AN ABSTRACT OF THE THESIS OF

<u>Paola M. Carrera-Ubidia</u> for the degree of <u>Master of Science</u> in <u>Wildlife Science</u> presented on <u>December 12, 2006</u>.

Title: <u>Giant Otters (*Pteronura brasiliensis*) and Humans in the Lower Yasuní Basin,</u> <u>Ecuador: Spacio-temporal Activity Patterns and Their Relevance for Conservation</u>

Abstract approved:

Dr. Selina S. Heppell

Giant otters (*Pteronura brasiliensis*) and humans in the Lower Yasuní Basin (Ecuador) have similar food and space requirements: they consume comparable arrays of fish species, and they use similar aquatic and terrestrial habitats. Resource partitioning could facilitate coexistence by allowing each species exclusive access to some resources.

My research examines the correlations between the use of spatial resources by giant otters and humans and the hydrological pulse of their ecosystem. My objectives were (1) to estimate the extent of terrestrial and aquatic habitat available for giant otters and humans; (2) to recognize the main patterns of space occupancy and its overlap between them; (3) to explain these patterns in relation to natural gradients in the watershed; (4) to describe the giant otter's diet; and (5) to depict the foraging activities of giant otters and humans relative to the distribution of prey. Between October 2004 and March 2005, I surveyed the Jatuncocha and Tambococha Creeks (Yasuní National Park) for direct and indirect signs of giant otters and humans, and I collected giant otter scat. Habitat availability was estimated by a geo-referenced map model that integrated virtual and field data, portraying four seasonal scenarios. Space use overlaps between giant otters and humans are a function of water level and the distance between terrestrial and aquatic habitats. The floodplain comprises 43% of the total study area during the flooding season, and is reduced to 25% of the total area at minimum water levels. Polygons obtained containing suitable habitat for giant otters are in average 41% larger than those obtained for humans; these contain areas that are inaccessible to humans (isolated pools and swamps, tributaries, and the upper portions of the main channel). Differences in space availability for and use by giant otters and humans depend on water level fluctuations. Area occupancy by both species is proportional to the estimated availability; but more so for giant otters, as humans increase area occupancy during the driest periods. Giant otter activity was primarily concentrated around the largest tributaries of each creek, and secondarily wherever the distance between suitable terrestrial and aquatic habitat was smaller. Human activity signs were distributed along the hydrographical gradient, *i.e.* in the lower portion of the Jatuncocha System (lagoon) or in the middle portion of the Tambococha Creek (large tributary).

To identify correlations between habitat use by giant otters and humans and prey availability, I analyzed scat samples and collected fish along several creek stretches. Giant otters consumed at least 47 of the 73 species available for them. Identifiable hard parts in the scat samples consisted primarily of *Hoplias malabaricus* (11.3%), *Hypselecara termporalis* (5.3%), *Acestrorrhynchus* sp. and *Prochilodus nigricans* (4.9% each). Foraging activity of giant otters was positively correlated with fish abundance and relative diversity, with some exceptions. Human activity patterns were related to fish abundance and diversity in Tambococha, but showed less correlation to fish distribution in Jatuncocha.

Overlap in resource availability and habitat use by otters and humans is highly variable. In the floodplain, extent and depth are critical variables that determine the distribution of resources in time and space, as well as the amount of resource partitioning possible. Competitive interactions during stressful conditions could be reduced by ensuring the availability of exclusive resources for giant otters during the driest periods, allocating suitable habitats within a short distance from one another along the longitudinal gradient of each watershed. Locally adapted and biologically sound regulations within this and comparable areas of the YNP could promote the persistence of giant otters without compromising the well-being of the local human inhabitants. © Copyright by Paola M. Carrera-Ubidia

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Giant Otters (*Pteronura brasiliensis*) and Humans in the Lower Yasuní Basin, Ecuador: Spacio-temporal Activity Patterns and Their Relevance for Conservation

By

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Paola M. Carrera-Ubidia, Author

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Black Elk Speaks, The Great Vision, (1932)

Giant Otters (*Pteronura brasiliensis*) and Humans in the Lower Yasuní Basin, Ecuador: Spacio-Temporal Activity Patterns and Their Relevance for Conservation

Paola Carrera-Ubidia

Wildlife Science (2006)

CHAPTER ONE: INTRODUCTION

1. RATIONALE AND OUTLINE

In response to rapid declines in biodiversity and ever growing threats to ecosystem function in the Yasuní National Park (Ecuador), the Wildlife Conservation Society (WCS) initiated in 2001 'The Living Landscapes Program', a conservation project aimed at protecting the 'landscape species' within the reserve. As a senior in Biology, I contributed to this effort with a BS thesis (Carrera, 2003). After collecting and analyzing data on fish availability, diet composition of giant otters (*Pteronura brasiliensis*), and fish harvest by humans, I obtained a few answers that lead to many more questions. Among the latter, I selected those that I considered relevant to conservation, interesting from an ecological perspective, and realistic under time and resource limitations.

This research identifies the major patterns of human and giant otter use of spatial resources within a 900 km² area of the Ecuadorian Amazon, aiming at better understanding the otter's conservation needs in this, and comparable, ecosystems. In this work, I have described the system and its main components in the context of ecological theory (Chapter 1), I have addressed some specific questions in two separate chapters, and I have identified those topics that apply significantly to conservation biology.

In Chapter 2, I describe spatial patterns of giant otter and human activities in space and time under the assumption that refuge and foraging spaces are fundamental habitats for both predators. By estimating the amount of habitat available for both predators according to water level variations, I compare these estimations with habitat occupancy and habitat overlap at a given time relative to changes in topology.

In Chapter 3, I hypothesize that foraging behavior is an explanatory variable for the activity patterns observed in Chapter 2, given that ultimately, ichthyofaunal information may lead to an improved ability to assess habitat suitability. I compare the relative abundance and diversity of potential prey items for giant otters and humans to the distribution of human and giant otter foraging activities. The data show that giant otter spatial movements are partially explained by prey distribution, although this variable did not explain the distribution in space of human activities.

Information on the minimum amount of space necessary for a top predator species to survive has been previously used to determine the size and shape of reserves. A detailed description of the variation in the availability of suitable habitat relative to seasonal change, and of the patterns of habitat use in response to these changes by giant otters and humans, can improve our ability to understand not only their resource requirements, but also to identify the critical periods when resource scarcity produces environmental stress and stimulates competitive interactions. My findings suggest that human activity should be regulated year-round within the watershed by establishing areas of exclusive use for giant otters in places where optimal distances between aquatic and terrestrial resources are found. This can promote the partitioning of resources, a reduction in competitive stress, and improvement of conditions at the population and metapopulation levels.

2. THEORETICAL BACKGROUND

2.1 Inter-specific competition and coexistence

According to ecological theory, competitive interactions are the driving forces responsible for the structure and diversity of natural communities (Morris *et al.* 2000). Yet, ecological practice has focused on a pattern more commonly observed in nature: the conditions that make coexistence possible between competing species (Abrams 1982, 1988). Early work around the concept of competition (Lotka, 1925; Volterra, 1926; Gause, 1934) suggested that competitive exclusion was the foremost cause of species extinction and biodiversity patterns (Ritchie, 2002). Extensive research has identified competitive interactions in more than 60% of species and systems studied (Ritchie, 2002) and across many animal taxa, including large mammals (Edwards, Croft and Dawson, 1996) and fish (Werner and Hall, 1979). Still, few studies have confirmed competitive exclusion (Ritchie, 2002), and many maintain that competition only occurs rarely and in times of extreme environmental stress (Grant, 1985), which suggests that most species avoid competition with adaptive strategies (Abrams, 1988).

Mobile organisms adapt particularly well to variations in resource availability (Connell, 1983) and sample the environment accordingly (Schoener, 1983), which results in habitat

partitioning, the exclusive use of resources in space and time, and thus, coexistence. Unlike classical Lotka-Volterra models, Tilman (1982) showed that coexistence is only possible when species compete for more than one resource; thus, habitat heterogeneity plays an important role in competitive coexistence (Abrams, 1988), and if competing species share a common resource type, heterogeneity in food size and density or habitat patch size is especially critical (Ritchie, 2002). Exclusive resources can also define a species' persistence regardless of competitive dynamics, carrying capacities, and rates of resource consumption (Ritchie and Olff, 1999). Hence, the number, density and size of resource patches encountered by a species imply that differences in foraging scale among species also contribute to coexistence. Large predators who live in close proximity to human populations (an increasingly common phenomenon) can be easily exposed to competition with humans over common resources; given that their real probability of "winning" the battle is narrow, those who do not find alternative resources eventually disappear (Yodzis, 1986). Thus, one of the main goals of biological conservation is to provide those conditions that minimize competition and favor coexistence with humans, inside and outside Natural Reserves (Terborgh, 1975; Du Toit, et al. 2004).

According to niche theory, differences among species in resource use reduce the per capita competitive effects between them (Levins, 1962). However, Schoener (1983) suggested that although exclusive resource use – the amount of exclusive resources divided by the amount of total resources – can lead to coexistence, other conditions might be involved as well. Ritchie (2002) asserted that the central question of inter-specific competition is what determines the availability of exclusive resources for each species. If exclusive resources are sufficiently abundant, they could support the persistence of a species despite competition for shared resources (Schoener, 1983).

Resource abundance is also scale-dependent, affecting the degree of habitat heterogeneity; at low resolution animals detect resources as a few large clusters (less choices), whereas more choices appear at a finer scale (Levins, 1962). The effect of scale on an animal's fitness and survivorship has been insufficiently explored by researchers (Ritchie, 2002). Optimal foraging theory (OFT) predicts that species will modify their behavior in response to resource density, distribution and quality, changing the scale at which they forage (Ritchie, 1998; Kotler and Brown, 1999). Habitat segregation can also arise from trade-offs between risk of predation, food availability and distribution, or abiotic conditions among habitats (Brown, Davidson and Reichman, 1979; Brown, Kotler and Mitchell, 1994). A second process affecting resource availability is that of temporal dynamics: seasonal or annual fluctuations expand the amount of choices for organisms and add a second dimension onto which resources are available (Chesson, 1994).

Combined information on resource density and distribution has been widely used to assess habitat quality, but this information can also be useful to predict the persistence of competing species by assessing the degree of current and potential resource partitioning within a system. Several models on competition for space exist (Klausmeier and Tilman, 2002), roughly grouped into either spatially implicit (SIMs) or spatially explicit models (SEMs). By monitoring the actual location and movement of my study organisms on the landscape (i.e. by using a SEM), I have examined the environmental conditions that elucidate their activity patterns. This allowed me to identify which features human behavior (the superior competitor) could be regulated to reduce their negative effects on giant otters (the inferior competitor and an endangered species) – given that both are large predators with similar resource requirements over a geographic extent.

Many variables affect the availability and distribution of resources in tropical ecosystems, and they are not always recognizable. This study focuses on the on the availability and distribution of refuge and foraging habitat relative to water level fluctuations. Other variables affecting water levels – i.e. precipitation, elevation, drainage, slope, geomorphology, topography, and vegetation (Tague, 2005) – have been tacitly integrated in the model on a three dimensional plane, so that water level acted as a surrogate for all the other features involved in a system's hydrodynamics.

This study aims at defining the main processes and variables related to the problem of resource availability, accessibility, use, and overlap patterns between humans and giant otters. Humans and giant otters are top predators with similar food and space requirements. Giant otters persist in those few Amazonian aquatic systems that have not been heavily impacted by humans, but cases of short- and medium-term coexistence have been observed within the past decade (Schenck and Staib, 1998; Ribas-Pereira, 2004). People in the Amazon basin still subsist on natural resources, obtained by traditional

means or by increasingly common unsustainable practices. Therefore, both predators rely on resources found in and around aquatic systems.

The Yasuní River basin, where this work took place, possesses complex geographical and topological features (Figures 1 and 2) that define the spatial conditions affecting this analysis. Some of these characteristics are unique to this system (geographical location, geo-political and economic conditions, local climatic and hydrographic patterns), but the area certainly reflects conditions found in many other areas where giant otters and humans compete and/or coexist. Many – although not enough – of the giant otter populations live inside protected areas, most of which lack realistic and scientifically based regulations or suitable enforcement. Giant otters are subject to many kinds of human activities that may have negative effects on their populations (INRENA, 1999; Rosas, 2004). Amazonian peoples, particularly the native tribes, suffer some degree of resource deficiency, socio-political marginalization, economic and educational dearth, and other adversities (Bromley, 1973; Smith, 1988; Butt and Boque, 1990, Curran *et al.* 2000). Many tribes have turned to ecotourism as a solution, but few have developed tourism activities that consider the giant otter's ecological requirements; ecotourists now represent a new threat rather than a partial solution.

Although my findings are obtained from a unique area of the Ecuadorian Amazon, they are intended to contribute to the knowledge and decision making regarding giant otter conservation in comparable places. I focused on specific questions related to the problem of resource availability, and on how water level affects the distribution, accessibility and topology of such resources, taking into account two different levels of scale where this variable can be analyzed: the landscape scale (basin) and the territory/home-range scale (watershed). Seasonality is also integrated in this analysis, and is understood as the environmental setting created within the floodplain by four hydrological stages: the maximum, high, intermediate, and low average water levels.

2.2 A note on spatial ecology

Why are the distribution and availability of space and food resources relevant to our knowledge of competitive interactions? The minimum quality and quantity of places where organisms can obtain resources varies enormously among species. Any type of space providing a functional service to species (i.e. habitat) is a key resource that most organisms compete for, particularly the space where basic activities occur: the places where the food is found (foraging areas), the places to hide the young and sleep (caves, dens, holes, trees), or the places to socialize and play can all be considered 'essential' habitat (Hanson, 1995). Many organisms find what they need in a relatively small area, but large carnivores usually live in areas where food and shelter are either scattered in the landscape or available only on a seasonal basis (Southwood, 1977). Spatial resources can be permanently accessible (i.e. geological formations, rivers, vegetation), or ephemeral (i.e. small water bodies, forest gaps, currents); which also determines the amount of time and energy that animals invest protecting an area and traveling in search of resources (Loreau and Holt, 2004). Most mammals delimit and protect areas around the space where they sleep and rear their young (territory), but they also explore areas beyond these limits (home range) in search of additional resources or a mate (Hanson, 1995).

The extent or location of giant otter territories during the rainy period is not well known (Duplaix, 1980; Laidler, 1984; Hoeinghaus *et. al.*, 2003), but during the rest of the year, giant otters use two main types of places: (1) Foraging areas in the water – shallow places within the main channels, deeper areas with aquatic vegetation, and pools, ponds, streams, or swamps (Carter and Rosas, 1997; Appendix 1); and (2) Shelter areas on land near the main channels – dens, campsites, and latrines. Only humans have similar spatial requirements, as people use equivalent places on land to establish their campsites, and comparable sites in the water to fish for food with the least effort. Even hunting occurs near the water during the dry season, and most hunting trails are accessed from water.

Similarities in habitat use and scale can result in species' competition for such spaces, but the characteristics found in a particular landscape can affect the magnitude of these competitive interactions in different ways. If, at a large scale, two species rely on one kind of habitat, an increase in compositional heterogeneity within that scale can imply a reduction in the amount of preferred habitat (causing a reduction in population persistence probability). At a finer scale such increases in heterogeneity can provide an advantage for the species, as habitats are partitioned into smaller samples of optimal and sub-optimal habitat, thus, reducing overlap between competing species and increasing the probability of population persistence (Fahrig and Nuttle, 2005). In this respect, "the outcome of interspecific competition will depend strongly on the rate of environmental change" (Fahrig and Nuttle, 2005), because the latter can have a large effect on the extinction threshold (i.e. the minimum amount of habitat required for population persistence). For the purpose of this study, seasonal fluctuations affecting habitat availability, connectivity, and configuration are considered local scale changes in the competing species' environment.

Lotic systems are highly dynamic, and so are the organisms that live in them, since they need to respond to fluctuations in depth, discharge, pH, visibility, and other seasonal changes within a watershed (Goulding, 1980). Fish consumers, including humans, have learned to predict the responses of their prey items to these changes (schooling, migration, or ovoposition events) in order to maximize their effort in obtaining food. Schoener (1971) analyzed the idea of "maximization" applied to previous knowledge of foraging behavior touching on the crucial question of whether all populations are constantly striving between cost-benefit situations, and if their survival and persistence depends on their ability to minimize costs and maximize benefits. Contributions to the understanding of foraging behavior were made by Rapport (1980), who showed that the degree of food selectivity for one prey type depends on its relative abundance and the relative abundance of alternative prey species.

The third chapter in this work will deal with the idea that the most important aquatic resources that giant otters and humans are competing for is that of foraging areas. Previous knowledge on the diet and foraging behavior of both giant otters and humans within the study area (Lasso, 2003; Carrera, 2003) and of variations in the dietary overlap between them (between 50-80% according to Carrera, 2003), suggest that both predators might obtain their food from the same places. Thus, foraging patterns might not only explain a large portion of their activity, but they might also represent a key element in their competitive interactions. The way in which patch selection, foraging path

and exclusiveness of foraging area (Schoener, 1971) are correlated with the spatial abundance of food resources and how these are tightly intertwined with the principles acknowledged in spatial ecology is discussed in the proceeding chapters.

3. GIANT OTTERS (*Pteronura brasiliensis*, Gmelin 1788)

3.1 Distribution and conservation status

Giant otter distribution is restricted to the Neotropical humid forests below 300 m elevation, where they establish territories along creeks, rivers, lakes, and swamps (Schenck, 1999). Once numerous and widely distributed in South America, only a small fraction of them has survived the intense pelt trade that took place during the 20th century (Carter and Rosas, 1997). Giant otters can still be found at low densities along most of their original range – the Guianas, and the Amazon and Orinoco basins – except for the La Plata basin in Argentina, where they are now extinct (Emmons and Feer, 1997). In Ecuador, giant otters are rare and have been reported from within the Yasuní National Park (i.e. the Ishpingo, Shiripuno, Tiputini and Yasuní watersheds), from scattered locations in the Cuyabeno Wildlife Production Reserve (i.e. the Cuyabeno, Tarapuy, Sabalo, Güepi, and Lagartococha watersheds), and from a few unprotected areas (i.e. the Morona Santiago, Pastaza, Tarapuy, and Zamora watersheds; Utreras & Tirira, 2001).

Due to the drastic reduction in their numbers, their vulnerability to human disturbances, and the emergence of new threats to the species – i.e. overfishing and habitat destruction (Staib & Schenck, 1994) – giant otters have been listed under the Convention on International Trade of Endangered Species of Flora and Fauna (CITES)'s Appendix 1 - i.e.a list of species In Danger of Extinction due to International Trade (2005) – since 1987, and to The World Conservation Union (IUCN)'s Red List of Endangered Species (2004) since 1990. In the Ecuadorian eastern lowlands, giant otter populations occupy isolated spots ever more exposed to human disturbance (Fersen *et al.* 1997), so they are considered a Critically Endangered Species in the Red Book of Mammals of Ecuador (Utreras & Tirira, 2001). For comparable reasons, they have been listed as a Critically Endangered species in the Red Book of Mammals in every other country where the species occurs, except for Brazil (IUCN, 2004; INRENA, 1999).

