BEHAVIOR AND ECOLOGY OF THE GIANT OTTER (*PTERONURA BRASILIENSIS*) IN OXBOW LAKES OF THE MANÚ BIOSPHERE RESERVE, PERÚ

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ABSTRACT

Lisa C Davenport: Behavior and Ecology of the Giant Otter (*Pteronura brasiliensis*) in Oxbow Lakes of the Manú Biosphere Reserve, Perú

(Under the direction of R Haven Wiley)

The Giant Otter (*Pteronura brasiliensis*) is an endangered otter of Amazonian lakes and rivers. It is the only otter of 13 extant species to breed cooperatively in family groups, with young of several years helping to raise younger siblings. I studied giant otters' behavior and ecology in 4 oxbow lakes (or "cochas") in the Manú Biosphere Reserve, Perú during 2003-2006. The objectives of this research were: 1) to investigate whether oxbow lakes return to random or predictable faunal communities after annual flooding; 2) to document seasonal and annual patterns in the diets of giant otters on two phytoplankton-dominated oxbow lakes; and 3) to document and characterize helping behavior in giant otters.

I initially classified the four study lakes into 2 lake types, phytoplankton-dominated lakes and macrophyte-dominated lakes. I obtained data on their faunal communities, limnology, and otter diet through four seasons of 2003, and during the dry-seasons of 2004-2006. I show that lakes' bird communities and caiman populations, and to a lesser degree fish communities, respond predictably by lake identity and type. Lake communities also responded to seasonal changes in 2003 data, but generalization to other years is complicated by the destructive flood in January of that year.

I studied giant otters' diet using visual observations, and demonstrated seasonal and annual changes not previously reported for the species. Giant otters shift to more intensive use of small cichlid prey found in edge habitats when with young cubs in the dry season.

In studying the giant otters' behavior, I showed that hunting skills and helping activities generally increase with age. This observation is consistent with a pattern of "slow learning" suggested by the Skills Hypothesis of Heinsohn (1991). I observed considerable variation in dispersal age and helping contribution within families, particularly with respect to defensive behaviors against potential threats.

Finally, the elderly matriarch in one family switched from being a provider of large prey to a beggar from other family members in 2007, apparently from the effects of old age. During 8 days of observation, her offspring assisted her through sharing prey and other types of assistance.

DEDICATION

To my best friend and husband, John Whittle Terborgh, who made this study,
as with so much else in our wonderful life, not only possible, but also way too much fun.

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Finally, the giant otters themselves tolerated my intrusive observations with great equanimity, for which I am forever grateful. Every day they taught me something new about their world, their individual personalities, their intelligence, and their abilities. I remain in awe of their fascinating lives, and hope to aid in ensuring their survival on this endangered planet.

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CHAPTER 1 INTRODUCTION

THE AMAZON

If there is any place on Earth still deserving of the term “wilderness,” it is surely the Amazon. First traversed accidentally by the Spanish explorer Francisco de Orellana in 1541, the subject of many failed mega-development projects, and one of the last places on Earth where uncontacted peoples still live nomadic existences, it remains a mythical, mysterious place that humanity has tried, but so far largely failed, to dominate. The diversity and majesty of its rainforests, animals, and indigenous cultures inspire awe and wonder in people around the world, which have led to increasing efforts to protect Amazonian habitats in parks and protected areas. Currently about 32% of the Amazon has been nominally protected in an attempt to preserve its biological and cultural riches, although most scientists consider a greater area to be required to maintain species diversity and ecosystem function (Soares-Filho et al., 2006; Terborgh, 1999). Although many Amazonian parks and protected areas are poorly defended, and deforestation rates both inside and outside protected areas are accelerating (Soares-Filho et al., 2006), the Amazon today still retains a mysterious hold on the human imagination, gaining increasing recognition as a treasure trove of not only diverse species, but also unimagined species- and ecosystem-level interactions, some of which are critical processes for maintaining the health of the planet.

The Amazon's mysteriousness extends to scientific understanding about its flora and fauna. After Franciso de Orellano's visit, it was nearly 200 years until the first scientist entered, and most scientific collecting has occurred only in the last century (Smith, 1990). Conservation efforts, sometimes stymied by lack of knowledge of where the most critical habitats and rare animals reside, have largely advanced only in the last half century, with many new additions to Amazonian protected area systems occurring only in the past decade. Dedication to understanding aquatic ecosystems has lagged behind advances in tropical forest ecology as has conservation of aquatic ecosystems and resources (Goulding, 1980).

THE GIANT OTTER

A vision of a mysterious and inexhaustible wilderness has also brought negative consequences for Amazonian forests and wildlife when unsustainable extraction has continued unabated. Unsustainable logging practices that continue today have reduced mahogany (*Swietenia macrophylla*) to 50% of its historic range, and brought it to commercial extinction in Bolivia, as is also likely in Peru in under a decade (Kornetter et al., 2004). Similarly, a legal trade in fur and skins continued through the 1950's and 60's that decimated populations of many animals, including caiman, large cats such as jaguar and puma, and other fur-bearers. The fur-bearer that earned the highest price for its pelt was the giant otter (*Pteronura brasiliensis*). Over 40,000 pelts of giant otter were exported from Brazil in the decade of the 1960's (Best, 1984, quoted in Carter and Rosas, 1997). By 1973, when the trade in otter pelts was stopped, the giant otter was considered one of the ten most endangered mammals in the world, with only small, isolated populations remaining in scattered corners of its former range (Carter and Rosas, 1997; Duplaix, pers. comm.). The Manú population, reportedly stable at about 80 individuals, is considered the largest in Perú (Groenendijk and Hajek, pers. comm.).

As the top predator of Amazonian rivers and lakes, the giant otter has the potential to be a keystone predator in the freshwater habitats where it lives, a role performed by its cousin the sea otter (*Enhydra lutra*) in kelp forests of the Pacific Ocean (Estes and Palmisano, 1974). However, in part due to its extreme rarity following the fur trade, no studies have yet been able to confirm the ecological interactions between giant otters, the fishes they prey upon, and any Amazonian freshwater ecosystem. My study aimed to fill in some of these gaping holes in our knowledge of the giant otter's natural history in at least one of its aquatic homes: oxbow lakes of the meandering Río Manú. The opportunity to work in the Manú River watershed, the entirety of which is protected in the Manú Biosphere Reserve, offers a privileged chance to study the dynamics of intact oxbow lake systems. Oxbow lakes of the Manú retain all their native fauna, including endangered fauna such as the black caiman (*Melanosuchus niger*) and the giant otter, and in the Tourism and Research Zones, oxbow lakes are protected from all human activities other than tourism.

I was interested in contributing not only to understanding the ecological role of giant otters in oxbow lakes, but also to better understanding their unique behavior. The only otter of 13 extant species to breed cooperatively, the giant otter's intra- and inter-familial behaviors and communication are among the most complex of any otter, and comparable to many other social carnivores. Although previous studies have documented hunting behavior and habitat use of giant otters in several Amazonian habitats, no other study has attempted to quantify helping behavior in the giant otter, even though helping behavior may be one of the most useful behaviors to aid understanding of the giant otter's use of a cooperative breeding system. Paradoxically, the giant otter might be one of the easiest top carnivores to observe, at least on oxbow lakes. Once habituated to human observation, my assistants and I were able to follow giant otters for complete 12-hour days whenever they were resident on my study lakes. Such continual access to the life of a top predator is a rare privilege, and an engaging topic for long-term study.

THESIS OUTLINE

I used a combination of techniques to better document the dynamics of oxbow lake communities and the otters' interactions within their environment and each other over several years (2003-2006). I combined behavioral observations with periodic sampling of fish, birds, caiman and water quality, including one full year of seasonal sampling in 2003. Chapter 2 reports on my sampling of oxbow lake fauna and water characteristics. In this investigation, I was particularly interested to see if after annual flooding, oxbow lakes returned to predictable or random assemblages of fish and other fauna, given the ongoing controversy on this topic. Chapters 3 and 4 report my data on giant otter diet, which represents the largest dataset ever collected on giant otter diet using visual species identification. Chapter 3 highlights the results of the strong seasonal variation in diet that I uncovered in 2003 work, and Chapter 4 uses additional dry season data to investigate an underlying cause for the variability, analyzing the suggestion that giant otters alter feeding behavior and diet in the presence of young cubs. I compare my own results on the giant otters' diet in Manú with other work on giant otters in Peru and elsewhere, and consider the potential consequences of dry season specialization on small Cichlids, including risk to young otters from caiman, and niche overlap with the sympatric Neotropical Otter (*Lontra longicaudis*).

In Chapter 5, I report on my observations of the behavior of giant otter helpers. Here I wished to not only quantify helping roles for the first time in the giant otter, but also to understand if giant otter families could be characterized by one of a number of possible behavioral syndromes that might give further insight into constraints on juvenile dispersal, and ultimately help explain cooperative breeding in the giant otter.

Finally, Chapter 6 reports on a rare, but fortuitous week of observations I made on an older breeding female, whose aged state caused her to switch from a provider of prey to a beggar from other family members. Since assistance to the elderly is rarely observed in animals other than humans, but may aid us to further understand the nature and significance of help provided by parents and offspring in cooperative animals, I provide a detailed report on these observations. I report on her begging success from other family members, consider the possibility that female menopause and multi-generational care may be found in giant otters in the wild, and speculate on its significance with respect to the "Grandmother Hypothesis" suggested for female menopause in humans.

For nearly every topic this thesis covers, the results reported are suggestive rather than conclusive about trends in oxbow lake ecology and giant otters' behaviors. Nevertheless, it represents one of the most intensive and quantitative efforts to understand the ecology and behavior of giant otters in the wild. I hope that the preliminary answers, as well as the multitude of remaining questions generated by this thesis, will enrich future investigation efforts and raise appreciation of the giant otter in the general public. Ultimately, scientific appreciation of the intriguing behaviors and ecological requirements of giant otters can and should lead to improved conservation of giant otters themselves and their threatened habitats throughout Amazonia.

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CHAPTER 2 COMMUNITY ECOLOGY OF FOUR OXBOW LAKES OF THE MANÚ BIOSPHERE RESERVE

ABSTRACT

The Piscivory-Transparency-Morphometry (PTM) Theory of floodplain lakes hypothesizes that Amazonian lake fauna return to distinct communities after annual flooding in response to top-down trophic cascades determined ultimately by morphometric and limnological characters of the lakes (Rodriguez and Lewis, 1994). Oxbow lakes of the Río Manú are observed in various states in the dry season, suggesting mechanisms of the PTM theory. Two of the most obvious lake states are phytoplankton-dominated lakes (Type 1 lakes) and macrophyte-dominated lakes (Type 2 lakes). I studied 4 oxbow lakes in the Manú river system, two of each lake type, measuring water quality parameters, and censusing fauna including fish, birds, and caiman during 2003-2006. I analyzed community data using Non-metric Multi-Dimensional Scaling ordination (NMDS) and partial Mantel's test, to test the hypothesis that fauna responded predictably across multiple years. Limnological measures showed few strong differences by lake, but bird community data showed strong site fidelity by lake in spite of changes from flooding, and type 1 lakes hosted more piscivorous birds than type 2 lakes. The fish and caiman communities responded to both year and lake during these observations.

INTRODUCTION

The study of tropical Amazonian lake habitats is still seeking to answer fundamental questions about the impact of various physical, chemical and biological forces on lake communities. For instance, disagreement continues on the basic question of whether fish communities of tropical floodplain lakes are random or predictable after annual flooding (Lowe-McConnell, 1987; Rodriguez and Lewis, 1994; Tejerino-Garro et al., 1998). In addition, authors debate the validity of models of hysteresis or "alternative stable states" in tropical lakes under real field conditions, and the predominance of top-down regulation, or trophic cascades (Didham and Norton, 2007; Scheffer, 1998; Schröder et al., 2005; Strong, 1992.). Classification of lake types and fish communities of the Amazonian region is also still in its early stages, in part because a thorough taxonomy of fish species is lacking (Ortega, pers. comm.). Oxbow lakes are particularly poorly studied, as few remain in a pristine state. In much of the world their formation has been curtailed by channelization, such as in the Mississippi River, and those that remain are rarely undisturbed by human activity. The Manú Biosphere Reserve, which protects the entire watershed of the Manú river, offers a unique opportunity to study the dynamics of intact, undisturbed oxbow lake systems. Oxbow lakes of the Manú retain all their native fauna, including endangered fauna such as the black caiman (*Melanosuchus niger*) and giant otter (*Pteronura brasiliensis*), and are protected from all human activities other than tourism.

Oxbow lakes: origins and classification

Oxbow lakes of the Río Manú, Peru, can all claim a common origin, having been formed during channel avulsion, a process in which the meandering river cuts off a large bend, abandoning one of its former curves to one of several possible fates (Goulding et al., 2003; Kalliola and Puhakka, 1993). Some former meanders quickly form low-lying "renacals" or swamp forests dominated by *Ficus trigona*, while others may temporarily become filled with grasses and tree seedlings and ultimately succeed to other forest types (Gentry and Terborgh, 1990). Other former meanders, however, will be left behind with enough sediment blocking the ends of the abandoned channel to form shallow lakes, called "oxbow" lakes or "cochas" (the local Quechua word for oxbow lake), which can persist as distinct bodies of water for decades or centuries. These lakes vary notably in a number of physical, chemical, and biological properties, many of which are immediately obvious to the naked eye. Some of the most obvious differences are seen in water color and transparency, development of marshy edges, densities of lake fauna (e.g. birds, snails, caiman and giant otter), and dominance of the water column by either phytoplankton, submerged aquatic macrophytes or floating macrophytes. The existence of such dramatic differences in lakes born of a common origin suggests a rich field of study for understanding the structuring mechanisms of aquatic communities.

Because oxbow lakes tend to reconnect to the main river channel several times a year during high water, they are considered "semi-open" ecosystems, and the nature of their interaction with the main river is probably critical to the observable differences among Manú lakes (Junk, 1997). In particular, certain Manú lakes retain year-round connections to the main river via narrow channels or a chain of multiple lake bodies, reminiscent of a string of pearls. Other lakes remain far more isolated, losing their connectivity to the main channel for most of the year, and only allowing interchange of river nutrients and fish during brief periods in the highest floods.

These hydrological differences likely underlie the fact that Manú lakes are found as a number of distinct lake types. However, before undertaking this study, it was not well understood if these presumed lake types represent different successional stages, stable ecological communities, or random assemblages of species that fluctuate from year to year, dependent upon the variable effects of the annual disturbance regime. Long-term experience at Cocha Cashu Biological Station led me to believe that Manú lakes are most likely distinct and fairly stable communities despite annual flooding: in most dry seasons, Cocha Cashu is observed to return to a phytoplankton-dominated state and to host high numbers of piscivorous fauna such as cormorants, caiman and otters.

Fish Communities in Oxbow Lakes of Amazonia: random or predictable?

Because the annual flooding regime is typical of lakes situated throughout Amazonia, various authors have questioned whether the semi-open systems of Amazonian lakes return to random or predictable lake states after annual flooding, particularly with regards to fish communities.   Until recently fish communities in Amazonian oxbow lakes were thought to be regulated by annual stochastic recolonization (Lowe-McConnell, 1987; Goulding, 1980). However, studies of lakes of the Orinoco River (Venezuela) and the Araguaia River (Brazil) suggest that Amazonian fish communities in oxbow lakes exhibit strong community integrity following floods, and return to distinct and predictable assemblages in the low water season, with communities regulated by the top piscivores (Rodriguez and Lewis, 1994; Tejerrino-Garro et al,. 1998; also see Pouilly et al., 2004). In the latter authors’ view, after flood levels recede, piscivorous fish suffer mortality dependent on water transparency and their adaptation to visual or non-visual methods of catching prey. They further suggest that water transparency is ultimately controlled by lake morphometry which should be relatively stable from year to year, thereby yielding fish communities that are regulated by the dominant suite of top predators accordingly. In proposing this "Piscivory-Transparency-Morphometry" hypothesis (or PTM Hypothesis) the authors showed that clear lakes dominated by visual predators evolved in two subsequent years along similar community paths; similarly, lakes dominated by non-visual predators (primarily electric fishes and catfishes) evolved towards a second distinct community type. Although the specific features of lake morphometry that control community structure remain vague under the PTM theory, the concept nevertheless gives us some underlying predictions to test about oxbow lake fish communities and potential community stability in the face of annual disturbance.

Study Objectives

As the Rio Manú watershed is located at the base of the Andes, the flooding regime is far shorter than for the oxbow lake systems studied by the authors in Brazil and Venezuela. While central Amazonian oxbow lakes may reconnect to the river for periods of up to six months, Manú oxbow lakes generally reconnect to the river for periods of a few weeks at most. With only short-term opportunities for exchanges of nutrients and fish from the main river, I predicted that Manú lakes should return to distinctive communities each dry season, and to evolve a community-level signature indicative of each lake type.

Moreover, I expected that Manú lakes with year-round connectivity to the main channel would behave distinctly from the most isolated lakes. Isolated lakes such as Cocha Cashu act as nutrient sinks in the dry season, and appear to be predictably dominated by phytoplankton. In line with the PTM theory, I investigated features of lake morphometry such as maximum depth, basin shape, and water chemistry measures such as transparency, conductivity, pH and alkalinity to understand possible correlations with the different lake types, seasonal changes, and faunal communities.

I expected to observe that Manú fish communities would exhibit strongest community similarity among all lakes in the wet season, evolving towards more distinctive communities, based on Lake Type, through the end of the dry season. Finally, I expected that these changes would mimic one another from one year to the next, with the dry season showing peak differences between lake types. Although the ideal sampling regime of completing multiple full years of seasonal sampling was not feasible due to time and budget constraints, my focus on dry season species assemblages aimed at demonstrating community resilience across multiple years.

STUDY AREA

My interest in studying Manú oxbow lake community ecology grew out of my parallel study on the behavioral ecology of the giant otter at the Cocha Cashu Biological Station. My choice of study sites therefore had as a primary criterion the choice of at least one comparison site for Cocha Cashu that allowed the study of giant otter under similar conditions. I chose to investigate if the seemingly distinct lake types of the region would result in measurably different communities of flora and fauna with an emphasis on the fish communities on which the giant otter depend. I determined site selection from among a number of lakes in the Manú Biosphere Reserve in 2002, and subsequently followed the four lakes from 2003-2006.

Manú Biosphere Reserve

My research was conducted in the lowlands (c. 400 m elevation) of the Manú Biosphere Reserve (MBR), Department of Madre de Dios, Perú (Figure 2.1). Specifically, the work was centered at the Cocha Cashu Biological Station, within the MBR reserve boundaries and on the shores of Cocha Cashu, the oxbow lake that gives the station its name. The lowland region of the MBR is dominated by the meandering Río Manú and a mosaic of tropical moist forest habitats. The river system is classified as a “whitewater” river, signifying that it carries abundant sediment from the nearby Andes (Barthem et al. 2003; Payne 1986). Average rainfall, as measured at the Pakitza Guard Station, is about 200mm per month (Gentry and Terborgh, 1990). Gentry and Terborgh (1990) describe the climate and terrestrial habitat. Barthem et al. (2003), Goulding et al. (2003) and Schenck (1999) describe oxbow lake habitats of the Madre de Dios region of Peru. Previous studies on giant otters in the Madre de Dios are described in Groenendijk and Hajek (2006), Staib (2002), Khanmoradi (1994), and Schenck (1999). Osorio and Ortega (2006) provided a photographic guide of the fish species collected in Cocha Cashu during this study. A history of the park’s contacted and uncontacted indigenous groups is contained in Macquarrie and Bärtschi’s 1992 book on the Manú.

Selection and Characteristics of Study Lakes

From many years of work at Cocha Cashu Biological Station, I knew that Cocha Cashu was isolated from the river in the dry season, and typically exhibited what I recognized as “phytoplankton dominated” features of lakes that are nutrient sinks. Water is typically turbid, and a cloudy green color from phytoplankton, and high densities of piscivorous birds (including cormorant, herons and kingfishers, among others) are present, as well as high densities of caiman and giant otter (Schenck, 1999). Relative to other study sites where giant otter have been found to have linear territories of 20 km or more, the size of the Cocha Cashu family's breeding territory (~2 km in length) is one of the smallest recorded (Laidler, 1984; Schenck, 1999). However, this family's extended territory does include outlying creeks and backwaters that are used in the wet season to an unknown extent.

In 2002 I visited nine Manú lakes, and collected chlorophyll a samples from six to obtain quantitative data on phytoplankton abundance and other water quality measures. I collected at least 3 water samples from each lake at varying depths using a horizontal sampler: one at the surface (0.0 m), 0.5 m and 1.0 m in depth. 250 ml of each sample was then strained through a Whatman CF filter, using a hand vacuum pump. Samples were stored in the dark with Dry-Rite at room temperature until processed in the lab. Chlorophyll a was extracted with 10 ml of acetone, and analyzed in a Turner Designs fluorometer. Since samples were not kept frozen between collection and processing, some degradation of the samples undoubtedly occurred, so that the data provide relative, not absolute measures of chlorophyll a concentrations (mg/l) in the lakes (Wetzel and Likens, 1991)

Low chlorophyll and high chlorophyll lakes were easily distinguished using the Kruskal-Wallis comparison for multiple samples (Table 2.1). Values of chlorophyll a varied widely, with a factor of 28 separating Cocha Salvador and Cocha Otorongo's maximum values. I chose Cocha Salvador as a second isolated, "phytoplankton-dominated" (hereby termed Type 1 lake) companion to Cocha Cashu, and two low chlorophyll lakes, Cocha Totora, and Cocha Otorongo, to represent connected, “macrophyte dominated” lakes (hereby termed Type 2 lakes). Relative locations of the 4 study lakes along the Río Manú are shown in Figure 2.2.

“Macrophyte dominance” for Cocha Totora and Cocha Otorongo refers to the extensive beds of “floating meadow” vegetation, floating mats of sedges and grass (i.e. *Scirpus cubensis* and *Pasalpum sp.*) and some floral species found only within these islands, such as an aquatic orchid (*Habenaria sp.),* plus members of the families Malvaceae and Onagraceae. Other characteristic plants of Type 2 lakes are the floating plants *Ludwigia helminthorriza, Utricularia sp.,* and aquatic ferns such as *Azolla macrophylla* and *Salvinia spp*. which occur in higher abundance along the edges of Totora and Otorongo than on Salvador and Cashu, where they are rare or absent. *Pistia stratiotes*, a floating macrophyte present on all lake edges, was seen prior to this study to completely cover Cocha Totora, but never any other study lake prior to the start of my study.

Size and morphometry of the four lakes varied, including length, width, depth, shape and depth profiles (Figures 2.3-2.6). As estimated by GPS coordinates in MapSource v. 6.11.1, Cocha Cashu is ~ 2.3 km in length, Cocha Salvador ~ 5.6 km in length, Cocha Totora ~ 0.7 km in length and Cocha Otorongo ~3.8 km in length. Maximum depth of Cashu and Totora were ~3 m and ~2 m, respectively (at the beginning of the study, prior to the input of a large sediment load in Cocha Totora) and ~5 m depth in both Salvador and Otorongo.

Cocha Cashu and Cocha Salvador demonstrated similar shape and edge vegetation that remained from their past history as river bends. Each lake is strongly curved, completing a full 180 degree curve, and in the case of Cocha Salvador, nearly completing a full loop with itself (Figures 2.3-2.4). On both lakes the shoreline internal to the loop (the shorter side of the loop), has along its edge a gradually sloping shore where river deposits once accrued. On Cocha Cashu, this shallow region promotes a convoluted shoreline where emergent grasses, sedges, *Heliconia*, shrubs and the occasional fig tree take hold. In contrast, the opposite and longer shoreline presents a sharp incline that changes abruptly from the water's edge into mature forest, with overhanging trees, vines and lianas, but almost no grasses or shrubs. Such a distinction between vegetation types on opposite shores is expected for former river bends, since loops form from the continual deposition of sediments on the inner part of the loop, and continual erosion of the outer edge of a loop. Although eventually inputs of sediment from the river and the surrounding forest should level out these profiles and fill in an oxbow lake, we know very little about the age of Manú oxbow lakes, and hence about the timescales or variability in the dynamics of these processes (Räsänen et al., 1991). Cocha Totora and Otorongo had predominantly steep-sided profiles along their borders, and s-curve shapes, rather than completing full loops in their main water bodies (Figures 2.5-2.6).

Perhaps the most important difference between the Type 1 and Type 2 lakes the fact that Type 2 lakes (Totora and Otorongo) maintain year-round outlets to the main river, which are fed by small creeks that descend from nearby uplands. The outlets to the river connect via long and narrow canals that are remnants of the formal river channel, and are choked up with long stretches of marsh grasses and floating meadow vegetation. In the densest and most persistent mats of floating meadow vegetation, small trees of the genus *Cecropia* can become established. In both Totora and Otorongo, the connector canals join with smaller sub-lakes before finally reaching the main river. I worked in only the largest single water body in each case.

METHODS

Data Collection Periods

Seasonal designations were constructed on the basis of rainfall data collected by park authorities at the Pakitza guard post (Figure 2.7). I collected seasonal data in 2003 in 4 periods: the “Dry” season (July-September); the “Dry to Wet” transition season (October – November); the flooding or “Wet” season (December – March); and the “Wet to Dry” transition season (April-June). Note that each season as defined here is of varying length – from 2 to 4 months – which I chose based upon a combination of the rainfall data and personal experience.

Other than the 2003 seasonal sampling, I collected data intermittently during visits between 2002-2006 (Table 2.2). Due to technical contraints, I did not sample birds in the wet season or fish in the dry season of 2005. In 2002, during my survey of suitable study lakes, I conducted bird censuses, caiman censuses and some water sampling, but no other data was comparable to later data. After 2006, Cocha Totora could no longer be satisfactorily sampled for fish communities, due to an altered drainage pattern (described below) that lowered the lake level to about 0.5 m in the 2006 dry season. Also, logistical difficulties precluded a dry season bird census at Cocha Otorongo in 2003.

It is important to note that in January of 2003 a rare (approximately 30-year) flood created extremely high-water conditions in all lakes. It brought strong currents, which destroyed extensive beds of littoral plants, and deposited fine sediments in the lake beds.