3.2 Relevant biology, natural history and population dynamics

Giant otters (*P. brasiliensis*, Carnivora, Mustelidae) live in family groups of up to 12 individuals (Duplaix, 1980; Staib, 2005), which is why they are locally known as 'river wolves'. They are among the largest predators in the Neotropics (Laidler, 1984) and their diets consist almost exclusively of fishes captured individually or in group hunts (Duplaix, 1980; Schenck, 1999). Giant otters have been observed eating fishes 10-40 cm long, ingesting up to three kg of fish daily (Duplaix, 1980; Schenk, 1999), and hunting prey that are weak, ill, slow, nocturnal, or that reside in benthic habitats (Gómez, 1999). Therefore, they play a key role in regulating and maintaining the integrity of fish communities (Staib and Schenck, 1994). Yearly and seasonal variations in the hydrological regime, and the fluctuation in abundance of fish prey, could determine the spatial distribution of giant otters (Duplaix, 1980). Migratory prey items may be significant resources for this type of predator, which could change its activity patterns (including its reproductive biology) in response to prey abundance (Willson and Halupka, 1995) or intense human disturbance (Schenck, 1999; Staib, 2005).

Researchers conducting extensive work during the last decade in Suriname (Duplaix 2002, 2004), Brazil (Ribas-Pereira, 2004; Rosas, 2004), and Perú (Schenck and Staib, 1998; Schenck *et al.*, 2002; Schenck, 2004, Staib, 2005) have been able to identify relevant aspects of giant otters' population structure and dynamics. A giant otter population consists of family groups of 5-12 individuals, and a series of solitary (sexually mature) individuals known as transients (Schenck and Staib, 1998). A single reproductive pair per family generates up to four cubs once a year during the dry season (Duplaix 2002, Rosas, 2004). In spite of the group's support during the rearing of the cubs, juvenile mortality is high; approximately 75% of otters disappear before age four (Schenck *et al.*, 2002). After 2-3 years, they reach sexual maturity and adopt a nomadic way of life, traveling more than 100 river km in search of a mate and their own territories (Schenck *et al.*, 2002). Dispersing transients also suffer high mortality, mainly due to their vulnerability to human disturbances, attacks from other groups in defense of their territories, predation, and/or

food scarcity (Duplaix, 2004; Ribas-Pereira, 2004). There is no overlap between family group territories, which typically include two or three oxbow lakes, and surrounding swamps, creeks and rivers; and group size and reproductive success are correlated to the surface area of ideal habitat available to the group (Schenck and Staib, 1998).

4. STUDY AREA: THE LOWER YASUNI BASIN, ECUADOR

4.1 The Yasuní National Park, Ecuador

Created in 1979, the Yasuní National Park (YNP - 00°10' to 01°45'S and 75°20' to 77°00'W) is part of the Upper Amazon Basin, and is the largest natural preserve in continental Ecuador, with 982,000 ha of protected land (Campos, 1998; Figure 1). At elevations between 175 and 400 m above sea level, the YNP is part of the "Napo Pleistocene Refugia" – a set of subtropical islands surrounded by savanna-type ecosystems that were preserved during the last glaciations, due to its proximity to the Andean foothills – which explains its exceptionally high degree of biodiversity and endemism among other Amazonian regions (Prance, 1985). Over 500 bird species, 700 plant species, 150 species of mammals and 100 species of amphibians have been found in the YNP - a level of biodiversity comparable to that of the entire United States in an area less than the size of the state of Connecticut (Campos, 1991 and 1998).

The YNP is limited on the north by the Napo, Tiputini and Tambococha rivers, on the east by the Yasuní River (near the Ecuadorian-Peruvian border), on the south by the Curaray River, and on the west by the Tiputini and Rumiyacu Rivers. According to Pitman (2000), only 10-23% of the YNP's area is covered by seasonally and permanently flooded forests and swamps, which surround the Tiputini, Yasuní, Tivacuno, Nashiño, Shiripuno and Cononaco watersheds, whereas the remaining 77-90% of the preserve corresponds to *várzea* and *terra firma* habitats (forest areas that remain dry temporally or throughout the year, respectively).



Figure 1. Geographical Location and Major River Systems of the the Lower Yasuní Basin in Amazonian Ecuador.

Upper left: Ecuador in South America; Lower left: The Yasuní National Park and the Lower Yasuní Basin in Ecuador; Right: the Napo River and the Lower Yasuní Basin (Geographical Coordinate System and Projection: Provisional South American Datum of 1956, UTM 185).

Amerindians and colonizers from other Ecuadorian regions and abroad inhabit the areas surrounding the YNP. The YNP-Napo buffer zone – the area between the northern limit of the YNP and the southern border of the Napo River (Figure 2) – is occupied by 11 Kichwa communities whose economy relies on activities such as natural resource use, tourism, agriculture, and sporadic work with the oil industry (GEF, 1998a). West of the Yasuní National Park lies the Huaorani Ethnic Preserve, a 678,220 ha area that was created in 1986 to protect the lives and culture of 1,700 Huaorani people (Toledo and Lara, 2001), whose livelihood still depends on hunting, fishing, fruit and seed gathering, and other natural resource extraction activities for their survival (Yost, 1981; Nations, 1988). Since ancestral Amazonian knowledge and culture have developed and subsisted for thousands of years in and around this area, in 1989 the United Nations Educational, Scientific and Cultural Organization (UNESCO) appended the area comprising the YNP and the Huaorani Preserve (known as the Yasuní Biosphere Preserve) to the World Network of Biosphere Reserves (Ruiz, 2000).

4.2 The Lower Yasuní Basin, Yasuní National Park

The study area corresponds to the Lower Yasuní Basin (LYB, Figure 2), located on the north-east corner of the YNP. It is limited on the north by the Napo River, on the east and west by a range of hills, and on the south by a series of Hoaorani settlements. Within an elevation range of 170 to 280 m above sea level, the area comprises:

(1) The YNP-Napo buffer zone on the north (with one human settlement, four Kichwa communities, one military settlement, and the Braga Creek), and the YNP-Perú buffer zone on the east (with one Kichwa community, one military post and two oil blocks);

(2) The YNP eastern corner, which includes the Tambococha Creek, the Jatuncocha Creek and Jatuncocha Lagoon which together form the Jatuncocha System, and the Yasuní River (Figure 2). This portion of the park (which covers approximately 900 km²) has been proposed as a "restricted" area – where human intervention with scientific purposes should be the only type allowed – due to the complex hydrological dynamics that have created characteristic ecosystems therein (Coello and Nations, 1989). A guard house located near the confluence between the Yasuní River and the Tambococha Creek, and established by the Ministry of the Environment for control and enforcement within the YNP, was occupied as the main camp site for the present study (Figure 2). The house sits at 230 m above sea level (18M 0452857 UTM 9892214), 300 m south of the mouth of the Tambococha Creek and 5.5 km north of the mouth of the Jatuncocha Creek.

4.3 Climate and Seasonality

The Yasuní National Park has a warm, humid weather, with average yearly precipitations of 3,000 mm (Romero-Saltos *et al.*, 2001). In the region, the average humidity fluctuates between 80 - 94% (Pitman, 2000), the average air temperature varies between 21 - 35 °C, and the average water temperatures range from 23 - 26 °C (GEF, 1998a). Climatic records in the LYB have estimated average yearly precipitations of 3,000 - 4,000 mm, and average daily temperatures of 25 °C, within a 15-38 °C range (Hicks *et al.*, 1990).

In the YNP, precipitations follow a bimodal trend, with a long rainy season between March and July, a short rainy period (*inviernillo*) between October and November, and a dry season from December until February (Saúl, 1975). In the lower Yasuní basin, however, the dry season follows the general pattern (December-February), but the rising water period is longer (February-May), the rainy period starts only in May, and the falling water period occurs by the end of August (Galacatos *et al.*, 2004, Figure 3).

Water and air temperature, as well as pH and conductivity were measured (as specified in the methodology section in chapter 3, Appendix 3) and although the water level is not necessarily the same in all three rivers studied, there is a strong correlation between the water level in Yasuní and Jatuncocha Creek (guard house and KM 7, respectively R = 0.86), and a less strong but still substantial correlation between the water level in Yasuní and Jatuncocha KM 7, respectively; R = 0.60, Appendix 4).



Figure 2. Geographic detail of the study area: major rivers, main human settlements, the Lower Yasuní Basin within the Yasuní National Park (horizontal lines), and its buffer zones (diagonal lines).

Within about 900 km², the study area comprises the north-eastern corner of the Yasuní National Park, its northern and eastern buffer zones, and the rivers that conform their limits. The town of Nuevo Rocafuerte, four rural communities, and two military posts are the main human settlements within the area.



Figure 3. Seasonal trends of precipitation and water level in the Yasuní National Park and in the Lower Yasuní Basin (Data Sources: Galacatos *et al.*, 2004, and INHERI, 2005, Graphic constructed by the author).



Figure 4. Average water level (black diamonds), and maximum and minimum values (grey lines) obtained for each time block of surveys at the Yasuní River between September 2004 and March 2005.

4.4 Hydrology and Geomorphology

4.4.1 The Napo River

The Napo is the largest river in the Ecuadorian Amazon (Terán, 1957). Its basin belongs to an extensive area filled with the Cretaceous-Tertiary sediments found between the Andes and the Brazilian Shield (Tschopp, 1953), and its channel contains basal sands from the Ordovician and Cambrian periods (Saúl, 1975). It originates at the Jatun Yacu, a river that at 4,000 m above sea level gathers the waters that flow from Andean volcanoes (Terán, 1957). Carrying large volumes of sediment from the Andean slopes, the Napo River causes large scale erosion at its banks, and a high ecological and demographic impact is produced due to its large discharge and erosive power during the flooding season (Sioli, 1975, 1984). With a high conductivity and a pH that is usually \geq 7.0, its water exhibits a turbid light brown coloration throughout the year (thus the name of "white-water" river).

4.4.2 The Yasuní River

The Yasuní River is born among the Zapota and Castañas mountain ranges, at the heart of the YNP, and flows east and north-east until it reaches the Napo River (Villavicencio, 1984). Covering a total extension of 186 km, this is the fourth largest river in the Napo basin (Terán, 1957). Although it is of local origin, it is usually considered a white-water river, due to its pH close to 7.0, the significant amount of sediments that it carries from the Amazonian hills, and the red clay soil found in its channel (Figure 5). In its lower portion, however, the Yasuní River can experience large variations in conductivity, pH and visibility/coloration, due to the black-water input from its tributaries, and the white-water input from the Napo River during significant floods (Galacatos *et al.*, 2004).

4.4.3 The Braga, Jatuncocha, and Tambococha Creeks

The three black-water tributaries that constitute the Lower Yasuní Basin originate locally, following the low, undulating and hilly terrain between broad swampy floodplains that dominates the landscape (Tschopp, 1953), and flowing eastward until they reach the Yasuní River (Figures 2, 5 and 6). Depending on the riparian vegetation found along their margins, these creeks range in width from only 5 m to about 50 m at the surface, and in

depth from 20 cm during the dry season to up to 7 m during the rainy season (*pers. obs.*); also, as a result of the topography, the depth profiles of the Jatuncocha Creek and the Tambococha Creek are comparable throughout most of their extension (Appendix 5). However, the Jatuncocha System has a more irregular geomorphology, which results in a larger number of white- and black- water tributaries, and associated pools and swamps, than those found in the Tambococha Creek (Figure 6). Most of the ecosystems formed by these creeks have been classified as Lowland Evergreen Forests Permanently Flooded by Black-Waters or *Igapós*, and a smaller portion is covered with *terra firma* forests (Sierra, 1999, Figure 7).

Black-water rivers originate from the surrounding swamps and flooded forests (Goulding *et al.*, 1988), where the water is rich in phenolic tannins, and poor in other compounds due to its high acidity – the pH can be as low as 3.8 and the conductivity can be close to null (Saúl, 1975). During the rainy season, black-water systems expand laterally towards the surrounding forests, incorporating associated river tributaries, oxbow lakes and swamps (Galacatos *et al.*, 1996). Previous studies in the Amazon have shown that black-water systems contain a high biodiversity (Goulding *et al.*, 1988; Henderson & Walker, 1990; Ibarra & Stewart, 1989), which has been attributed to the energetic contribution from allochthonous nutrient sources during the seasonal floods (Goulding *et al.*, 1988).

The Braga Creek flows over 16 km within the YNP-Napo buffer zone before reaching the Yasuní River. Once pristine, this watercourse is now navigable only in its last three km (*pers. obs.*), whereas the remaining portion has suffered intense eutrophication due to the input from agricultural runoff and logging. The upper portion of the Braga Creek is easily accessible by land from the YNP-Napo buffer zone (two-hour walk from the Napo river banks), and most people that possess land in this area have built structures that allow them to cross the creek (*pers. obs.*). The lower portion of the Braga is subject to eventual floods from the Napo River, and during such events, the area between the two water bodies becomes a large swamp that surrounds the town of Nuevo Rocafuerte, and that can remain flooded for months or years, depending on the intensity of the floods (*pers. obs.*, Figures 5 and 7).



Figure 5. Distribution of soil types within the study area according to their pH (Source: Dr. Rodrigo Sierra, University of Texas; Map created by the author).

The pH distribution in the soil pattern shows how areas nearby the Napo River are more exposed to white-water floods with neutral pH, and how areas in the Lower Yasuní basin are rather subject to acidic water floods, from black-waters that originate in the rainforest. Notice the average pH soils found at the lower portion of the creeks, and the difference between each side of the Yasuní River.

The Tambococha Creek flows over 26 river km, and represents the YNP's northern limit throughout its last 18 km (Figure 2). Due to its topography, its upper seven km are accessible only during the rainy season, and remain dry during the rest of the year. In its last five km, the channel becomes an elongated lagoon (2 km²) which is also suffering intense eutrophication. Thus, most of the Tambococha Creek can be accessed by canoe from the Yasuní River, and by foot from the YNP-Napo buffer zone (a four-to-five hour walk from the Napo River banks). Although the Tambococha Creek is mostly a blackwater body, it can be subject to extreme changes in water coloration, visibility,

conductivity and pH, due to the contribution upstream from the Aguas Blancas Creek (a large white-water tributary, Figure 5) that carries some sediment from the south-western hills (Figure 6), or from the Yasuní and Napo Rivers downstream, which during high water levels invade the creek with white-water floods (*pers. obs.*).

The Jatuncocha Creek 's full extent has yet to be defined, since the area where it originates is covered by riparian vegetation. It is likely that its origin is a large swamp located near the central portion of the Yasuní River (*pers. obs.*), but at least the last 22 km are navigable during the dry season. Similarly to the Tambococha Creek, the Jatuncocha Creek widens in its last portion, creating a 2.2 km² lagoon (the Jatuncocha Lagoon) that narrows down in the last two km (Figures 5 and 6). The Jatuncocha System can only be accessed by canoe, although old trails that were previously used by the aboriginal tribes – which connected it to several points in the Tambococha Creek – are eventually used by the experienced hunters (*pers. obs.*).

4.4.4 Vegetation

Plant diversity in the YNP is enormous; Balslev and Renner (1989) found up to 228 species of trees over 10 cm diameter at breast height in one ha of *terra firma* forest, and 146 species in the floodplain forest (394 species total in only one ha, only 19% shared). In the LYB, three main types of vegetation occur: *terra firma* forest, which is located on the higher grounds and remains dry throughout the year; *várzea* forest, which is subject to seasonal floods, usually by white-waters; and *igapó* forest, which are permanently flooded throughout the year, usually by black-waters (Figure 7, Appendix 6).

Terra firma forests are characterized by a high canopy (15-25 m) and occupied by members of the Myristicaceae, Moraceae and Sapotaceae families, though trees with stilt roots are also frequent. The under-story is usually open with smaller trees and shrubs, and abundant lianas (Neill, 1988), whereas the ground layer is not very developed (Balslev *et al.* 1987). The *várzea* forest is only inundated during major flooding events that happen every few years. It corresponds to a 200-1000 m wide strip along the Napo River, with a fertile soil that has been enriched with Andean sediments (Figures 5 and 7).


Figure 6. Digital Elevation Model (3 arc-second) and Hydrography layer from the study area (Sources: www.usgs.gov/seamless and the author, respectively).

Elevation and topography are key factors in determining changes in water level within the area; according to direct observations, the areas below 195 m elevation (the Jatuncocha Lagoon and the lower portion of the Tambococha Creek) remain flooded throughout most of the year, whereas the portions upstream (levees) can dry out completely once the rainfall is reduced. The distribution of black-water (BW) and white-water tributaries is part of the hydrography.



Figure 7. Vegetation at the landscape scale in the study area (Source: Dr. Rodrigo Sierra, University of Texas; Map created by the author).

At this scale, vegetation distribution follows a simple pattern: most of the Lower Yasuní Basin is covered with Lowland Palm and Black Water Forests (or igapó), but some of the areas within the YNP-Napo buffer suffer eventual white-water floods, and are currently being modified into agricultural land (pers. obs.). A smaller portion of the area, as determined by elevation, is covered with terra firma forests, which are found on the levees located between the upper portions of the Tambococha Creek and Jatuncocha Creek.

In average, the *várzea* canopy is higher (35-40 m) than in *terra firma*, and is characterized by the presence of Kapok tress (*Ceiba pentandra*) and fig trees (*Ficus* spp.) that can reach up to 50 m. A common palm-tree in the under-storey level is *Phytelephas macrocarpa* (vegetable ivory seed). *Igapó* forests occur along the upper and middle portions of the Yasuní River tributaries, and consist of permanently flooded areas (swamps), and temporarily flooded areas that might be exposed during intense draught periods. Characteristic swamp vegetation includes the palm *Mauritia flexuosa*, and the trees *Virola surinamensis* and *Symphonia globulifera*. Common tree species in the temporarily flooded forests are *Macrolobium acaciifolium* (or "*mandi*", which forms riparian colonies called "*mandiales*"), the freshwater mangrove tree *Coussapoa trinervia*, and the palm *Astrocaryum jauari* (or "*chontilla*", which forms riparian colonies called "*chontillales*"). *Igapó* and *várzea* forests also include several species of floating plants that grow in low-current zones and that are able to occupy large portions of the surface during eutrophication processes (Balslev *et al.* 1987; Appendix 6).

4.5 Giant otters and Humans in the Lower Yasuní Basin

According to the local inhabitants, giant otter populations had been extirpated from the area, and the ones currently found within the LYB had re-colonized the area during the last decade (G. Merino, *pers. comm.*). Researchers that had previously worked in the LYB (Lasso, 2003; Utreras *et. al.*, 2005) determined during surveys conducted in 2001-2002 the presence of two family groups: one of five giant otters living in the Tambococha Creek, and one of six individuals occupying the Jatuncocha System. Lasso (2003) found that most of their latrines were located along the flooded forest and that a smaller amount of them were in *terra firma*; in contrast, most dens were distributed in the *terra firma* areas. In the Tambococha Creek, Utreras *et al.* (2005) concluded that the home range occupied by the resident group was of 0.6 km² during the dry season and of 7.7 km² during the rainy season. In the Jatuncocha Creek, the total extent of the area occupied by giant otters during the dry season was of 2.8 km² and of 20 km² during the rainy season. In Lasso's opinion, (2003) the LYB is still a suitable habitat for giant otters, due to its ecological and geomorphologic features, and to the relatively infrequent disturbances in the area.

Carrera (2003) studied the dietary niche width of giant otters and its overlap with the human fisheries, and found that: (1) from the 98 fish species available, humans and otters consumed only about 50%, half of which were rare within the system, (2) the giant otter

diets are slightly more specialized than humans', but both forage in an opportunistic manner, and (3) depending on fish availability, their diets overlapped between 54-82%. Duplaix (1980), and Staib and Schenck (1994) emphasized how indirect competition for food with humans could aggravate giant otter survival.