All lakes suffered damage, but Cocha Totora was particularly affected, as the flood altered the drainage pattern of its main water body, changing it from a backwater area tangential to an upland creek's input, to an area with continual internal flow between the creek and the main river. The new drainage pattern subsequently cut Cocha Totora's outlet to the river deeper every year, lowering the average water depth from about 1.5 m in the dry season of 2002 to about 0.5 m in the dry season of 2006.

Finally, although no data collection was planned for the dry season of 2006, I included new data from that year after observing a rare phenomenon at my main study site of Cocha Cashu. In that year, beginning about February or March, the lake was covered with a native floating plant, *Pistia stratiotes*. I estimated that about 1/3 of the total surface area of Cocha Cashu was covered by *Pistia* in 2006.

Limnology and Lake Morphometry

During the course of the 2002-2006 sampling, I measured a variety of limnological parameters at each lake. Conductivity (µS/cm^2) and temperature (C°) were measured every 0.5 m up to 2.5 m depth using a YSI 30 multimeter. Oxygen (mg/l) was taken every 0.5 m up to the maximum depth using a YSI 51B meter with model 5739 probe. Total alkalinity (ppm $CaCO_3$) was measured at the surface, using a LaMotte Alkalinity Kit 3467 model DR-A. Transparency (Secchi depth in meters) was estimated with a LaMotte Secchi Disk and a line marked to cm divisions, which also served to determine maximum depth. pH was measured using a digital IFSET MiniLab model IQ125 pH meter. I did not continue to take chlorophyll a measures throughout the multiple years of the study, due to the difficulty of properly storing and freezing samples under the field conditions available.

I documented depth profiles of the 4 lakes, using an Eagle "Portable FishEasy" sonar fish-finder which I attached to the side of the sit-on-top kayak. At approximately every 200 m I followed a transverse transect across the lake. Only a portion of these transects are represented in Figures 2.3-2.6. I then summarized each lake's morphometric signature by calculating the Volume Development Index, (VDI) from all transects. VDI = 3* Z_{mean}/Z_{max}, where Z refers to depth. VDI relates the shape of the lake basin to an inverted cone with height equal to the mean depth (Z_{mean}) and base equal to the lake's surface area. A value of 1 would represent a perfect cone, while higher values of VDI indicate greater volume development, or a more "U" shaped basin. Lake morphometry is expected to influence the ability of submerged macrophytes to develop, which could in turn influence, transparency, fish community structure, and other features of lake states (Beklioglu et al., 2006, Håkanson 2005).

I took multiple limnological measures at each lake in different seasons as able. I present only dry season data, for which each lake's repeated measures for that season are averaged for each year.

Bird Community Sampling

I surveyed birds from canoes or kayaks, using Canon 12 x 36 image-stabilizing binoculars, with one or two observers counting all birds seen. We conducted censuses in the morning, following the circumference of a defined study area. Morning censuses usually occupied 2-3 hours beginning around 0700 h local time. If birds were flushed by the observer, they were only counted if they flew behind the observers' boats or to the opposite shore if that shore had already been censused. Flushed birds were not counted if they flew in front of the boats or to the other shore if that shore had not yet been censused. In the case of Cocha Cashu, Cocha Totora and Cocha Otorongo, all open water areas were circumnavigated. In the case of Cocha Salvador, only about one half of the southern portion of the lakeshore was censused, an area that included forested and marshy habitats. A handheld GPS (Garmin Etrex Legend) was used to trace the distance traveled during the census, and all counts were relativized by the calculated lake perimeter (MapSource Version 6.11.1). All recognized birds were censused by the observers, and based upon expert opinion, I classified each species as lake-dependent or forest-dwelling, and classified each to a feeding guild (fish, aquatic insects, plants, snails) (Terborgh, pers. comm.). I also used expert opinion to classify birds as resident, northern migrants, southern migrants, or local (intra-tropical) migrants.

All ordinations used the Non-Metric Dimensional Scaling (NMDS) procedure in PC-Ord Version 4.41 (MJM Software), using Sorenson distance measures on numbers of animals per 100 m shoreline. NMDS does not assume an underlying linear or monomodal response to environmental variables, and so is the most appropriate ordination for repeated measures of plots followed over time (McCune and Grace, 2002). I ran NMDS using the "slow and thorough" autopilot mode in PC-Ord; multiple runs were compared visually to ensure a consistent result emerged, and I chose as the final run the result with the best correlation between Sorenson dissimilarity and ordination distance.

I restricted the dataset to only those species that were lake-dwelling species, and removed northern and southern migrants (primarily transient shorebirds). When multiple censuses were available for a sampling period, I restricted the dataset to one census chosen at random per period. The multi-year dataset comprises 33 samples at the 4 study lakes. I ordinated both abundance and presence/absence data of the multi-year dataset to compare differences between lakes with and without the effect of abundance. As lakes differentiated easily even with presence/absence data, those data are presented here.

While the main question of community resilience is focused on dry season communities, I also was interested in looking at whether or not I could detect directionality in compositional change over the seasons. I therefore conducted a separate NMDS ordination on the seasonal data I collected in 2003 (15 plots with 55 species).

For all ordinations, a Post-hoc measure of the % of variance obtained by each NMS ordination is reported as the r-squared coefficient of determination for each axis. This statistic represents the correlation between Euclidean distances in NMS ordination space and Sorenson distances between each pair of samples (McCune and Grace, 2002).

Finally, to characterize whether the dataset was significantly clustered based on Lake ID, Year, Season, or Lake Type, I conducted Mantel's tests using R (version 2.4.1) and the "ecodist" module. When run with contrast matrices, Mantel's test is essentially a MANOVA procedure that compares within-group variability to among-group variability (McCune and Grace, 2002; D. Urban, pers. comm.). Contrast matrices are distance matrices constructed such that 0 indicated the equivalent lake, year, etc., and 1 indicated a different lake, year, etc. I ran multiple models including simple Mantel's tests, and partial Mantel's tests using contrast matrices, to partial out the effects of the other factors. Prior to running the Mantel's tests, I visually inspected Shepard diagrams of the ordinations used (from PC-Ord output), to assure linearity in the plots of Sorenson distance vs. Euclidean distance in the ordination.

Once I determined that birds were sensitive to my a priori designations of Lake Type, I also ran the Indicator Species Analysis Procedure in PC-Ord 4.41 on the 33-sample (multi-year) dataset. I report species and their feeding guilds for those species identified as significant indicators for Lake Type at the $p < 0.05$ level by descending Indicator Value.

Caiman

Caiman census procedures followed identical shoreline routes as the bird censuses, but were done at night with headlamps (Petzl E50 Duo) to catch eyeshine. I counted all caiman regardless of species, although it was clear that nearly all caiman observed on oxbow lakes are black caiman (*Melanosuchus niger*). The smaller white caiman (*Caiman crocodilus*) are primarily seen in the river.

Each animal spotted was classified as small (< 1 m length), medium (1-3 m length), or large (> 3 m length) dependent on the apparent size and brightness of the eyeshine, and where possible, by estimation of head-size (Magnusson, 1983). Despite known limitations of these survey methods under different observing conditions (Magnusson, 1982), on my study lakes I achieved highly repeatable results at all sites across multiple years, and revealed strong differences in caiman densities between sites. On the two study sites nearest the Cocha Cashu Biological Station (Cocha Cashu and Cocha Totora) I conducted multiple repeated censuses to better demonstrate change over time. Because I undertook caiman censuses at Cocha Cashu and Cocha Totora as early as 2001 (before the initiation of other animal censuses), some of my censuses pre-date the 2003 flood, allowing us to compare before and after data.

To test for differences of caiman densities among lakes, I applied the non-parametric Kruskal Wallis test for differences between the median abundances of caiman densities, and also report post-hoc pairwise tests using a Bonferroni correction for significance (XLSTAT 2006).

Fish Community Sampling

Beginning in 2003, I undertook intensive sampling of the fish community at the four study lakes, under permit from the Ministry of Fisheries of Peru to the Museo de San Marcos, Lima, whose personnel oversaw all sampling efforts. To sample fish broadly among different size classes and different lake habitats, I used 3 different fishing methods. Five fish sampling regions were set up in each lake, and a standard sampling regime was followed at each station and for each method. For small to large fish in shallow grassy edge zones, I used a seine net of 6m length, 1.2 m height, and mesh diameter of ¼ inch. One sample consisted of 5 repeated hauls, spaced at 10 min intervals, and at regular distances in the region. For medium sized fish in central lake habitats, a gill net of 20 m length, 4 m height, and 2-inch mesh was set for periods of 1 hour per station. Finally, a throw-net of 4 m diameter with 1.5-inch mesh was used to sample with less size-class selectivity than the gill net, again in the center and along forested “log zones” of the lake. The throw-net was thrown 5 times at random locations and intervals, centered within each of the same 5 recognized sampling regions.

Fish were identified in the field, and measured for weight, height, standard length, and total length, after which they were released. Nearly all specimens collected were identifiable to species or morpho species. Voucher specimens of all species collected were sent to and identified at the Museo de Historia Natural, San Marcos with the help of Dr. Hernan Ortega.

As with bird census data, I report on two different runs of NMDS ordinations on the fish community data. For 2003 seasonal data, I combined presence/absence data from all 3 net sampling techniques and relativized the data using Beals Smoothing. A 3-dimensional result was recommended by the auto-pilot procedure, of which 1 projection is reported here. Mantel's models were also generated using R, to test if results were significantly clustered by Lake ID, Season, or Lake Type, as with the bird community data.

The Beals Smoothing procedure used on the fish data emphasizes patterns in the data based on joint occurrences of species, and is useful for data with many 0's such as this fish community dataset. Using presence/absence data with Beals smoothing loses information on differences in species abundance from lake to lake and across time, however. Community differences may not be fully represented by this method, and so I also analyzed the full dataset by calculating the Catch Per Unit Effort (CPUE = g/man-hour) for each species in each sample by the 3 net methods. Since different species with different average weights are caught with the 3 different methods, total CPUE differs by orders of magnitude for each method. Therefore, to combine the 3 methods without unduly favoring one method over the others, I standardized the values for each method by dividing each value in the species/sample matrix by the total CPUE for each method and multiplied by 100, thereby transforming the matrix elements' CPUE values into percent of total CPUE for that fishing method. I then created an aggregate sample unit by taking the average percent total CPUE across the 3 methods for each matrix element. Averaging the values of the 3 different methods creates a new entity that represents the centroid value of the 3 methods (McCune and Grace, 2002).

I ordinated aggregate CPUE samples for all samples in all years, using NMDS to visualize sample similarities, and again compared the significance of sample similarities with Mantels' models.

RESULTS

Limnological Measures.

Limnological measures showed few strong differences by lake, and none proved to be a good predictor of my Lake Type designations. The least variable measure by lake was pH, which showed very little variation among lakes or years (Figure 2.8). I expected oxygen levels to have been higher in Type 1 lakes due to oxygen production by phytoplankton, but oxygen concentration did not provide any indication of differing by Lake Type. Oxygen concentrations vary considerably throughout the day, as demonstrated by one 12-hour survey I conducted on Cocha Totora early in the study (Figure 2.9). The majority of my oxygen measures were taken in mid-day or late afternoon, when phytoplankton should have been maximizing its contribution to oxygen levels. However, other factors such as wind, clouds, and temperatures also affect these results, and probably resulted in sufficient variation to overwhelm the signatures of the different lake types.

Conductivity of the 4 lakes was highest for Totora (mean ~300 $\mu S/cm^2$), probably as a result of its smaller size and shallower depth. Stratification of water in deeper lakes should restrict mixing and lower ion concentrations in the water column. Also, evaporative concentration of nutrients will raise conductivity in a smaller water body. Conductivity correlated strongly with alkalinity (Pearson r = 0.94), suggesting that the preponderance of ions present are of calcium carbonate origin.

Transparency, measured as Secchi disk depth (m), also did not vary as I had expected for the Type 1 and Type 2 lakes. While Otorongo did maintain one of the highest transparency measures in all years, the other high transparency lake was Cocha Cashu, rather than Totora as I would have predicted from its lower phytoplankton concentrations in its early years. The flood of 2003 seems to have confounded expectations of high transmparency in Type 2 lakes by turning Totora into a shallow mudflat, albeit with sufficient flow to be inhospitable to its usual floating macrophytes. Cocha Cashu also increasingly clarified over the study as a result of first submerged (2004) and later (2006) floating macrophytes (predominantly *Najas aguta* and *Pistia stratiotes*, respectively). Salvador's low transparency was due to high phytoplankton concentrations in all years, so was the only lake to fulfill its expectations as a Type 1 lake.

The Volume Development Index (VDI) provided by lake transects gave the following values: Cashu = 2.0, Salvador = 1.4, Totora = 3.0, and Otorongo = 2.1. The sample size was insufficient for detailed comparison, although the expected pattern of lower VDI values for Type 1 lakes (Cashu and Salvador), and higher VDI for Type 2 lakes (Totora and Otorongo), suggests that a broader survey of Manú lakes could find this morphometric measure useful as a predictor of Lake Type, perhaps most effectively in combination with other limnological measures such as Secchi Depth and chlorophyll a.

Bird Community Sampling

Bird community data showed strong patterns in seasonal and Lake Type community signatures. Analyzing the 15 seasonal plots from 2003, the NMDS procedure resulted in a 2-axis solution that resolved 82% of the variance in dissimilarities (Figure 2.10). The 2003 dataset separates by Lake ID on Axis 1, but shows a seasonal progression on Axis 2. Mantel's test statistics also suggest a similar effect of both these factors with statistically significant results for both factors (Mantel's r =0.17 for Lake ID, p = 0.01; and Mantel's r =0.28 for Season, $p < 0.01$). Mantel's r was improved for both Lake ID and Season by running partial Mantel's tests removing the effect of the other significant factor.

The two Type 1 lakes (Cashu and Salvador, 1 and 2 respectively) did lay alongside each other in ordination diagrams, but the two Type 2 lakes (Totora and Otorongo, 3 and 4 respectively) did not, falling onto opposite sides of Axis 1. Because of this feature of the results, Lake Type did not produce significant results in a Mantel's test as expected.

Connecting the lakes' samples in date order, on Axis 2 there is a progressive change from the wet season (March) into the dry season (September and August) for all lakes but Otorongo, where the dry season sample was missed. Two of the lakes (Cashu and Totora) also appear to cycle back towards wet-season conditions with the onset of rains in October/November.

For the multi-year dry bird community dataset, analyses based on abundance and presence/absence were similar, although differences among lakes were even more pronounced with presence/absence data, and are reported here (Figure 2.11). The 2-axis solution explained 79% of the variation, and is shown with two color coding schemes to highlight the nested factors of Lake Type and Lake ID. Compared to 2003 seasonal data alone, the Mantel's tests on the multi-year dataset showed a strong response to Lake Type (Mantel's r = 0.32, $p < 0.01$), a similar effect of Lake ID (Mantel's r = 0.22, $p < 0.01$), and no significance for Season or Year. Because no significance was seen for season or year, no partial correlation models were run. In Clustering of Type 1 lakes, Cashu and Salvador are noticeably tighter in the ordinations than Type 2 lakes, with Cocha Totora presenting the most widely varying samples of all.

To further investigate indicator species by Lake Type, I applied the Indicator Species Analysis available in PC-Ord 4.41. This analysis was based on the two a priori categories of LakeType, and on the multi-year abundance dataset of lake samples (n=33). Seventeen of the 61 species included in the analysis were found to be significant indicators (at $p < 0.05$) for the Lake Type 1 designation, but only 3 species were found to be good indicators of Lake Type 2 designation (Table 2.5). The top 5 Type 1 indicators are all piscivorous species, and include some of the large and medium-sized herons (*Ardea cocoi, Tigrisoma lineatum,* and *Butorides striatus*), cormorants (*Phalacrocorax brasilianus*) and kingfishers (*Ceryle torquata* and *Chloroceryle aenea*). Also indicative of Lake Type 1 are birds that depend on flying or aquatic insects such as the Sunbittern (*Eurypyga helias*), Purple Gallinule (*Porphyrula martinica*) and Gray-breasted Martin (*Progne chalybea*).

In contrast to the top-trophic level species typical of Lake Type 1, the two best indicators for LakeType 2 sites are both herbivorous, including the arborial leaf-eating Hoazin (*Opisthocomus hoazin*) and the more terrestrial horned screamer (*Anhima* *cornuta*). The third species considered an indicator of Lake Type 2 is the Snail Kite (*Rostrhamus sociabilis*), an aerial predator on snails that typically is seen flying over marshes or floating meadows.

Caiman Densities

Both Cocha Cashu and Cocha Salvador had high populations of caiman, with significantly higher numbers compared to Cocha Totora and Cocha Otorongo (Figure 2.12). The difference in density between the maximum value recorded at Cocha Cashu and at Cocha Otorongo exceeded an order of magnitude (4.8/100 m vs. 0.43/100 m respectively) and the Kruskal-Wallis test of the medians was significant to $p < 0.001$. Post-hoc pairwise comparisons demonstrated that the Lake Type groups were significant with Bonferroni corrections applied when all size classes were pooled (Table 2.6), but were not significant when only large caiman were included (Table 2.7).

Cocha Cashu caiman censuses showed considerable variation over time, and to investigate this structure, I plotted all datapoints of size-class data in date order and fit a smoothed spline, nn=45 (Figure 2.13; SAS Enterprise Guide 3.0). This presentation demonstrates the drop in caiman numbers after the flood of January 2003, when many juveniles probably suffered low survival. Populations recovered fairly rapidly, until numbers dropped again in 2006 with the coverage of the lake by *Pistia*.

Oxbow Lake Fish Communities

As in the bird community analysis, I created separate ordinations on 2003 seasonal data and 2003-2006 multi-year data to look at compositional change over the year. When the data from all years were combined based on aggregate CPUE samples, a 2-axis solution was derived, and a cumulative r-squared of 0.61 was obtained (Figure

2.14). Visual inspection and Mantel's test results (Table 2.4) indicated that Lake Type, Lake ID and Year are factors explaining clustering in the plots, but not Season. Partialling out the effect of Year and Season gave the highest Mantel's r statistic for Lake ID. In Figure 2.14, I emphasize the role of Year by delineating 2003 points, which largely separate out on the right half of Axis 1, although clustering by Lake ID is also present.

When I ordinated the seasonal raw data from 2003 (average CPUE from all 3 net methods), the data lacked obvious structure, so a satisfactory ordination was not found until data were transformed with Beals Smoothing. Using this procedure, a 3-dimensional solution resolved 95% of the variance (Figure 2.15). Here, LakeID is the strongest factor structuring the data, separating out the lakes on Axis 3, and giving a Mantel's r of 0.21 ($p < 0.01$). Lake Type had a weaker r value of 0.15 ($p = 0.01$), as Lake Types 1 and 2 did not line up as predicted. As with bird samples, lakes separated out fairly cleanly on an NMDS axis (Axis 3 in Figure 2.15), but showed somewhat cyclical internal patterns. Unlike the bird community results, fish communities did not show consistent directionality in change with season.

DISCUSSION

Overall, my results showed that faunal communities in tropical shallow lakes maintain community structure by lake, and to a lesser degree by the two designated Lake Types. I also demonstrate some directionality in seasonal changes in my 2003 seasonal dataset, but this result may be specific the the 2003 conditions as a result of the 2003 30-year flood. Few other studies exist on shallow tropical lake fauna other than fishes, so comparison with other studies is limited. In addition, no other study known has looked at different lake types as I did here to compare differences in patterns and community stability. Given the usefulness of recognizing my 2 Lake Types, and including this classification in my analysis, other studies on tropical lakes may benefit from also attempting preliminary classifications before analyzing community-level data.

Bird Sampling

I demonstrate support for the suggestion that bird communities return to predictable rather than random assemblages on oxbow lakes in the Manú. My two a priori LakeType designations performed well as predictors of bird communities across multiple years, with the nested factor of Lake ID showing even more integrity across all years. If stochasitic recolonization and community assemblage after annual flooding were the norm, I would have expected to see no pattern in the clustering of annual datasets, or that Year or Season would structure the NMDS ordinations of lakeshore bird communities. I found that, even with the abnormally strong flood year of 2003 being included in the dataset, individual lakes' community structure (Lake ID factor) overrode both Year and Season effects. Moreover, using Indicator Value analysis, I demonstrated a distinction between Type 1 and Type 2 lakes' bird communities. Type 1 lake samples are characterized by a richer piscivore guild, while Type 2 lakes are characterized by herbivores and snail specialists.

When considering only the seasonal sampling from 2003, the NMDS ordination suggested that in addition to Lake ID, the effect of Season was important to structuring bird communities, even when migratory birds are removed. The seasonal progression and cycling observed in the 2003 dataset may be typical of Manú lake bird communities in all years, demonstrating responses to changes in nesting and feeding behaviors by season. It may also reflect a response to changes in the recovering littoral vegetation underway after the January 2003 flood, so may be a feature peculiar to this dataset.

The 2003 dataset did not initially indicate support for my suggestion that the Type 1 and Type 2 lakes would behave most similarly based on Lake Type, since Type 2 lakes did not appear closely aligned in their community compositions. However, inclusion of the multi-year dataset, using only dry season samples, provided evidence that my study lakes did respond predictably from year to year reflective of these two Lake Type classifications, based both on visual examination of the ordinations and on the MANOVA analysis provided by the Mantel's test using contrast or design matrices. Geographical location may have been responsible for the unexpected results by Lake Type in 2003, with lakes nearer to one another appearing more similar based on local fish congregations and movements following the flooding.

Although I did not find the factor Year to be as important as Lake ID to bird community structure, I did observe one intriguing phenomenon during the study: an infestation of the floating plant *Pistia stratiotes* that covered at least 1/3 of the surface of the lake in 2006. Because of positive feedback mechanisms that suppress phytoplankton and submerged plants, a switch to *Pistia* dominance can be considered an alternative stable state (Scheffer et al., 2003). Changes observed in the bird fauna with *Pistia* dominance include lower abundance of piscivorous birds, such as the herons and kingfishers, that normally abound on the lake. Also, the *Pistia* brought a greatly increased number of two specialist insectivores, Wattled Jacana (*Jacana jacana*) and the Least Grebe (*Tachybaptus dominicus*). The population of jacanas had increased from a few dozen on Cocha Cashu prior to *Pistia*, to over 200 by mid-2006, and least grebes increased from a scanty three or four to over a dozen. Jacanas are adapted to walking on floating plants on long toes, and they hunt for spiders and other insects that the plants harbor. The Least Grebe also probably benefited from the abundant small insects living in *Pistia*, and perhaps equally importantly from improved refuge from caiman (*Melanosuchus niger*) provided by the floating vegetation.

The new lake state's bird community was distinct from other Cocha Cashu samples in my analysis of abundance-based but not presence/absence-based data, and changed its community structure to appear more similar to a Type 2 lake (not shown here). The same pattern was also seen in the multi-year fish abundance-based dataset. I therefore suggest that, although presence/absence studies can distinguish the strongest lake-to-lake differences in community structure, it is important to include abundance estimates if we want to be able to distinguish more specific classifications of oxbow lake types, and identify the significance to faunal communities of alternative states within a single lake.

I did not find indications of long-term successional change structuring the bird dataset for my study lakes, at least over the ~5 y time window that I collected bird censuses. If successional changes were taking place, I would have expected each lake's samples to be progressively more dissimilar from one year to the next, but no such pattern was observed with the multi-year dataset.

As I predicted from casual observation, the two Type 1 lake samples are more similar to each other than they are to Type 2 lakes in the ordinations of the multi-year dataset (but not 2003 data alone). There is also a pattern in the ordination of presence/absence data suggesting that species assemblages are “tighter” from year to year in Type 1 lakes than in the Type 2 lakes. This feature of my ordinations also appeared in fish community analyses. Warwick and Clarke (1993) suggested that ecosystems stressed by external factors will show more dispersed community signatures. Since my Type 2 lakes remain connected to upland streams and the river year-round, greater variability in water level fluctuations might be considered a stress factor to Type 2 lakes. Type 2 lakes have both lower species diversity and lower overall densities of birds and caiman (see next section). And, although migratory birds were removed from the analyses, Type 2 lakes appear to host more transient and rare species, such as shorebirds, storks, spoonbills, and Orinoco Geese. Frequent water level fluctuations may create conditions in Type 2 lakes that are preferred by birds that are more adapted to fluctuating, ephemeral resources.

The Piscivory-Transparency-Morphometry (PTM) theory (Rodriguez and Lewis, 1994; Tejerrina-Garro et al.1998), developed for oxbow lake fish communities in the lower Amazon, is confirmed in this work to also extend to bird communities. Bird community data showed predictable, and not random community assemblage structure in my Manú oxbow lakes. Compared to fish surveys, bird censuses are comparatively easy and efficient to collect, so they might prove as the most useful indicators of lake classifications and lake states in Manú oxbow lakes. Further work to verify and more narrowly classify a larger sample of lakes is needed, as well as analysis of individual species’ sensitivity and preference to differing conditions.

Caiman Densities

Measurements of caiman density fluctuate to some degree based on seasonal patterns, flooding and juvenile survivorship, and sampling difficulties such as changes in detectability in different conditions. In spite of these issues, however, the strong differences between sites resulted in significant differences among my four study lakes, and between Lake Types.

Cocha Cashu and Cocha Salvador had significantly higher densities of caiman than Totora and Otorongo across all years, as predicted from initial conditions observed. Maximum densities on Otorongo and Cashu differed by over an order of magnitude (Table 2.4). These results corroborate previous authors working in Manú Biosphere Reserve, who found similar relative densities to ours in 1998, and also found Cocha Cashu to host the highest known density of black caiman of any Manú oxbow lake (Schenck, 1999). Clearly, some longstanding features of Type 1 lakes make them preferred habitat for breeding caiman.

Differences among lakes were seen within all size classes, but were particularly striking in the smallest two size classes, which represented approximately 1-year-old juveniles and the smallest reproductive-sized animals. These size classes were largely absent from Cocha Totora and Cocha Otorongo, so it appeared animals on these lakes had very low reproductive success. Type 2 lakes may support fewer caiman simply based on the difference in primary productivity in these lakes. If that were the case, we would not expect to see the similar number of large caiman, but rather all size classes should be affected. Instead, it appears likely that specific features of Type 1 lake morphometry cause caiman to prefer Type 1 lakes for reproduction. Specifically, I suggest that black caiman need a combination of forested and grassy edges for juvenile survivorship, which is better provided for on Type 1 lakes. Young caimans fall prey to many predators, including birds, cats, otters, and even other caiman. On Type 1 lakes, I have observed that medium and large caimans prefer to set up territories on shaded, forested edges, while young caiman are at highest density in grassy patches, where they can find more cover. In spite of the maternal care provided in caiman, the combination of forest and grassy edge habitats in near proximity may be critical for juvenile survivorship, and caimans may only find the desired combination of habitats in Type 1 lakes such as Cashu and Salvador where well-developed shallow littoral zones exist together with abrupt forested edges.