Colonization within the YNP's boundaries is forbidden, but there are human settlements along its borders. The town of Nuevo Rocafuerte is located less than 1 km West from the border with Perú (Figure 2), and occupies 2-3 km of the southern Napo River bank. According to the last population census conducted by the National Institute of Statistics and Censae (INEC) in November 2001, Nuevo Rocafuerte had 1,400 inhabitants (826 in the urban center, and 579 in the peripheral rural areas) – which then included the communities of Alta Florencia, Baja Florencia, and Santa Teresita (INEC, 2002). While field work was carried out, the new Kichwa community of Bello Horizonte was settling in the last unclaimed lands: the YNP-Napo and the YNP- Perú Buffer zones. Once the property limits are established among community members, they log the forest for construction material, and then they burn down a portion of their land for agricultural purposes. After building their homes, community members establish the physical limits of the community to make the process official (*pers. obs.*).

During the last 40 years, oil exploration and exploitation companies have been the largest source of income for many in the Amazonian regions in Ecuador (GEF, 1980). People can find temporary employment in transportation, construction, mechanics, security, telecommunications, and health services for the industry. Those who do not work for oil companies make a living out of natural resource trade, agriculture, subsistence and commercial fishing and hunting, public education, and other public services (*pers. obs.*). Though the land is not suitable for long-term agricultural exploitation, local communities do not manage sustainable domestic and wildlife species, nor fabricate artisan products from local resources, nor develop sustainable eco-tourism projects, which are common sources of income in other Amazonian regions (Smith, 1980); there is no marketplace where the local products can be commercialized either (*pers. obs.*).

4.6 Conservation Status in the Study Area

The Global Environmental Fund (GEF, 1998a and b) conducted studies in the YNP and developed a management plan for the park, which concluded: "the persistence of the YNP's ecosystems relies on detailed knowledge of certain fauna species, such as the large predators (due to their role in the trophic chain), [...] and the aquatic organisms". This report insists on prioritizing the conservation of aquatic environments, particularly in the northern and central portions of the park, due to their exposure to oil-related activities (Appendix 7). It also underlines that the future of the aquatic fauna is possibly more fragile than terrestrial wildlife, in view of the high levels of pollution registered in the rivers, the massive riparian deforestation observed, and the frequent use of indiscriminate fishing methods (GEF, 1998b).

Ecuadorian legislation forbids commercial hunting, fishing, and logging within the YNP, or subsistence fisheries that employ indiscriminate methods (i.e. poisons, explosives, and nets). However, people from the surrounding communities and military settlements have performed large scale hunting, fishing, and logging on a regular basis before and since the YNP was created (Coello and Nations, 1989). My personal observations in the LYB during 2004-2005 have led me to conclude that efforts to improve law enforcement within the LYB have failed or are nonexistent, that the use of dynamite as a fishing method has become an exceedingly common practice; in response to the rising demand for food from other Amazonian localities and the precarious economic conditions in the area, people that used to hunt and fish for subsistence are now augmenting their efforts to a commercial level. The lack of regulations in natural resource extraction could have significant negative effects on the local biodiversity and ecological integrity in a long term.

A larger scale threat, however, is the one posed by the imminent exploitation of the oil fields within the Ishpingo - Tiputini -Tambococha (ITT) block (Appendix 7). Over 900 million barrels of oil – the largest known oil reserve in Ecuador – lie under this block, which is under development since 2006. Though the last pristine portions of the Yasuní National Park would be affected, it has been announced that extraction activities would start by 2007 or as soon as an international partner is found for the task. Development

following oil activity summed to the existing human disturbances in the area could represent the "coup de grace" for the resident wildlife.

In summary, in an area of approximately 900 km², the study area contains:

- a small town and four rural communities that suffer economic and political distress,
- two military posts, each on either side of an international border,
- a relatively pristine portion of a natural preserve (and its buffer zones), where no environmental enforcement exists due to its remoteness and lack of resources,
- three small black-water systems (one within the buffer zone, one which represents the northern limit of the natural preserve, and another that is more remote); these drain into a larger watercourse that is a seasonally black- or white-water river and which constitutes the international border; in turn, this one flows into a larger white-water river the suffers great human impact; and
- a set of environmental hazards of variable distribution, magnitude and duration the most relevant: habitat destruction (water and sound pollution, oil exploitation and road construction), overfishing and the use of dynamite and poisons, and unregulated practices of tourism and other recreational activities.

5. METHODOLOGICAL APPROACH AND FIELD LIMITATIONS

Field work was conducted from September 26 to December 19, 2004 and from January 11 to March 10, 2005 (N total days of field work = 145). Two Kichwa assistants with previous experience in giant otter research helped with preparation and installation of field equipment, and with canoeing, data collection, camping and fishing. Navigation within creeks was done by rowing on a $7m \times 1m$ fiberglass canoe, and a 15 HP outboard motor was utilized in larger areas (Yasuní River and Jatuncocha Lagoon).

Table 1. Time distribution and distances covered in each of 10 time blocks during the field season (JS=Jatuncocha System, TC=Tambococha Creek).

During surveys, giant otter and human direct and indirect signs were georeferenced, water level records were obtained, and other characteristics of habitat – i.e. extent of vegetation cover, terra firma and stream-tributary-trailhead accessibility and navigability – were registered.

Total	Location	Activity	Day	Route (KM)		Total KM
days				Start	Finish	/ Day
2	Main	Planning, Equipment	1	0		0
Z	Campsite		2			
4	Yasuní - JS - Yasuní	Watershed Surveys	3	0-5 YR	0 – 15 JC	20
			4	15 – 10 JC	10 – 20 JC	15
			5	20 – 15 JC	15 – 25 JC	15
			6	25 – 0 JC	5 – 0 YR	30
3	Main Campsite	Data entry, Equipment maintenance	7			
			8	0		0
			9			
3	Yasuní - TC - Yasuní	Watershed Surveys	10	0 TC	10 TC	10
			11	10 – 5 TC	5 – 15 TC	15
			12	15 – 20 TC	20 – 0 TC	25
2	MC - NR - MC	Equipment maintenance, supplies	13	0 YR	5 NR	5
			14	5 NR	0 YR	5

The field season was divided into 12 different time blocks of 12-14 days each, where surveys were conducted in each water body at 3-4 day intervals (Table 1). The main campsite was located by the Yasuní River, 5 km south of the Napo River, 0.3 km south of the Tambococha Creek's mouth, and 5 km north of the Jatuncocha System's mouth (Figure 8). Other research campsites were located on KM 15 and 22 in the Jatuncocha System, and on KM 8 and 18 in the Tambococha Creek. Water level gauges – 8 m wooden poles with bands at 10 cm intervals grounded in the mid portion of the main channel – were installed throughout the field season on KM 7, 14 and 21 in Jatuncocha

System and on KM 7 and 14 in Tambococha Creek (Figure 8); an additional water level gauge and a precipitation gauge were permanently installed by the main campsite. Readings of water level were recorded 3 times daily in Yasuní and once daily in the creeks during surveys.

The identification and ageing of giant otter indirect signs (dens, latrines, tracks, and scratch-walls) and direct observations (sightings and hearings) were done according to Groenendijk *et al.* (2005). To avoid overlaps in time estimations, only the most recent signs – up to 1 week old – were considered for my seasonal analyses. Traces of human presence (refuse, footprints, or fire remains) and direct encounters with humans were treated likewise, but in this case, the skills of the native assistants, *ex situ* accounts (i.e. records of people entering the YNP by the main campsite), and camera traps placed in specific locations in each system (Figure 8) were used as the most reliable estimates of sign age. For each river km, biodegradable Bright-Glo tape flags were tied in visible places by the river banks during the first day of surveys (intermediate water levels).

Activity signs found during the first time block were identified by an 8-10 letter code that included river km marks and 250 m distance marks for those occurring within the same km, and a code number from 1-4 at the end when the signs were active more than once (1=occurred within the last 24 hours, 2=is one to three days old, 3=between 7 and 10 days old, and 4=more than 10-12 days old). For instance, the point JCDN-KM7+1 was a den located in the Jatuncocha Creek, approximately 250 meters upriver from the KM 7 flag, and was active at least until the previous day; whereas the point THCS-KM5-4 was a human campsite located in the Tambococha Creek, near or exactly at the KM 5 flag, and had not been used for at least 12 days, or since the previous time block. This way, even if a locale was used various times, each of the points recorded in the GPS unit had a single identifier. Direct observations of giant otters were an exception in the coding procedure. As these already correspond to active signs (category 1), the final digit in the code matched the number of individuals seen each time, as a means of keeping track of the family group members. For instance, the point JLSG-KM2++7 is a giant otters sighting in the Jatuncocha Lagoon, approximately 500 m upriver from the KM 2 flag, where 7 individuals were seen at that time.



Figure 8. Distribution of kilometer flags, camera traps, research campsites and water level gauges within the study area.

During each time block, the entire length of each watershed was surveyed as far upstream as possible, both in the main channel as well as in all accessible tributaries. Accessibility in most cases was restricted by the riparian vegetation, and channel width and depth; in other cases, restrictions were represented by a combination of transversal logs of varying diameter and water level fluctuations, particularly near the head of each creek. Thus, the distance covered during each time block was never the same, but it was usually possible to cover the last 18 km in the Tambococha Creek and the last 21 km in the Jatuncocha System. When the water level was at its minimum and all of the tributaries in the second half of the watersheds were dry, these portions were explored on foot as far as possible.

The frequency and distribution of time blocks was designed to assure that each watershed was surveyed at equal time intervals and for a comparable amount of time. However, adjustments were eventually necessary due to supply shortages, health issues of the crew members, or other incidental circumstances. Therefore, time intervals between surveys in each watershed could vary from three to six days, and the starting and finishing time on the first and last days were also variable. Surveys never started later than 8 am and never ended sooner than 5 pm. Fish sampling was mostly conducted between 5.30-8.30 am and 6.00-9.00 pm, with 30 minute margin of variation.

Not all giant otter or human activities could be tracked over their entire range. In the Tambococha Creek, many people accessed the watercourse by land, in most cases to perform illegal fishing or hunting; it was possible to observe efforts to erase signs of presence, or active avoidance of direct encounters (hiding behind the vegetation or within tributaries). Giant otter activity in this creek was also hard to survey, as in most cases the signs found were those of a transient, solitary individual, who exhibited very inconspicuous behavior and fled immediately after seeing us.

In the Jatuncocha System, human and giant otter activities were easier to survey; all access to this watershed by humans is done by river through the Yasuní River, while the giant otter family group was large and conspicuous, so observations of presence and activity were very easy. On a few occasions, otters left the main channel and escaped by land, not to be seen again until the next day, so their exact location could not be determined due to physical restrictions (vegetation and swamps). The otters were also impossible to

track if they were too far upstream, where the vegetation (transversal logs) or channel width did not allow us to physically reach those areas. In that case, a GPS point was collected and only an estimate distance in kilometers was given to the point and later corrected on the map.

Errors in age estimations of otter and human signs can also occur. After a heavy rain, the fecal material in the latrines is washed off and its smell becomes bland, so they might appear older. Tracks on the clayish substratum become wet and more defined, giving the impression of a fresh print. We combined the experience and honesty of the native assistants in assessing sign age (particularly for human signs) with suggestions found in the literature (particularly for giant otter signs). In any case, only during the first time block or when a new sign was found, this represented a real challenge; once a sign was identified, it was possible to recognize subsequent changes (with few exceptions). The camera traps also represented a challenge because water level could vary enormously between and within time blocks, so convenient locations turned inconvenient after small periods of time, as re-adjustments were not possible daily. Nevertheless, the cameras hidden at the mouth of each watershed did well in keeping track of human activity; whereas the cameras placed upstream were not an adequate method to record giant otter presence.

CHAPTER TWO: HABITAT OVERLAP BETWEEN GIANT OTTERS (*Pteronura brasiliensis*) AND HUMANS: LANDSCAPE HETEROGENEITY PROMOTES COEXISTENCE BETWEEN TWO LARGE PREDATORS

1. INTRODUCTION

A species that uses large, ecologically diverse areas and often has significant impacts in the structure and function of natural systems is known as a 'landscape species' (Redford *et al.*, 2000). The large area requirements of these species also make them particularly susceptible to human use of landscapes (Sanderson *et al.*, 2002). Unlike in other functional categories used in conservation biology – focal, umbrella, keystone or flagship species –, the requirements of each population of the landscape species are used to define in extent and grain the area targeted for conservation, as such species rely on the composition and configuration of the landscape rather than simply on its total area (Sanderson *et al.*, 2002). It is thus acknowledged that organisms use heterogeneous landscapes (i.e. "mosaics of habitat patches across which they move, settle, reproduce, and eventually die"; Forman, 1995), which makes it possible to conserve the structures and functions that the landscape provides along with the target species (Redford *et al.*, 2000). Due to their spatial and ecological requirements, giant otters (*Pteronura brasiliensis*) ideally match the landscape species concept, which has turned them into the ambassadors of Amazonian aquatic systems (Duplaix 2004).

In optimal conservation practice, natural habitat would be maintained in its most pristine state and remain unaltered by human impact through the creation of isolated reserves (Terborgh, 1975). However, failed attempts over the last decades have proven such goals not only unrealistic, but also impractical (Dunning, Groom and Pulliam, 2006). Instead, effective management strategies recognize the importance of social and economic influences on the landscape, and account for the complex and diverse needs of both wildlife and people (Sanderson *et al.* 2002). Efforts intended to aid sustainable economic growth in addition to conserving biodiversity have proven more feasible on a long term, particularly in regions where people survive on natural resource extraction. Humans – a generalist predator with its own requirements and patterns of resource use – are seldom included in scientific studies as another species affecting the landscape (Forman, 1995).

Integrating humans as a species that eventually competes for resources with another predator could be a more realistic approach in conservation science, but is a challenging idea.

Ecological theory describes the long-term persistence of two species that share (or compete for) the same space or food items as 'coexistence' (Ritchie, 2002), which results from habitat partitioning and the exclusive use of fundamental resources (Connell, 1983). This is particularly true for mobile organisms, as they can sample diverse environments in different ways (Schoener, 1983). It was thought that coexistence was only possible when species compete for more than one resource or under a narrow range of supply rates for each type of resource (Tilman, 1982), but Grant (1985) has showed how behavioral changes in the use of resources can diminish the overlap in feeding niches. Habitat heterogeneity – defined as spatial and/or temporal differences in habitat patch size and food size, distribution and density (Abrams, 1988) – is a critical factor in competitive coexistence, and a conceptual link between competition and coexistence theory and conservation biology at the landscape level. But because there are several kinds of heterogeneity that can be identified on the landscape, the key for conservationists is to define the kinds of heterogeneity that control the ecosystem under threat, whereas the key for ecologists is to recognize the main processes responsible for those influences (Dunning, Groom and Pulliam, 2006).

Space is a fundamental resource for which all living organisms compete, particularly the space where basic daily activities take place – i.e. foraging areas, shelter spots (caves, dens, holes, trees) – or the places where socialization and play occur (Hanson, 1995). Most mammals delimit and protect the areas where they sleep and rear their young (i.e. their territories), but actively explore the areas where additional resources or a mate can be found (i.e. their home ranges; Hanson, 1995). The permanency in time of a resource can also be essential in determining the amount of time and energy that animals invest in competing for space (Loreau and Holt, 2004). If large carnivores usually live in heterogeneous landscapes where primary and secondary resources are scattered in patches or available only on a seasonal basis, then the size, shape and distribution of territories and home ranges can vary in accordance with the animal's ability to move, colonize, and defend them (Southwood, 1977).

I have explored, through the application of ecological theory in a spatially explicit framework, how the concept of coexistence can contribute to biological conservation of an endangered species (the giant otter). In the system under study, coesistence between humans and thislarge, predatory mammakl may be enhanced by the ability of individuals to partition resources that are not accessible to humans in a portion of the animal's range. My study also illustrates how informal ecological theory can benefit from nonexperimental data (Grant, 1985).

Little is known about the extent or location of giant otter territories during the rainy period (maximum water levels), when most of the forest is flooded and the fish are scarce or unavailable (Duplaix, 1980; Laidler, 1984; Hoeinghaus *et. al.*, 2003). During the rest of the year, giant otters are known to use two main types of habitat:

- Foraging areas: usually shallow areas in the main channel of rivers and lakes, or deeper areas with riparian or aquatic vegetation, and pools, ponds, streams, or swamps (Carter and Rosas, 1997; Appendix 1); and,
- Shelter areas on land but close to the water where they can breed (single dens), or rest, play, and mark their territories (campsites and latrines). Such places can vary in size, quantity, and quality depending on the geomorphology of the areas they occupy, but in most cases these are places located in *terra firma* forests (Schweitzer, 1986; Lasso, 2003; Appendix 2) and nearby a good foraging spot (Duplaix, *pers. comm.*).

No other mammal in the lowland Neotropics has similar spatial requirements, except for humans. People need comparable places on land to establish temporary campsites or permanent shelters, and equivalent sites in the water in order to fish for as much food as possible with the least effort. Thus, hills and levees located near the water (i.e. the highest places in the watershed), and water bodies that persist during the dry season (i.e. the lowest places in the watershed) are highly valuable for people and giant otters. Reasonably, the places where both occur within a short distance are ideal locations for both predators (*pers. obs.*). Given that they also share similar prey items (Schenck 1999; Carrera, 2003; Staib, 2004), their interaction is that of natural competitors.

The presence of giant otters in the study area implies that they have been able to coexist with humans so far and to some degree; but could present and future conditions eventually lead them to competitive exclusion? Identifying the factors that contribute to resource limitation could show us how to regulate human activity where giant otters occur (i.e. reduce competitive stress) so that humans persist without jeopardizing the survivorship of giant otters.

Seasonal fluctuations in water level can play a key role in determining the availability of resources for both species. Higher water levels pose a challenge since most of the land is flooded and the fishes hide within the forest (Goulding, 1980). Intermediate water levels (observed during the falling and rising water seasons) are likely more favorable situations: shelter places become available and there is still enough water to preserve the fish prey items within reach. Conversely, during the dry season many places on land are available but foraging areas can be scarce, and depending on the local geomorphology and hydrography, there might be only a few places (or none) where both shelter and food are found within a short distance (*pers. obs.*). If such ideal places disappear during the dry period, people and otters must travel longer distances to find them, and this might be the critical time when the probability of direct encounters and competition for space is the greatest.

In light of the dynamic resource overlaps and potential for competition between giant otters and humans, and based on existing knowledge of the giant otter's life history and its conservation status within the area, this study's objectives were:

- 1) To obtain a realistic estimation of habitat availability for giant otters and humans according to seasonal water level fluctuations,
- To identify patterns of seasonal resource use (occupancy) and habitat use overlap between the two species, and
- 3) To identify those patterns of habitat use by both species that are related to topology (relative distance and location) which may allow remote sensing of available habitat on larger spatial scales.

My results call attention to the importance of concepts such as habitat heterogeneity and connectivity, environmental gradients, seasonal variability, and the problem of scale; these might enhance our ability to effectively manage comparable landscapes, and to successfully meet conservation goals for giant otters and other landscape species.

2. METHODOLOGY

2.1 Habitat availability estimations

The places within the basin that could be considered suitable habitat (foraging and shelter areas) for otters and humans are: (1) the large water bodies (i.e. the superficial extent of the main channels, used for transit), (2) the areas subject to permanent flooding (i.e. the areas adjacent to the main channel that are flooded during most of the year and that are used as foraging/fishing sites, such as tributaries, pools, ponds, submersed vegetation colonies, and swamps); and (3) the areas adjacent to the watershed that can be used as shelter or resting sites, such as the lower *terra firma* forests and the *levees* immediately bordering the watershed. Therefore, floodplain extent and the limits between where it expands and contracts are hereby used a substitute for habitat availability.

I created a three-dimensional geographic model (map) simulating four seasonal scenarios of water level variation and floodplain extension through the year. These simulated natural patterns previously reported by Blandin-Landívar (1976) and INHERI (2004):

- A. Rainy season or flooding period: a constant increase in precipitation occurs, the maximum levels of water level are reached and the floodplain extends laterally filling all available spaces. This season is simulated in the model but no data was collected during the time when it actually occurs (April September).
- B. High water season: local precipitation decreases, the floodplain retracts, and the water level suffers little variation.

- C. Transitional or intermediate period: precipitation is sporadic, the water recedes from the floodplain at a higher rate, and the water level shows a steady decline.
- D. Dry season: local precipitation is scarce, the basin is drained to its minimum extent, and the water level reaches its minimum values. External events such as significant precipitation in the Andean slopes produce short events of water level increments.

The following extant geographic information from the area was used to build the floodplain extent and water level model:

- A Digital Elevation Model (DEM) resolution: 3 arc-seconds (0.00083 degrees) or 90 m – obtained from the United States Geological Service (USGS)'s Seamless Data Distribution System (Shuttle Radar Topography Mission, 2006). In order to optimize the usefulness of the DEM as a template for watershed analysis, the original file was translated to hydrographical language (by the application of the ArcHydro Tools for GIS 9.1), which prevents the creation of false water-bodies based solely on elevation, by integrating the slope and topography variables in a raster model of water direction and water flow;
- Recent soil, vegetation, and precipitation layer files resolution 3 arc-seconds,
 (0.00083 degrees or 90 m; courtesy of Dr. Rodrigo Sierra and MSc. Manuel Peralvo,
 University of Texas); and
- A high resolution ortho-photo file from the area (1 arc-second or 30 m resolution) obtained from the NASA Landsat Orthoimagery Mosaic download service (2006).

These layers were combined with real geographic information obtained *in situ* (GPS records imported to ArcGIS 9.1; average resolution recorded by GPS unit = 18 m, N records = 887) from observations of vegetation cover extent, water level and flood extent, and physical barriers for navigation and human access. Once the maximum and minimum water level limits and floodplain extent limits were determined in the model, equal elevation intervals of 2 m per season average (within a 4 m range) were established following the vertical (topography), longitudinal and transversal (geomorphology) axes, resulting in a three dimensional analysis of water level variations in the basin used to

predict availability of foraging (pools, swamps, river and lake banks) and terra firma (camping) sites. Then, a polygon representing the area available for humans and giant otters was created manually for each season (grain = 200 m) according to water level fluctuations, vegetation cover, and ease of access following physiological, ecological and ethological requirements and capabilities of each species.

2.2 Spatial occupancy and habitat use analysis

I estimated the use of space by giant otters and humans in space and time using points obtained in the field (with a Garmin E-Trex Vista GPS). At the landscape scale, the use of space by both species was estimated in two time scales: (1) the total survey time in the entire basin (N days = 70; all the GPS points collected during that period of time were used) which corresponds to the high, intermediate and low water level periods (N signs of human presence = 252; N signs of giant otter presence = 283), and (2) for each survey time block (N=10, 14 days each). In this case, only GPS points of recent signs were used and time blocks were analyzed as discrete time units (and not as time sequences) because the climatic pattern found was not that of a typical year. At the watershed scale, only the total survey time (70 day data) was used, due to small sample sizes.

GPS points were assigned a different icon according to the type of sign identified: human campsites, trail-heads, local and research fishing boats, and other indirect signs; and giant otter dens, individual latrines, tracks and scratch walls. Additionally, a 1 km radius buffer (resulting in 2 kilometer diameter circles) was created around each of these points in order to account for the estimated range of activity around the signs. The 2 km diameter was chosen as a minimum activity distance based on previous observations of human activity patterns within the area as well as on reports of giant otter ethology and behavior (Duplaix, 1980; Staib, 2005), following the criterion that both species could move in any direction 500 m around the sign, and that they traveled at least 1500 m to get to that point (this is the minimum distance found between active signs within a time block).

The polygons created for giant otters account for most of the floodplain (main channels, lakes, tributaries and swamps), plus the adjacent *terra firma* sites within 500 m from each

side of the floodplain, minus the areas that are known to be inhabited by people (except for the lower portion of the YNP-Napo buffer zone, where giant otter signs were found); whereas the areas available for humans account for the floodplain and its adjacent *terra firma* sites within 500 m from each side, plus the areas known to be inhabited and used as fishing grounds year-round, minus the swamps, the upper half of the tributaries, and the portions where vegetation limits canoe access.

Water level averages obtained at the Yasuní River were used to estimate seasonal variations in habitat use at a large scale. Although water levels can differ in each watershed (as shown by the quartile variation, Table 2), the daily average levels in the Yasuni River showed a strong correlation with those measured in KM 7.0 of the Jatuncocha System (r = 0.80) and a slightly weaker correlation with the water level measured in KM 7.0 of the Tambococha Creek (r = 0.66) during the same time frames (Table 2). Also, the probability that the variances between the Yasuní River and the Jatuncocha System and Tambococha Creek are not significantly different is relatively high (F-test = 0.1 and 0.5, respectively). Thus, the use of the water level in the Yasuní River is considered a good estimate of average water level in the entire basin, according to the field data collected for this study.

Table 2. Statistic summary for water level values obtained in the Yasuní River, and the Jatuncocha System (JS) and Tambococha Creek (TC).

The values used to compare the Yasuní River with each of the creeks are values obtained within the same time block, therefore there is a double set of values for Yasuní. The values for the creeks were registered 7 km from the confluence with the Yasuní.

YASUNI	and Js	YASUNI	YASUNI AND TC					
MODE (cm)								
YASUNI	JS	YASUNI	TC (cm)					
250	360	150	150					
STANDARD DEVIATION (cm)								
YASUNI	JS	YASUNI	тс					
53.31	69.66	63.41	54.9					
QUARTILES 1-4								
YASUNI	JS	YASUNI	тс					
190	268.5	150	62.5					
220	330	200	125					
250	363.5	250	160					
310	440	340	200					
SLOPE								
0.	61	0.76						
CORRELATION								
0.	.8	0.66						
	F-1							
0	.1	0.4	0.48					

2.3 Habitat overlap analysis

A similar procedure was used to estimate the overlap between the habitats used by giant otters and humans. The polygons estimating the total area used by giant otters and humans (including the 2 km buffers) were added to a 25 m diameter buffered polygon of the "River" feature, in order to account for the average minimum space used by either species to move from one place to another. At different scales, the giant otter use, human use and buffered river features were combined under the "Intersect" tool of the ArcGIS[™] 9.1 Spatial Analyst tool set.

The polygons obtained by the "Intersect" tool corresponded only to those areas where all three features overlapped, therefore excluding those areas overestimated by either buffer, particularly for those sites on land that are not necessarily used for transit by both species. Each layer was subsequently analyzed individually, and areas where isolated points located between two areas of overlap occurred were estimated and added to the total overlap value. The percent overlap calculations correspond to the total area overlap multiplied by 100 and divided by the total area used by both species. This last estimate equals the distance between the furthermost point upstream minus the lowermost point downstream from either species (maximum – minimum distance from mouth in km) multiplied by the buffer estimate (2 km).

It must be noted that for most time blocks, water level values that corresponded to the high, intermediate or low categories at the landscape level (those measured in the Yasuní River), were analogous to those used for the watershed scale (obtained from water level gauges located at km 7 in each of them); but some exceptions exist due to variations in small scale precipitation and the topological effect of the local hydrographic dynamic – i.e. the Tambococha Creek was more subject to water level variations in the Napo and Yasuní Rivers, whereas variations in water level were less dramatic in the Jatuncocha System, probably due to the relatively longer distance from the Napo River and to the buffer effect that results from a wider catchment area (the lagoon).

2.4 Patterns of habitat use as a function of topology

Topology represents the relative distance between certain features of the landscape and a place of interest (i.e. quantitative description) and their positional relationship with that feature (vicinity, containment, function...i.e. qualitative description). Due to the nature of watercourses, there is a high probability that certain resources are distributed along an upstream-downstream gradient, and this might explain some of the patterns of activity

observed. Therefore, relative distance was measured in this case from the mouth of each watershed upstream. The distance from the mouth could correspond to an implicit gradient of resource distribution and water level variation, as is usual for rivers and streams and as can be inferred from elevation gradients (although this is not necessarily applicable to all kinds of resources). For this part of the analysis, both recent (categories 1 and 2) and older signs (categories 3 and 4) of otter and human activity were considered. Relative frequencies of presence of signs were considered every two kilometers in order to maintain consistency of scale throughout the analysis.

3 RESULTS

3.1 Habitat availability for giant otters and humans

According to the model maps, of the total surface of the study area (902.81 km²), 63% (566.3 km²) is at least partially flooded during the rainy season, (green and blue layers in Figure 9), but only 43% (388.2 km²) corresponds to the floodplain in the LYB (the area south of the Napo River and west of the Yasuní River). During this time of the year, the Braga, Tambococha Creek and Jatuncocha System are connected, at least in their lower potions, by a series of swamps and by the overflow of their tributaries.

Due to the geomorphology of the basin (particularly, the slope of the hill situated between the Tambococha Creek and the Jatuncocha System), scarcely any sites of *terra firma* remain dry in the wet season (red and orange layers, Figure 9A). As the water recedes progressively into the dry season (Figure 9D), the floodplain within the LYB is reduced to only 25% (225.7 km²), and much of the connectivity between water bodies is lost, whereas the availability of dry land increases, although most of it is located upstream. The average difference in habitat availability for humans and for giant otters (4 seasons) is 41%, but it is more significant during higher water level periods (57 and 46%), than it is during the drier seasons (38 and 22%, Figure 10).







Figure 9. Geographic model of habitat availability within the Lower Yasuní Basin, predicting fluctuations in water level and floodplain extent during the rainy season (A), and during high (B), intermediate (C) and low (D) water level periods.

The polygons estimating the total area available for humans (black) and for giant otters (white) follow the elevation average between minimum and maximum values within a 4 m elevation range for each season. Areas in blue represent the minimum elevations covered by water at that level, green and olive correspond to permanent or temporary swamps, and cherry colored areas match terra firma sites that can be flooded during the maximum water levels within a season. (DEM Source: USGS, Maps created by the author).



Figure 10. Seasonal variation of habitat availability for giant otters and humans expressed in absolute area extension. The grey boxes represent the percentage area available for humans from the total available for giant otters.

The model shows that less than 25% of the total area corresponds to suitable habitat available for both species permanently - this may even be an overestimate because the main channels are included but are not suitable habitat for shelter or foraging. From the total extent of the study area, only 5% (46.83 km²) corresponds to foraging areas – i.e.

the lower portions of the watershed that do not dry out –, and 3% (27.67 km²) correspond to *terra firma* – the highest parts of the watershed that do not get flooded at any time during the year.

From the graphic image derived from this model map, the permanently available areas on land are more accessible to giant otters than for humans, as these are located in upstream portions of the watershed and more than 500 m away from the main channel. The contrary occurs for foraging areas, which are easily accessible for humans through the main channel, but that are higher risk areas for giant otters, since they are far away from *terra firma* places where resting and demarcation of territory occur.

3.2 Spatial occupancy by giant otters and humans

At the landscape level, area occupancy was highly correlated with estimated space availability for both humans (r = 0.83) and giant otters (r = 0.86). The proportion of area available for the two species decreases proportionally with water level (Figure 10). Giant otters use only between 20-31% of the area available for them (Figure 11), whereas humans use most of the space available for them (44-95%). In both cases, the smallest proportion of available area used occurred during the high water period, when giant otters use only 20% of the area available for them, and humans use only 44% of accessible areas. Excluding the flooding season – when the amount of available area presented is only an estimate – the average area used by giant otters within the basin during high, intermediate and low water levels was 51 km², whereas the average area used by humans was 46 km².

At the watershed level, patterns in habitat use relative to space availability are different than at the basin (landscape) level. In the Jatuncocha System, the areas available for giant otters range between 52 km² in the dry season to 95 km² in the flooding period, whereas the areas they actually occupy range between 23-44 km², during the same periods. Giant otters used in average 41% of the space available for them (excluding values from the flooding season). However, there was an inverse correlation between use of space and water level: use of space represented 37, 42 and 45% of the area available during the

high, intermediate, and low water level periods, respectively (Figure 12 A). The areas available for humans ranged between 33-50 km² and the areas that they actually used ranged between 26-37 km². Humans used larger proportions of the areas available for them: the areas used by them represented 57, 66 and 88% of the areas available during the high, intermediate and low water level periods, respectively. The average extent of the areas used by humans, excluding the flooding period, was of 70 km².



Figure 11. Area (km²) used by giant otters and humans (void columns) compared to the total area available for them (bold columns) within the LYB.

The values used for the flooding period were estimated from the total area used by each species during the entire field season. The values used for the high, intermediate and low seasons correspond to the average among time blocks equivalent to each water level range (high: TB5, 7 and 10; intermediate: TB2, 3, 4 and 6; low: TB1, 8 and 9). In the Tambococha Creek, a comparable pattern is observed. The areas available for giant otters ranged between 30-90 km²; whereas the areas available for humans ranged between 20-45 km². Giant otters used between 46-78% of these areas (flooding and high water level periods respectively), and humans used 61-94% of the areas available for them during the same periods (Figure 12B). The average use of space by giant otters was 64% of the availability (14-45 km²) whereas the average for humans was 81% of the availability (17-26 km²), excluding the flooding season.

For the two watersheds analyzed, the patterns of area use by giant otters and humans are comparable: (1) there is more absolute area available for giant otters than for humans (average difference = 35 km^2 in the Jatuncocha System and 24 km^2 in the Tambococha Creek); (2) the absolute areas used by both are comparable (average difference = 2 km^2 in the Jatuncocha System and 7.7 km² in the Tambococha Creek); and (3) the percentage area used from the space available is higher for humans than it is for otters (29% higher in the Jatuncocha System and 25% higher in the Tambococha Creek).

At the basin scale and during each of the time blocks considered, humans used smaller areas than those used by giant otters, except for the second time block (intermediate water level), where the area used by humans was 12% larger than the area used by giant otters (Figure 13). Giant otters used areas of approximately $17 - 41 \text{ km}^2$, although the average extent recorded during each time block was of 26.5 km²; whereas humans used areas between $12 - 33 \text{ km}^2$, covering an average extent of 20.7 km² in each time block.

A linear regression model shows that the range of activity of the two species at the landscape scale is proportional to one another: in general, for every km² used by humans, giant otters occupy areas that are approximately 1.2 times larger (Figure 14).





Figure 12. Habitat use by giant otters and humans in the Jatuncocha System (A) and in the Tambococha Creek (B).



Figure 13. Total area used by humans and giant otters compared to average water levels at the Yasuní River for each time block; white boxes contain the percentage area used by humans when compared to that used by giant otters.



Figure 14. Linear regression model explaining the relation between area extent used by giant otters and humans in the Lower Yasuní Basin, based on signs observed during 14 day sampling intervals.

The proportion of area used by each of the species is similar to this pattern at the watershed level. In general, giant otters used larger areas than humans within each time block in each of the watersheds, except for time blocks 2 and 6 in the Jatuncocha System (Figure 15A) and time blocks 4 and 5 in the Tambococha Creek (Figure 15B). These time blocks correspond to intermediate and high water level periods. In the Jatuncocha System, giant otters used areas of 20 km² in average (min=13 km², max=27 km²), whereas humans used areas between 10-22 km² (17 km² in average). The use of habitat in the Tambococha Creek was analogous: between 7-24 km² by otters (15 km² in average) and between 5 and 20 km² by humans (13 km² in average).

In the Jatuncocha System, local variations of only 1 m in average water level determined 10 km² fluctuations in the extent of the areas used by humans; a comparable variation in the use of area by giant otters was also observed. In the Jatuncocha System, both species seem to use larger area extents at low and high water levels, whereas the areas used are smaller at intermediate water levels; but in the Tambococha Creek, humans reduced the area extent used during the highest water levels recorded locally.

3.3 Habitat use overlaps between giant otters and humans

Bilateral overlaps between humans and giant otters are not comparable between the two spatial scales. When the whole basin is accounted for, the extent of areas where overlaps occurred ranged between 2.5 km² and 30.9 km² (respectively 7% and 68% of the total area used by both species). The average overlap between humans and giant otters corresponds to approximately 11 km² (or 29% of the total area used by both). The largest percentage of habitat overlaps occur during low and high water levels (25 – 68%), and minimum values of overlap in the use of space are found during the intermediate water level periods (7 – 15%, except for time block 2 where the overlap is 38%; Figure 16).



Water level and time blocks

Figure 15. Spatial extent of habitat use by giant otters and humans in the Jatuncocha System (A) and the Tambococha Creek (B); the water level categories and the average water level used (scattered line) correspond to the values obtained locally at KM 7 in each of the watersheds.



Average water level and time blocks



The white diamonds correspond to the absolute extent of area overlapped, whereas the bold digits represent the average percent bilateral overlap (i.e. the average between the unilateral overlap of areas used by humans with areas used by otters and viceversa).

Patterns of overlap at the watershed scale were different from those found at the basin scale, and between each other. In the Jatuncocha System, the average overlap in use of space between species was 44% (13 km²) across time blocks over a 30 – 60% range (8-20 km² range), (Figure 17 A). In this system, overlaps between 30-45% occur during the high and intermediate water level periods, whereas overlaps between 50-60% occur during intermediate and low water level periods.





Average water level and time block



The white diamonds correspond to the absolute extent of area overlapped, whereas the bold digits represent the average percent bilateral overlap (i.e. the average between the unilateral overlap of areas used by humans with areas used by otters and viceversa).

Spatial overlap in the Tambococha Creek ranged from 34-64% which corresponds to a range of 4-16 km². In average, the overlap in this creek was of 51% across time blocks (10.5 km²), (Figure 17B). During intermediate water levels, the overlap between areas used by giant otters and humans ranges between 34-46% of the total area used by both; the range of overlap during the high water level periods is 41-52%; and the highest overlaps in the use of areas occur during the low water level periods, in a range of 57-64% of the total area used.

There were qualitative differences in the results obtained among scales. At the basin scale, the relationship between water level and the percentage overlap of areas used by humans and giant otters is not clearly defined, given that the water level at the Yasuní River represent the variations of water level at the basin scale only to a certain degree (Figure 16). At the watershed scale, on the other hand, there is a more defined correlation between water level and the percentage overlap observed. In both the Jatuncocha System and the Tambococha Creek, the smaller overlaps occur during the intermediate and high water level periods, whereas the higher overlaps were registered during intermediate and low water levels (Figure 17).

3.4 Patterns of habitat use as a function of topology

At the landscape scale, giant otter signs were predominantly found in the Jatuncocha System and Tambococha Creek watersheds (Figure 18). Although signs were found by the Braga Creek, this watershed remained unexplored due to limitations in accessibility. Nevertheless, it must be noted that sightings and vocalizations of giant otters in the vicinity of the Braga Creek were frequently reported by the locals. The signs found upstream of the Braga Creek and around one if its tributaries (a 2 m width stream) were reached by foot through a hunting trail accessed from the Napo River. No dens, latrines, tracks or scratch walls were found along the margins of the Yasuní River, although otters were frequently seen going up and down this river.



Figure 18. Distribution of giant otter signs within the Lower Yasuní Basin; only signs one week old or less (direct observations and vocalizations, active dens, recently marked latrines, and fresh tracks and scratch walls) were included.
Nearly all signs found in the Jatuncocha System were the product of activities carried on by a family group of giant otters that was known to occupy this watershed since 2001, as confirmed by the identification of individual collar patterns. Between October 2004 and January 2005, there were 2 adults, 2 sub-adults, 1 juvenile and 3 cubs in this family group. The cubs were observed outside the den for the first time during the first week of November 2004. By the end of the field season, two cubs had disappeared and one of the sub-adults was separated from the rest of the group.