On Type 2 lakes, large caiman may use lakes more for feeding than reproduction, and seek out other lakes in which to reproduce. The large caiman on Type 2 lakes may also be those that have lost territorial battles, and so are largely transients or short-term residents. Further field studies on the behavior and reproduction of the caiman are obviously needed to confirm these suggestions.

Fish Ordinations

The most striking feature of the fish community datasets is the effect of the 2003 flooding in the ordinations. As with bird community data, Lake ID and to a lesser degree, Lake Type remain as important factors, in spite of this confounding effect. As with bird data, Season appears to have only a weak effect on structuring communities.

In the 2-dimensional NMS ordination of the aggregate fish samples, Axis 1 strongly differentiates the 2003 series of species data from the 2004-2005 series of data for all lakes. The 2004-2006 points outside the 2003 cluster also group by Lake ID.

Mantel's r values demonstrate the relative importance of the various factors that are significant in structuring the dataset under various simple and partial models (Table 2.4). In 2003 data, Lake ID is the strongest factor, and in the multi-year dataset, both Year and Lake ID are important factors. Lake Type is a significant factor, but with a somewhat lower Mantel's r compared to the other factors. Partialling out the effect of Year on Lake ID and Lake ID on Year provides only marginal improvements in the multi-year models Compared to bird community data, the greater effect of Year suggests that there is more year-to-year variability in fish communities. Yearly changes likely are the result of disturbance from flooding and recovery in all years, and resultant effects on juvenile survival. Finally, large numbers of fish migrate into and out of lakes during high water, which may be an important factor affecting yearly species abundance (Fernandes, 1997). Separating out these various factors that affect yearly changes still needs further study.

There is no support from the 2003 dataset for the prediction based on the PTM theory that oxbow lake fish communities are most similar in the wet season during reconnection to the river, and then diverge to distinct communities based on LakeType. In fact, the wet season position of the plots in my 2003 ordination shows the most dissimilarity for the four plots of any season.

The effect of Lake Type in structuring fish communities is not as strong as for bird communities in the multi-year datasets (Mantel r of 0.17 for fish communities, vs. 0.32 for bird communities). Also, as with bird data, in 2003, Cocha Otorongo and Cocha Salvador fish communities overlap despite being considered different Lake Types. Again I suggest that, after the strong 2003 flood, the close geographic proximity of Otorongo and Salvador allowed local fish migrations to dominate community structure. I did not test the explanatory effect of geographic distance as a contributing factor, due to the low explanatory power of so few samples, but a larger study at more sites should consider this factor.

Recovery from the effects of the 2003 flood were apparent during 2004-2006 work. Submerged aquatic vegetation along lakeshores recolonized on all lakes, littoral grasses and plants such as *Heliconia spp*. recolonized, and floating meadows and other floating macrophytes regained some of their coverage on Otorongo (but not Totora where drainage changes precluded floating plants). This recovery process seems to have allowed more gradual return of the fish fauna to "typical" conditions by Lake Type for fish than it did for birds.

As with bird data, multi-year fish ordinations show Cashu and Salvador maintaining more discrete centroids of points that are more similar to each other's species composition across years than Otorongo and Totora. Totora's dramatic community shifts dominate the ordination results. Undoubtedly, Totora's successional path and high dissimilarities in 2004-2005 are due to its undergoing rapid hydrological changes, that by the dry season of 2004 left it extremely shallow (<1m), which drastically changed conditions for resident fish.

Lateral Fish Migrations

One factor not accounted for in my sampling regime during this study was the importance of lateral fish migrations, or bi-directional movements of fish between the lakes and the main river during the wet season (Fernandes, 1997; Winemiller and Jepsen, 1998). The numbers of fish involved in these lateral migrations can be impressive, especially during the first flood of the year to reconnect a given lake. Fish aggregations are reported and used by local residents for their own consumption, and occasional feeding congregations of birds are observed at outlets to the river. Although I did not take data directly on these migrations until after the study period reported here, preliminary results (from Cocha Cashu 2005 and 2006) indicate that the species involved can change from year-to-year (Osorio, Alvarez and Davenport, unpublished results). Most species participating in such movements are detritivorous or piscivorous fish that enter the oxbow lakes to feed during the subsequent dry seasons, taking advantage of the higher primary productivity provided by lakes relative to the Manú River. After feeding in the lakes during the drier months, animals leave again in the following wet season ready to reproduce, and probably spawn further upriver in clearer upland streams with higher oxygen concentrations (Goulding, pers. comm.). The species captured in the connection channel between the river and Cocha Cashu varied significantly between 2005 and 2006, and so may be an important random factor effecting changes in fish communities in Manú lakes.

SUMMARY AND CONCLUSIONS

My results on the community ecology of four Río Manú oxbow lakes give new insights into the classification and dynamics of oxbow lake ecosystems and their faunal communities. These results are unique, as oxbow lakes are so little studied. My results can primarily be compared to studies from other watersheds such as Venezuela and Brazil, where the flooding regimes are considerably more extended in time (Okada et al., 2003; Rodriguez and Lewis, 1994; Tejerina-Garro et al., 1998).

I began the study with the expectation that the Type 1 and Type 2 designations would maintain more similar limnological characteristics and patterns in fishes' responses to seasonality than I actually observed. The heavy flooding of 2003 undoubtedly altered the normal resilience of communities in my lakes well beyond the normal disturbance regime. Although it confounded my analysis to a degree, the event was nevertheless instructive in demonstrating how shifts in lake states can be triggered, particularly in the shallowest lakes of the region. The loss of Cocha Totora as habitat for fishes, due to major hydrological changes, and the shifts in Cocha Cashu from an algae-dominated lake, to a lake dominated by floating macrophytes are, I believe, long-term impacts from the altered edge vegetation, sediment load and nutrient regime from the 2003 flood.

Strikingly, in spite of the various changes in lake state on Cashu and Totora, certain components of the fauna community, most notably birds and caiman, retained predictable community and population signatures through several dry seasons on most lakes.

Further work on oxbow lake classification and community ecology can take from this study that bird communities and lake morphometry may be the most promising indicators of lake type to develop better classification of oxbow lake types, and give predictive capacity about flora and faunal associations. Where satellite imagery can be evaluated, chlorophyll a is probably the most direct indicator of lake types, but is likely to be strongly bimodal, and offer less sensitivity to sub-categories of lake types than site visits. Time series measures of chlorophyll a should be used to evaluate its stability as an indicator, and ground-truthed as to its effect on fauna. Water level fluctuation, determined by connectivity of the lakes to upland creeks and the main river, may also play a major role in determining lake type and faunal associations.

Chlorophyll a (mg/l)

Lake	N	Minimum	Maximum	Mean	Std. deviation
Cashu	23	2.093	17.896	9.288	4.882
Salvador	2	10.844	25.704	18.274	10.508
Totora	11	2.384	6.840	4.132	1.510
Otorongo	2	0.570	0.924	0.747	0.250
Gallareta	3	3.316	4.536	4.067	0.657
Juarez	3	1.128	4.792	2.912	1.834

Multiple pairwise comparisons using the Dunn's procedure / Two-tailed test:

Sample	Frequency	Sum of ranks	Mean of ranks	Groups		
Otorongo	2	3.000	1.500	A		
Juarez	3	31.000	10.333	A		
Totora	11	171.000	15.545	A		
Gallareta	3	48.000	16.000	A	B	
Cashu	23	659.000	28.652		B	C
Salvador	2	78.000	39.000			C

Table 2.1: Chlorophyll a Extraction in 6 Manú Lakes, 2002. Non-parametric analysis of differences in chlorophyll a in 6 Manú Oxbow Lakes (XLSTAT 2006). In Dunn's multiple pairwise comparisons, tests are Bonferroni corrected to significance level of 0.0033.

	2003				2004				2005				2006			
	Wet	W to D	Dry	D to W	Wet	W to D	Dry	D to W	Wet	W to D	Dry	D to W	Wet	W to D	Dry *	D to W
	Dec-Mar	Apr-Jun	Jul-Sep	Oct-Nov	Dec-Mar	Apr-Jun	Jul-Sep	Oct-Nov	Dec-Mar	Apr-Jun	Jul-Sep	Oct-Nov	Dec-Mar	Apr-Jun	Jul-Sep	Oct-Nov
Fish	X	X	X	X			X	X	X						X	
Birds	X	X	X	X			X	X			X				X	
Caiman	X	X	X	X			X	X	X		X				X	
Water Quality	X	X	X	X			X	X	X		X				X	

* Cocha Totora was not included in fish sampling in 2006 due to excessive shallowness that year

Table 2.2: Sampling Regime Realized on 4 Manú Lakes. Timing of seasonal and dry-season visits to Manú lakes 2003-2006.

2003 data only

Model	Mantel r	2-tailed p-value
Birds~Laketype	0.10	0.11
Birds~LakeID	0.17	0.01
Birds~Seasons	0.28	<0.01
Birds~LakeID + Seasons	0.26	<0.01
Birds~Seasons + LakeID	0.32	<0.01

All Years, Presence/Absence Data

Model	Mantel r	2-tailed p-value
Birds~Laketype	0.32	<0.01
Birds~LakeID	0.22	<0.01
Birds~Years	0.04	0.65
Birds~Seasons	0.03	0.74

Table 2.3: Mantel's Test Models on Bird Community Data. Simple and partial Mantel's Test statistics on Bird Community Data. Factors partialled out with contrast matrices denoted by "+" sign.

2003 data with Beals Smoothing

Model	Mantel r	2-tailed p-value
Fish~Laketype	0.15	0.01
Fish~LakeID	0.21	<0.01
Fish~Seasons	0.01	0.86

All years, Aggregate Samples

Model	Mantel r	2-tailed p-value
Fish~Laketype	0.17	<0.01
Fish~LakeID	0.24	<0.01
Fish~Years	0.25	<0.01
Fish~Seasons	0.05	0.25
Fish~LakeID + Years	0.26	<0.01
Fish~LakeID + Years + Seasons	0.27	<0.01
Fish~Years + LakeID	0.28	<0.01
Fish~Years + LakeID + Seasons	0.28	<0.01

Table 2.4: Mantel's Test Models on Fish Community Data. Simple and partial Mantel's Test statistics on Fish Community Data. Factors partialled out with contrast matrices denoted by "+" sign.

Species Name	**LakeType**	**Indicator Value**	**p**	**Feeding Guild**
Ardea cocoi	1	72	0.001	Fish
Butorides striatus	1	71	0.002	Fish
Tigrisoma lineatum	1	70	0.001	Fish
Phalacrocorax brasilianus	1	67	0.005	Fish
Ceryle torquata	1	61	0.011	Fish
Mesembrinibis cayennensis	1	59	0.004	Snails
Progne chalybea	1	55	0.003	Insects
Chloroceryle aenea	1	51	0.002	Fish
Porphyrula martinica	1	48	0.025	Insects
Heliornis fulica	1	44	0.027	Insects
Eurypyga helias	1	43	0.012	Insects
Gallinula chloropus	1	39	0.014	Insects
Agamia agami	1	35	0.016	Fish
Tachybaptus dominicus	1	33	0.022	Aquatic Inverts
Aramides cajanea	1	33	0.029	Insects
Cochlearius cochlearius	1	28	0.048	Aquatic Inverts
Anhima cornuta	2	65	0.007	Plants
Opisthocomus hoazin	2	59	0.038	Plants
Rostrhamus sociabilis	2	39	0.046	Snails

Table 2.5: Indicator Values and Feeding Guilds of Manú Lake Birds by Lake Type. Based on abundance data with migrants removed, by Lake Type where 1=Isolated and 2 = Connected lakes. Species significant at $p < 0.05$ are shown in descending order of Indicator Value for each Lake Type. As these tests are a posteriori, however, species for which p-values are not $\ll 0.05$ may be suspect.

Sample	Frequency	Sum of ranks	Mean of ranks	Groups	
Otorongo	7	56.500	8.071	A	
Totora	15	231.500	15.433	A	
Salvador	10	337.000	33.700		B
Cashu	23	915.000	39.783		B

Table 2.6: Multiple Pairwise Comparisons of Caiman Densities on Manú Oxbow Lakes. Results of non-parametric comparisons of multiple means with all size classes pooled (XLSTAT 2006). Groups that are significantly different are designated by letter. Significance determined by Bonferroni correction.

Multiple pairwise comparisons using the Dunn's procedure / Two-tailed test:

Sample	Frequency	Sum of ranks	Mean of ranks	Groups
Otorongo	6	103.000	17.167	A
Totora	15	310.500	20.700	A
Cashu	22	622.000	28.273	A
Salvador	6	189.500	31.583	A

Table 2.7: Multiple Pairwise Comparisons of Large Caiman Densities on Manú Oxbow Lakes. Results of non-parametric comparisons of multiple means for large size class only (XLSTAT 2006). Groups that are significantly different are noted by letter. Significance determined by Bonferroni correction.

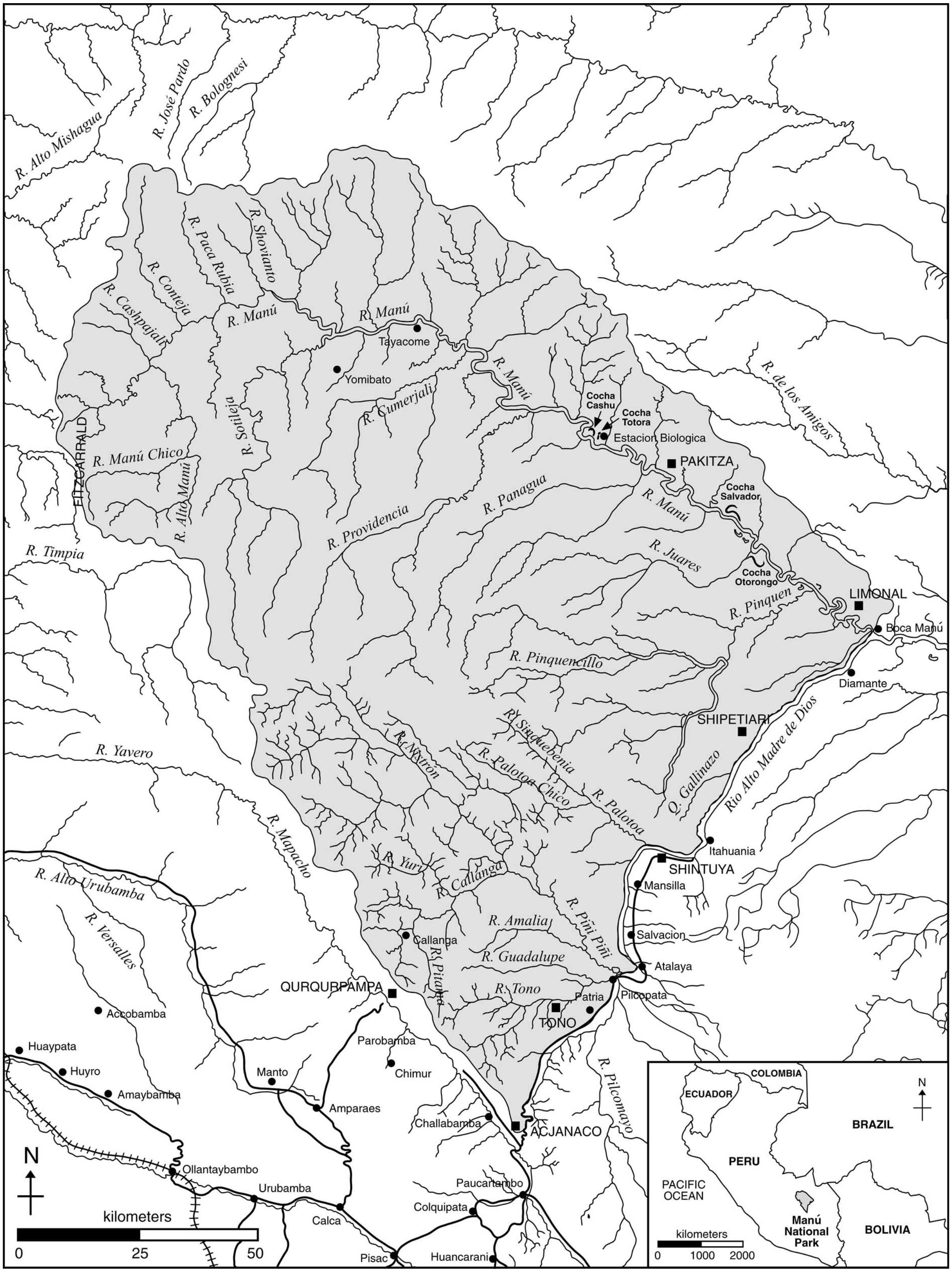

Figure 2.1: Study Site Locations within Manú National Park, Perú. Redrawn from Macquarrie and Bärtschi, 1992 and Shepard et.al., 2007.

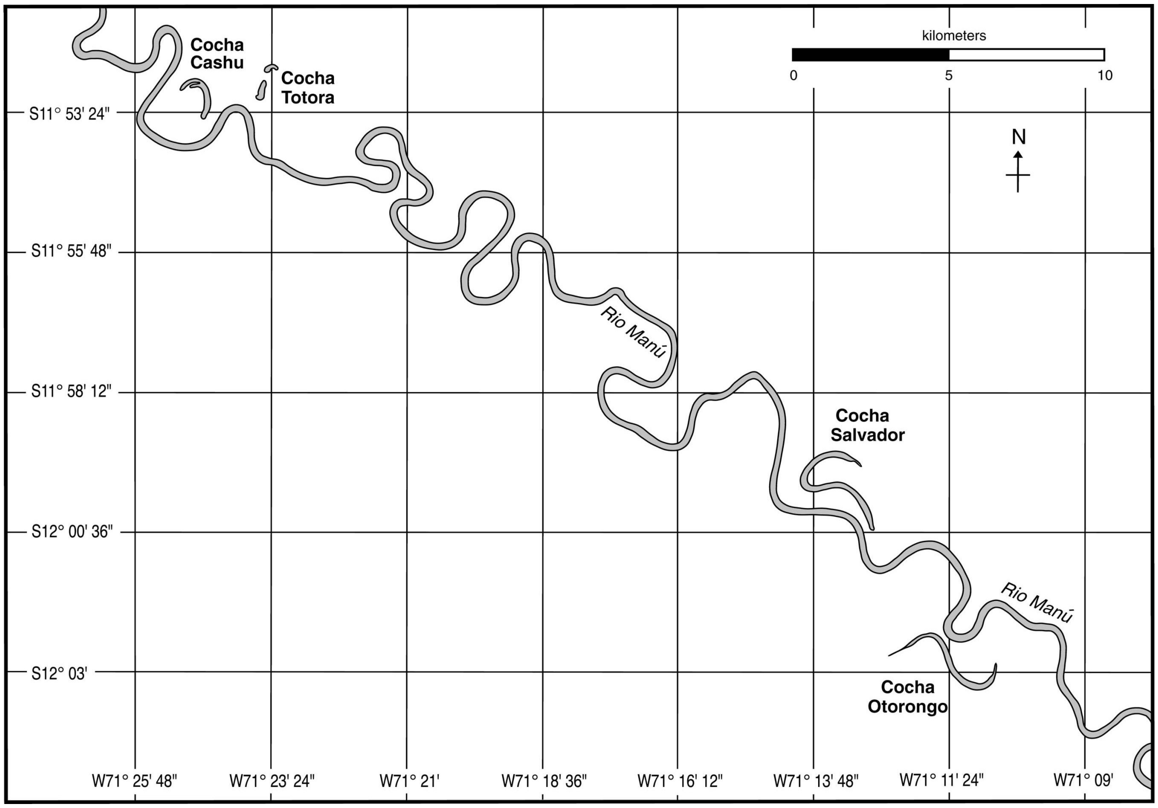

Figure 2.2: Locations of the Four Study Lakes along the Río Manú.

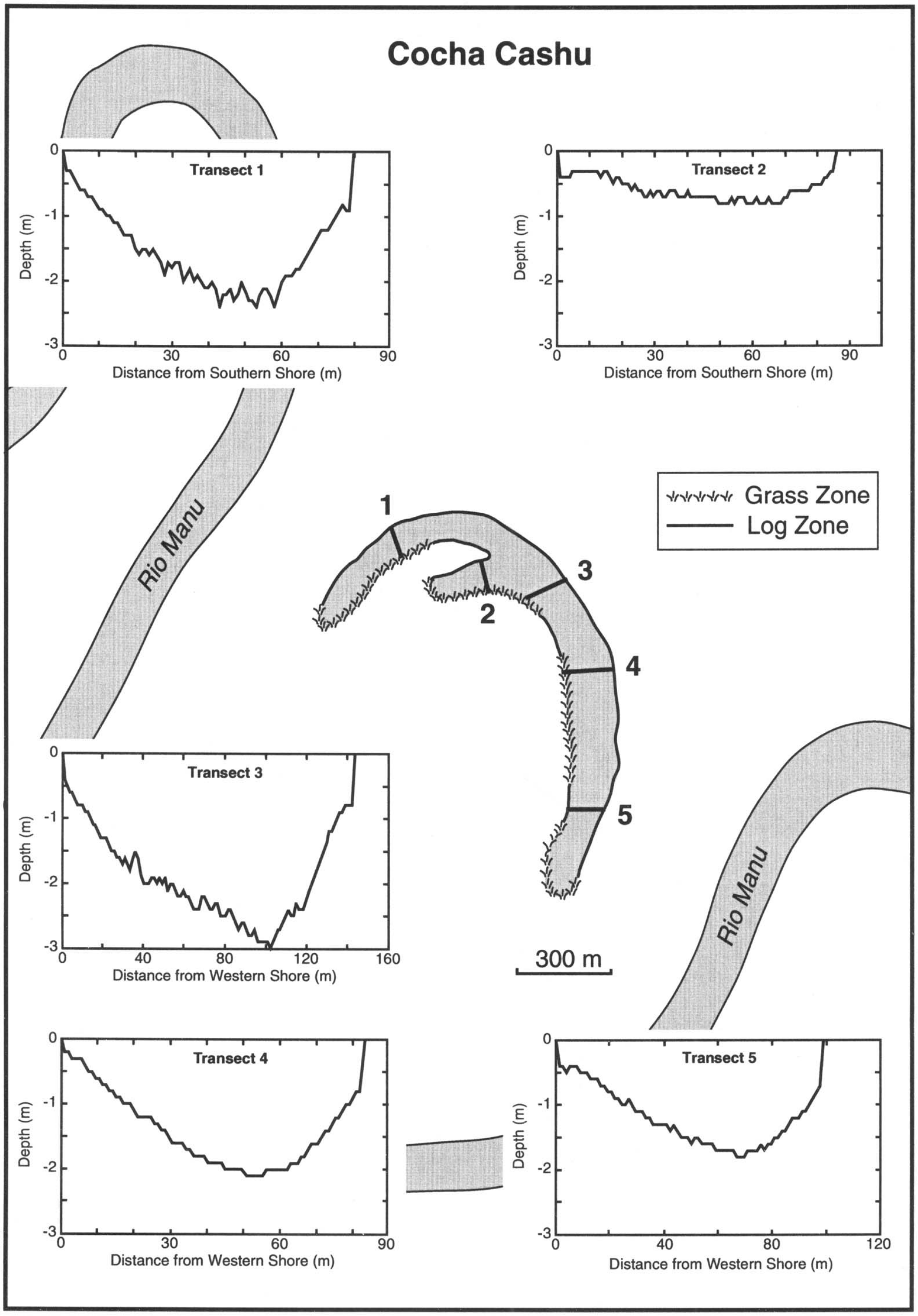

Figure 2.3: Vegetation and Depth Profiles of Cocha Cashu.

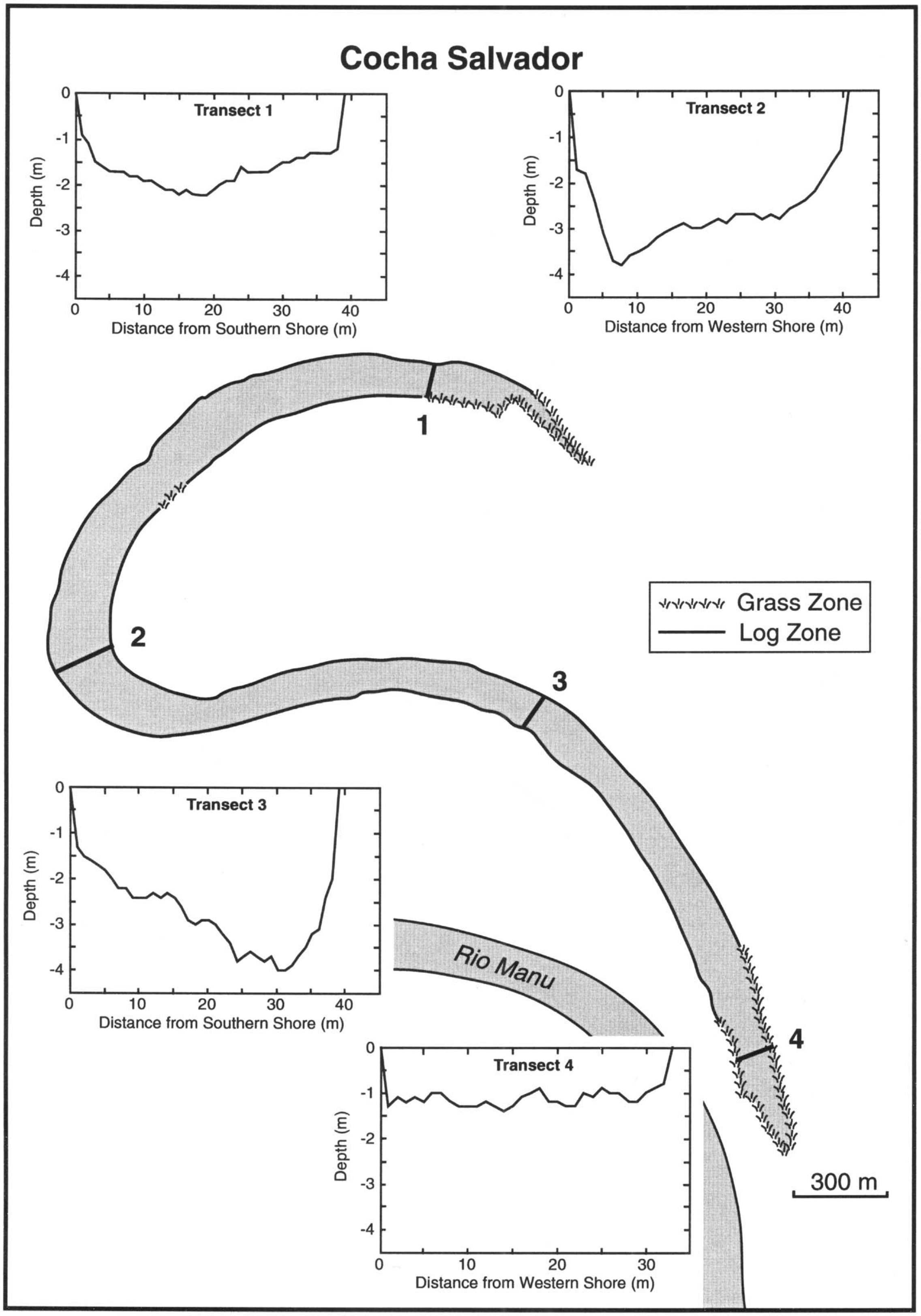

Figure 2.4: Vegetation and Depth Profiles of Cocha Salvador.