Signs from this group were found along the entire watershed, although most of them were concentrated in the upper portion of the system, whereas smaller proportions were found in the middle portion and in the northern banks of the lagoon (Figure 18). Direct observations of this group were done during at least 1 minute (detection, periscoping, alarm snore, escapee), to as long as 30 minutes (usually while the group was fishing and the conditions allowed for good camouflage). When in contact with other humans, the members of the group showed a more cautious behavior.

Many latrines were used regularly throughout the field season (unless they were flooded), though at least one new latrine was found each time a new survey was conducted. No specific pattern of latrine use was observed, aside from the fact that the most frequently marked latrines were always close to a tributary. According to my observations, most dens were never occupied for more than 2-3 days. The dens that were used more frequently were always located in levees with the following characteristics: there was an ample range of vision to both sides of the river, there was a tributary within 100 m, and there were logs along the river that could be used for resting or as lookout points.

In the Jatuncocha System, most of the signs (25%) were found in the upper portion of the creek (i.e. between KM 16–18), in the surrounding areas (18% in KM 14–16, 18% in KM 18–22), and in the middle portion of the creek (11% in KM 8–10; Figure 19A). Lower densities of giant otter signs of activity occurred between KM 2–8 (4.2%) and 24–26 (1.8%).





Most of the signs registered in the Tambococha Creek belonged to a single (transient) individual that was seen exploring the watershed at least once every time block, and although its collar pattern could not be identified, its tracks were easily recognizable since the left forepaw missed the fourth and fifth claws. Direct observations of this individual were always short (1-5 minutes), and usually after feeling our presence it quickly disappeared by river or by land. All dens (with one exception) and most latrines at the Tambococha Creek (Figure 18) were used by this transient individual, as indicated by its characteristic tracks.

Other giant otter records in the Tambococha Creek include the sighting of 10 giant otters of varying sizes observed during the first time block and within the first kilometer surveyed. They displayed an attack behavior towards two other adults, until they saw us and disappeared by land. This group was never again seen in the Tambococha Creek, but several reports were obtained from the Braga Creek afterwards, which suggests that this watershed was their territory. Also, a group of four large individuals was seen once at the mouth of the Aguas Blancas Creek (KM 21 of the Tambococha Creek), occupying a den in KM 22, though no other signs were found before or beyond this point (this portion of the creek could only be accessed twice). Most giant otter signs found in the Tambococha Creek were not registered in consecutive days or in consecutive time blocks, except for a few latrines where scat or tracks were found on a regular basis.

Approximately 48% of giant otter signs found in the Tambococha Creek watershed were distributed in the middle portion of the watershed (KM 6 – 12), but high densities were also found around KM 14–16 (14%), 0 – 2 (11%), and 0-4 (20%), (Figure 19). Lower giant otter sign densities were found between KM 4–6 (2.5%) and 16–20 (8%).

Human presence within the LYB was distributed in a similar pattern to that of giant otters: most of the people concentrated their activities in the YNP watersheds, and only activities of transit and wood extraction were conducted along the Yasuní River (Figure 20). The Jatuncocha System was accessed by motor or paddle canoes, whereas the Tambococha Creek was also accessed by land from the Napo River or the Braga Creek. People accessing the Tambococha Creek by trail used the middle and upper portions of the watershed (avoiding the control point at the mouth of the river), where they kept dugout canoes for short distance navigation.

In the Jatuncocha System, human activity took place in the lagoon and in the mid-section of the creek, whereas less activity was recorded in the upper portion, showing a pattern of reduction in human activity as the distance from the mouth increased (Figure 21A). Almost 48% of human signs were found in the lagoon (KM 0 - 6), where most of the signs were campsites (ample space for camping and easy access to fishing spots). At least 31% of human signs were found in the middle (KM 10-14) and mid-upper (KM 16-18) portions of the creek; whereas human signs were less frequent in the upstream portions of the system: only 11% between KM 18-24 and 1% between KM 14-16.

In the Tambococha Creek, the distribution of human activity seemed to be concentrated on 3 different areas (upper, middle and lower portions of the creek), interspersed by places where no human activity occurred (Figures 20 and 21B). Between KM 14 – 18 (upper portion) 16% of human signs were found; 66% were distributed in the middle portion (KM 4–12), where the largest percentage corresponded to the stretch between KM 6 – 8; whereas 14% of human activity took place within the first two km by the river mouth.



Figure 20. Distribution of signs of human activity within the Lower Yasuní Basin; only signs that were less than one week old (direct observations, active campsites, recently used fireplaces, and fresh tracks) were included in this map.



Figure 21. Distribution and frequency of human signs relative to the distance from the mouth of the Jatuncocha (A) and Tambococha (B) watersheds (2 km categories); the best fitting models for the data correspond to a logistic regression in A, and to a polynomial curve of the fourth order in B.

4 CONCLUSIONS / DISCUSSION

The results have shown that quantitative and qualitative differences can be observed in the total extent of area available for and used by giant otters and humans when the spatial and temporal scales under analysis change. At low spatial resolution (basin scale) the difference between area availability and use is larger than at higher resolution (watershed scale), mostly because at the basin level the model accounts for secondary areas (such as the Yasuní River and isolated watercourses) that are not included at the watershed level. Also, the values obtained for the area used by giant otters and humans are only a rough estimate at the basin level (additive). When two time scales are considered (season and time block) the results obtained are also different, mainly because at the seasonal time-scale all the values are averaged and matched to a water level value, whereas at the time block scale is possible to observe more detailed variations in the use of space when compared to water level. In conclusion, at high resolution (smaller scale) humans used smaller areas than otters, and at low resolution (larger scale) the areas used by humans could be smaller or larger than those used by giant otters, depending on the temporal scale under analysis.

The territory and home range extent of large predators have commonly been used as a way to estimate the size and shape of natural reserves, because they determine how much space is necessary for an animal to meet its ecological needs (Sanderson *et al.*, 2000). Previous territory estimations for giant otters reported extents from 2-4 river km in Guyana (Duplaix *et al.*, 2004) and 1.1 km² in Peru (Schenck *et al.*, 2005) to 20 km² in Suriname (Laidler, 1984). In the LYB, Utreras *et al.* (2005) measured the extent of giant otter home ranges for the two resident groups of otters during the dry season and produced an estimate for the rainy season. They measured the distance between the two most remote signs from giant otters found along the longitudinal gradient of the creeks, and added to it a buffer based on the maximum distance found between the river bank and a giant otter sign on land. They concluded that in the Tambococha Creek the home range occupied by the resident group was of 0.6 km² during the dry season and of 7.7 km² during the rainy season. In the Jatuncocha Creek, the total extent of the area occupied by giant otters during the dry season was of 2.8 km² and of 20 km² during the rainy season (Utreras *et al.*, 2005).

Field observations and the results derived from them in the present work are qualitatively similar to those obtained by Utreras et al. (2005) but quantitative differences arise from the methodology employed to estimate these areas and from the way seasonality affects area availability. In both cases, the use of space by giant otters in the LYB corresponds seasonally to a large portion of the watercourse and some of the surrounding terrestrial habitats, and the difference in the areas obtained relies on the estimates of these adjacent areas (300 m buffer zones in Utreras et al., 2005 vs. 2 km buffer zones in this work). The estimation of habitat availability by means of a virtual model allowed me to show that many areas within the basin could be used by giant otters to complement for the areas adjacent to the main channel when fish become scarce or when human density becomes threatening. Also, during 13% of the total observation time (113 min) in the Jatuncocha System, giant otters could only be heard but not seen during surveys, and in 17% of the total survey time (115 h), giant otters were not seen at all, although fresh signs were found within the area. This is presumably because they were actively using the adjacent swamps and ponds far away from the main channel during that time. Thus, higher distance values were assigned to the buffers representing these adjacent areas in the polygons derived from the field data.

One important disparity is that of the home range sizes obtained for the two main seasons. While Utreras *et al.* (2005) concluded that the home ranges of giant otters during the dry season were dramatically smaller than during the rainy season ($6 - 17 \text{ km}^2$ smaller), my results indicate a different pattern: larger areas are used by giant otters during *both* the low and high water level periods, and smaller when the water level is at an intermediate stage. Although Utreras *et al.* (2005) do not specify the water level thresholds between these two seasonal stages, the dry period in their study would be comparable to the lower water level period in this study, but the same is not true for the rainy period (only habitat availability is estimated here for that time of the year). Such differences, again, are most probably due to the methods employed for the estimations, which underscores how much caution must be taken in the interpretation of numerical results, and the importance of standardized methods for estimating home range sizes.

In addition to the existence of suitable supplementary habitat for giant otters within the basin, the three-dimensional geographic model obtained (Figure 9A) showed the possible

amount of connectivity between watersheds during the flooding periods and also the permanent availability of terrestrial habitat in the upper portions of the watershed. In general, giant otters had more access to suitable terrestrial habitat than humans during this period. This is in agreement with the idea that giant otters do not disappear in flooded forest during the rainy period as they might do in the lower parts of the Amazon basin, where they abandon the dry season territories and move to a different area (Ribas-Pereira, 2004; Groenendijk, 2005). They seem to only shift their territories up-river without abandoning the ones downstream, which might be available occasionally thanks to the extreme water level fluctuations that result from high elevation range in the area. Environmental stress associated with refuge and foraging habitat scarcity would definitely be the real challenge for giant otters during this time of the year, particularly if cubs were born late in the dry season and did not develop the necessary skills to be effective hunters (Schenck *et al.*, 2002).

Giant otters might also take advantage of the connectivity in the floodplain to find resources or a territory/mate in the case of transient individuals. Connectivity offers access to the middle portion of the Yasuní Basin in the South and to the middle portion of the Tiputini Basin in the Northwest, allowing for genetic exchange among populations, although the current status of the Tiputini populations is not well known. Schenck *et al.* (2002) and Brecht (1983) had already noted how connectivity and access to secondary habitats can be key factors in the survivorship of giant otter populations.

In the LYB, only 1 m variations in water level can produce 10 km² (or 5 river km) differences in area occupancy by either species, so further considerations about the importance of the 3-dimensional scale must be accounted for. It is likely that home range estimations based on 1- or 2-dimensional characteristics of the landscape can provide a good idea of the minimum area necessary to maintain a population at that scale; but the 3-dimensional characteristics of the floodplain must be included when considering habitat availability or use in the case of metapopulations, because not only differences in connectivity and habitat accessibility can be established, but because water level ranges (and not only averages) can profoundly affect seasonal restrictions in habitat accessibility, availability and quality. An important consequence of this idea is that the minimum home range estimations for viable giant otter populations are likely not comparable between

Andean and lower Amazonian ecosystems. Near the Andes, water level variations could represent a change in habitat use on a three dimensional scale, whereas in the lower Amazon, water level variations are probably more significant on the vertical axis (depth).

During the lowest water level periods, connectivity among watersheds is lost and several alternative habitats suitable for refuge or foraging disappear, so the use of space by giant otters is restricted to each creek. Refuge habitat is more available and some foraging habitat remains, which are favorable conditions. However, the distance between refuge and foraging sites increases (higher energy expenditure), human density and frequency increase (producing competition for foraging sites as only 25% of available space is suitable habitat Figure 9D), and the likelihood of disturbance related stress (cub sequestration, noise pollution, inappropriate tourism practices) augments. Thus it is during this period when most of the competitive interactions between giant otters and humans might occur. Such statement has been supported by the findings of Zucco and Tomas (2004), and Schenck *et al.* (2002). The absence of competing groups of otters within the Jatuncocha System, which according to home range estimations could provide resources for three family groups of otters (Duplaix, 1980; Schenck, 1999; Shenck *et al.*, 2002; Staib, 2005; Utreras *et al.* 2005,) could be a sign of this lack of connectivity, of low transient survival rates, or a combination of both.

Humans, on the other hand, used at least 60% of the space available for them; this suggests an ability to explore and exploit suitable habitat to its full extent. Particularly during intermediate water levels, more foraging sites such as tributaries and ponds are accessible for humans, which might explain why the areas they use are smaller during those water level periods than they are during the high or low water levels. Yet, a large proportion of suitable habitat for both (75%) corresponds to habitat constantly visited by both species, which can be understood as the amount of area where some degree of overlap always occurs regardless of water level. These could be areas that provide primary refuge or foraging within a particular section of the river that are explored in at least a two-dimensional scale (larger overlap), or areas of transit that are only utilized linearly (smaller overlap).

The average overlap between areas used by giant otter and humans was about 30% of the space used by both; but it could be as low as only 7% and as high as almost 70% between time blocks. Although such overlaps could not be linearly related to variations in water level, most of the large overlaps occurred during the dry season, whereas the smaller overlaps occurred during intermediate water levels. It is not surprising that the pattern in overlap was similar to that of habitat use, as during the dry season (when less suitable habitat is available) both species have fewer choices, and move longer distances than during other seasons, so the probability that they will use common areas is higher.

Dissimilar trends were found when overlaps were analyzed at the watershed scale. In the Jatuncocha System, habitat overlap was inversely related to water level variations (higher overlaps occur at lower water levels), and it was not comparable to the pattern of habitat use. This watershed offered habitats that became progressively unavailable with water level changes and with distance from the mouth (i.e. there was a constant decrease in elevation towards the mouth of the system), so at lower water levels otters and humans were presumably left with fewer dry places to camp near foraging areas, and vice-versa. If larger distances must be traveled by both species, it is expected that more overlap will occur in their use of space, particularly when the availability of suitable sites is restricted.

At any scale, giant otters concentrated their activities within the watersheds and in the areas adjacent to the main channels. Although other aquatic habitats are available for them during parts of the year, the main channel offers quick access to both refuge and foraging places, by facilitating movement from one place to another and easy escape from predators and other threats (Staib, 2005). Once giant otters detect the presence of humans or other animals in the area (primarily by smell or hearing, and secondarily by sight) they immediately dive in the water, and only then they assess the magnitude of the threat. It is harder to tell what sort of escape strategy giant otters would use if threatened in secondary habitat, such as permanent swamps or while crossing *terra-firma* areas, but direct observations suggest that they can use certain kinds of vegetation (such as colonies of the long spiked *Astrocarium* palm tree) as a refuge when access to the main channel is not immediately available. Such would be a life threatening situation mostly when cubs are still young and depend on the protection of the adults (at intermediate water levels,

or when the water level starts to decline), befalling vulnerable to caimans (particularly *Melanosuchus niger*), jaguars (*Panthera onca*), or humans.

Conditions seem to be still suitable for survivorship and persistence of giant otters in the Jatuncocha System. The presence of the same family group as the one found by Lasso during the dry season of 2001-2002 supports this statement, although the disappearance of three of its members by the end of our surveys renders such idea questionable when extrapolated to the population level. This group's annual home-range corresponds to the entire watershed (at least 50 km²) although they used the upper and middle portion of the creek more frequently. However, the lagoon was visited on a regular basis, and usually only the northern border of the lagoon was explored; only in the absence of humans (except for the researchers) giant otters explored the lagoon's southern banks. On the other hand, the campsites and latrines located near the mouth of the system (KM 0 – 2) were almost always marked (in 8/10 of the survey time blocks) even if the nearby den was not actively used, and even when 50% of human activity was concentrated in the lagoon.

This suggests that giant otters avoid overlaps in foraging areas with humans whenever possible, but that they take the risk of encountering humans regardless of the stress this might produce for the sake of territory marking and defense. After all, the lagoon constitutes excellent foraging habitat, and provides enough foraging sites for these and many other large predators (such as the piscivorous fish *Arapaima gigas*, pink dolphins *Inia geoffrensis*, white caiman *Caiman crocodilus*, black caiman *Melanosuchus niger*, several species of piscivorous birds, and possibly the Neotropical otter (*Lontra longicaudis*). Thus, the few terra firma places available for giant otter use (mainly, two latrines on islands in the mid-portion of the lagoon and a campsite covering 500 m of the northern border) must be claimed from human and other giant otter groups at some risk.

High densities of signs from the transient otter in the middle portion of the Tambococha Creek suggest that this area (which is the drainage area of a relatively large tributary) offered easy fishing and good refuge for a single otter, so most likely this individual used the middle portion for basic survival, and it was seen in other parts of the creek or in the Yasuní River during its search of a mate. As described by Schenck *et al.* (2002), the risk of

local extinction occurs when the rate of re-colonization of an area by a transient is low, or at least if it is lower than the mortality rate of the local group. As they have clearly stated in their latest research, "it seems reasonable to suppose that the bottleneck for a successful colonization is whether a [transient] meets a potential mate at the right time and place".

Management decisions should be made based on considerations from multiple scale perspectives, since conditions may be favorable for the competing species at the local scale, but unfavorable for the persistence of the metapopulation at the landscape scale. Reductions in the rate of human disturbances within the watershed should be combined with improvements in connectivity between watersheds and among basins. The use of motor powered canoes in all water-bodies should be restricted to 25 HP, and human incursion in the upper portions of the creeks when water levels reach minimum values should be forbidden; this would reduce competitive pressures between giant otters and humans by removing disturbances that force giant otters to expand their range of activity (which increases the probability of direct encounters with humans) and by facilitating resource partitioning on a spatial scale. Future research should focus on the comparison of giant otter area use among regions with different elevation ranges, when all else is comparable. If significant differences were found between giant otter response to water level variations, then regulations for conservation should be modified accordingly If giant otters switch to habitats that are nor accessible to humans during the rainy period they are less vulnerable than if only slight shifts in territory use are done during that time of year (due to facilitated human access) as has been observed for the Lower Yasuní Basin.

CHAPTER THREE: FORAGING PATTERNS OF GIANT OTTERS (*Pteronura brasiliensis*) AND HUMANS IN THE LOWER YASUNÍ BASIN

1. INTRODUCTION

In order to survive, defend a territory, find a mate, or escape from predation, an animal needs sufficient food (energy), and many carnivorous animals must learn where to find it (Wilson, 1976). Moreover, top predators with high metabolic rates must allocate a substantial amount of time and energy to find food, because their overall survivorship depends on their ability to efficiently forage (Schoener, 1971). However, energy intake maximization during foraging activities depends on the densities of prey, and this affects the behavior of the forager, as prey distribution is linked to the dynamics of the whole system (Krivan, 1994). Additionally, it has been shown that dietary specialization is correlated with the relative abundance of both preferred and non-preferred food items (Rapport, 1980). These patterns have been observed for giant otters and humans in the Lower Yasuní Basin (LYB), as they are both top predators who feed almost exclusively on the fishes obtained in its aquatic systems (Carrera, 2003).

Previous research on the diet, foraging behavior, and seasonal responses of giant otters to prey abundance highlight the variability of giant otter diet across landscapes (Duplaix, 1980; Rosas *et al.*, 1999; Zucco and Tomás, 2004), and the need to integrate the spatial component of prey availability and human presence more explicitly (Gómez, 1999; Staib, 2005). Furthermore, Carrera (2003) had shown that an overlap of 54-82% exists between the giant otter's diet and the local fisheries, so foraging behavior could represent one of the main causes of direct or indirect competition between them, since it is possible that they are obtaining their prey in overlapping foraging sites. My study describes the composition of the giant otter's diet, and examines giant otter and human foraging behavior by comparing the distribution of giant otter and human activity over time to the relative abundances and diversity of fishes in the LYB.

Giant otters are semi-aquatic mammals that live along creeks, rivers, lagoons and flooded areas of the Amazon, Orinoco and La Plata river basins (Emmons and Feer, 1997) and in similar portions of the Guyana Shield (Duplaix, 1980, 2004; Laidler, 1984). Once abundant and widely distributed, about 3000 giant otters were estimated to have survived the intense pelt hunting that took place from the 1940's to the 1980's throughout their entire home-range (Carter and Rosas, 1997). Population viability estimations predict that their population size may be reduced by 50% over the next 20 years (Groenendijk, 2004, Schenck *et al.*, 2002). In the Ecuadorian eastern lowlands, most giant otter populations exist in isolated spots ever more exposed to various degrees of human disturbance, and thus are considered a Critically Endangered Species in the Red Book of Mammals of Ecuador (Utreras and Tirira, 2001). Within the Yasuní National Park (YNP, Figure 1), giant otters have been designated as a conservation priority species, due to their role as top predators and charisma, because of their sacred rank in Amerindian mythology, and because they are increasingly exposed to water pollution, oil exploitation, the deforestation of riparian forests, and the effects of illegal fishing methods (GEF, 1998b).

Giant otters live in highly cohesive family groups of three to ten individuals (Schweizer, 1986; Schenck, 1999), but super-groups of 12 to 20 can be seen when abundant food resources are available (Duplaix, 1980). Once they have reached sexual maturity, transient individuals do solitary explorations outside of the family group's territory (Carter and Rosas, 1997; Schenck *et al.*, 2002). Giant otters feed almost exclusively on teleost fishes and are able to consume up to 3kg of those daily (Duplaix, 1980). Strictly diurnal, they hunt alone or in groups during early morning (Laidler, 1984) and mid-afternoon hours (Carter and Rosas, 1997). They prefer black or clear water-bodies, likely because of their transparency and the large diversity of fishes present (Schweitzer, 1992). Giant otters usually capture fishes between 10-40cm in length (Duplaix, 1980), although they have been observed eating fishes of up to 100cm (Carter and Rosas, 1997; Carrera, 2003).

Fishes from the Characoidei, Perchoidei and Siluroidei suborders are commonly consumed by these mammals, but crustaceans, snakes, turtles or even small caiman (mainly, *Melanosuchus niger*)) can also be part of their diet (Carter and Rosas, 1997). Studies conducted in Guyana by Duplaix (1980) showed a prevalence of *Hoplias malabaricus* (Characoid) which was found in 73.5% of the samples. Rosas *et al.* (unpublished) found that Characoids were present in 87% of the samples analyzed, and Best (1984) found that *Schizodon* sp. (also a Characoid) prevailed in the scat. Conversely, Laidler (1984), and Carter and Rosas (1997) found remains of Cichlids in 97% of their samples, Schenck (1999) concluded that the cichlid *Satanoperca jurupari* was present in 75% of the samples, and Duplaix (1980) and Laidler (1984) noted that catfishes and crabs were common in 34% and 40% of giant otter scats, respectively. Seemingly, fish species are consumed according to their abundance and vulnerability to giant otter predation (Carter and Rosas 1997), but no research so far has addressed the question of how tightly giant otter diet is dependent on prey abundance and distribution.

Information on prey abundance and distribution might contribute much to our understanding of giant otter conservation issues related to over-fishing and water pollution. Sheldon (1988) noted that ecosystem integrity has decreased in areas where fish diversity has been homogenized. Thus, data on the dietary specialization of giant otters and its relationship to seasonal variations might demonstrate whether a few fish species must be protected from over-exploitation or if maintenance of the local diversity is a more effective conservation action in areas subject to different degrees of disturbance. Higher order interactions with humans (i.e. direct encounters, competition for space or food) and other fish predators might be expected as well and should be considered in a conservation plan.

The LYB is currently exposed to such disturbance; the Yasuní River drains into the Napo River, which is heavily impacted by human transit and organic pollution (GEF, 1980). Due to its geography, the accelerated population growth in the surrounding human settlements, and the lack of enforcement of ecological regulations, the remaining wildlife in this area could be acutely threatened. Massive fish depletions have already taken place within the YNP because of habitat fragmentation, the high sensitivity of fishes to sudden changes in water pH (Fausch *et al.*, 1990) and the exponential increase in fishing efforts (GEF 1998a).

In the Napo basin, 562 species of teleost fishes have been reported (Galacatos *et al.*, 2004). Almost 400 of these species exist within the YNP (Barriga-Salazar, 2001) and around 280 species have so far been found within the LYB (Galacatos *et al.*, 2004). In spite of this enormous diversity, substantial threats to the fishery from the irrational use of poisons and dynamite (GEF 1998b), and the potential for fishery depletion to restrict

food availability for giant otters and other piscivorous animals, no efforts have so far focused on the preservation of aquatic habitats and fish species in the YNP.

Here, the relative abundance of dietary items, their spatial distribution and its variations according to seasonal changes have been combined to identify the foraging patterns of giant otters and humans. The temporal and spatial abundance of food resources has a major effect on the way two competing large predators such as giant otters and humans (Carrera, 2003) use their habitat. From data collected on distance covered between foraging and resting sites, I discuss the implications of competition for food to the overall vulnerability and exposure of giant otters to human disturbances.

2. GOAL AND OBJECTIVES

The main purpose of this study is to expand our knowledge of giant otter ecology and identify those aspects of giant otter foraging behavior that are relevant to the development of a management strategy, and improve the ability of park managers to facilitate the long-term persistence of giant otters. Specifically, my objectives are:

- 1.1. Describe the food availability for giant otters and humans in terms of the relative abundance of fish species (number, diversity and distribution) that fall within a suitable range for their consumption,
- 1.2 Reveal the dietary items consumed by giant otters from prey items found in scat samples; and
- 1.3 Compare the distribution of known and potential prey to the distribution of giant otter and human activity paths.

3. METHODOLOGY

The data on fish species availability and consumption by giant otter and humans were collected from the two main black-water tributaries of the seasonally variable Yasuní River's lower basin: the Tambococha Creek (18 river km) and the Jatuncocha Lagoon and Creek (22 river km) – hereby mentioned as the Jatuncocha System (Figure 1). The base-camp stood by the confluence of the Tambococha and Yasuní rivers at 75°25'W, 00°58'S (at 230m elevation). In 145 days between September 2001 and March 2002 – which included the falling water, dry, and rising water seasons – the fieldwork was conducted on a 7m • 1.3m boat (Johnson 15HP outboard motor) and one 5.5m • 0.8m dugout canoe, with the help of two local assistants.

3.1 Food availability

Fish sampling design criteria were based on previous reports of giant otter diet contents (Duplaix, 1980; Best, 1984; Laidler, 1984; Carter and Rosas, 1997; Schenck, 1999; Lasso, 2003) and on tropical fish diversity (Goulding, 1980, 1985, *et al.* 1988; Angermeier and Karr, 1983; Henderson and Walker, 1990; Galacatos *et al.*, 1996, 2004). A 10-100cm total length range was selected for the target fish so that all potential prey items among the fish community were included – thus, young-of-the-year and adult specimens from some species were excluded – and a variety of fishing methods (nets, traps, hook and line) were applied. Length, depth and knot-to-knot mesh sizes were different among nets, and the strength and length of hook and nylon were also variable (Table 3); the nylon lines with hooks were used with float or cane, and with live worms, fishes, insects, or lures as bait.

In order to avoid disturbance to the giant otters' daily activity patterns and to increase catchment per unit effort (CPUE), the fish sampling occurred from ~04.30 to ~08:30 and from ~17:00 to ~21:00 every survey day. Surveys were conducted for four days in the Jatuncocha System and for three days in the Tambococha Creek, covering different sections of each watershed on different days (Table 1). With some exceptions, every kilometer in each watercourse was sampled at least once with suitable methods. All 15 methods used were randomly dispersed along all suitable sites within 3 km transects to ensure that an equal amount of fishing effort was applied along the watercourse (5

different methods were applied every km), except where no suitable habitats existed for net sampling. In those cases, traps and hook and line were applied. For the last km of each creek, at least 2 different methods were set at the confluence with the Yasuní River. Each site was sampled once in the morning and once in the evening every time surveys were conducted in each watershed (i.e. every 12-14 day time block) over a 12 time bock period (total days of sampling = 84, daily average = $7.3h \cdot d^{-1}$, n = 624h). All sampling methods were applied for an equivalent amount of time and were used in pools, river margins with low current, stream mouths or flooded swamps depending on their suitability to each of these types of habitat.

Table 3. Methods used for fish sampling within the study area.

Method 14 has five hoops with a gradually increasing diameter (200cm each time within the specified range) which is proportional to the increasing volume of the trap's net. The capture prey range refers to the average standard length of fishes that can be caught with each method, as specified in the user's manuals.

	Method	Measurements (cm)				Capture
No.		Mesh size (cm)*	Length	Depth	Diameter	prey range
			(horizontal)	(vertical)	(arc)	(cm)
1	Beach Seine	2	5800	200		15 - 100
2	Gill Net 1	1	4190	160		10 - 30
3	Gill Net 2	5	6240	170		20 - 100
4	Gill Net 3	8	4170	170		40 - 100
5	Gill Net 4	1.2	3120	180		10 - 30
6	Gill Net 5	6.3	3120	240		40 - 80
7	Cast Net 1	3		320		20 - 70
8	Cast Net 2	3.5		300		30 - 100
9	Cast Net 3	0.6		90		10 - 50
10	Hand Net	1.9		41.9	31.3	20 - 60
11	Hooks (small)			1.0 - 2.2		10 - 30
12	Hooks (medium)			2.2 - 4.6		30 - 50
13	Hooks (large)			4.6 - 9.0		50 - 100
14	Hoop net	4.5	500	43 - 58	43 - 58	25 - 100
15	Bottom trap	1.5	150	40		10 - 40

* Mesh sizes are stretched knot to knot measurements

All the fishing gear was set upon arrival to the fishing site and retrieved in the same order at the end of the fishing period, and only after release of all fish trapped. For every fish caught and released, the place and time, the common and scientific name were registered, standard length (cm) and total weight (gr) were measured with the help of portable scales of varying capacities, and a photographic record was taken. Fishes were identified *in situ* using taxonomic keys – Géry, 1977; Lowe-McConnell, 1978 and 1987; Taphorn and Lilyestrom, 1987; Swing and Ramsay, 1989; Burgess, 1989 – at least to the genus level.

3.2 Diet analysis

Giant otter scat collection: During surveys, it was possible to identify one transient individual who was frequently seen going up and down the Tambococha Creek, and at least two family groups, one that occupied the upper portion of the river (two sightings) and one that plausibly used the Tambococha Creek and the Braga creek alternatively (one sighting in the Tambococha Creek, one sighting in the Braga Creek). A group of nine individuals was seen occupying the Jatuncocha System and both alpha adults were positively identified as the same group found in this watercourse in 2001-2002 (as described in Lasso, 2003 and Utreras *et al.* 2005).

Due to the differences in otter densities among the population, the quantity and quality of scat samples varied greatly between the two creeks. Only 13 scat samples were collected from the 27 latrines used by the transient otter in the Tambococha Creek (recognized by an incomplete track from its left forepaw), of which only four were useful for analysis, given the scarcity of material collected. These small latrines were hard to find unless they were very fresh, they were usually placed between 10-50 m inland, in inconspicuous areas that could not easily be noticed or accessed from the river, and that were hardly ever used more than once, with a few exceptions. Whenever new latrines were set in an area where land was scarce or during high water level periods, the new spot could be even 1-2 m apart from the old ones. Scat samples from these latrines posed some difficulty in collection, since they were scarce and scattered across the soil and spread in the surrounding vegetation, and material from two nearby latrines could be

mixed. In almost every occasion, the pungent smell characteristic from recent markings could be detected, but no sample could be found.

In contrast, the 41 different latrines found in the Jatuncocha System were conspicuously placed in campsites at the margin of the river bank, had abundant material, and at least half of them were marked regularly (particularly those located near dens). Two otter campsites occupied up to 30 m² (15•2 m) of the river bank – sometimes on both sides of the river, if the place was narrow – and more than one latrine was usually found in these areas. Other latrines were smaller (5-15 m²) but in most cases they were located by the river bank and only on a few occasions they were placed up to 30 m inland. Most of the scat samples from these latrines contained fecal material from more than one individual, and only in a few cases individual scats were found.

Scat material was collected with a stainless steel shovel in tightly locked 250cc and 500cc plastic containers (small samples) or in 1000 ml zip-loc plastic bags (large samples) from every latrine, campsite and den found in the study area. In the latter case, samples were collected only once the den had been abandoned by the group. From all latrines identified, 42 scat samples (29 from the Jatuncocha System and 13 from the Tambococha Creek) were collected in the area and subsequently analyzed for diet characterization. All the latrines and campsites were geo-referenced with a GPS (Garmin E-Trex Vista), and marked for future recognition with flagging tape. A unique identifier 10-letter code was created for each sample/GPS point, where the watershed, river kilometer, latrine, date, and sample age were recorded. Immediately after collection, samples were taken to a nearby tributary, at least 1 km away from the latrine, and immediately rinsed with river water while simultaneously stirred in a 0.3mm mesh. After rinsing, the material was placed in a clean container with two layers of absorbent paper and a sachet of silica gel. After each survey, the samples were sun-dried for 2-4h, and stored in labeled plastic containers.

In the laboratory all the fecal material (containing fish scales, otoliths, bones and vertebrae) was submersed in a solution of 5% potassium hydroxide (KOH) for 2-5min, rinsed in distilled water, and dried by hand with rice paper. For each scat sample, the contents were classified according to condition (complete or partial piece), size (3)

categories) and shape (3 main categories for scales and otoliths). Then, otoliths were placed in 2 cc glass tubes with an identifier and a cotton top. Non-regenerated scales (or those closest to this criterion) were selected and pressed between up to 10 glass slides per sample (the number of slides differed with sample size and scale diversity) and an additional slide per sample was created with regenerated and atypically shaped scales. All other material (vertebrae, maxillae, spines, rays and other bones), was placed in the original plastic container.

Once the fecal material was clean, and the preserved parts were recognized and classified, it was ready for identification. This was done by comparing the fish parts with a reference collection of scales, otoliths and skeletons collected in situ and created for this purpose by Carrera (2003), which is now in possession of the Vertebrate Museum at the Pontifical Catholic University of Ecuador in Quito (QCAZ#: 634-976). The scat contents and the reference material were finally compared under a dissecting microscope (10x, 40x and 100x), aiming for identification at the species, genus, or family level.

Taxonomic keys (Géry, 1997; Lowe-McConnell, 1978; Taphorn and Lilyestrom, 1984; Burgess, 1989; Swing and Ramsey, 1989; SINCHI, 2000), reference literature (Goulding, 1980; Goulding *et al.* 1988; Crawford, 1991; Galacatos *et al.*, 1996, 2004; Silva, 2000; Barriga-Salazar, 2001; Stewart *et al.*, 2002, Lasso, 2003), and on-line references (especially <u>www.fishbase.org</u>) were consulted when no matches were found in the reference collection.

3.3 Fish distribution and foraging sites

Although all signs of giant otter presence were geo-referenced during each survey, only the ones where active fishing was observed – 92% of sightings and vocalizations – and all the active or recently active latrines were included in the analysis of foraging paths. After depicting the position of these signs on a map (ArcGIS 9.1), 2 km buffers were created around them to simulate the potential area of activity around each point (500 m radius) and the minimum distance traveled to reach that point (1500 m radius). The river distance between the two most distant buffers on the watercourse was measured as an estimate of the total foraging path length. Then, the relative frequencies of giant otter and human sign distribution were grouped according to 2 km river transects and compared to the relative frequencies of fish abundance and fish diversity. The best regression model fitted to each pattern was obtained by selecting the one that gave higher R² values, but if differences were only at the centesimal level (i.e. linear regression R² = 0.723 and polynomial regression on the 2nd order R² = 0.747), the simpler model was chosen even if it had a slightly higher R² value.

4. RESULTS

4.1 Food availability

Relative abundance - From all sampling sites, a total of 1862 fish specimens were collected $(\bar{x} = 15.3 \text{ fish} \cdot \text{d}^{-1}, \text{SD} = 0.6)$, which belonged to 8 orders, 21 families, 65 genera and 73 species (Appendix 8). From all the specimens captured, 56% were Characiformes, 29% were Perciformes, and 9% were Siluriformes; the 6% remaining corresponded to the other five orders registered. Within the Characiformes, the families with most specimens were the Characidae (25%), Curimatidae (11%), Erythrinidae (12%) and Prochilodontidae (11% of total individuals). Within the Perciformes, Cichlids were most abundant (16%), whereas Pimelodidae had the largest number of individuals within the Siluriformes (7% of the total fish collected). The most abundant species in the community were *Plagioscion* squamosissimus (9.8%) and Prochilodus nigricans (7.1%, Appendix 8, Figure 22); these and six additional species represented almost 50% of all individuals caught within the study area, all of which were Characoids and Percoids, except for Parauchenipterus galeatus, a Siluroid. There were 43 rare species, each corresponding to less than 1% of the total fishes captured (Figure 22). Most of the abundant species were also widely distributed within the study area, with the exception of few cichlids that were restricted to the Jatuncocha Lagoon and to lower portions of the black water systems. From the total specimens, 36% were caught in the Tambococha Creek and 64% in the Jatuncocha System. In this watercourse, the largest proportion of fishes (61%) was captured in the Lagoon.



Cumulative Frequency (%)

Relative Frequency (%)





Figure 23. Total number of specimens and of species obtained in the Jatuncocha System (A) and the Tambococha Creek (B) arranged according to the longitudinal distribution of sampling sites (KM 0 corresponds to the mouth).

Relative diversity - Among all species registered, the majority belonged to the orders Characiformes (42%), Siluriformes (34%) and Perciformes (10%). The families with the highest numbers of species were Characidae (27%), Pimelodidae (15%) and Cichlidae (9%). The Jatuncocha System was the richest in relative diversity (n = 62 species), when compared to the Tambococha Creek (n=51). Inside the Jatuncocha System, the largest number of species were found in the lagoon (36%, KM 1-6), and secondarily a large proportion was also found in the lower (29%, KM 7-10) and middle (21%, 13-15) portions of the creek (Figure 23A). Fish diversity was slightly higher in the middle portion of the creek than in the lower portion (lagoon). Both relative abundance and diversity of fish were relatively low in the upper portion of the creek.

In the Tambococha Creek, 65% of the fish captured were found in the mid-portion of the creek (KM 7-11) with significantly lower fish abundances towards either extreme in the longitudinal gradient. The highest numbers of species were also captured in KM 7-8, but relatively high values were also obtained from the lower portion (KM 2-3) and the area adjacent to and upstream from the mid-section (KM 9-11).

4.2 Diet analysis

At least 47 species of fish (5 orders, 17 families) were identified from the 42 scat samples analyzed (Figures 24 and 25, Appendix 9). These species represented 65.3% of the species available (an approximation, since certain fish remains in the scats were not identified to the species level). According to their frequency in the diet, the main orders appearing in the giant otter diet were the Characiformes (63.5%), Perciformes (30.1%), and Siluriformes (9.0%), whereas the remaining 2% was represented by Osteoglossiformes (*Osteoglossum bicirrhossum*, or Arawana), Gymnotiformes (*Gymnotus carapo*, or mild electric fish), and unidentified fish remains appearing in one sample.

Among the Characoids (Figure 24A), the families with the highest relative abundance among all scat samples were the Erythrinidae, Characidae and Serrasalmidae; the perches (Perciformes, Figure 24B) had its two extant families (Cichlids and the Sciaenids) largely represented; and for the catfishes (Siluriformes), mainly the Loricariidae, the Pimelodidae (long-whiskered catfish), and several unidentified remains that appeared in a smaller proportion, were the main representatives of this order (Figure 24C).



Relative frequency in the diet

Figure 24. Relative frequency of fish families in the diet of giant otters expressed as a percentage of appearance in the total scat samples analyzed (266 sets of fish remains from 42 samples); only the families from the three most common orders (Characiformes, A; Perciformes, B; and Siluriformes, C) are represented.