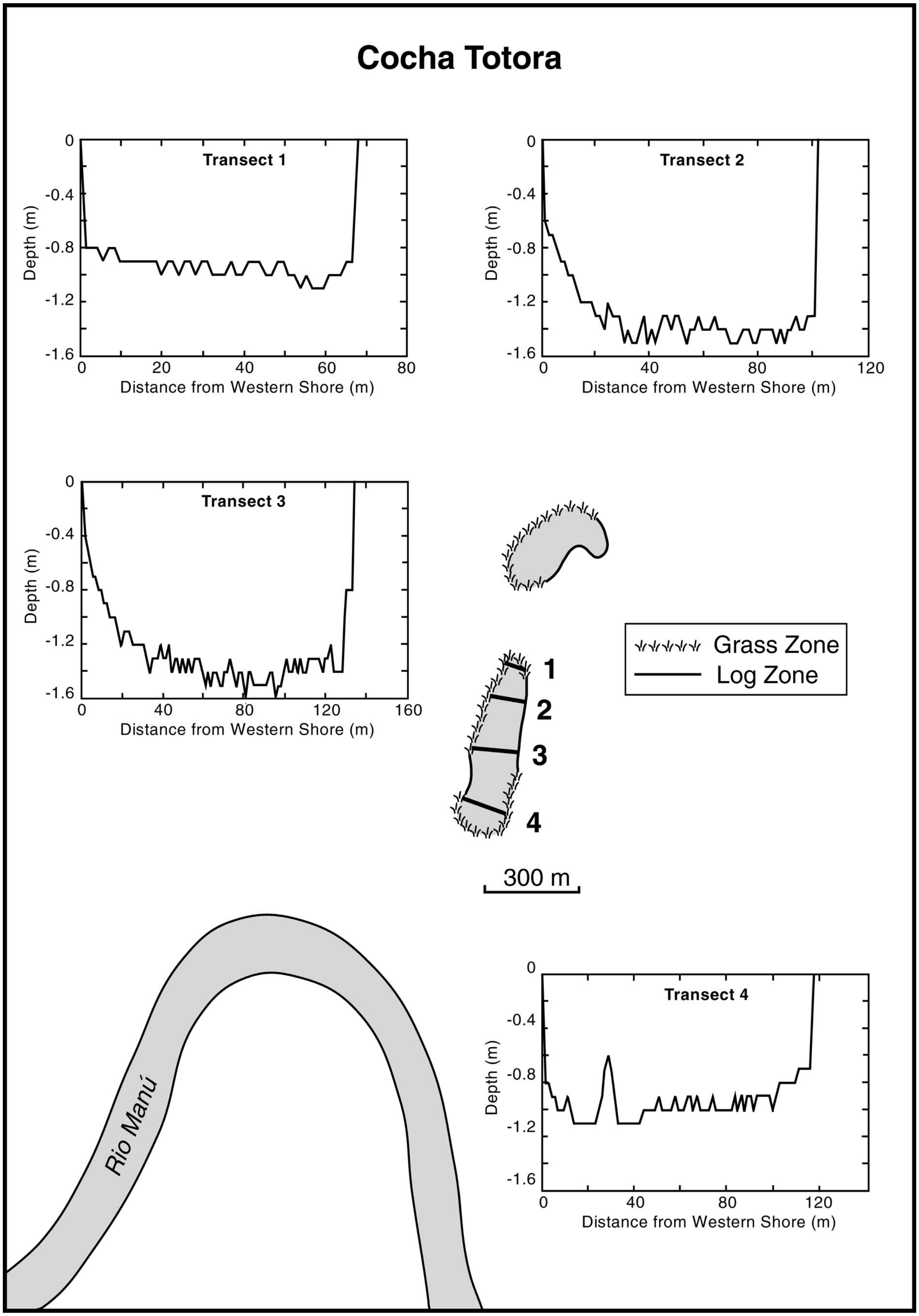

Figure 2.5: Vegetation and Depth Profiles of Cocha Totora.

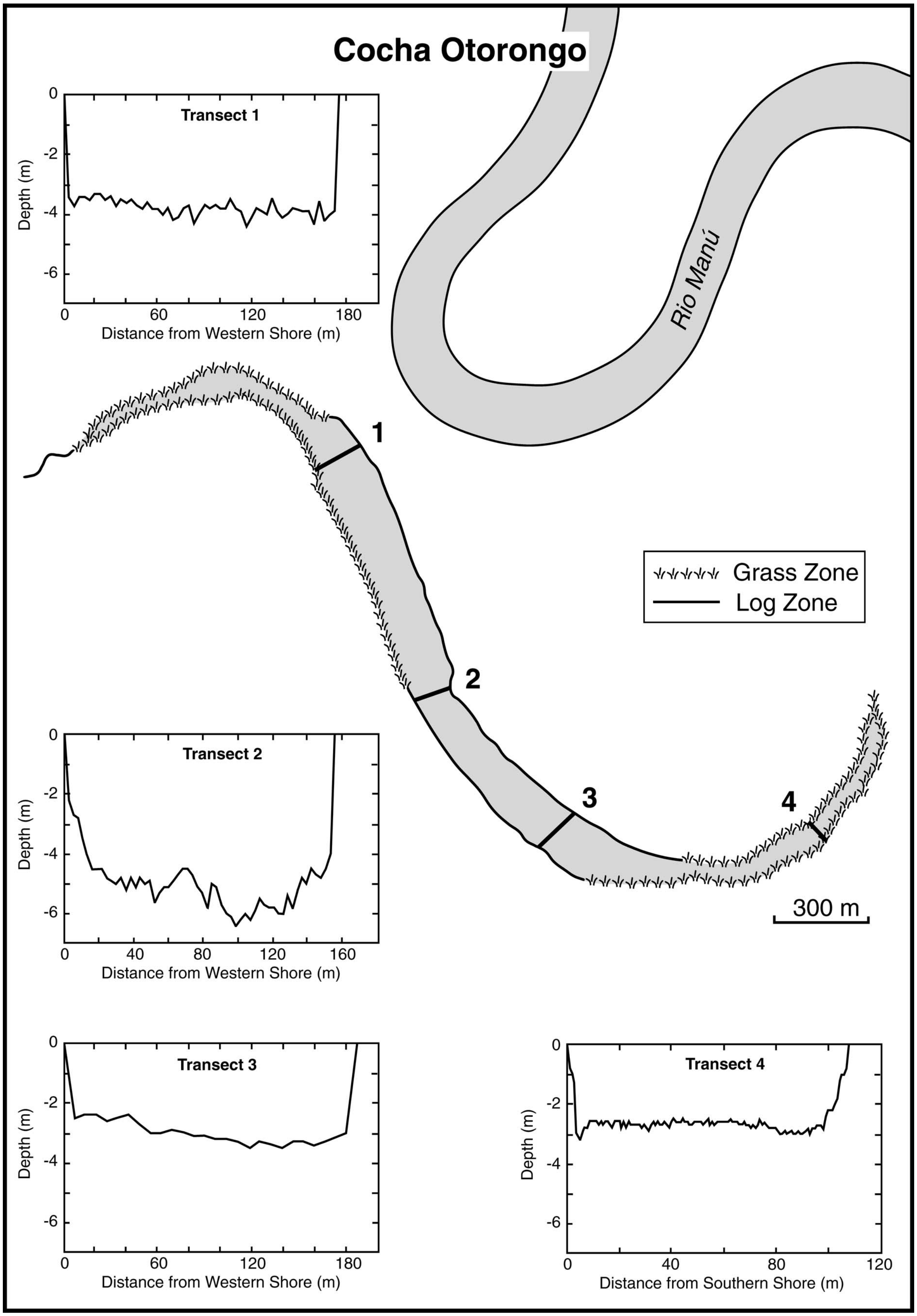

Figure 2.6: Vegetation and Depth Profiles of Cocha Otorongo.

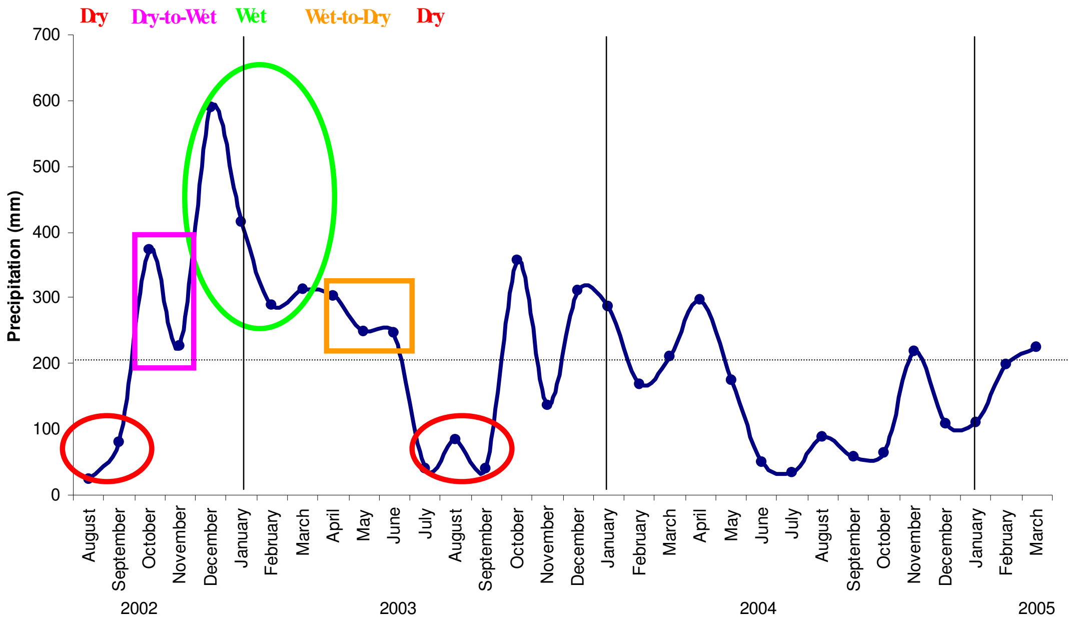

Figure 2.7: Monthly Precipitation and Season Classification. Precipitation data from 2002-2005, Pakitza Guard Station, Manú Biosphere Reserve, Perú. Colored ovals and squares designate monthly groupings that helped determine my classification of the Dry, Dry-to-Wet, Wet, and Wet-to-Dry seasons.

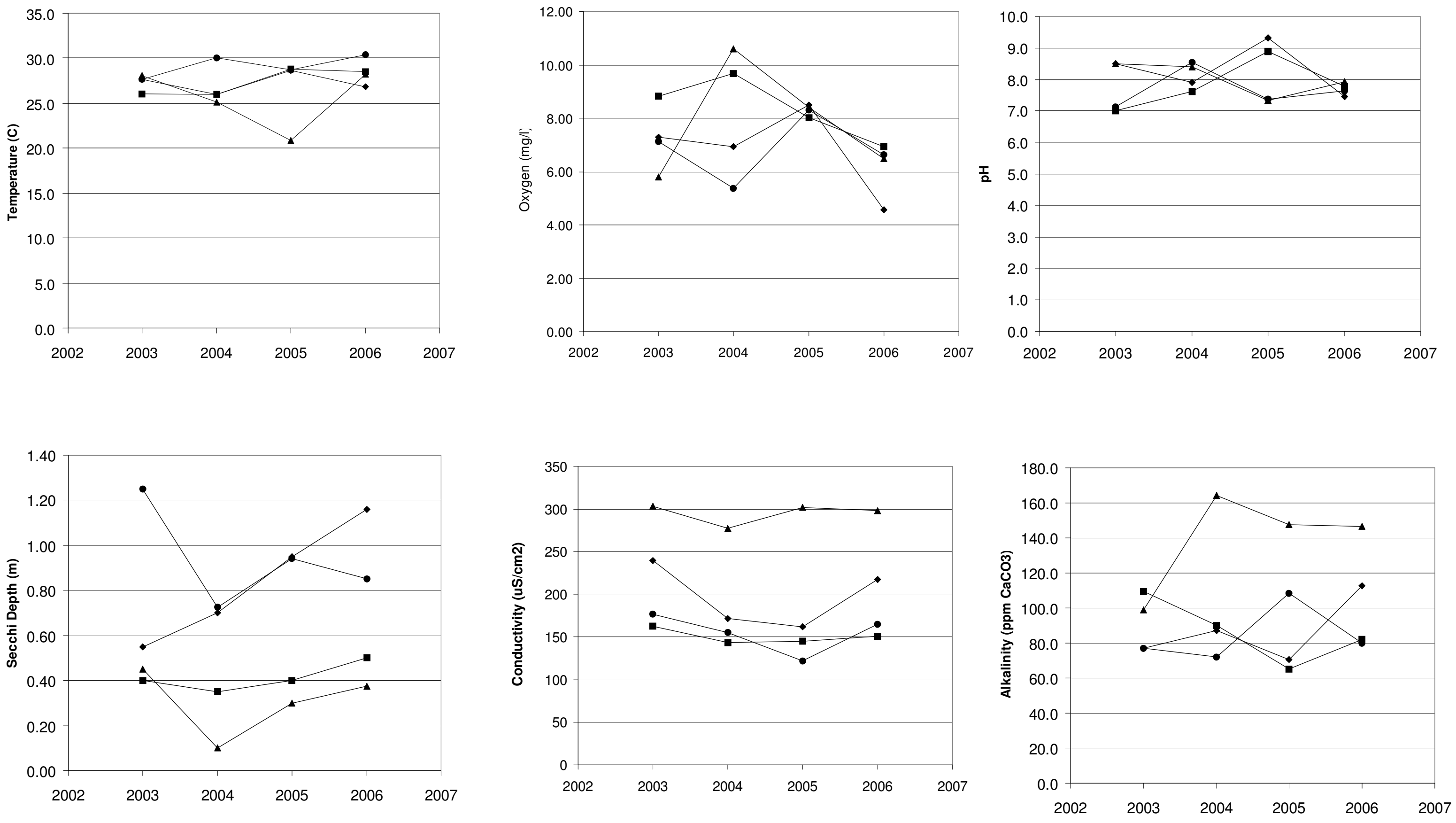

Figure 2.8: Dry Season Temperature, Oxygen, pH, Secchi Depth, Conductivity and Alkalinity on 4 Manu Oxbow Lakes. Diamonds = Cashu; Squares = Salvador; Triangles = Totora; Circles = Otorongo.

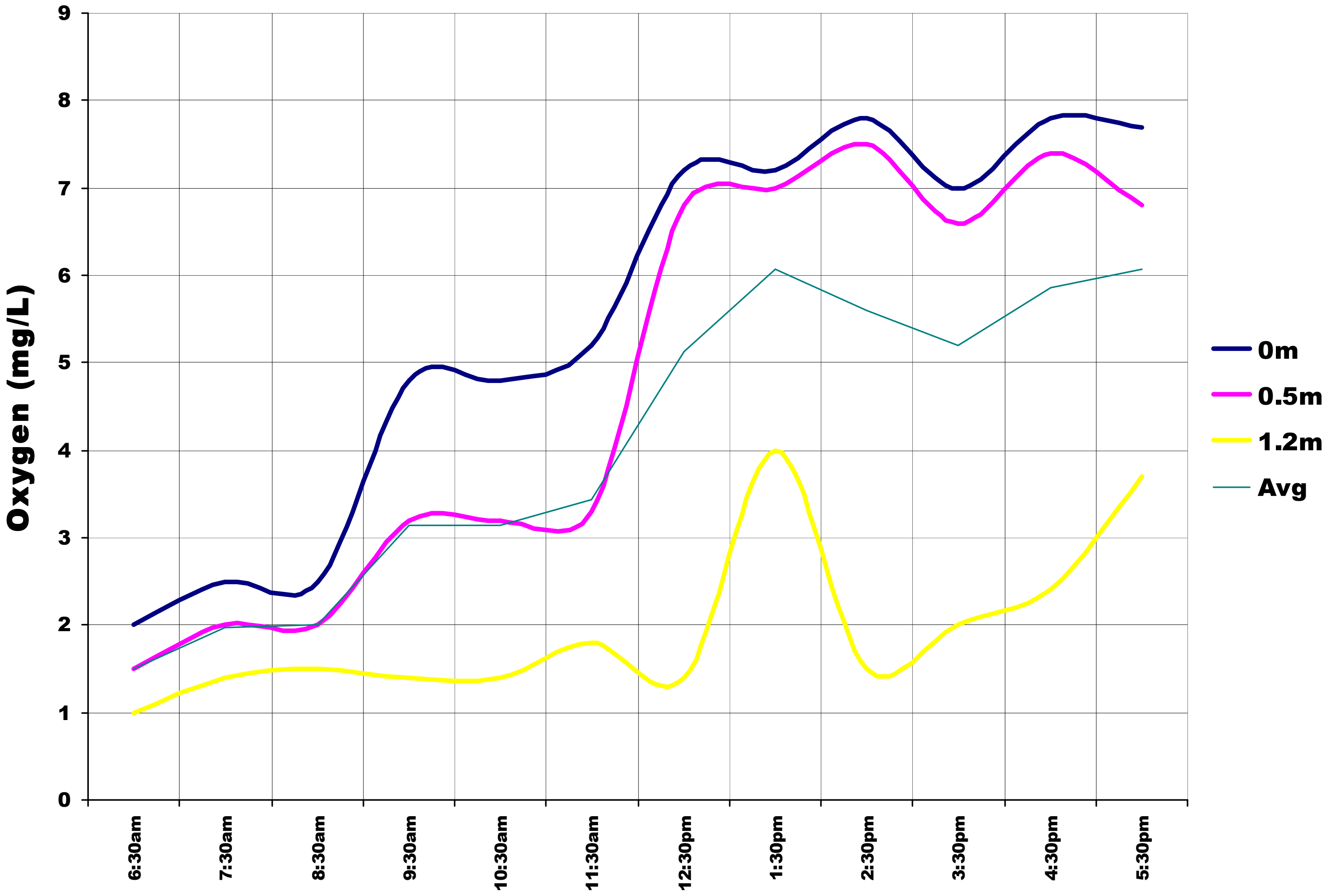

Figure 2.9 Hourly changes in Oxygen Concentration on Cocha Totora, August 19, 2002.

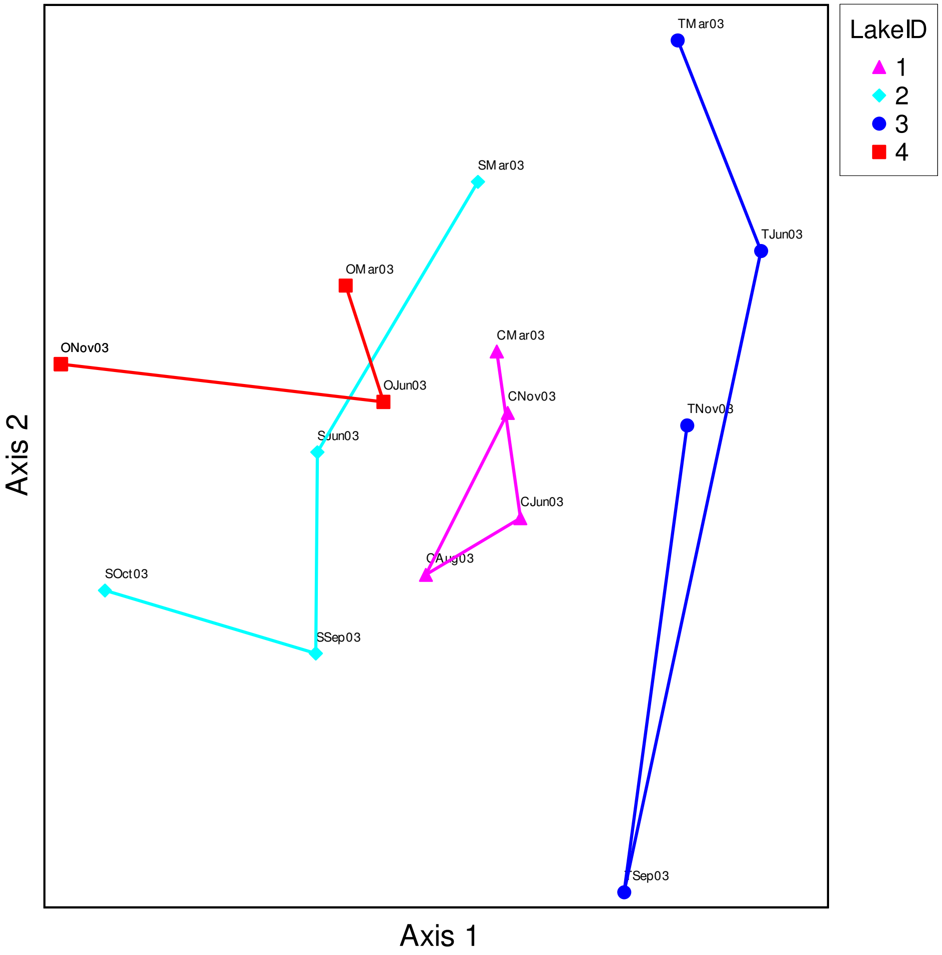

Figure 2.10: Non-metric Multidimensional Scaling (NMDS) Ordination of 2003 Seasonal Bird Censuses by Lake. Vectors connect datapoints in date order. 55 species of resident and local migrant species are included. LakeIDs are coded as 1=Cashu; 2=Salvador; 3=Totora; 4=Otorongo. Sample labels also denote the lake names' initial, month and year of samples.

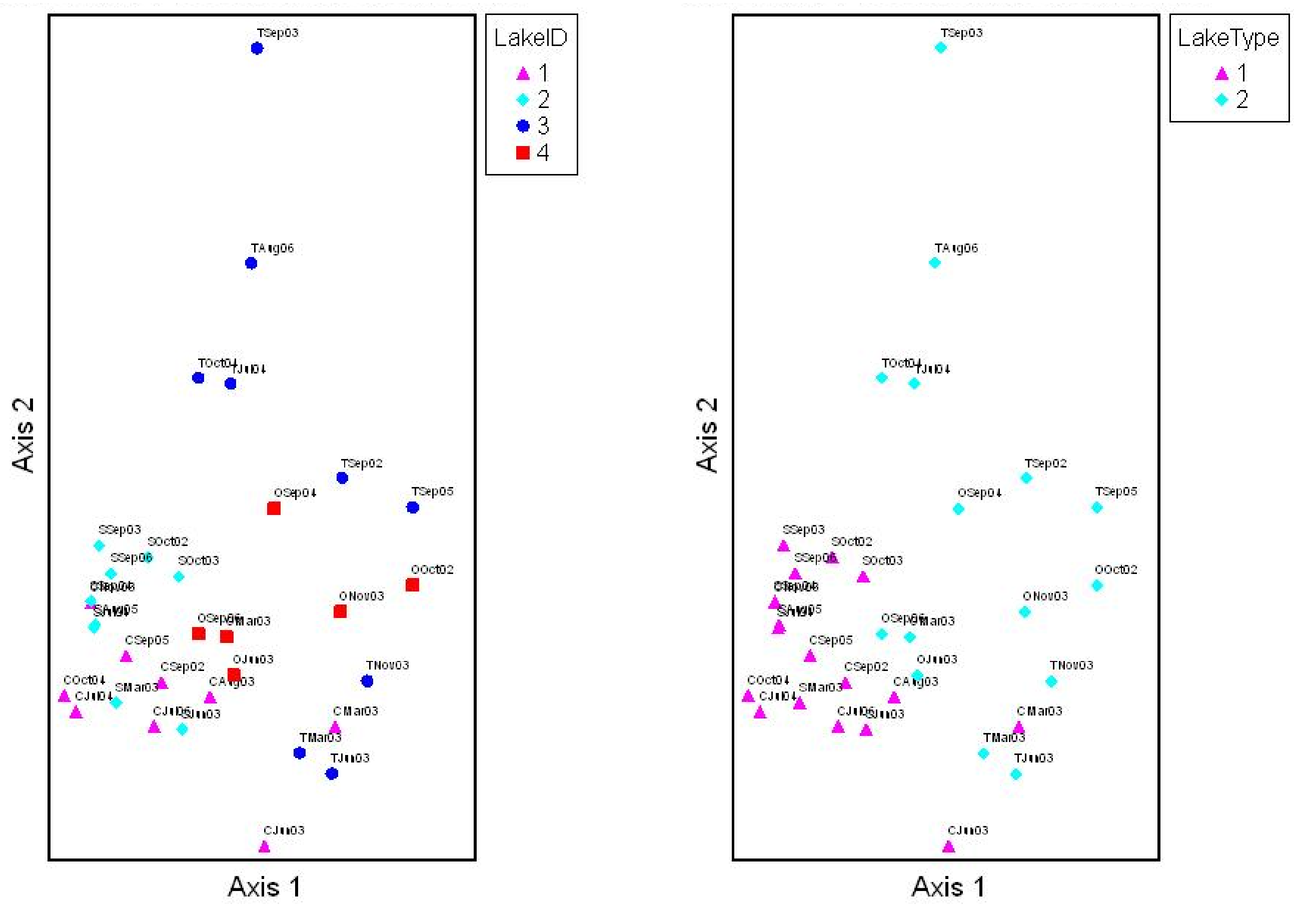

Figure 2.11(a-b): Non-metric Multidimensional Scaling (NMDS) on Presence/Absence Bird Censuses. by (a) Lake ID, (b)Lake Type. Lake IDs are coded as 1=Cashu; 2=Salvador; 3=Totora; 4=Otorongo. Point labels also denote the lake names' initial, month and year of sample. See text for details of species and sample selection.

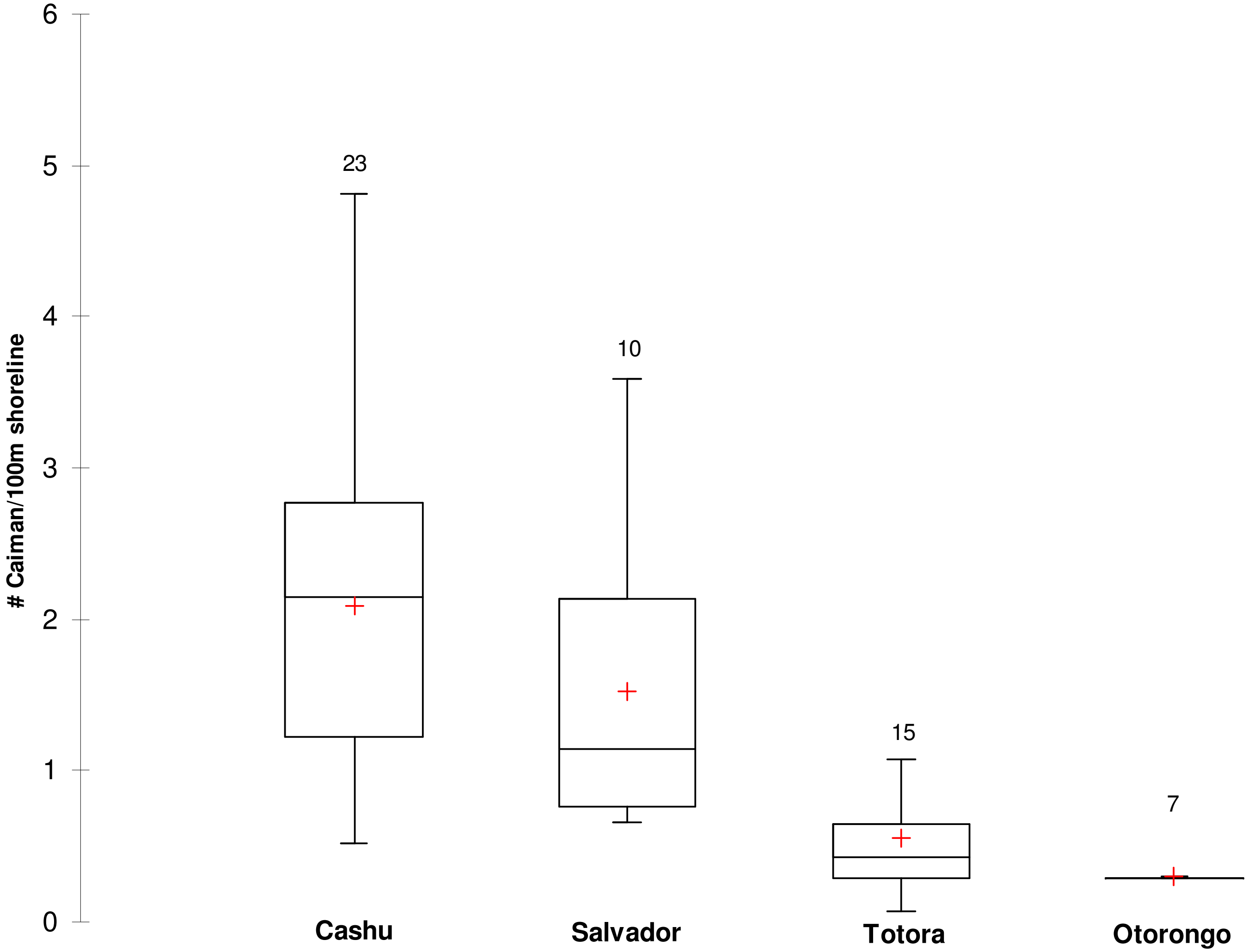

Figure 2.12: Abundance of Caiman on 4 Manú Oxbow Lakes. Boxplots display # of caiman per 100m shoreline. Boxes outline 1st quartile, median, and 3rd quartile values. Mean is marked with a "+" and minimum and maximum values are displayed at either end. Numbers above report sample number (n) taken on multiple dates between 2002-2006.

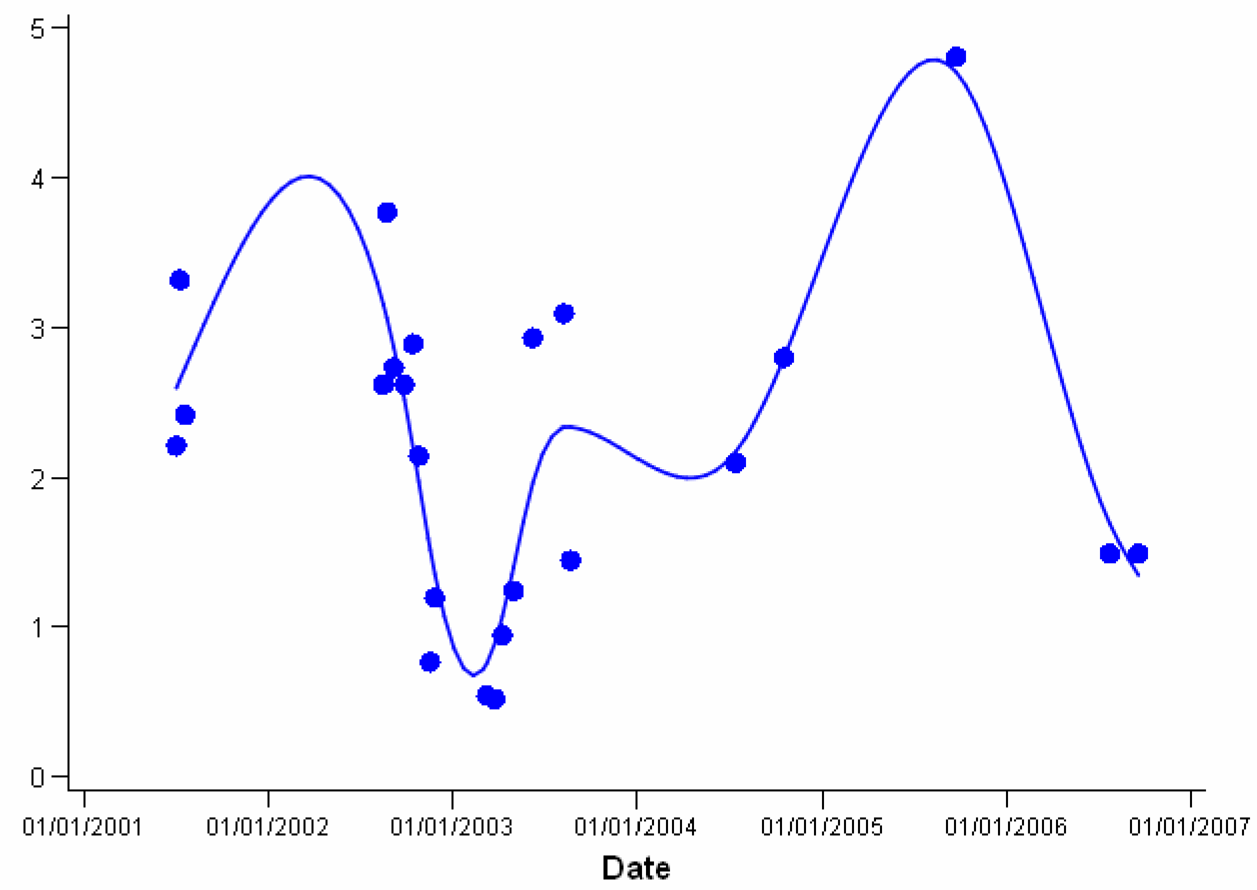

Figure 2.13: Change in Caiman Density on Cocha Cashu 2002-2006. Total # of caiman per 100m shoreline on Cocha Cashu. Datapoints are connected by an interpolated spline in date order. Note the drop in 2003 caiman numbers after flooding and again in 2006 with *Pistia* coverage.

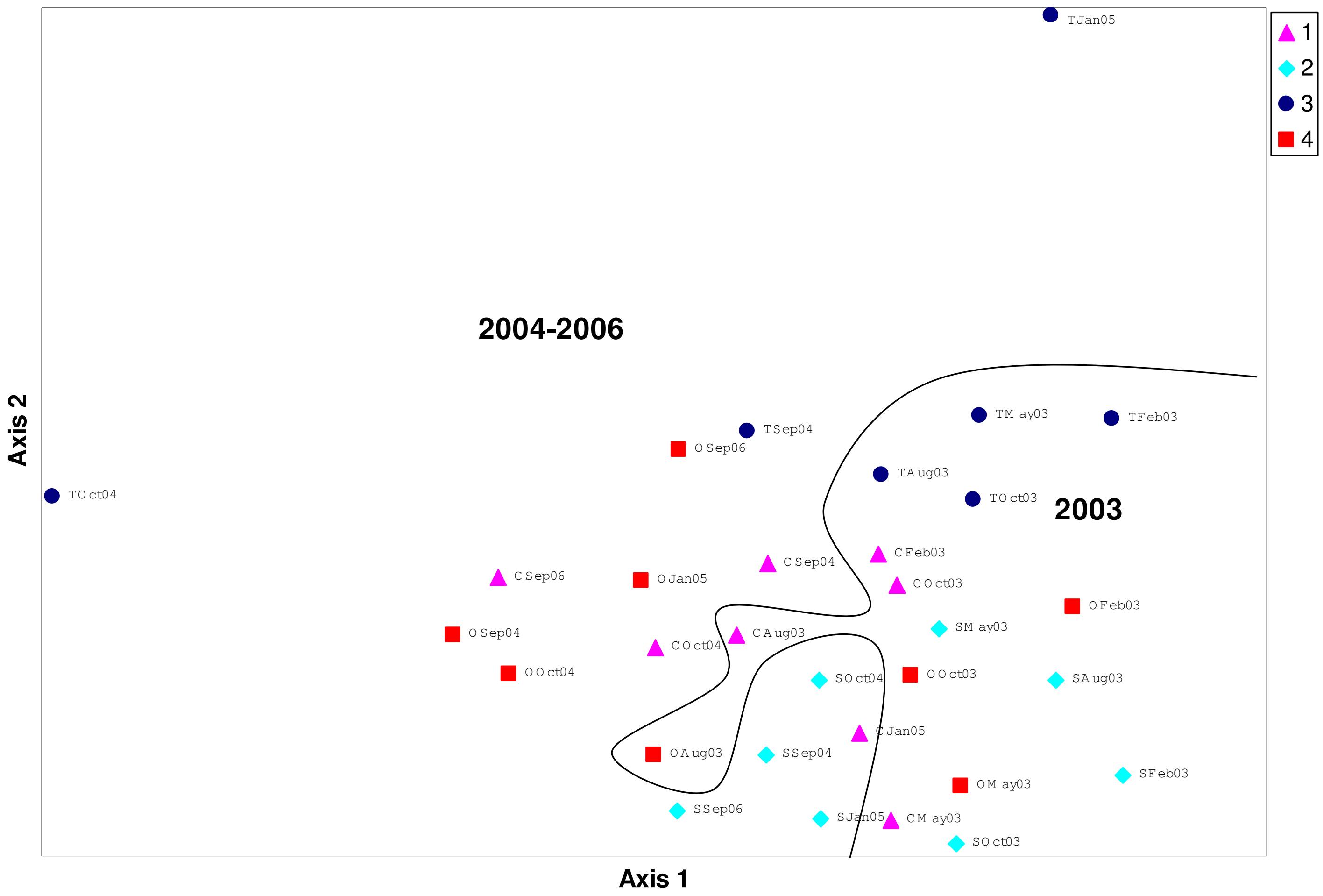

Figure 2.14: Fish Community NMDS Ordination by Lake ID. Based on aggregate samples using relative CPUE for all 3 net types. LakeID values are: 1=Cocha Cashu; 2=Cocha Salvador; 3=Cocha Totora; 4=Cocha Otorongo. Each point's label also denotes Lake initial, month and year of sample. 2003 seasonal datapoints are separated from 2004-2006 points by a dividing line.

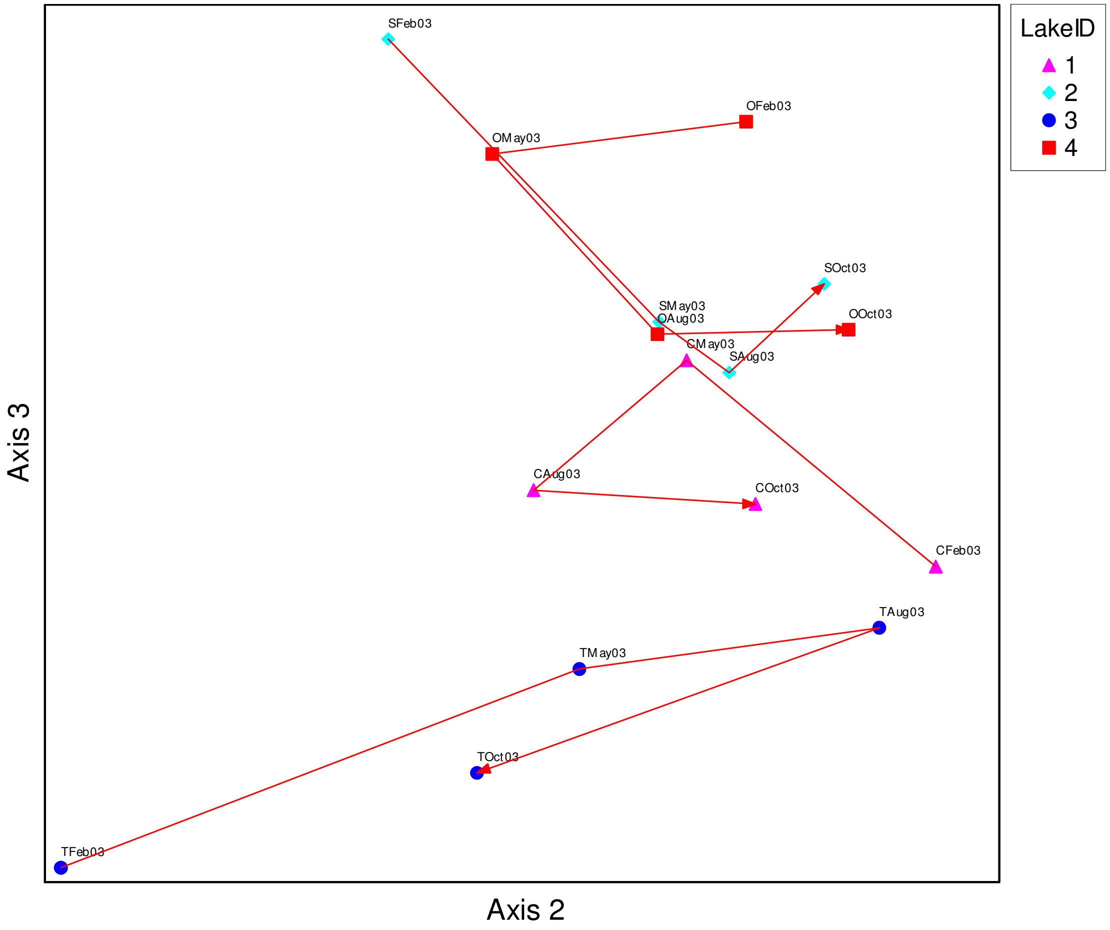

Figure 2.15: 2003 Seasonal Fish Community NMDS by LakeID. 2003 data using all 3 netting methods, and all species. Data are transformed to presence/absence with Beals Smoothing algorhythm. Samples are connected by vectors in date order. Lake ID values are: 1=Cocha Cashu; 2=Cocha Salvador; 3=Cocha Totora; 4=Cocha Otorongo. Each point's label also denotes Lake initial, month and year of sample.

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CHAPTER 3 SEASONAL VARIATION IN THE DIET OF GIANT OTTERS (*PTERONURA BRASILIENSIS*) IN OXBOW LAKES OF THE MANÚ NATIONAL PARK, PERÚ

Submitted to the Proceedings of the IXth International Otter Colloquium, Meeting of the IUCN Otter Specialist Group, June 4-10, 2004, Frostburg, MD, USA.

ABSTRACT

The giant otter (*Pteronura brasiliensis*) is an endangered otter of Amazonian lakes and rivers, for which much basic ecological information is lacking. I studied giant otter diet and fish abundance in 4 oxbow lakes ("Cochas" in Quechua) in the Manú National Park, Peru, during 4 seasons in 2003. The lake with the most distinct species composition was Cocha Totora, the smallest lake with the largest ratio of edge to open water. Cocha Cashu was the only lake in which wet and dry season fish communities differed substantially. Giant otter diet showed strong seasonal shifts in prey selection, with the most specialized diet occurring in the dry season, when 43% of prey items consumed were small insectivorous *Crenicichla cf. semicinta* (Cichlidae). I suggest that switching to small cichlid prey could be the result of the giant otters choosing hunting methods that accommodate the limited swimming and feeding abilities of very young cubs (<2-3 months old).

INTRODUCTION

The Giant Otter

The giant river otter (*Pteronura brasiliensis)* is an endangered predator of Amazonian lakes and rivers, for which much basic ecological and behavioral information is lacking. To ecologists, giant otters are of interest because, as top predators, they may impart "top-down" regulation of fish and even plant community structure in Amazonian waters, similar to the effect of the sea otter (*Enhydra lutris*) in nearshore Pacific kelp forests (Estes and Palmisano, 1974). Studies of shallow lakes in both temperate and tropical ecosystems have demonstrated the importance of predatory fish to maintaining lake communities (Carpenter and Kitchell, 1993; Rodriguez and Lewis, 1994), as have studies of food webs in rivers (Power, 1990). However, never has any study of a tropical shallow lake extended our ecological understanding to include the upper-most predators such as otters, caiman or birds.

One difficulty in studying the giant otter and its ecological role is its extreme rarity. Prior to its near extirpation for the fur trade, banned in 1973, the giant otter probably was common throughout most watersheds east of the Andes (Duplaix, 1980; Schenck, 1999). Today it is virtually absent from central Amazonia, and it primarily remains only in small, disjunct populations on the edge of its former range (Carter and Rosas, 1997; Olson et al., 2001). Thus, despite its wide former distribution, very little is known about comparative aspects of giant otters' feeding ecology, habitat preferences, or social behavior in different parts of its former range.

In the Manú Biosphere Reserve (MBR), giant otters have been relatively well-studied. They prefer to raise young in shallow oxbow lakes (or "cochas" – the Quechua word for oxbow lakes), former river channels that have been cut off from changes in the river's course (Schenck, 1999; Staib, 2002). Very little is known about the ecology of these lakes, however, with little information available beyond compiled species lists (Ortega, 1996).

Fish Communities in Shallow Oxbow Lakes

Until recently, fish communities in oxbow lakes of Amazonia were thought to be regulated by stochastic flooding and recolonization (Lowe-McConnell, 1987; Goulding, 1980). Recent studies of lakes of the Orinoco and the Araguaia Rivers dispute this claim, however (Rodriguez and Lewis, 1994; Tejerrino-Garro et al., 1998). These studies suggest that tropical lakes do exhibit strong community integrity following floods, and return to distinct and predictable assemblages of plant and animal species, regulated by piscivorous fishes' responses to lake morphometry and limnology via the Piscivory-Transparency-Morphometry (PTM) Theory. The applicability of these studies to other Amazonian lake systems has yet to be confirmed, and as the top predators of their aquatic ecosystems, giant otters may well play an important role in affecting these trophic cascades and the community ecology of oxbow lakes.

Shallow lakes in both temperate and tropical zones can exhibit alternative states with respect to their floral and faunal communities, and preliminary observations suggest that oxbow lakes of the Manú and elsewhere in Perú and Bolivia do as well (Scheffer, 1998; T. Killeen, pers. comm.). Manú oxbow lakes exist in 1 of 3 possible states: 1) algae-dominated, with abundant phytoplankton, few floating plants, and few to no submerged plants; 2) floating plant-dominated, with considerable surface coverage of floating aquatic plants including *Pistia stratiotes*, *Ludwigia helminthorriza, Azolla* spp., and others, with clear water but little-to-no submerged aquatic plants; or 3) submerged aquatic vegetation (SAV) – dominated water, with clear-water and extensive beds of submerged aquatics in shallow regions, including especially *Najas* spp., but also potentially including multi-species assemblages and some floating plants. At Cocha Cashu Biological Station, two lakes within the trail system are frequently visited by researchers, Cocha Cashu and Cocha Totora, and have been observed over a 30-year span to experience occasional switches between these states, although monitoring of the factors that might cause these switches has not been undertaken, and, therefore the mechanisms for changes between states are not understood (Terborgh, pers. comm).

Research Objectives

The goal of this study was to combine observations on fish abundance and giant otter habitat use and diet to improve our understanding of the ecological causes and consequences of their prey selection on oxbow lake habitats. Here I report on the first year's data collection from a multi-year study. 2003 was the only year in which sampling was conducted in the 4 study lakes during all four seasons, so the results here focus on seasonal changes in fish fauna from the 4 study lakes within the Rio Manú floodplain, and giant otter diet from 2 of these lakes.

STUDY AREA

I collected data on 4 oxbow lakes in the lowland portion of the Río Manú in the Manú National Park and Biosphere Reserve, Perú (MBR). The region is dominated by tropical moist forest, and a description of the terrestrial habitat can be found in Gentry and Terborgh 1990. A description of oxbow lake habitats was presented by Goulding et al, 2003 and Barthem et al, 2003 (cf. Chapter 2). The river system is a “whitewater” river, with abundant sediment brought down from nearby Andean slopes. The park encloses the entire watershed of the Río Manú, and hosts one of the highest populations of giant otters known in Perú. The otters primarily breed on the 6 largest oxbow lakes in the park, but also use numerous smaller oxbow lakes, creeks, palm swamps, and backwater wetlands (Schenck, 1999). The population of resident otters in the park is estimated to be stable at about 80 individuals (Hajek, pers. comm).

I conducted fish sampling on four oxbow lakes of the Río Manú: Cocha Cashu, Cocha Totora, Cocha Otorongo and Cocha Salvador. I also collected data on the diet and behavior of resident giant otters on 2 of these lakes: Cocha Cashu and Cocha Salvador. Previous visits to these 4 lakes indicated that Cocha Cashu and Cocha Salvador generally maintained algae-dominated states year-round, while Cocha Totora and Cocha Otorongo tended to maintain clearer water conditions, with more extensive beds of submerged and floating aquatic plants. Cocha Totora is unique among the 4 lakes in being known to have its entire surface periodically covered by *Pistia stratiotes*, a floating aquatic plant common throughout Amazonia, although just prior to the initiation of this study (January 2003), a strong flood removed all the lakes’ floating vegetation (Terborgh, pers. comm.).

METHODS

I collected data during periodic visits to each of the 4 lakes during 4 periods: the wet season (January – March); wet to dry transition season (April-June); the dry season (July-September); and the dry to wet transition season (October – December). I collected data on giant otter data at both Cocha Cashu and Cocha Salvador when feasible, but only

Cocha Salvador data are reported here for all but the dry-to-wet season, when both lakes' data are shown. The sample size from Cocha Cashu was limited during 2003 after the severe flooding of January. It was the only year since the breeding pair took up residence at Cocha Cashu (in 1997) that the otters raised young at a location outside of Cocha Cashu. Therefore, they were only occasionally seen on the lake before October 2003, when newborns were old enough to travel with the family, and the family returned to using Cocha Cashu on a regular basis.

Fish Community Sampling

Here I report fish sampling in wet and dry seasons only, to compare fish communities when lake samples should be maximally distinct. To sample the 4 oxbow lakes' fish communities, I set up five sampling stations in each lake, and followed a standard sampling regime at each station. I used 3 fishing methods for 3 distinct microhabitats within each lake. For shallow grassy edge zones, I used a seine net of 6 m length, and 1.2 m height, with mesh diameter of 0.63 cm. A seine net sample consisted of 5 hauls, spaced in >10 min intervals in non-overlapping sections of the region. The 10 min delay between samples allowed for any effect of disturbance from the previous sample to subside. In central lake regions, I set a gill net of 20 m length, 4 m height, and 5cm mesh for a period of 1 h per station. Finally, a throw-net of 4 m diameter with 3.75 cm mesh was used to sample more discrete areas than could be sampled by the gill net within the "log zone" of the lake, which was estimated to extend about 20 m deep alongside forested lake edges, and is an area where many fallen logs provide shelter for fish. The throw-net was thrown 5 times at random locations and intervals in the designated sampling region at each station. Fish were identified, weighed, and measured for standard and total length in the field before release.

I report fish community results in two forms. First I compiled presence/absence data combining all 3 net methods to generate species lists by lake (Table 3.1). From these data I report Sorenson similiarity indices for the 4 lakes (Table 3.2). Secondly, I plotted the 4 lakes' seine net samples using Nonmetric Multidimensional Scaling analysis (NMDS, PC-Ord, Version 5; MJM Software) for the dry and wet seasons. Catch data were not relativized before running the NMS procedure . Only seine net samples were used in this analysis because they captured the majority of species present, and because seine-net sub-samples showed higher repeatability than throw net or gill net sub-samples.