At least ten species of fish were present in 50% of the scat contents: the characoids *Hoplias malabaricus, Acestrorrhynchus* sp. (dog fish), *Prochilodus nigricans (bocachico*), a few unidentified myelinids (four different species of silver dollars) and serrasalmids (three common species of piranhas); and the cichlids *Hypselecara termporalis, Crenicichla* sp., *Aequidens tetramerus, Astronotus ocellatus* (oscar) and one unidentified set of remains (likely, *Heros appendiculatus*), are all represented in between 3–11% of the samples (Figure 25). On the other hand, 25% of the dietary items corresponded to 10 fish species of intermediate abundance in the environment, and the remaining 25% was made of rare species, mostly of Characiformes (Figure 25). Among other species identified, another 20 appear with a frequency between 2-3%, and the remaining fishes appear rarely in the scat samples (less than 2%).

When compared to the relative abundance of each fish species as offered in the environment, the frequencies of appearance of each prey item present two main patterns: only the dietary items with intermediate frequencies (to the center of the *x* axis, Figure 25) are consumed in proportion to the frequency of abundance in the environment; in contrast, dietary items in either extreme of the scale appear in either significantly larger, or smaller frequencies than in the samples collected by fishing methods. In particular, *H. temporalis, Acestrorrhynchus* sp. and *A. tetrameurs* appear in very high proportions in the giant otter's diet even though they are relatively scarce in the environment. On the other hand, *P.nigricans, A. ocellatus* and *C. monoculos* are found in a low proportion in the giant otter's diet when compared to the frequencies in the environment. *H. malabaricus* is one of the only species that was found in a large percentage of the giant otter's scat samples and that is also very abundant in the environment.



Fish species

Figure 25. Relative and cumulative frequencies (%) of identified prey remains from giant otter' scat analyses.

When fish remains in the spraints were not positively identified to the species level, they were grouped within the next taxonomic level, unless it conflicted with information on local fauna diversity. The relative frequencies of these fish in the environment are presented in gray columns for comparison.

4.3 Fish distribution and foraging paths

Remarkably similar patterns are observed when the distribution of active giant otter latrines and direct observations of active foraging behavior are plotted against the distribution of fishes available in both watersheds (Figure 26). In the Jatuncocha System, however, not many giant otter sightings and latrines are found within the last portion of the watershed (KM 0-10) although the highest fish abundances were found in KM 4-6 (upper lagoon) and KM 8-10 (lower creek). Relatively lower abundances were found around the mid portion of the Creek (KM 14-16) where the highest densities of otter signs occurred (Figure 26A). Also, concurrent frequencies were found within the 2 kilometer section nearby the mouth of the watershed, as well as within KM 10-2. The pattern found for plotted distributions of giant otter signs and fish diversity was analogous to the one for fish abundance (these were highly correlated). The distribution of human signs, on the other hand, could not be correlated to the distribution of fish abundance or diversity in this watershed, except for a small overlap between KM 4-6, 12-14 and 16-18 (Figure 26A). From the overall pattern observed in the Jatuncocoha System, giant otter signs were highly correlated with fish abundance and diversity, except where high densities of human activity occurred (Figure 26A).

A much closer correlation is observed between the foraging patterns of giant otters and humans, and the relative fish abundance and diversity in the Tambococha Creek (Figure 26B). Nearly 60% of giant otter activities concentrated between KM 6-12, which is the segment of the river where most of the fish collected (nearly 65% of specimens and species) were found. Giant otter sign density was slightly higher than the one found for fish abundance and diversity in the lower (KM 0-2) and upper (KM 14-18) portions of the river, but are still proportional in frequency to those obtained in fish sampling. Human and giant otter activities in the Tambococha Creek are not identical, but do follow a similar pattern, and large overlaps can be observed in KM 6-10 and 14-18 (Figure 26B).



Figure 26. Distribution of giant otter foraging activity signs compared human activity signs and fish abundance and diversity in the Jatuncocha System (A) and in the tambococha Creek (B).

Distance from mouth (km)

In the Jatuncocha System, 87 active latrine markings and 47 sightings during fishing activities were found, and 99 signs of human presence were recorded. In Tambococha (B), 37 active giant otter latrine markings and 20 sightings during fishing activities were recorded, while 50 signs of human presence were registered.

5. CONCLUSIONS / DISCUSSION

5.1 Food availability

A large diversity of suitable prey for giant otters and humans is available in the Lower Yasuní Basin. The structure of the fish community (within the size ranges obtained during the surveys) is comparable to other Amazonian regions in terms of relative abundance of the most common members of the Characiformes, Perciformes and Siluriformes orders (as shown in Goulding, 1980; Saint-Paul *et al.*, 2000; Galacatos *et al.*, 2004). There were significant differences between sampling sites in terms of fish diversity and relative abundance in both creeks. In the Jatuncocha System, most of the fish collected were caught in the upper portion of the lagoon, in the lower portion of the creek, and at the mouth of a large tributary around KM 14 in the creek. In the Tambococha Creek, the largest amount of fish sampled was caught at the mouth of a large tributary in KM 7. Total abundance and diversity were tightly correlated, which suggests that that a larger diversity would have been found with a higher sampling effort.

In fact, higher relative abundances and diversity were found during similar research conducted during a comparable period of time in 2001-2002 (Carrera, 2003). A total of 95 species (identified from almost 2900 specimens) were found in the area, which also accounted for 14 species exclusively found in the Yasuní River. The lower diversity found in 2004-2005 is probably explained by the lower total catch obtained (only 73 species from almost 1870 specimens). However, the effort applied in both studies was comparable: in 2001-2002 sampling was done in 98 days (629 h, 6.6 h/day in average), whereas in 2004-2005 sampling was done in 84 days, but the daily effort was greater (7.3h•d⁻¹), resulting in a similar amount of total sampling time (624h). Also, sampling distribution was slightly different between the two studies: a block design, with discrete, nested fishing sites was used in Carrera (2003) while the sampling effort in this study was more evenly spread throughout the watercourses' longitudinal gradient, applying most methods within equivalent distances. The same equipment was used in both studies, but no estimate of CPUE effort *in situ* is available in order to know how slight variations in age and placement affect the results obtained.

The community structure (for the size range sampled) is quite similar between Carrera (2003) and that obtained here. One exception applies for members of the Curimatidae family, which appear less frequently in all the comparable fishing sites. *Psectrogaster* essequibensis (Curimatidae) and *S. fasciatum* (Anostomidae), which are commonly found in giant otter's diets and in the human fisheries, were especially absent from all sampling sites in 2004-2005, even in the lagoon, where higher abundances were obtained in previous studies (Carrera, 2003; Galacatos et al., 2004). Hardly any fish were captured in the upper portions of the Tambococha Creek, even though there were suitable and accessible places for our fishing gear. Dynamite fishing was heard on several occasions in both watersheds, but it is a fairly common practice in the Tambococha Creek where there is easy access from land without notice from the park authorities, little time and effort required by the explosives for effective fishing, and easy harvest of dead fish with canoes hidden in the smaller tributaries for that purpose. According to many local inhabitants, much of the fish consumed around the area is captured by fishermen that only use dynamite. It is hard to determine with complete certainty that this watershed is already being depleted by the indiscriminate use of such methods, but the very scarce fish obtained with 15 different methods applied for 7 hours each time within a range of 6 kilometers throughout the dry season, and the fact that in some occasions not a single fish could be captured by any of these methods, is certainly pointing in that direction.

5.2 Diet analysis

From all the samples obtained, 47 species of fish were identified from giant otter scats (representing around 65% of the fish available within suitable size range). These represent almost two thirds of the 73 species that constituted the giant otter diets obtained by Lasso (2003) and Carrera (2003) (54% of the species available). This could be due to the fact that the number of samples obtained in this study (42) represents approximately half of the samples obtained in 2001-2002 (88) by Lasso (2003), so fish diversity in the scats would probably increase with a larger sample size. But it could also mean that the overall fish diversity within the system has decreased, and that this is revealed in the composition of giant otter's diets. Is this difference is due to an overall decrease in fish diversity or to

an expansion in dietary preferences from the part of the otters? It is not unlikely that both are occurring simultaneously, and that one (expansion in dietary range) is the result of the other (local population decline). A more detailed study would need to be done to prove this point, but it is largely known that because of their adaptability and opportunistic habits, giant otters are excellent bio-indicators of a system's biological integrity.

From the 10 prey items most frequently consumed by giant otters in 2001-2002 and 2004-2005, many correspond to the same species: *H. malabaricus* (4.9% and 11.3% respectively), *P. nigricans* (13% and 4.5% respectively), and the five most common species of Cichlids (that together sum up 27.5% and 15.4% respectively). On the other hand, species that were very common dietary items in 2001-2002, such as *S. fasciatum* (7.3%), *H. unitaeniatus* (4.1%), and *T. angulatus* (3.2%, Carrera, 2003) are largely absent from giant otter's diet in this study. *S. fasciatum* and *H. unitaeniatus* are articularly desirable for people and otters as a prey, because of their fleshy bodies and high fat content. It is hard to tell whether these differences are significant over time or if they are depicting a trend in fish declines. Only continued surveys in the area with comparable methodologies would allow us to clarify this.

Changes in dietary contents are common among opportunistic mammals, especially if they forage in heterogeneous and dynamic environments (Kotler and Brown, 1999) and particularly in tropical systems, where the distribution of migratory and non-migratory fish can vary greatly (Angermeier and Karr, 1983; Henderson and Robertson, 1999). Giant otters are no exception to this rule, and have been proven to behave like opportunistic foragers in their entire distribution range (Gomez, 1999; Rosas *et al.*, 1999; Staib, 2005). Their diets can contain dozens of different species, or be more specialized according to local diversity and distribution of fishes; for instance, Schenck (1997) found a 75% frequency of *Satanoperca jurupari* in giant otter scat samples. In the case of a varied diet, they seem to rely on a large proportion of species that are rare in the environment, so diversity is an important component of a suitable habitat for them, offering more choices in terms of availability and vulnerability of prey. In the case of dietary specialization, giant otters rely on the ability of few abundant species to maintain their populations, so over-fishing of such species or the destruction of essential habitat supporting their populations could be very detrimental to giant otter persistence within an area. The methods employed to identify dietary items from fecal samples also vary in efficiency, accuracy, and approach, so a detailed standardization of such methodology (collection, preparation and reference information used, as well as target taxonomic level for identification), and the creation of locally obtained, broadly sampled fish reference collections would improve our ability to compare dietary contents among populations. Only in that way can we use the dietary items as a more precise surrogate for monitoring fish diversity and biological integrity in the aquatic systems inhabited by giant otters.

5.3 Fish distribution and foraging sites

Comparisons between suitable prey distribution and giant otter foraging activities (represented by active latrines, sightings and vocalizations) suggest that their spatial foraging patterns are only partially linked to their prey's abundance and diversity. Opportunistic in their predatory behavior, giant otters spent much of the daytime attending those areas where higher fish densities occurred, with the exception on the Jatuncocha Lagoon. Human activity, on the other hand, was not directly related to fish abundance or diversity in the Jatuncocha Creek, likely because other activities take place aside from fishing; in the Tambococha Creek, human and giant otter activities did follow a similar pattern to that of fish distribution, with a few exceptions. In the Tambococha Creek, fish abundance seems to be a particularly important variable for the residing transient individual otter, as places with high fish densities ensure some success in capture. Also, the large tributary that converges with the Tambococha Creek at KM 7 is where most of the human activity was concentrated. This might explain the high degree of overlaps in the areas used between giant otters and people in the previous chapter, as well as a high probability of competitive stress for both.

The largest abundance of fish was distributed in the Jatuncocha lagoon, but giant otters do not visit this area with proportional frequency. Several reasons might explain this pattern. First, there might be a higher predation risk for the cubs (*Panthera onca* has been seen swimming across the lagoon). Second, not many refuge and resting places are available around the lagoon (as most are occupied by humans); the closest dens up and

downstream of the lagoon are more than 8 river km apart, and this might be a long distance for cubs to cover if there are no places to stop and rest. And third, and most importantly, this is the area where human activity is most frequent. On the other hand, the middle portion of the creek, where most giant otter foraging signs were found, seems to be ideal when considering food availability, predation risk (refuge sites and available terra firma places found within shorter distances) and human absence. Given these patterns, we may ask why giant otters fail to restrict their activity to the mid-portion of the watershed and avoid human presence and predation risk in the lagoon.

Duplaix (1980) and Ribas-Pereira (2004) have stated that giant otter's family groups need only a few kilometers of river stretch as a home range, as the territories within are easier to defend. In areas where water level variation can have extreme effects on the extent and depth of the floodplain (see chapter 2), territories and home-ranges can be significantly larger. The giant otter family group living in the Jatuncocha System needs to ensure that the lagoon will remain available for stressful conditions, so they are willing to take the risk of predation and the probability of stressful encounters with humans in order to defend this territory from other groups. This potentially explains why giant otters periodically visited the campsite located at the very entrance of the Jatuncocha System (KM 1), even though human activity in the area was very frequent. The den near the main campsite in this location was only used twice over the 7-month period when we conducted our surveys, but the campsite was frequently marked, usually very early in the morning. After fishing for a few minutes in a nearby tributary, marking the latrines and resting, giant otters always returned to the upper portion of the system once people arrived. On the one occasion when there was no human activity in the lagoon giant otters were seen foraging in many places in the lagoon all day long. Aside from a valuable territory to defend, giant otters might find it easier to fish there, due to the higher transparency of the waters and to a difference in the plant composition of the riparian zone, which might also facilitate foraging for the cubs.

Schenck (1997) had found that fish availability and other habitat factors did not lead to a clear explanation of giant otter absence in suitable Peruvian lakes. Abundance, diversity and habitat quality are related, but giant otters learn where the most fishes or the better prey can be caught, especially when the family group contains members of diverse age
and experience. If, additionally, these places are constantly visited by humans who explore the area with motor canoes, then habitat quality is reduced, the fish are scared away by the noise of the motors, and fishing success of giant otters is diminished.

Managers at the YNP and other protected areas that harbor giant otter populations can use this information to monitor the impact of water pollution (from organic origin or due to oil spills and similar waste-related issues) in the system. If fish populations were greatly affected by a large disturbance event and were removed from the system for a long period of time, activity patterns of giant otters would change in response to the distribution of their prey items. Thus, the presence or absence of giant otters in a watercourse is most likely indicative of large-scale declines in the fish populations, even if the habitat is suitable in terms of terrestrial resources. Although more evidence would be needed to prove this statement, it is reasonable to infer that the current absence of a family group of giant otters in the Tambococha Creek is due to the depletion of their target prey by the uncontrolled human use of dynamite. Giant otters, due to their energetic requirements and their susceptibility to anthropogenic disturbance, have also been catalogued as bio-indicator species; the information on how tightly their activity patterns are connected with the distribution and density of their prey items illustrates the useful role of these mammals as aquatic ambassadors.

CHAPTER FOUR: IMPLICATIONS FOR ECOLOGY, MANAGEMENT AND CONSERVATION

Tropical ecosystems are subject to great environmental variations at different magnitudes, which in part explains their spatial heterogeneity and biodiversity (Golley and Medina, 1975). Dynamic hydrological processes and the resulting variation in water level and floodplain extent have been shown elsewhere to affect movement and migration (Sheldon, 1988; Galacatos *et al.*, 1996; Silva, 2000), reproductive behavior (Duplaix, 1980; Laidler, 1984; Rosas and de Matos, 2003), and population distribution and density of organisms (Wishen, 1998; Kotler and Brown, 1999). Grant (1985) has showed how in such fluctuating environments, the variances in resource utilization traits by organisms become severely restricted at times of intense environmental stress. In this thesis I have quantified and assessed the potential for coexistence between giant otters and humans, using a GIS approach for habitat overlap analysis. These results should provide evidence for the protection of critical areas that support giant otters during stressful conditions.

There are several ways to quantify resource availability and distribution, and many mathematical models can be built to estimate resource limitation through the use of these parameters. The goal of this study was not to establish the carrying capacity of the system as a whole, but to explore the choices that giant otters and humans have in terms of refuge and foraging space (suitable habitat), based on their tight dependence on the floodplain's pulse (Hederson and Robertson, 1999; Hoeinghaus *et al.*, 2003) and the distribution of fish prey (Saint-Paul *et al.*, 2000; Petrey *et al.*, 2003). Such explorations lead to the conclusion that human activity patterns (or behavior) can be regulated in ways that reduce the magnitude of human impact on the local giant otter populations, by ensuring permanent access to some fundamental resources within the LYB.

Whether giant otter occupation of the basin has been permanent or intermittent, they have coexisted there with humans for a few generations; this suggests that giant otters have persisted in the area until now in spite of the gradual increase in human disturbances. Some degree of habitat partitioning and exclusive access to resources for giant otters must have facilitated their coexistence with humans so far, but human population growth and the concomitant need for resources will eventually change the conditions that make this habitat partitioning possible. The results of my research should help managers prolong conditions that promote coexistence and anticipate how giant otters may be affected by stronger disturbance and new threats.

The partitioning of spatial refuge resources in the area is guaranteed by the longitudinal and transversal distribution of such resources: levees and hills in the upper portion of watercourses or near the main tributaries of those watercourses are not easily accessible for people but are ideal locations for giant otters, especially for family dens; all other land resources (*terra-firma* places and levees located in the middle or lower portions of the watershed) are accessible to humans and have the potential to become exclusively used by humans. In order to guarantee reduced competition for space between giant otters and humans, and to avoid the impact of human presence in the area, human access should be confined to the lower and middle portions of the watercourses all year around, but permanent land areas within the middle and lower portions of the watershed for exclusive use by giant otters should be designated.

The partitioning of food resources (prey items and foraging areas) is a more complex aspect of otter and human competition. The differences in diet composition among giant otter populations can be significant depending on the region where they live, and on the fish prey availability and vulnerability; analogous dietary differences can be found among human populations in the Amazon (Butt and Boque, 1990; Smith, 1981; Uquillas, 1984; Carrera, 2003; Zucco and Tomas, 2004). However, in the case of the LYB, overlaps between giant otter and human diets vary between 55 – 82% whether fish availability and dietary preferences were included or excluded, respectively. Although both giant otters and humans behaved as generalist and opportunistic predators, at least 50% of their diets were supplemented with less abundant species that were targeted either due to their nutritional value or vulnerability. Resource partitioning might occur for those dietary items that are found in areas that can be exclusively accessed by giant otters (swamps and tributaries) and for those species that are not used by humans (i.e. Loricariidae, Doradidae), but aside from these, all fishes are susceptible to human harvest, particularly if non-selective methods such as dynamite and poisons are frequently used.

Does the distribution of foraging areas allow for resource partitioning? Foraging habits of giant otters in the LYB were determined by a combination of relative abundance and diversity of fish variables with topological variables. As noted in Smith (1981), Castro (1991) and Carrera (2003), the fishermen learn quickly where the highest abundances of fishes occur and frequently visit those 'good spots' in order to maximize their fishing effort. It is possible that fish diversity does not play a role in determining the distribution of foraging activities of humans, particularly if there is commercial interest for certain species. Thus, habitat partitioning of foraging sites only occurs where fish resources are isolated from human access (or where common fishing methods are restricted), i.e. in the shallow portions of the main channel, and in tributaries, oxbow lakes, ponds, pools and swamps that are not in contact with the main channel. In such case, these types of areas must also be protected from human access all year round, in addition to those areas that are commonly used by humans and otters but that are the only foraging sites during the dry season (i.e. ponds and tributaries in lower portions of the main channel and the lagoon). By protecting areas that combine abundance, distribution and proximity of spatial and feeding resources along all of the available habitat, resource partitioning and long-term coexistence could be ensured in this and similar areas. Overlaps in habitat use and diet vary with seasonal changes because the density and distribution of spatial and food resources vary with floodplain extent and depth.