Otter Observations

I observed giant otters from a one-person, sit-on-top kayak, using image-stabilizing binoculars (Canon 12x 36 IS), a digital voice recorder (Olympus DS330), and a Palm-pilot using a customized PocketC event recorder program (Lorch, 2002). Once habituation of each otter family was complete, otters were followed by a single observer at a time for full days, using continuous sampling. Usually, a series of observers rotated in shifts, completing 3 hours of observation per shift. The palm pilot event recorder allowed us to note 9 behavior states and 9 instantaneous events, including the time of every prey capture observed. Prey captures were identified visually to species or guild and size category, both of which were dictated into the voice recorder. Size classes were designated as Very Small (0-10cm); Small (10-20cm); Medium (20-30cm); Large (30-40cm) or Very Large (>40cm). I verified visual species identifications where possible by immediately collecting samples of fish scales left on logs or other feeding sites after a meal. These scales were stored in envelopes labeled with time/date/preliminary species identification of the sample. Under a microscope, I compared the samples to scales extracted from known specimens and corrected visual identifications as needed.

Data Preparation and Analysis

When a prey item was not identifiable to species, but guild could be estimated by shape, size and location of capture (i.e. edge vs. open water), identifications were lumped into 5 larger species groupings; including:

1) Open Water Detritivores: Fish primarily from the families Characidae, Curimatidae and Prochilodontidae, with narrow bodies and white or silver coloring. These very small to very large fish form multi-species schools, and are primarily detritivorous. They were typically caught by the otters in "open water" habitats, in the central and deepest parts of the lakes. Medium and large species (>20cm) within this group include *Acestrorhyncus* sp., Curimatidae spp., *Potamorhina altamazonica,* and *Prochilodus nigricans.* Small and very small species (<20cm) include a number of Characidae such as *Astyanax* and *Charax* spp., *Roeboides* spp., *Steindachnerina* spp., *Tetragonopterus argenteus*, and *Triportheus* spp..
2) Cichlidae: Very small (<10cm) to small (10-20cm) fish of the family Cichlidae consumed in large quantities along forested and grassy edges. According to Goulding et al (2003), these Cichlids are territorial and insectivorous, feeding on aquatic invertebrates and smaller fishes. The two common species observed, *Crenicichla cf. semicinta.* and *Aequidens tetramerus* were visually distinctive, and usually identified to species unless ingested too quickly.

3) Pimelodidae (“vagres”): scaleless small to large catfish with body shapes for both bottom-dwelling and open-water lifestyles. With no scales, species identifications could not be confirmed from remains at feeding sites, and most without distinctive spots or stripes were grouped under the family.
4) Loricariidae (armored catfish or “carachamas”): slow-moving, small to large detritivorous fish that live on the bottom or on submerged logs, have heavily armored scales for the length of their body, and a sucker mouth. Several species are recognizable to species in the field, but questions remain for the taxonomy of several similar small species. Although not a preferred prey item of adults, these fish are easily caught and frequently given to juveniles learning to hunt and handle food, although I often saw they were not fully consumed. I did include in the dataset all captures of these fish, even if only partially consumed.
5) Anastomidae (“Lisas”): a family with several members of small to medium striped, typically bottom-feeding detritivorous fish, the 2 most common of which are *Leporinus friderici* and *Schizodon fasciatus*.

For analysis of giant otter diet, all prey that were observed and could be assigned to guild or species categories were counted as individual catches, and presented as % occurrence in giant otter diet by season. All unknowns were removed. Using percent occurrence rather than biomass means that large species that are less frequently caught may be more important to otter nutrition than implied here, but % occurrence gives better insight into the relative effort allocated into catching different types of prey and in hunting within different microhabitats.

RESULTS

Fish Communities of Manú Oxbow Lakes

Combining fish sampling of all 3 net types for the 4 study lakes revealed similar species lists and Sorenson indices for Cocha Cashu, Cocha Salvador, and Cocha Otorongo, and a more distinct fish community for Cocha Totora, (Tables 3.1 and 3.2). Sorenson similarity indices suggest that Cocha Otorongo is most similar to Cocha Totora of the 3 remaining. Being the smallest lake, Cocha Totora had more edge habitats compared to open water of all the lakes, and its fish fauna was distinguished by having numerous small Characidae not found in the other lakes. It also was the only lake to contain members of the family Cynodontidae, very large carnivorous fish more typical of rivers than lakes (Table 3.1).

The Nonmetric Multi-dimensional Scaling (NMS) iteration procedure resulted in an optimal solution in 3 dimensions. The final stress of the 3-d solution was 0.38, and the post-hoc r^2 value for correlation between the ordination and original Sorenson distances for 1,2,and 3 axes was 0.4, 0.4, and 0.5, respectively (PCOrd 5). Cocha Cashu showed a strong separation from the other samples in its dry season fish community composition (Figure 3.2). However, all other samples clustered by lake rather than by season.

Giant Otter Diet in Cocha Salvador

Giant otter diet in Cocha Salvador demonstrated strong seasonal shifts in prey selection during the year (Figures 3.3a-d). From January through June (Figure 3.3a-b), including the most intense flooding season when high water reconnects oxbow lakes to the Rio Manú, giant otter diet is fairly evenly distributed among a number of species of medium size *(i.e Hoplias, Prochilodus* and other Open Water Detritivores, *Serrasalmus*, and Loricariidae), and a nearly equivalent proportion of the small Cichlid *Crenicichla* cf. *semicinta*. However, in the dry season (Figure 3.3c), the latter fish constitutes the vast majority (43%) of prey captures on Cocha Salvador, despite its very small size. Other Cichlids, including *Aequidens tetramerus* and small Cichlids identified only to family, combine to make all Cichlids in giant otter diet account for 71% of all prey items. The dominance of *Crenicichla* in the diet diminishes again by the time the rainy season gets under way again (between September and October; Figure 3d), when the Open-water Detritivores predominate but to a lesser degree (49% in Cocha Salvador and 36% in Cocha Cashu).

Cocha Cashu vs. Cocha Salvador Diet

In the one dry-to-wet season where data were available from both Cocha Cashu and Cocha Salvador, results were similar at both lakes. Both otter families predominantly preyed on the Open-water Detritivore guild, and also on the bottom-dwelling sit-and-wait predator, *Hoplias malabaricus* (Figures 3.3d and 3.4). The Salvador family showed a greater reliance on *Crenicichla* prey than the Cashu family, and Cashu animals showed greater reliance on *Serrasalmus* species (piranha).

DISCUSSION

Oxbow Lake Fish Communities

The finding that Cocha Totora was distinct in its fish community composition relative to the other lakes is not very surprising, given that it is the smallest and shallowest lake, and also the least isolated from the main river. It has a year-round connection to an upland creek, and also has a continuous outlet to the river, allowing more frequent movements of fish movements between the lake and the river. Totora had the only samples of certain large carnivorous fish known as “chambira” (*Cynodon* and *Raphiodon*), which are usually more closely associated with river habitats (Barthem et al., 2003). Their presence in Totora may be a result of lateral migrations of these species from the river to the lakes to hunt in the clearer waters found in lakes. Totora’s small size ensures that it has a greater proportion of grassy edges and shallow water habitats relative to open water habitats compared to the other lakes, and it usually has much of its area covered by the floating aquatic plant *Pistia stratiotes*. The greater diversity of small Characid species found in Totora can understood from this fact, as small Characids frequent dense vegetated areas for refuge and feeding.

Otorongo is similar in several respects to Totora. It, too, maintains a year-round connection to the river through a long meandering arm that eventually forms an outlet to the main river. It also has extensive edge and floating vegetation, especially the floating macrophyte *Ludwigia helminthorriza*.

The distinctiveness of Cocha Cashu in the dry season compared to other lakes is likely explained by its attainment of an unusually clear lake state in the dry season of 2003. Sediment brought by the river typically lowers all the lakes’ transparency during the wet season (<0.1m Secchi depth), and transparency typically remains low into the dry season (<0.3 m Secchi depth) due to phytoplankton blooms that dominate the water column and shade submerged plants. In Cocha Cashu’s 2003 dry season samples, however, the lake had developed extensive patches of submerged aquatic vegetation (SAV) in shallow areas, predominantly of *Najas aguta.* The SAV-dominated lake state at

Cocha Cashu, allowed water to clarify throughout the lake, improving transparency relative to any other lake or to wet season conditions (approx. 0.6 m Secchi depth). Water clarification and changes in habitat structure provided by the *Najas* likely favor visual predators, change food availability, and provide refuge for small fish and zooplankton, altering trophic food webs and community composition (Rodriguez and Lewis, 1994; Tejerina-Garro et al., 1998).

Giant Otter Diet

Prior to this study, the best data available on giant otter diet came from analysis of giant otter latrines from the Madre de Dios, Manú, and Tambopata rivers (Schenck, 1999). While I used scales found at feeding sites to confirm visual identifications, I did not analyze scats in this study. Schenck's scat analysis found that the highest percentage of scales in giant otter latrines (40% in the Manu watershed) belonged to a single "boquichico" species, *Prochilodus caudifasciatus*. The second most important prey item (22% in the Manu watershed) in the scat analysis was a Cichlid, *Satanoperca jurupari*. I similarly found that close relatives of both these fish, (*Crenichla semicinta* in the Cichlidae and *Prochilodus nigricans)*, were major components of giant otter diet at mysites, but also found that their % occurrence varied strongly among seasons.

As fish community composition at Cocha Salvador did not change markedly between dry and wet seasons, the strong seasonal changes in prey selectivity at Cocha Salvador need to be explained by factors other than changes in prey availability. First, it is possible that giant otters switch prey as a result of changes in water quality, and particularly to oxygen availability or transparency in oxbow lakes. While transparency may influence giant otter prey selection in some lakes in the region, Cocha Salvador remained algae-dominated, with low transparency throughout this study, so that that factor is not likely to be important. More likely is the possibility that low oxygen conditions could slow the physiological abilities of fish attempting to escape the otters, making them more vulnerable to predation. Anoxia can be considerable in shallow lakes during the dry season when windy days are infrequent, and may even lead to large fishkills in Manú lakes (Terborgh, pers. comm).

Second, it is possible that fish behavior may change during the seasons and affect giant otter diet. Reproductive behaviors of year-round residents may make species more susceptible to the otters' hunting methods in certain parts of the reproductive cycles. We do not have data on the reproductive schedules of most Manú fish, but we do know that most Cichlids set up breeding territories in shallow edge habitats, and the increase in consumption of *Crenicichla* may be a response to nesting behavior that makes them more vulnerable to capture by giant otters.

A third reason for the seasonal shift in diet may be that giant otters are choosing different hunting methods in different seasons in order to accommodate young cubs, specifically their limited swimming abilities and poor handling skills. The use of *Crenicichla* may be a feeding strategy favored by the families when traveling with young cubs less than 2-3 months old. Cubs are typically born in the middle of the dry season in the Manu, when the peak in *Crenicichla* consumption occurred. *Crenicichla* were nearly always observed being caught in shallow waters where the cubs have plenty of access to logs and open forested edges to perch on while adults hunt. *Crenicichla* are also small, floppy, easy prey for young cubs to handle. Few other prey items were shared in their entirety with cubs, with most larger fish being consumed by adults until only a tail remained, at which point it was directly offered to a begging cub, or allowed to be "stolen" when a cub grabbed the fishtail from the adult's mouth. At Salvador in particular, Iobserved long hunting bouts where the whole family hunted in a tight pack along the forest edge while the cubs perched on land or logs nearby, crying for food until a whole *Crenicichla* (and occasional other items) were caught and brought directly over to the cubs. Further analyses on giant otter hunting behaviors at both study sites will be conducted with more longitudinal data to look in greater detail at these hypotheses (see Chapter 4).

Some additional points to note about my visual observations relative to previous analyses of giant otter diet is the importance of *Hoplia*s, Gymnotids, and piranha (*Serrasalmus spp.*) as year-round prey items for giant otters in Manu lakes. While *Hoplias* has previously been recognized as an important year-round food item for giant otters at various study sites in Amazonia, the latter two groups of fishes have been less prominent (Schenck, 1999; Laidler, 1984; but see Rosas et al., 1999). The scales of both Gymnotidae and *Serrasalmus* are miniscule, especially in the Gymnotids, and so are probably poorly conserved in latrine samples. In my visual observations, these two groups of fishes are unmistakable, and they remained steady components in the otters' diet throughout the year. The nocturnal Gymnotids hide in the day in the mud and roots of plants in floating islands and in cavities of logs. When focused on hunting in these areas, giant otters were able to pull out many of these fishes in a short period of time, regardless of season. It may be worth considering if Gymnotids therefore constitute a keystone resource that supports the otters through the wet season when lake levels are highest, schooling fish most dispersed, visibility at its lowest, and edge habitats (where

Cichlids are most easily caught) flooded well above average water depth. If catching Gymnotids requires only tactile senses, they may offer an important interim resource when lake conditions are non-optimal for hunting other prey species.

SUMMARY AND CONCLUSIONS

This is the first paper to quantify seasonal differences in giant otter diet on oxbow lakes. One cautionary conclusion it draws is that season does matter. If conclusions about diet in any otter species are drawn from one season alone, they may be based on incomplete or biased sampling. Year-round observations, especially from the wet season when otters are most difficult to follow, are still needed from many sites. Additionally, my speculations about the importance of piranha and gymnotids in wet season diet are still preliminary, and should be verified in additional observations on Manu lakes and additional sites. That migratory fish have an important role in oxbow lake communities and giant otter diet is another factor that is little understood, and will be addressed with further study of these two giant otter families' diet and behavior in ongoing work.

Family	Species	Cashu	Salvador	Totora	Otorongo
Anastomidae	Leporinus fasciatus	x			
	Leporinus friderici	x	x		x
	Schizodon fasciatum	x	x	x	x
Characidae	Acestrorhynchus altus	x	x	x	x
	Aphyocharax alburnus	x	x	x	x
	Astyanax bimaculatus	x	x	x	x
	Brachychalcinus sp.				x
	Characidae "black tail spot"		x		x
	Characidae "Glass fish"			x	
	Characidae "orange tail"			x	
	Characidae "red tail"			x	
	Characidae "silver stripe"				x
	Characidae "yellow tail"				x
	Characidium purpuratus	x			
	Charax sp.		x	x	x
	Cheirodontinae		x	x	
	Ctenobrycon sp.	x	x	x	x
	Cynopotamus amazonus			x	x
	Holoshestes sp.	x		x	x
	Holoshestes sp2.				x
	Moenkhausia dichroura	x	x	x	x
	Odontostilbe sp.	x			
	Phirrulina sp.	x		x	
	Pygocentrus nattereri		x	x	x
	Roeboides affinis	x		x	
	Roeboides myersi	x	x	x	x
	Serrasalmus rhombeus	x	x	x	x
	Serrasalmus spilopleura	x	x	x	x
	Tetragonopterus argenteus	x	x	x	x
	Triportheus albus		x		
	Triportheus angulatus	x	x	x	x
Cichlidae	Aequidens tetramerus	x	x		x
	Apistogramma sp.			x	
	Crenicichla cf. semicinta	x	x		
Curimatidae	Curimatella alburna			x	x
	Curimatidae cf. Steindachnerina		x		
	Potamorhina altamazonica	x		x	x
	Psectrogaster rutiloides	x			
	Steindachnerina bimaculata	x	x	x	
	Steindachnerina dobula	x	x		
	Steindachnerina sp.			x	x
Cynodontidae	Cynodon sp.			x	

Family	**Species**	**Cashu**	**Salvador**	**Totora**	**Otorongo**
	Raphiodon vulpinus			x	
Erythrinidae	Hoplias malabaricus	x		x	x
Gymnotidae	Eingenmannia sp.			x	
Loricaridae	Ancistrus sp.	x			
	Hypoptopoma sp.	x			x
	Hypostomus emarginatus	x	x		x
	Liposarcus disjunctivus	x	x	x	x
	Loricarinae		x		
	Psudohemiodon sp.	x	x		x
Pimelodidae	Pimelodella gracilis			x	x
	Pimelodus blochii	x		x	
	Pimelodus maculatus	x		x	
Potamotrygonidae	Potamotrygon motoro	x			x
	Prochilodus nigricans	x	x	x	
Sciaenidae	Plagioscion squamossisimus	x	x		
Species Totals	**57**	**35**	**28**	**35**	**32**

Table 3.1: Presence/Absence of Fish Species in 4 Manu Lakes. Three net methods combined.

	Cashu	**Salvador**	**Totora**	**Otorongo**
Cashu	1.00			
Salvador	0.56	1.00		
Totora	0.39	0.30	1.00	
Otorongo	0.57	0.52	0.49	1.00

Table 3.2: **Sorenson Similiarity Index on Fish Species Presence/Absence.**

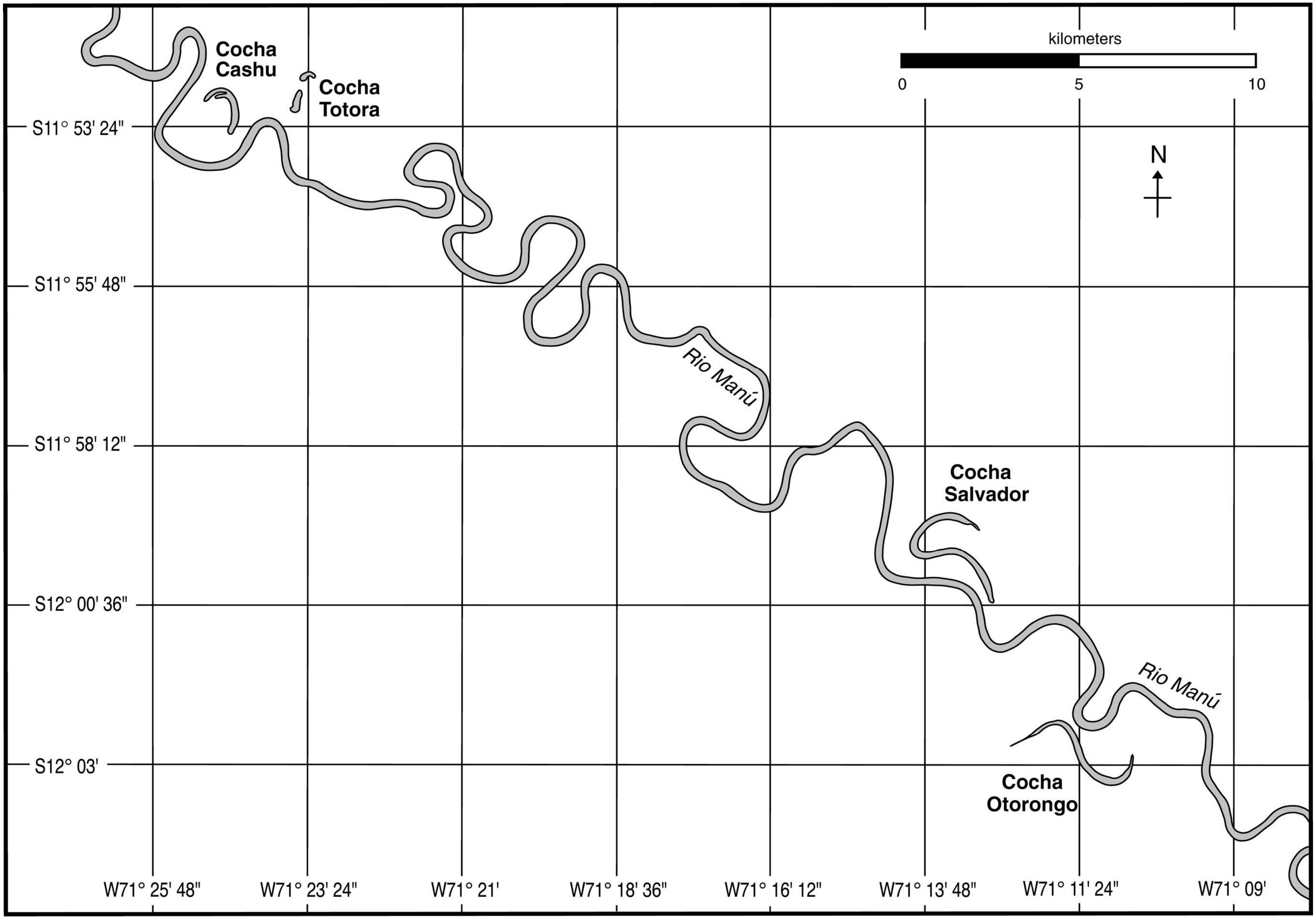

Figure 3.1: Location of the Four Study Lakes in Manu National Park, Peru. (adapted from Schenck, 1999)

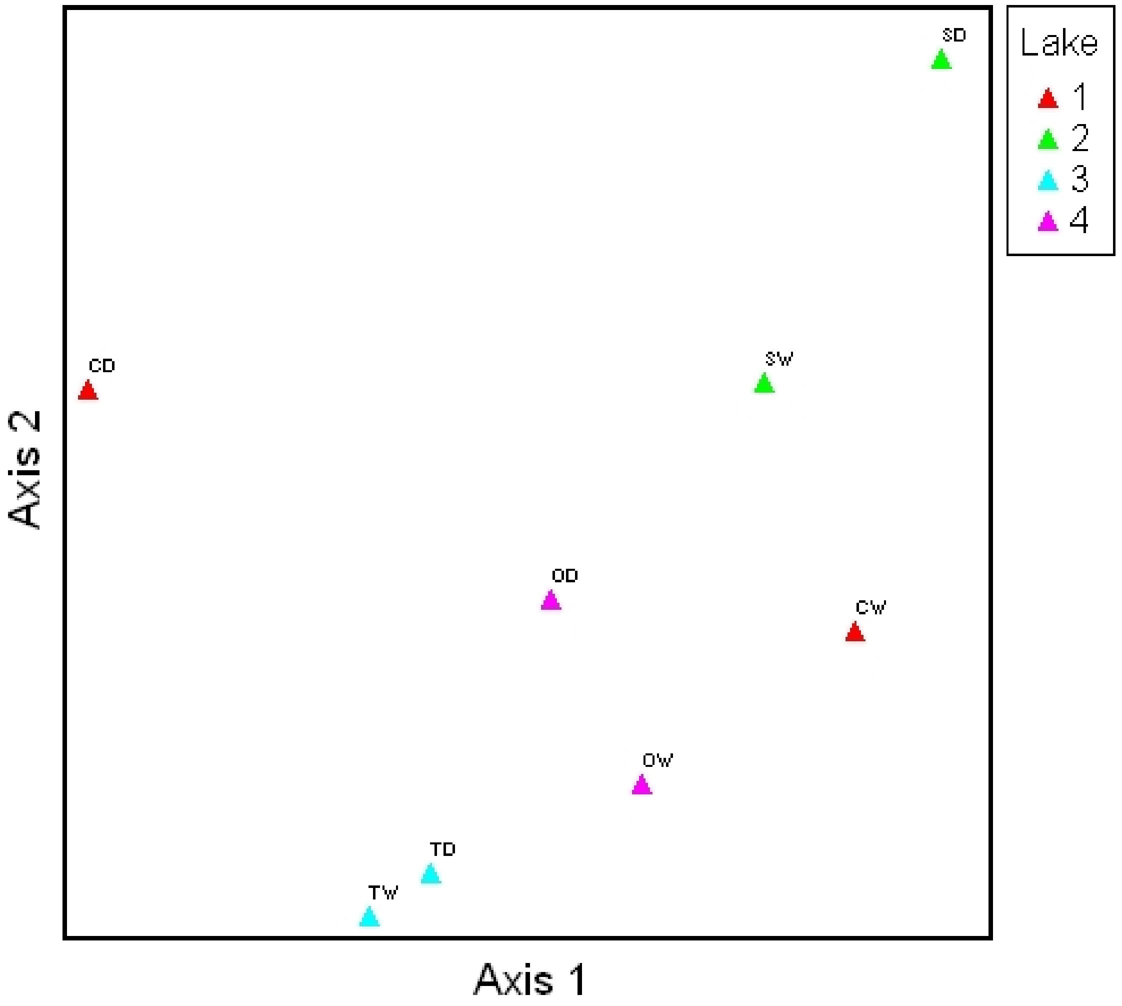

Figure 3.2: **Non-metric Multidimensional Scaling (NMDS) Analysis of Manu Oxbow Lake Fish Communities.** Lake 1 = Cashu; Lake 2 = Salvador; Lake 3 = Totora; Lake 4 = Otorongo. Labels alongside the points represent Lake and Seasons: CD=Cashu Dry; CW = Cashu Wet; SD = Salvador Dry; SW = Salvador Wet; TD = Totora Dry; TW = Totora Wet; OD = Otorongo Dry; OW = Otorongo Wet.

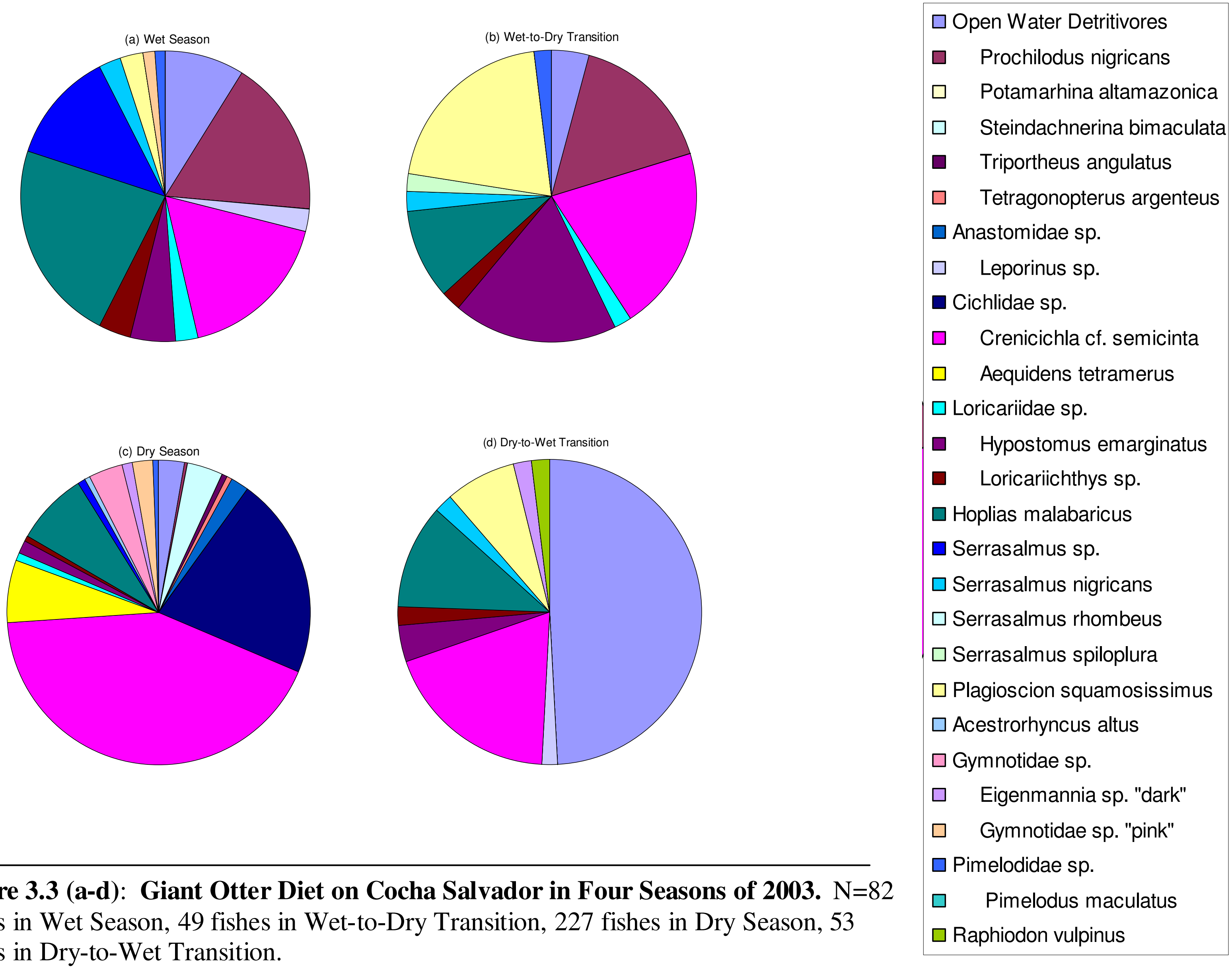

Figure 3.3 (a-d): **Giant Otter Diet on Cocha Salvador in Four Seasons of 2003.** N=82 fishes in Wet Season, 49 fishes in Wet-to-Dry Transition, 227 fishes in Dry Season, 53 fishes in Dry-to-Wet Transition.

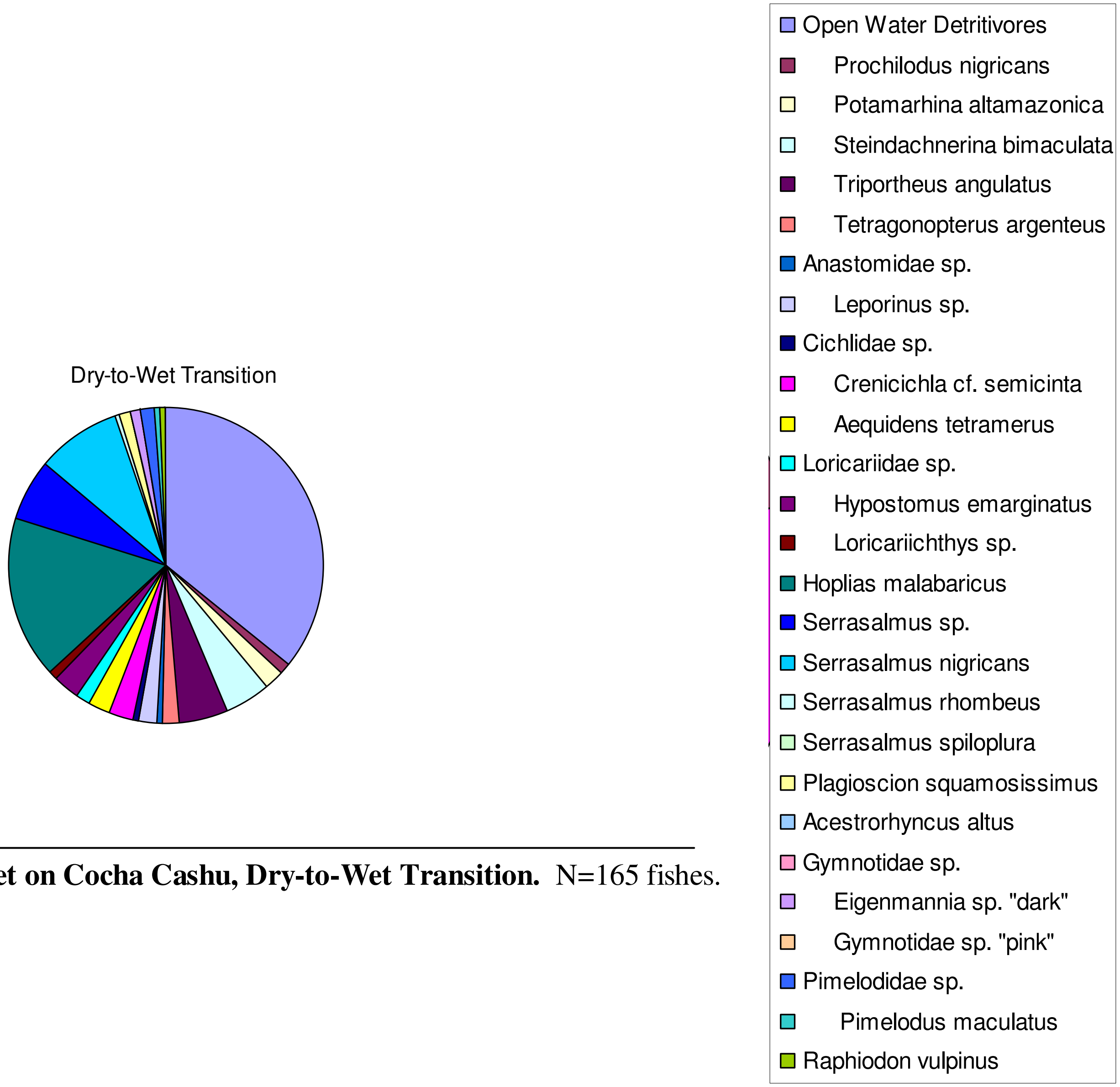

Figure 3.4: Giant Otter Diet on Cocha Cashu, Dry-to-Wet Transition. N=165 fishes.

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CHAPTER 4   GIANT OTTERS EAT A LOT OF BABYFOOD: CONSEQUENCES OF HUNTING WITH INCOMPETENT YOUNG

ABSTRACT

In an earlier report based on 1 year of data (2003), I showed that giant otters change their diets seasonally, with diet shifting from a broad use of many medium (20-30 cm) and large (>30 cm) fishes known collectively as “Open Water Detritivores” to a highly specialized diet of small (<20 cm) fishes of the family Cichlidae, which are primarily found along forested lake edges (Davenport et al., in press; cf. Chapter 3). I analyzed additional data from multiple dry seasons (2004-2006) to examine the hypothesis that the shift to Cichlid prey is primarily driven by swimming and feeding limitations of young cubs. I followed two families of habituated giant otters on oxbow lakes in the Manú National Park and Biosphere Reserve, Peru, and observed hunting bouts when young cubs were present and absent. I visually classified all prey taken as “Cichlids,” “Open Water Detritivores,” or “Other.” Results demonstrate that the use of small Cichlids (the “babyfood”) by both families increased dramatically in the presence of young cubs in all years. By comparing only dry season observations, the shifts in prey use could not be explained by seasonal fish migrations, changes in prey size classes, or seasonal changes in oxbow lake limnological characteristics. Otters may have an incentive to prey heavily on the small but abundant Cichlids because they are easily handled by young cubs, or they may choose to hunt along edge habitats (where Cichlids are most abundant) as

young otters can more easily follow the family's movements along edges. Two potential consequences of the giant otters' change in diet and micro-habitat use and diet are: 1) a higher risk of cub predation by caiman (*Melanosuchus niger*); and 2) lower niche separation with the sympatric Neotropical Otter (*Lontra longicaudis*).

INTRODUCTION

Optimal foraging theory contends that, when choosing among feeding patches or prey items, animals should forage for prey in a manner that maximizes nutritional intake for the time and energy expended on capture and consumption (Emlen, 1966; MacArthur and Pianka, 1966). Prey or habitat selectivity should therefore reflect an optimization of effort based on the availability and profitability of different prey items and habitat types. Shifts in prey use should occur in response to factors that change prey profitability, such as changes the prey's relative abundance, prey size, or behavioral responses to predators.

In a previous report, I documented strong seasonal shifts in the diet of giant otters across 4 seasons of a single year ((Davenport et al., in press; Chapter 3). Diet in 2003 shifted from a broad use of many medium (20-30 cm) and large (>30 cm) "Open Water Detritivores" in the wet season to a highly specialized diet of small (<20 cm) Cichlids in the dry season. A number of seasonal factors affecting prey abundance and capture success could explain the change from a generalized diet to a specialized diet in the dry season. Limnological changes in oxygen availability or transparency in the dry season could affect otters' capture success by species. Also, seasonal development of emergent, submerged, or floating macrophytes could provide refuges that alter prey detectability.

Prey abundance could be directly altered by lateral fish migrations during high water, and survival and growth of juvenile fishes could affect prey profitability throughout the year.

As an alternative to processes that directly affect prey abundance and detectability, I hypothesized that the shift to small cichlids was due to changing needs of the otter families. Specifically, I hypotheisized that the emergence of young cubs in the dry season affected the giant otters' hunting behavior, including choice of micro-habitat and prey selection. To analyze this hypothesis further, I combined 2003 dry season data on diets of giant otters with additional data from the dry seasons of 2004-2006. By analyzing diet and habitat use under dry season conditions only, and observing otters hunting with and without young cubs, I eliminate the potential influence of the seasonal factors that could directly affect prey abundance, detectability and profitability directly, and focus on the choices the otters make when selecting habitat and prey while raising young cubs.

Giant Otter Reproductive Behavior

In Manú oxbow lakes, giant otter cubs may emerge from the den any time between March and September (Schenck, 1999), although they typically emerge in the dry season (July to September). Cubs suckle for about 5 months, adding increasing amounts of fish to their diet as they age (Sykes-Gatz, 2005). Once they emerge from the den, they travel with the family on hunting bouts with increasing frequency, but also remain in the den for long periods with a babysitter (a parent or older sibling) while the family engages in hunting bouts of 1-2 hours (Duplaix, 1980; pers. obs.). No food is brought to the babysitter or cubs when the family returns from hunting, so that eventually a new hunting bout commences in which the babysitter and cubs participate. This alternation of hunting parties with and without cubs provided an opportunity to test whether giant otters' diets and habitat use varied with respect to presence of cubs while other factors that could directly affect prey profitability should not vary.

METHODS

Study Site and Observation Methods

The study site, behavioral methods and procedures for assessing diet visually are as described in Chapter 3. I collected all data presented here dry (July – September) or dry-to-wet transition (October – November) seasons before annual rains and flooding. All data presented here are from my own sessions with the otters to remove any observer bias.

I classified microhabitats within the lakes as "Log Zone", "Grass Zone", and "Middle Zone. " The Log Zone category denoted regions of the lake bordering an abrupt transition to forest. Characteristic features of the zone included deep shade conditions; steep shores with little to no development of emergent aquatic macrophytes; considerable leaf litter input; and numerous half-submerged logs. Black caimans (*Melanosuchus niger*) are also characteristic inhabitants of the Log Zone, preferring to rest underwater or along the shore in the shade during the day. I defined the Log Zone to extend about 20 m from shore, or the average perpendicular distance between the shore and the extremities of fallen logs. I defined the Grass Zone region to occupy an area of equal width (~20 m) perpendicular to the lake edge, but at sunny sites along shores with shallow inclines that developed stands of semi-aquatic plants (mostly sedges, grasses and *Heliconia spp*.). The

Middle Zone habitat included deep, open water sections of the lake not denoted as Log Zone or Grass Zone, and made up the majority of lake surfaces.

I mapped the lakes and microhabitat zones in 2002 using a Garmin GPS unit (Garmin eTrex Legend) and digital voice recorder (Olympus DS330). I used Garmin's MapSource program (Version 6.13.07) to download reference points and calculate distance and area measures. I created the maps from a sit-on-top kayak, by completing a track around each lake's perimeter, and noting changes in edge vegetation along the track, including the presence of onshore grass, heliconia, bamboo, and trees and shrubs. For this analysis, all edge locations were broadly classified as either Log Zone or Grass Zone. The areas encompassed by these two habitats were calculated from the length of the perimeter occupied by each vegetation type. Errors in these measures could arise from variation in water level, and curvature of the lake edge, which would distort the calculated area of edge zones in curved portions. However, these problems should not significantly distort relative measures of area for the purpose of these analyses. The area of the remaining "Middle Zone" habitat was calculated by taking the total area encompassed within the perimeter's track (computed in MapSource software), and subtracting the combined areas of "Log Zone" and "Grass Zone" regions calculated previously.

For observations on behavior and diet, I used a Palm-pilot with customized event recorder software running on the PocketC compiling language (Lorch, 2002), and a digital voice recorder with a timestamp function (Olympus DS330 digital recorder or Tungsten C Palmpilot running Audacity DVR software; Audacity Audio, 2007). At the start of each session, the internal clocks of the two devices were synchronized to the second. On the event recorder, I continuously recorded the family's use of lake microhabitats and exact times of events such as fish catches and other behaviors (i.e. caiman encounter, sharing of prey). I dictated additional information regarding behavioral events into a digital voice recorder, noting presence of cubs, information on prey species caught, identity of otters involved in catching or sharing fish, or defending against caiman or other threats.

Observation Periods

Data from Cocha Salvador result from intensive visits of 8-14 days per year in which I observed the otter family for at least two 3-hour sessions per day. Data from my home base at Cocha Cashu extend over 2-3 months, and include observations of at least one 3-hour session per day. Collection dates from the two lakes do not overlap. At both lakes, I attempted to balance observation sessions evenly between morning and afternoon sessions, in order to avoid introducing biases from differing activity patterns over the course of a day (Table 4.1).

I was not able to make comparisons of hunting with and without young cubs in all years at both lakes. In 2003, the Cocha Cashu otter family did not raise cubs on the lake, and only visited with cubs beginning in October, at which point the cubs traveled with the family continuously. The Cocha Salvador family had very early cubs in 2005 and 2006, so that my observations coincided with cubs aged 2-3 months, who already traveled with the family at all times.

Data Processing and Analysis

Behavioral observations were entered chronologically into an Excel spreadsheet. Data from the event recorder were downloaded first, providing exact records of the start and end times of behavioral states and events. I next interpolated information transcribed from the voice recordings, including information on prey size and species, identity of otter catching the prey. I removed time periods in which otters were resting or out of sight, and then calculated accumulated time with and without cubs in each of the three microhabitats. Finally, I calculated prey selection in the presence or absence of cubs as simply the total number of fish caught and identified to species or guild during the observation period.

For this analysis, I assigned all fish catches to one of just three categories: Cichlids, Open Water Detritivores, and Other. As described in Chapter 3, the category Open Water Detritivores is a grouping of fishes with similar physiology and appearance that live in multi-species schools in open water. In Manú oxbow lakes, they are primarily from the families Characidae, Curimatidae, and Prochilodontidae. I present Results as percent occurrence of each prey category in the diet of each otter family with and without young cubs.

Finally, I tested the hypothesis that the percent occurrence of Cichlids in the diet correlated with percent time in the Log Zone (Pearson correlation coefficient), using proportion data transformed with the arcsin squareroot transformation. And I tested the hypothesis that otters use increased proportions of Cichlids in their diet in the presence of young cubs by calculating a paired, one-tailed Wilcoxon Sign Test using each lake in each year where I had comparable data (n=5).

RESULTS

Results represent 2973 fish catches from Cocha Cashu and 2168 from Cocha Salvador during the dry seasons of 2003-2006. In all combinations of lake and years where I could make comparisons, the proportion of cichlids in the giant otters' diet increased in the presence of cubs (Figure 4.1(a-h)). The result of the one-tailed Wilcoxon Sign Test comparing Cichlid use with and without cubs was statistically significant at $p = 0.03$. The strongest shift in diet is seen in Salvador 2004, where the percent occurrence of Cichlids in the diet jump from 1% to 69%. More typical was a doubling or tripling of cichlids in the diet in the presence of cubs. One caveat is that sample sizes without young cubs were invariably smaller than sample sizes with cubs, so that diet without cubs may reflect sampling error.

Cocha Salvador otters took greater proportions of Cichlid prey than did Cocha Cashu otters in all years, but also had a greater area of Log Zone habitat where cichlids are predominantly captured. On Cocha Salvador, about 79% of the perimeter was classified as Log Zone edge habitat (and the remaining 21% as Grass Zone), while on Cocha Cashu, 62% of the perimeter was classified as Log Zone (Table 4.2).

In Cocha Cashu 2006, very few Cichlid prey were taken either with or without cubs, not exceeding 10% of prey items in either situation. Instead, Cocha Cashu otters overwhelmingly concentrated on catching Open Water Detritivores, which constituted 90% of captures without babies, and 77% with babies.

The percent of time in the Log Zone correlated significantly with the percent of Cichlid Captures ($p < 0.01$, Pearson correlation coefficient, $r = 0.77$; Figure 4.2), demonstrating that Cichlids are caught when otters hunt in the Log Zone region of the lake.

DISCUSSION

The analyses I present in this report confirm my earlier suggestion that the giant otters' dramatic shift in diet in the dry season is primarily explained by the emergence of young cubs at that time. By comparing dry season hunting bouts only, and comparing prey selection with and without young cubs, I excluded the potential effects on diet that could result from seasonal changes in prey abundance, chemical changes in the water, or physical changes in microhabitats. A clear trend from both the Cocha Cashu family and the Cocha Salvador family shows that when with young cubs, giant otters specialize on Cichlid prey found in Log Zone forested edge habitats. Other, less dramatic shifts in the otters' seasonal diet changes may well reflect changing conditions in the resource base of Manú oxbow lakes, but the effect of cub rearing on the diet of all family members is large and irrefutable, having been demonstrated from two different families in multiple years.

The proportion of Cichlids consumed by giant otters correlates closely with the proportion of time spent in the Log Zone microhabitat on Manú oxbow lakes, demonstrating the critical role of this specific microhabitat in the otters' shift to a specialized diet. The change in behavior and diet could therefore be equally well considered a shift in microhabitat use in the presence of cubs. Increased specialization in Log Zone habitats and Cichlid prey could impart a number of consequences to giant otters' interactions with other species such as black caiman (*Melanosuchus niger*) and the

Neotropical otter (*Lontra longicaudis*) that are also believed to depend on this microhabitat, as discussed below.

Cocha Salvador vs. Cocha Cashu Observations

I observed an increase in predation on cichlid prey for both families of otters when hunting with young cubs. However, I also observed that the Cocha Salvador family consistently took a higher proportion of Cichlid prey when with cubs than did the Cocha Cashu family (Fig. 4.1). This difference is probably a consequence of differences between the two lakes'morphometry and availability of microhabitats. Based on my mapping and classification of edge habitats, on Cocha Salvador, edges classified as Log Zone comprised 79% of the total perimeter, while on Cocha Cashu, Log Zone comprised 62% of the perimeter. While Cichlids are present in both edge zone types, they are particularly common in the leaf litter below forested edges found in the Log Zone. Grass Zone areas in Cocha Salvador are also located only at the farthest ends of the lake, while in Cashu, extensive Grass Zone regions were found all along the western edge, providing otters access to Grass Zone habitat throughout the lake.

It may also be a greater imperative for Cocha Salvador otters to stay along edge zones when with young cubs because of the greater width of Cocha Salvador's waterbody. On Cocha Salvador, schools of fish being pursued by otters can travel greater distances away from the shoreline, so adults may be more likely to lose contact with young stationed on the edge. Cubs that are more frequently out of contact with the adult hunters may be more heavily preyed upon by caiman or other predators, or fed less frequently, lowering their growth and fitness.

The Importance of the Constraints on Giant Otter Cubs and their Caregivers

Constraints on young cubs during skill development and growth should put pressure on adults to forage in ways that give young otters opportunities for hunting and socializing with the family, but which don't also sacrifice their own nutritional requirements and optimal foraging strategies. Mustelids have high metabolisms relative to other mammals, so that nutrition pressures may be more severe on otters than on most other mammals (Iverson, 1972; McNab, 1986). My observations help to shed light on this interesting feature of giant otter life: how families of giant otters cope with the presence of "incompetent" young (relative to adults) while still hunting efficiently, and maintaining family cohesion.

Other studies have shown that juvenile animals evolve age-specific behaviors that optimize survival while they develop skills (Holekamp and Smale, 1998). While this observation is likely to be true of young giant otters, their limited swimming and hunting abilities limit the range of movement and behaviors of adults when traveling and hunting together. I suggest that giant otter families solve this problem through the observed increase in hunting along edges for Cichlids when cubs are present. This hunting method is not the most efficient method when cubs are absent, but offers advantages when with cubs. Edge hunting for Cichlids offers abundant (if small) prey that 1) are a useful item for "babyfood" due to their small size and ease of handling; 2) exist in high enough numbers that all family members can feed on them together despite their small size; and 3) are found in a microhabitat where the cubs can easily follow adults when swimming and long-distance communication skills are poor. This behavioral and dietary flexibility suggests a high adaptability of otters to different conditions, and highlights the importance of long-term and seasonal sampling to properly characterize giant otters' use of prey resources.

Comparisons with other Field Sites

While no other study has correlated diet and microhabitat usage as in this study, several other studies on giant otter diet elsewhere in South America have reported on the importance of Cichlids to giant otters. Differences in methodologies and sampling periods may affect conclusions, but regional differences at the family level probably do reflect real differences in prey availability and habitat preferences of the local otters. Prior to this study, the best data from the Manú came from analyses of the remains of scats by Khanmoradi (1994) and Schenck (1999). These authors concluded that a single species of Cichlid (*Satanoperca jurupari* – rarely found in my study) made up 44% of giant otter diet, and so corroborate my own visual observations.

In northern South America, where primary productivity of aquatic habitats are lower than in Manú, results are mixed. Duplaix (1980) observed giant otter diet in Suriname visually, and found Perciformes (including Cichlids) to be less preferred than both Characiformes and Siluriformes. However, Laidler (1984) analyzed scats from giant otters in Guyana, and found that seven species of Cichlids (including the introduced *Tilapia*) constituted the most important group of prey for giant otters. Laidler also found no evidence of seasonal change in diet.

In Brazil, Rosas and coauthors compared scats from two sites, and found Cichlids to be heavily used in the Amazon, but of low importance in the Pantanal (Rosas et al., 1999). Waldemarin corroborated these results in the Pantanal, also reporting low presence of Cichlid remains in scats (Waldemarin et al., 2004). Most of these studies, including my own, still lack multiple years of comparative data in all seasons, which would improve interpretation about giant otter prey and habitat use. More wet season data is needed, since my 2003 seasonal sampling demonstrated wide variation in seasonal diet. However, wet season data are lacking from most study sites because otters are difficult to follow and observe during high water.

Effect of *Pistia* on Giant Otter Diet at Cocha Cashu

The unusually high use of Open Water Detritivores and low use of Cichlid prey at Cocha Cashu in 2006 probably demonstrates a dramatic effect of the floating plant *Pistia stratiotes* on oxbow lake ecology, giant otter behavior and diet. *Pistia stratiotes* is a floating aquatic macrophyte that aggressively colonizes through asexual reproduction under the right nutrient conditions (Junk and Piedade, 1997). Although low numbers of *Pistia* are always present on Manú oxbow lakes, for unknown reasons, a *Pistia* bloom began in the wet season of 2006 on Cocha Cashu. It covered approximately 1/3 of the surface of Cocha Cashu by the time of my 2006 measurements. These lake conditions were highly unusual: 2006 was the first year known (in over 30 years experience on the lake; Terborgh, pers. comm.) in which Cocha Cashu was covered by *Pistia.* During a *Pistia* infestation, phytoplankton and submerged vegetation decline from shading and competition for nutrients. Oxygen levels also decline from the loss of photosynthesis in the water column, and reduced wave action. Water clarifies from the reduced sediment suspension and loss of phytoplankton. Populations of many fish species decline in response to these changed conditions, probably mostly due to the low oxygen conditions and loss of the phytoplankton-based food web (Scheffer et al., 2003).

The mechanism that lowered the otters' use of Cichlids in 2006 is unclear without further study of Cichlid population changes, but it may be a direct effect of *Pistia* on Cichlid abundance along the edges. By lowering oxygen levels and blocking light, *Pistia* may affect the ability of Cichlids to live and breed successfully along lake edges. It may also badly impede the otters' ability to locate and capture Cichlids as a visual and physical impediment to capture.

In central regions of the lake, otters hunt in and around *Pistia* in spite of a number factors that should negatively affect hunting success, such as lower light transmission, and physical drag from its roots and leaves. *Pistia* may also impart beneficial factors to the otters' hunting success, however. Water clarity improves with *Pistia* as it shades out phytoplankton and reduces wave action and sediment resuspension in shallow areas. Fish also congregate under masses of *Pistia* for protection from aerial predators, but may find escape from otters more difficult with the *Pistia* acting as a barrier to vertical flight.

Edge Hunting and Caiman

Spending more time in edge habitats puts the otters at increased risk of encountering their most likely aquatic predator, the black caiman (*Melanosuchus niger)*, as well as terrestrial predators such as jaguars and puma. Black caimans exist at high densities on both Cashu and Salvador (cf Chapter 2), and are potentially a source of mortality of young. During the daytime, caiman spend most of their time at rest in the same shaded Log Zone regions where giant otters catch small Cichlids. Several authors have suggested that minimizing the threat of predation is one reason animals evolve sociality (Cresswell, 1994; Elgar, 1989; Lima, 1995; Powell, 1974; Pulliam, 1973; Roberts, 1996; Terborgh, 1983; van Schaik, 1983; van Schaik et.al, 1983), so understanding the interaction between the two species could have far-reaching implications.