The increase of human density in the area would not represent a major threat if areas for exclusive use by giant otters are designated, because spatial overlaps between otters and humans usually occur within and around the main channel of watercourses. On the other hand, the effects of water pollution (water quality and noise pollution) or habitat destruction associated with the oil industry could hardly be prevented by these measures. If an oil spill occurred at the upper reaches of the basin, the immediate death of the fish fauna by anoxia would negatively impact the survivorship of giant otters and humans in a short and medium terms, whereas the noise pollution produced by constant transit along the Yasuní River would intermittently interfere with the fishing activities of both species, but would affect giant otter foraging success in a larger proportion.

Could variations in home range size in response to changes in water level mean that both species are modifying their scale to adapt to changes in resource availability? If only 1 m

fluctuations in water level produce 10 km² variations in home range extent (otters) and area use (humans), then the 6-10 m yearly variations in water level could certainly generate modifications of scale in the use of space (total distances covered during daily activities). Changes in water level not only produce alterations of number, size, density, or distribution of resources – certain habitats suffer qualitative transformations (i.e. from dry land to swamp, from swamp to flooded forest, from pond to marsh to varzea forest), so the scale of resource heterogeneity is also transformed. Alterations of the climatic regime produced by global warming could represent a magnified scenario of water level variations (Galarraga-Sanchez, 2006). For now, the model created here can portray an estimate of the extent covered at maximum water level values during an intense flooding event. In that case, giant otters would probably be at an advantage due to their ease of access to swampy areas, but such changes in scale would imply a switch from a longitudinal use of space along the watercourse gradient to a two-dimensional or circular pattern of resource utilization. Managers must keep in mind that there are many different ways to analyze the landscape (i.e. depending on the number of dimensions included). Determining which one is more realistic and takes into account all possible variables is an important and relevant for conservation in face of large scale threats.

My conclusions agree with those of Utreras *et al.* (2005) and van Damme and Wallace (2005): the amount of adjacent habitat that is susceptible to flooding during regular and irregular rainy seasons must be taken into account for protection, and not only the lakes, rivers and immediately adjacent shores. Such habitat allows for resource partitioning in the face of competitive interactions with humans and provide dispersal or access paths to other primary resources during extreme environmental conditions. New studies involving giant otter habitat use, home range and territory size, or exploring options for reserve creation or area protection must take into account elevation ranges and gradient, because these two variables determine how the floodplain behaves according to water level variations, which in turn affects the way resources are accessed and distributed across the landscape.

Although static measurements of home range size are useful for determining the minimum amount of habitat that a population needs to survive, I have shown here that many other considerations about habitat and the way it changes with water level fluctuations must be included when designating protected habitat, or when making decisions about environmental regulations. Relying solely on 'effective home range size' might lead to underestimations of the size and the quality of the areas needed for protection, as human activities that have the potential to negatively impact wildlife populations represent an additional challenge to the one already posed by natural environmental fluctuations.

Predictably, the effects of human disturbance and management solutions might vary greatly among Amazonian regions, simply because the floodplain dynamics in the Andean slopes (Colombia, Ecuador, Peru and Bolivia) or in the Guyana shield (Orinoco and Guyana basin) might be affected at different magnitudes by water level variations than in the central Amazon (central Brazil), or in the lower Amazon basin (such as the Brazilian Pantanal). Most, if not all, of the areas used by giant otters in Ecuador lie within relatively large elevation gradients, and are thus dramatically affected by the flood dynamics of the system. A regional model predicting habitat suitability for giant otter persistence or re-introduction could be built based primarily on this critical variable.

The activity patterns observed from the LYB indicate that hills, levees, and lower *terra-firma* land – optimal terrestrial habitat – located near the water (i.e. the highest places in the watershed), and adjacent water bodies that do not dry out during the dry season (i.e. the lowest places in the watershed) are highly valuable for people and giant otters. Most importantly, the maximization in the use of these resources is determined by the distance between them and the ease of access to them. Giant otters (more than humans) do not "choose" their range of activity based on where a basic feature is located, but based on where it stands relative to another critical feature and on how easy they are accessed. Ideally, the places where both occur within a very short distance are optimal habitat for both predators. In conclusion, an ideal situation for both species is that where these requirements are met:

• From all the resources available, some must only be accessible for one species, or a subcategory of a resource type must not be used by both species in the same proportion. In this case, from all the habitat available for humans and otters, the upper portion of tributaries and the main watercourses, annexed swamps, and areas with certain kinds of vegetation growth that make canoe navigation impossible

should only accessible for giant otters, which offer alternative - although suboptimal - habitat during stressful conditions.

- Basic resources (food and shelter) must be found within short distances. Given that seasonal fluctuations in water level play a key role in determining the availability of such places, the distance between fundamental spatial resources increases linearly (dry season) or vertically (rainy season) during these extreme conditions. Falling and rising water levels are probably more favorable situations, since shelter places become available, but there is still enough water to maintain the fish prey items within reach. The findings of this study support the idea that shorter distances are covered during these transitional periods in water level fluctuation.
- Access between terrestrial and aquatic habitats must be faciliated. Connectivity
 between resources is especially critical during stressful conditions because it allows
 each species to adapt to changes in resource number, density and distribution
 rapidly while minimizing exposure to predation and other risks. In the LYB, the
 main channel of each watershed is the connector between resources, but for otters
 it is also a resource in itself. Giant otter accessibility to the lagoon responds to
 human presence and density, and if these increased progressively, a critical resource
 during the dry season would no longer be available for giant otters.

These conditions might reduce competition between giant otters and humans and could ensure persistence (and even population growth) over the long-term. The use of camping and foraging areas by humans should be regulated, and limits for human access should be placed in order to provide giant otters with sufficient alternative resources for times of stressful environmental conditions. Likewise, fishing activities and methods must be regulated accordingly; there are numerous means of regulating artesian fisheries so that they guarantee the sustainable use of this resource. Regardless of the approach, neither giant otters nor humans will be able to survive or persist in this area if the indiscriminate use of non-selective methods such as dynamite eliminates the fish fauna from the system. A thoughtful and efficient partitioning of the Lower Yasuní Basin would not only favor coexistence between giant otters and humans, but would probably increase overall biodiversity, improve ecosystem functioning and guarantee human and wildlife welfare.

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APPENDICES



Appendix 1. Examples of foraging and fishing areas found in the study area

ABOVE: riparian vegetation along deep areas in the main channel (Tambococha Creek on the LEFT and Braga Creek on the RIGHT) where the fishermen place their nets or hooks along the vegetation, and where otters corner the fish against the vegetation in order to capture them. CENTER: floating vegetation in Tambococha Creek such as grass, lilies and logs also represent good refuge structures for fish; giant otters have been seen diving below this type of vegetation, which is also a favored place for fishermen to throw dynamite in. BELOW: in places like this fishing becomes easy during the dry season, since the water level is low enough that even the main channels (left) are good places to fish, whereas the pools (right) dry out completely. (PHOTOS: PAOLA CARRERA).



Appendix 2. Examples of areas on land used by giant otters and humans

Giant otters and humans need similar places to rest and sleep, and in both cases these are known as "campsites". UPPER LEFT: giant otters carve dens in hills or levees along the river bank; these can have several chambers and entrances. UPPER RIGHT: an abandoned giant otter campsite during the dry season; several latrines are located above this main entrance and across the river. CENTER LEFT: fallen trees and their buttresses seem to be ideal alternatives for campsites when levees are not available. CENTER RIGHT: a multiple latrine used actively by otters until February 2005; in March, people used the same place to clean the bushmeat they had captured (LOWER RIGHT). LOWER LEFT: people also favor levees for installing their campsites, particularly if they are next to a tributary; this campsite remained active for three weeks (PHOTOS: PAOLA CARRERA).



Appendix 3. Abiotic data recorded daily in the study area during the field season (October 2004 – March 2005).

Appendix 4. Depth profile and visibility obtained in 2002 from the two main tributaries in the Lower Yasuní Basin (Data obtained in 2002).



Depth is represented with a solid line, whereas visibility corresponds to the striped areas. All measurements were done in cm every 500 m following the main course of each river, and through the straight line uniting the mouth and head of the Jatuncocha Lagoon (the lentic portion of the system starts 1.3 km from the mouth). Measurements in the Yasuní River were done from the confluence with the Napo River (KM 0) to 1 km south of the mouth of the Jatuncocha Creek-Jatuncocha Lagoon System (KM 20). Measurements were taken during comparable water level periods in each river (rising water season).



Appendix 5. Examples of RIPARIAN VEGETATION CHARACTERIZING THE STUDY AREA

Várzea forests are characterized by the presence of tree species that form a thick, relatively tall canopy, and a lesser dense under-storey with a few riparian shrubs (UPPER LEFT). Lentic habitats that are subject to variations between white-water and black-water floods (such as the lower portion of the Tambococha Creek, UPPER RIGHT) can have both forest types present within the same area, with floating meadows – several species of Graminea – and palms growing next to the *várzea* forests. *Coussapoa trinervia* (false mangrove; CENTER, LEFT) are distinctive species of the black-water flooded systems, and so are the *chontillales – Astrocarium jaguarii* – palm tree colonies that dominate large portions of the river banks within the study area (CENTER, RIGHT). *Ranuncularia* sp. and the water jacinth (...) are typical floating plants in low-current zones (BELOW; Photos: Paola Carrera).



Appendix 6. OIL FIELDS INSIDE AND AROUND THE YASUNÍ NATIONAL PARK, ECUADOR

Amazonian Ecuador is rich in crude oil due to its proximity to the Andes; the oil boom during the 1980's gave rise to exploration activities, after which the land was partitioned in blocks, and assigned to several different national and international companies. Eight of these blocks are inside the Yasuní National Park or the Hoaorani Ethnic Reserve territories, and over the years, the industry has caused significant ecological damage to the land and aquatic systems. Declared "intangible" by the national government during the 1990's because of its uniqueness, the ITT block – where the study area is located – has already been scheduled for development. Rigorous control and enforcement of environmental laws must accompany this process; else, once the oil extraction and related activities (i.e. camp installation, road construction, and colonization) get started, the future of the wildlife and the people that reside inside and around the Lower Yasuní Basin will be threatened. Future oil development inside the new blocks assigned within the neighboring Peruvian areas, do not leave much choice for the re-distribution of disturbed wildlife species. (Source: www.saveamericasforest.org).

Appendix 7. Water level averages obtained for each time block, and compared between the Yasuní River, and the Jatuncocha System, and between the Yasuní River and the Tambocoha Creek.





Appendix 8. Fish availability expressed as number of specimens (NI), relative frequencies (RF%) and cumulative frequencies (CF%) of the 1862 fishes collected during the field season.

Family	Species	Ni	RF(%)	CF(%)
Sciaenidae	Plagioscion squamosissimus	183	9.83	9.8
Prochilodontidae	Prochilodus nigricans	132	7.09	16.9
Erythrinidae	Hoplias malabaricus	116	6.23	23.1
Curimatidae	Potamorhina altamazonica	99	5.32	28.5
Characidae	Triportheus elongatus	82	4.40	32.9
Characidae	Pygocentrus nattereri	79	4.24	37.1
Cichlidae	Astronotus ocellatus	78	4.19	41.3
Cichlidae	Cichla monoculus	63	3.38	44.7
Curimatidae	Psectrogaster esseguibensis	55	2.95	47.6
Auchenipteridae	Parauchenipterusgaleatus	50	2.69	50.3
Curimatidae	Curimata vittata	49	2.63	53.0
Characidae	Metynnis sp.	46	2.47	55.4
Cichlidae	Chaetobranchus flavescens	45	2.42	57.8
Characidae	Serrasalmus rhombeus	43	2.31	60.2
Ervthrinidae	Hoplervthrinus unitaeniatus	41	2.20	62.4
Cynodontidae	Rhaphiodon vulpinus	40	2.15	64.5
Characidae	Myleus cf. rubripinnis	36	1.93	66.4
Anostomidae	Schizodon fasciatum	35	1.88	68.3
Characidae	Mvleus sp.	34	1.83	70.1
Characidae	Brvcon whitei	33	1.77	71.9
Cvnodontidae	Cvnodon aibbus	32	1.72	73.6
Ctenoluciidae	Boulengerella maculata	32	1.72	75.3
Loricariidae	Hypostomus emarginatus	30	1.61	77.0
Cichlidae	Satanoperca iurupari	27	1.45	78.4
Pimelodidae	Pimelodella sp. 1	26	1.40	79.8
Characidae	Acestrorrhynchus falcatus	25	1.34	81.1
Cichlidae	Aequidens tetramerus	24	1.29	82.4
Osteoglossidae	Osteoglossum bicirrhosum	22	1.18	83.6
Characidae	Piaractus brachypomus	21	1.13	84.7
Curimatidae	Steindachnerina bimaculata	21	1.13	85.9
Ageneiosidae	Ageneiosus brevifilis	18	0.97	86.8
Cichlidae	Hypselecara temporalis	17	0.91	87.8
Characidae	Charax gibbosus	16	0.86	88.6
Prochilodontidae	Semaprochilodus insignis	16	0.86	89.5
Pimelodidae	Pimelodus sp.	16	0.86	90.3
Cichlidae	Heros efasciatus	15	0.81	91.1
Characidae	Triportheus angulatus	13	0.70	91.8
Pimelodidae	Pimelodella sp. 2	12	0.64	92.5
Osteoglossidae	Arapaima ajaas	12	0.64	93.1
Pimelodidae	Calophysus macropterus	12	0.64	93.8
Characidae	Mvlossoma duriventre	11	0.59	94.4
Curimatidae	Curimata sp.	8	0.43	94.8
Characidae	Astvanax fasciatus	8	0.43	95.2
Pimelodidae	Pseudoplatystoma fasciatum	8	0.43	95.6
Cichlidae	Crenicichla cincta	8	0.43	96.1
Doradidae	Anadoras grvpus	8	0.43	96.5
Loricariidae	Ancistrus alga	6	0.32	96.8
Pimelodidae	Sorubim lima	5	0.27	97.1
Hemiodontidae	Hemiodus unimaculatus	5	0.27	97.4
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	Total specimens	1862		
	Total species	73		
Ramphichthydae	Ramphychthys sp.	1	0.05	100.0
Ramphichthydae	Gymnoramphichthys cf. rondoni	1	0.05	99.9
Characidae	Hydrolicus scomberoides	1	0.05	99.9
Callychthydae	Hoplosternum littorale	1	0.05	99.8
Loricariidae	Loricaria sp.	1	0.05	99.8
Archiridae	Hypoclinemus mentalis	1	0.05	99.7
Anostomidae	Leporinus trifasciatus	1	0.05	99.7
Pristigasteridae	Pellona castelnaeanus	1	0.05	99.6
Engraulidae	Lycengraulis batesii	2	0.11	99.6
Loricariidae	Pterygoplichthys sp.	2	0.11	99.5
Characidae	Acestrorrhynchus falcirostris	2	0.11	99.4
Pimelodidae	Sorubimichthys planiceps	2	0.11	99.2
Anostomidae	Leporinus agassizii	2	0.11	99.1
Pimelodidae	Hemisorubim platyrhinchos	2	0.11	99.0
Loricariidae	Hypostomus sp.	2	0.11	98.9
Cichlidae	Crenicichla anthurus	2	0.11	98.8
Doradidae	Oxydoras niger	2	0.11	98.7
Anostomidae	Leporinus cf. muyscorum	3	0.16	98.6
Characidae	Colossoma macropomum	4	0.21	98.4
Potamotrigonidae	Potamotrygon cf. motoro	4	0.21	98.2
Cichlidae	Crenicichla protheus	4	0.21	98.0
Anostomidae	Pseudanos trimaculatus	4	0.21	97.8

APPENDIX 9. RELATIVE FREQUENCIES OF FISHES IDENTIFIED IN THE GIANT OTTER SCAT ANALYSIS ACCORDING TO TAXONOMIC HIERARCHY.

NS is the number of samples (N=31) where each of the species appeared, and all relative frequencies are percent estimates of the total 265 fish parts that were identified at some level. NI are those parts that were no identifiable at the species level, but family affiliation was usually possible in most cases. Parts classified under these categories do not necessarily correspond to one single genus or species, and in some cases might belong to either species already listed.

TAXONOM	IICAL HIERARCHY	OF IDENTIFIED FISHES	Relative Frequencies			
ORDER	FAMILY	GENUS-SPECIES	NS	Species	Family	Order
	A	Leporinus frederici	1	0.38	2.01	
	Anostonnuae	Schizodon fasciatum	7	2.63	5.01	_
		Acestrorrhynchus sp.	13	4.89	10.53	
	Charaaidaa	Brycon whitei	6	2.26		
	Characidae	NI Characoid	4	1.50		
		Triportheus elongatus	5	1.88		
		Curimata vittata	4	1.50		-
	Curimatidae	NI Curimatid	1	0.38	3.76	
		Potamorhina altamazonica	4	1.50		
		Steindachnerina dobula	1	0.38		
		Cynodon gibbus	1	0.38		-
	Cynodontidae	NI Cynodonitd	7	2.63	3.76	
Characiformes		Raphiodon vulpinus	2	0.75		62.41
		Hoplerythrinus unitaeniatus	7	2.63		-
	Erythrinidae	Hoplias malabaricus	30	11.28	16.17	
	-	NI Erythrinid	6	2.26		
	Hemiodontidae	Hemiodus sp.	3	1.13		-
		Myleus rubripinnis	3	1.13		-
	Myelidae	Mylossoma duriventre	5	1.88	7.52	
	5	NI Myelinid	12	4.51		
		Prochilodus nigricans	13	4.89	7.14	
	Prochilodontidae	Semaprochilodus insignis	6	2.26		
	Serrasalmidae	NI Serrasalmid	9	3.38	10.53	-
		Pvgocentrus nattereri	2	0.75		
		Serrasalmus rhombeus	3	1.13		
Gymnotiformes	Gymnotidae	Gymnotus carapo	1	0.38	0.38	0.38
Osteoglossiformes	Osteoglossidae	Osteoglossum bicirrhossum	4	1.50	1.50	1.50
	0	Aequidens tetramerus	9	3.38	28.57	20.09
	Cichlidae	Astronotus ocellatus	9	3.38		
Perciformes		Chaetobranchus flavescens	4	1.50		
		Cichla monoculos	2	0.75		
		Cichlasoma bimaculatum	5	1.88		
		Crenicichla sp.	11	4.14		30.08
		Hypselecara temporalis	14	5.26		
		NI Cichlid	13	4.89		
		Satanoperca jurupari	9	3.38		
	Sciaenidae	Plagioscion squamossissimus	4	1.50	1.50	-
	Ageneiosidae	Ageneiosus sp.	1	0.38	0.38	
Siluriformes		NI Ageneiosid	1	0.38		
	Doradidae	NI Doradid	2	0.75	0.75	
		Hipostomus sp.	- 1	0.38		9.02
	Loricariidae	NI Loricariid	7	2.63	3.01	
		Callophysus macropterus	1	0.38	2.63	•
	Pimelodidae	Pimelodella sp	6	2.26		
	Siluroidea	NI Siluroid	6	2.26	2.26	-
Unidentified	Unidentified	Unidentified	1	0.38	0.38	0.38
	Surgentined		1	0.00	0.20	0.20
Total Orders > 5	T. Families > 17	Total species > 47	$\Sigma = 265$	$\Sigma = 100$	$\Sigma = 100$	$\Sigma = 100$