Observing interactions between black caimans and otters suggests the potential for a role of black caiman in giant otters' juvenile mortality, but actual sightings of juvenile mortality events are so rare as to be almost unknown (Groenendijk, pers. comm.). One other study did attempt to look at interactions between black caiman and giant otters on Cocha Cashu to assess this potential source of mortality, but with little success (Duft and Fittkau, 1997). During my observations, I observed giant otters disrupt and harass caimans sleeping along edges almost daily, but caiman usually retreated underwater rather than escalating the incident. Both families of otters engaged in coordinated attacks on large caiman (presumably females) during the caiman's nesting period, a time when caiman may be less likely to retreat from intruders near a nest. In one case, an adult otter was seriously injured (observation reported in Groenendijk and Hajek, 2006), and on 2 occasions, it seemed likely that the adult caiman was badly injured. I also observed large caiman stalking solitary otters on occasion, including when the otters were injured or eating large fish. Finally, I observed the otter family at Salvador coordinate raids on nests of baby caiman, which usually provoked a counter-attack by the mother caiman upon hearing distress calls from her young. In spite of these numerous and varied observations of inter-species aggression, I never directly observed the death of either otters or adult caiman from any of these clashes.

In spite of the lack of direct evidence that caiman predate giant otter cubs, first-year cubs experience a mortality rate of about 36% of cubs each year in the Manú that is almost entirely unexplained (Groenendijk and Hajek, 2006). Mortality rates may vary in oxbow lakes, or in other habitat types that lack caiman, and may well relate to caiman predation. Annual cub survival may be higher where caiman are less dense, or where shallow edge habitats (and Cichlid prey) are not available, such as in deeply-contoured lakes like Cocha Otorongo. A comparative study of cub survival, microhabitat use, and caiman density is not been being done anywhere to my knowledge, but could demonstrate if increased edge hunting does raise predation risk for young giant otter.

Effect of Using Small Prey on the Sympatric Neotropical Otter

Seasonal shifts in giant otter diet could also be relevant to our understanding of the giant otter's relationship with its sympatric relative, the Neotropical otter (*Lontra longicaudis*). In general, the smaller Neotropical otter is thought to be more of an upland species of small creeks, including at higher elevations where giant otters are not found (Laidler, 1984). Neotropical otters are also present in the lowlands, however, and although rarely seen around Cocha Cashu Biological Station, are known to be present from spraints at "Playa Bonita" within the trail system at Cocha Cashu (pers. obs.). "Playa Bonita" is a small (typically 2-3 m wide) clear creek that originates in the uplands, and enters Cocha Totora. Despite their presence nearby, Neotropical otters have never been observed using the local oxbow lakes (Cocha Cashu and Cocha Totora) where giant otters breed. Tourist guides also report occasional sightings of Neotropical otters on the river, but never from oxbow lakes where giant otters live (R. Huanca, pers. comm.).

Carnivores are typically intolerant of one another, and chase off or kill would-be competitors (Palomares and Caro, 1999), so it is perhaps to be expected that the giant otter, as the larger of these two piscivorous otters, would dominate the higher productivity oxbow lake habitats in the Manú. However, at other lowland sites such as the Pantanal of Brazil, giant otters and Neotropical otters occur at similar densities and are believed to be highly tolerant of one another (Waldemarin and Barroeta, 2004; Waldermarin, pers. comm.). According to Waldemarin, both species use oxbow lakes and rivers in the Pantanal, and co-occur on the same stretches of river. She suggests that the two species reduce interspecific competition by dividing the lake microhabitats and fish resources. She observed that giant otters were more likely to hunt in deeper lake regions, and used rivers less than Neotropical otters. The sizes of bones and scales in scat also suggested that giant otter take larger prey than Neotropical otter in the Pantanal (Waldemarin and Barroeta, 2004).

It has long been known that various otters, including *Lutra* spp. and *Aonyx* spp. can co-exist in the same areas. The clawed *Lutra* spp. tend to be more specialized on fish, while the clawless *Aonyx* spp. tend to specialize on crustaceans they locate with their sensitive toes (Kruuk, 2006; Kruuk et. al., 1994). For example, *Lutra sumatrana* and *Aonyx cinerea* were observed to interact peacefully in Southern Thai peat swamps, even being photographed together on the same logs (Kanchanasaka, 2007). Kanchanasaka showed that they can maintain this peaceful co-existence at least in part by specializing on different types of prey.

The implication for the relationship between giant otters and Neotropical otters seems to be that if incompetent young are the cause of a seasonal shift to small Cichlid prey and edge habitats in giant otters, the one that suffers the consequence may be the Neotropical otter. Giant otters should be more likely to displace Neotropical otters from their territories if the needs of dependent young cause greater overlap in the size and location of their prey.

A significant difference between the Pantanal and Manú might be one of geomorphology and ecology. The densely forested Manú floodplain creates edge habitats that receive large quantities of leaf litter. In comparison, the Pantanal hosts a mosaic of forest and grassland, and generally lacks such tall and complex forests on the periphery of oxbow lakes. Such qualities of the edge habitat might favor dense numbers of the territorial Cichlids, especially *Crenicichla*, in the Manú, compared to the Pantanal. In addition, it should be noted that fish species diversity is considerably lower in the Manú than the Pantanal, particularly as oxbow lakes have less diverse fish communities than rivers and creeks (Ortega, 1996). The lower species diversity could increase the importance of *Crenicichla* and other Cichlids to giant otters on oxbow lakes of the Manú.

Further comparative studies of fish communities and otter diets between the two sites (and others) would help to determine how important the seasonal specialization on Cichlid prey in the Manú is to the co-existence of giant otters and Neotropical otters. The two species, may, like other sympatric otters, be fairly tolerant when niche differentiation is achieved. Either this niche differentiation has been undermined in the Manú by the mechanism I suggest, or the low abundance of Neotropical otters on Manú lakes must be explained by other constraints on Neotropical otters in the Manú that we do not understand.

	Cashu				Salvador				
Session	2003	2004	2005	2006	2003	2004	2005	2006	***Total***
AM1	4	19	7	9	6	8	5	5	***63***
AM2	3	7	7	5	5	6	7	5	***45***
PM1	4	13	10	5	6	9	3	4	***54***
PM2	4	10	4	7	4	4	3	1	***37***
Grand Total	***15***	***49***	***28***	***26***	***21***	***27***	***18***	***15***	***199***

Table 4.1: Distribution of Sessions on Cocha Cashu and Cocha Salvador, 2003-2006. AM1=6am-9am; AM2=9am-12pm; AM3=12pm - 3pm; AM4 = 3pm - 6 pm.

	Lake			
Lake Parameters	Cashu	Salvador	Totora	Otorongo
Total Area (ha)	34.5	91.8	10.1	54.6
Length (km)	2.3	5.6	0.8	3.8
Average Depth (m)	1.2	2.3	1.1	3.3
Max Depth (m)	4	4.4	1.7	6.4
Volume Development Index	0.9	1.6	1.9	1.5
Average Width (m)	112	160	113	155
Microhabitat Coverage				
Grass Zone Perimeter (km)	1.7 (38%)	2.2 (21%)	.9 (63%)	4.3 (57%)
Log Zone Perimeter (km)	2.8 (62%)	8.8 (79%)	.5 (37%)	3.3 (43%)
Grass Zone Area (ha)	3.4 (10%)	4.6 (5%)	1.8 (17%)	8.6 (16%)
Log Zone Area (ha)	5.6 (16%)	17.6 (19%)	1.1 (10%)	6.6 (12%)
Middle Zone Area (ha)	25.5 (74%)	69.6 (76%)	7.3 (72%)	39.4 (72%)

Table 4.2: Shape and Habitat Parameters of 4 Oxbow Lakes of the Río Manú. See text for details of microhabitat calculations.

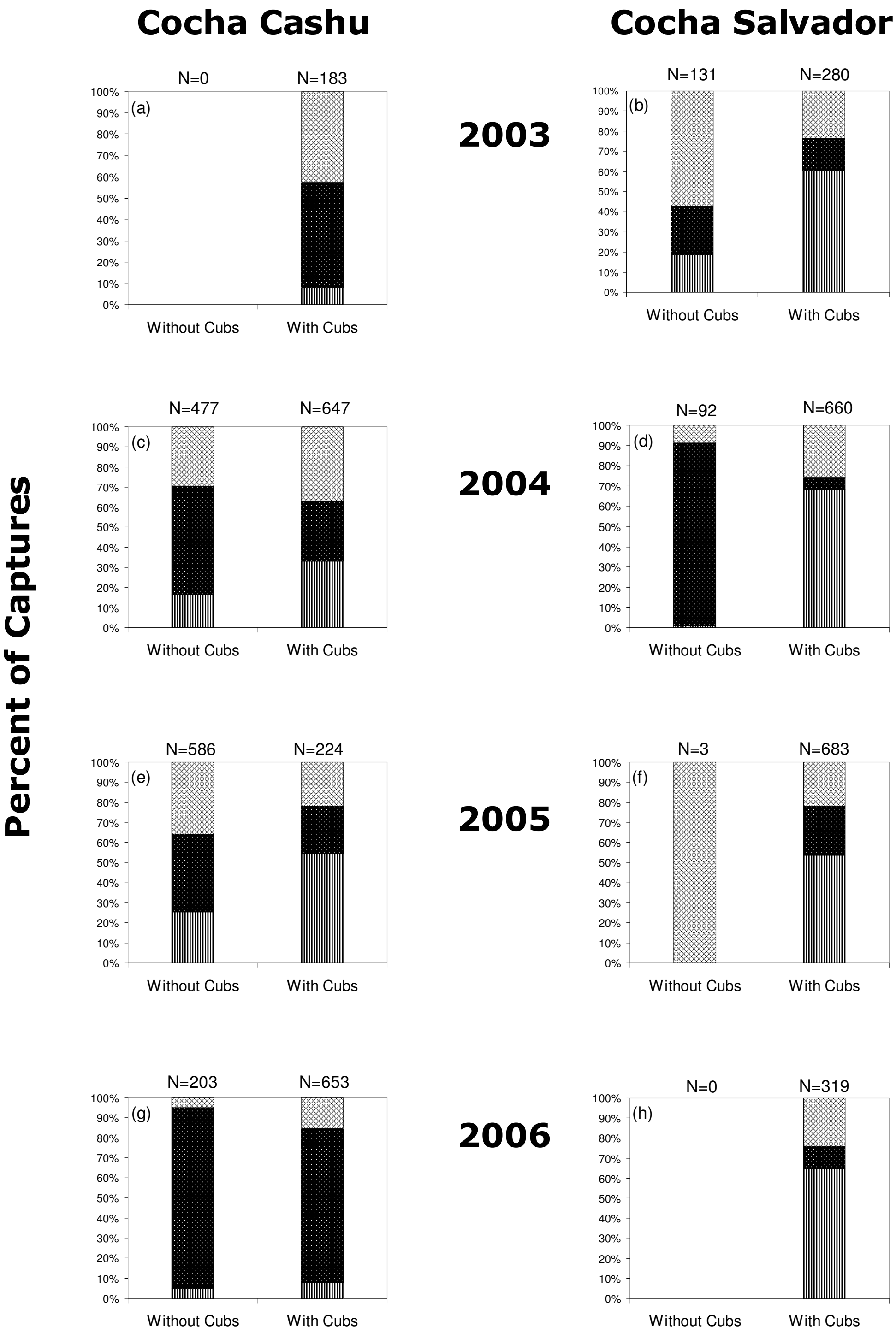

Figure 4.1 (a-h): Cichlids and "Open Water Detritivores" as Percent of Captures in the Presence and Absence of Young Cubs on Cocha Cashu and Cocha Salvador 2003-2006. (a) Cashu 2003, (b) Salvador 2003, (c) Cashu 2004, (d) Salvador 2004, (e) Cashu 2005, (f) Salvador 2005, (g) Cashu 2006, (h) Salvador 2006. Sample sizes (N) are the total number of prey items identified. Vertical stripes = cichlids; Spots = "Open Water Detritivores;" Cross-hatches = Other.

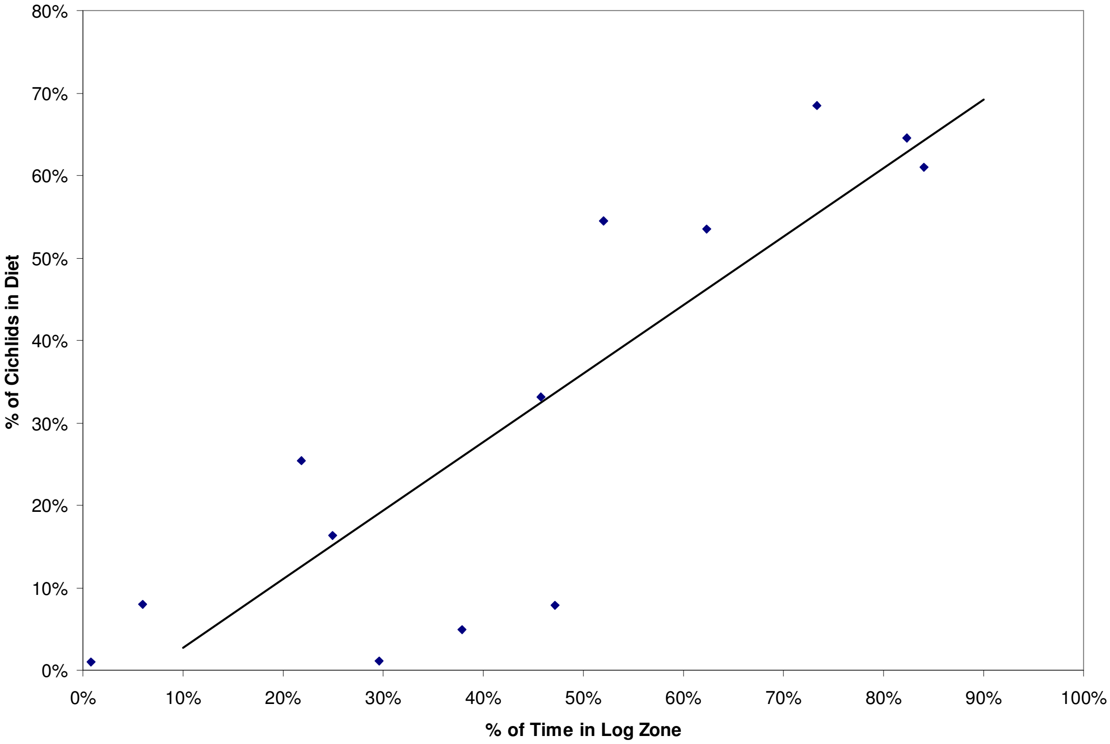

Figure 4.2: Correlation Between Time Spent in Log Zone and Percent of Cichlids in Diet. Data include Cocha Cashu and Cocha Salvador observations with and without cubs, as in Figure 4.1, correlated with time spent in Log Zone for the same observation periods.

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CHAPTER 5 HELPERS IN GIANT OTTER FAMILIES (*PTERONURA BRASILIENSIS*): SOCIAL CLIMBERS, SPECIALISTS, OR SLOW LEARNERS?

ABSTRACT

Of the 13 extant species of otters in the world, the giant otter is the only species to breed cooperatively, with juveniles of previous years helping to raise newborn cubs. I asked 3 questions regarding philopatric animals in giant otter familes. First, I asked if giant helpers really help raise their younger siblings. Second, I asked if helpers are variable in type or amount of help, and in skill development. Third, I asked if we can characterize patterns in helping behavior as characteristic of animals who are social climbers, behavioral specialists, or slow learners. I show that helpers do help, that family members do differ in the level of skills and help provided, and that giant otters best conform to predictions for the "Slow Learning" or Skills Hypothesis (Heinsohn, 1991).

INTRODUCTION

Sandell (1989) argued that solitary living is, in essence, the default breeding strategy in carnivores: in the absence of evolutionary forces that select for the complex social behaviors required of cooperative breeders, we would observe only solitary social systems. We are thus challenged to improve our understanding of cooperative species' life history, ecology, and behavior to explain the causes and consequences of the rise of cooperation in carnivores and other animal societies. A large literature explores the theme of the evolution of cooperative breeding, with comparative, long-term studies of birds providing the preponderance of empirical evidence. For the giant otter, only the most preliminary examination of its natural history, social system and dispersal patterns have been completed to date (Duplaix, 1980; Schenck, 1999). This study is the first to document dispersal and helping behaviors in giant otters in an attempt to clarify which of the many theories of cooperative breeding might best describe the underlying causes of their social system.

The Evolution of Cooperative Breeding

Helpers in a cooperative breeding system choose to delay dispersal from the natal territory and forego their own reproduction rather than dispersing to attempt independent reproduction. Their apparent altruism raises a number of issues regarding the cost-benefit structure of this choice, understood as an application of Hamilton's rule of inclusive fitness (Hamilton, 1964).

The effort to understand the forces that make dispersal costly or philopatry beneficial to helpers in cooperative families has generated multiple theories, some of which emphasize the costs, and others emphasizing the benefits. Of the major hypotheses suggested to clarify the evolutionary causes of cooperative breeding, three of the most prominent include: the Ecological Constraints hypothesis; the Life History hypothesis; and the Benefits of Philopatry hypothesis. I discuss each in turn, including some specialized formulations of each hypothesis, and consider current thinking on each.

Under the Ecological Constraints or "Habitat Saturation" hypothesis (Brown, 1974; Emlen, 1982; Koenig et al., 1992), cooperative breeding is believed to arise due to ecological limitations on dispersal or reproduction off the natal territory, thereby emphasizing the prohibitively high cost of dispersing and “floating." Limitations might include a lack of denning sites or high mortality risks from dispersal, or, within a specific formulation of the theory known as the Resource Dispersion Hypothesis, the patchiness of food resources. Proponents of the Resource Dispersion hypothesis suggest that quality and dispersion of food resources can predict group size in animals ranging from antelope, mustelids, to primates (Bacon et, al., 1991; Carr and Macdonald, 1986; Kruuk, 1989; Kruuk & Macdonald, 1985; Jarman, 1974; Johnson et al., 2000; Macdonald, 1983; Powell, 1979; Powell, 1989; Symington, 1987). Most authors now consider ecological constraints to be a potential contributing factor, but rarely the sole underlying cause of cooperative breeding (Cockburn, 1998; Ekman et al., 2001; Kokko and Ekman, 2002; Perrin and Lehmann, 2001). Conflicting findings about potential ecological constraints for certain species (such as being feeding specialists or generalists) have caused confusion about its general applicability (Arnold and Owens, 1998; Arnold and Owens, 1999). In addition, several authors have argued that non-cooperative species face similar ecological obstacles as cooperative species, and that the Ecological Constraints hypothesis can not account for the lack of delayed dispersal in these non-cooperative species (Ekman et al., 2001; Koenig et al., 1992; Stacey and Ligon, 1991).

Arnold and Owens (1999) offered an alternative view or expansion of the Ecological Constraints hypothesis using phylogenetic mapping of bird species’ behavior on ecological and life-history traits. The Life History hypothesis envisions cooperative breeding evolving as a two-step process. A life-history trait, such as low annual mortality, provides a pre-disposition to cooperative breeding that is then strengthened by ecological conditions, such as living in an invariable climate, where species can maintain territories year-round (Arnold and Owens, 1999). This hypothesis also stresses the limits on dispersal and independent breeding, as opposed to benefits of staying and helping on the natal territory. As Pen and Weissing (2000) state: “Thus, the Ecological Constraints and Life History hypotheses both stress that the direct fitness benefits of seeking independent breeding opportunities are too small to outweigh the indirect inclusive fitness benefits of helping relatives.”

A number of authors have commented on the importance of large body size as a particularly important determinant of life history traits and sociality (Bekoff et al., 1981; Berrigan et al., 1993; Boyce, 1988; Cole, 1954; Johnson et al., 2000; Promislow and Harvey, 1990). As a further refinement of these observations, the Slow Learning, Skills hypothesis, or Maturational Constraints hypotheses (Brown, 1987; Heinsohn, 1991; van Schaik et al., 2006) suggest the significance of the high cost of training or developing brains in the juveniles of larger-brained species. Developing a larger brain imparts physiological delays on juveniles’ acquisition of an adult level of ecological competence, lengthening the time to independence from the family, and delaying dispersal in these species (van Schaik et al., 2006). Species such as top carnivores that occupy challenging feeding niches may be particularly prone to evolve philopatry and cooperative breeding systems through this path (Heinsohn, 1991).

The Benefits of Philopatry hypothesis emphasizes benefits to staying on the natal territory and helping (Ekman et al., 1994; Ekman et al., 2001; Kokko and Ekman, 2002; Pen and Weissing, 2000; Stacey and Ligon, 1991). In some cooperative species, so-called “helpers” may not actually help survival of siblings, indicating that direct benefits from staying within the natal territory are instead causing delayed dispersal (Kokko and Ekman, 2002). Stacey and Ligon (1991) point out that under the Ecological Constraints and Life History hypotheses, there is insufficient explanation of why, while waiting for the opening of breeding opportunities, adult helpers in cooperative breeders stay in the natal territory, rather than floating and avoiding the costs of helping.

Ekman et al (2001) suggest that the timing of dispersal is a decision of both parents and offspring: differences between cooperative and non-cooperative species may lie in parents' tolerance of older offspring at the start of a breeding season, and willingness to continue conceding food and other forms of aid. On the other hand, all family members might benefit from natal philopatry if advantages accrue to living in a group of larger size. Living in larger groups may help all family members benefit from the ability to confuse, detect or defend against predators (Alexander, 1974; Brown et al., 1999; Foster and Treherne, 1981; Landau and Terborgh, 1986; Powell, 1974; van Schaik et al., 1983a); increase prey size or hunting efficiency in carnivores (e.g. wolves; Miller, 1975; Macdonald, 1983); or compete with kleptoparasites (e.g. wild dogs; Creel and Creel, 2002). Other suggestions of benefits to philopatry to individual dispersers include gaining the right to acquire the natal territory, and acquisition of skills through helping (Beauchamp, 1998; Cockburn, 1998; Komdeur, 1996; Pulliam, 1973; Ridley and Raihani, 2007; Ridley et al., 2008; Roberts, 1996; Wiley and Rabenald, 1984; Woolfenden and Fitzpatrick, 1978; Woxvold and Magrath, 2005).

Ultimately, understanding the underlying causes of sociality in any particular species will require detailed understanding of its ecological and behavioral traits, to characterize the relative importance of various costs and benefits in dispersal and helping choices. Comparisons with the ecology of closely related species and phylogenetic analysis can help us to better understand the causes behind the evolution of cooperative behavior, its maintenance, and evolutionary consequences in different lineages.

Giant Otter Breeding Biology and Behavior

The giant otter (*Pteronura brasiliensis*) is unique among the 13 species of extant otters in being a facultative cooperative breeder, and the ease of observing its social and feeding behaviors in Manú oxbow lakes makes it an interesting species for documenting relevant features of cooperative breeders, such as helping behavior, skill development of young, and flexibility in breeding and dispersal strategies. In Manú oxbow lakes, families of giant otters defend territories, typically with a breeding pair raising young with the assistance of young from previous years ("helpers-at-the nest" in the terminology or ornithological studies). Giant otter cubs tend to appear in the dry season (July to September), although they have been observed to emerge from the den in any month between March to September (Schenck, 1999). The mated pair remains together year-round for their entire reproductive history (Duplaix, 1980; Groenendijk and Hajek, 2006). Established family groups include up to 10-12 individuals, and older offspring assist young-of-the-year through various tasks such as feeding, babysitting, defense, grooming, and playing.

As in all facultative cooperative breeders, giant otter juveniles receive care from parents and non-breeding helpers, but the breeding pair can successfully rear young without the presence of such helpers (Clutton-Brock, 2006). Juvenile otters are thought to gain reproductive maturity around 2 y of age, but may stay with their natal family for ~ 1.5 to 4 years before dispersing (Groenendijk and Hajek, 2006; Sykes-Gatz, 2005; pers.

obs.). As suggested by the wide range of age at dispersal, some juveniles stay with the natal family for several years beyond reproductive maturity, while others depart to exist as "floaters" in multiple territories, sometimes in coalition with other dispersing family members, or unrelated individuals (pers. obs., and Groenendijk and Hajek, 2006). Little has been published about dispersal distances of floaters or territory inheritance in giant otters, although Groenendijk and Hajek (2006) report that males disperse greater distances than females, and that it is more often females who inherit a natal territory after the loss of the breeding pair.

To date, no consensus exists on the question of why giant otters are the sole member of the Lutrinae to breed cooperatively. In other otter species, social cooperation is frequently observed, but not as part of raising young. For example, male foraging congregations have been observed in *Lontra canadensis* (Blundell et al., 2002; Larivière, 2001). *Aonyx capensis*, the African clawless otter, is primarily solitary (79% of observations), but will travel in groups of 2 adults with 1-3 young, (Rowe-Rowe 1978a, quoted in Larivière, 2001; van der Zee, 1982 quoted in Larivière, 2001). For all other otters for whom the reproductive biology is known, young disperse at around 1 y of age, and the father does not associate with the mother except to mate.

The Role of Helpers in Giant Otters

In a cooperative breeding system, the work of feeding and defending the family, and particularly care for young-of-the-year, is shared among many helpers. Helping can carry fitness costs, and the level and type of help provided may differ substantially among individuals, and be affected by sex and/or age of the helper (Cant and Field, 2001; Clutton-Brock et al., 2003; Clutton-Brock, 2006; Heinsohn and Legge, 1999; Komdeur, 2006). Where one sex is more philopatric, and therefore more likely to help, adults should alter sex ratios of young to produce more of the helping sex, according to Emlen's "repayment model" (Emlen et al., 1986; Griffin et al., 2005). Helpers may also help disproportionately based on relatedness or expectation of future rewards, particularly the acquisition of the breeding territory, although authors differ in whether animals with the highest rank, and likely to gain a territory should help more or less (Balshine-Earn et al., 1997; Cant and Field, 2001; Cant, 2003; Cant and Field, 2005; Cant and Field, 2006).

For the giant otter, little is known about its ecology or behavioral interactions, including the role of helpers in a family. Knowing more about intra-familial interactions and quantifying helping behaviors could illuminate changing needs and pressures on family members of different ages, and suggest predictable patterns in juveniles' development and dispersal strategies. This study is the first to quantify helping behavior in a wild family of giant otters to address these issues, and I suggest that we can gain insight into underlying mechanisms driving social organization if we can differentiate between contrasting behavioral syndromes from field observations of animals' behaviors.

In this study, I pose three successive questions regarding the role of helpers in giant otters. First I ask: do giant otter helpers help? Although our understanding of helper contributions within species is still too poor for accurate predictions, one useful benchmark for comparison is the level of adult skill and/or help (Heinsohn and Legge, 1999, Maclean, 1986). Since parents and siblings have equal relatedness to young-of-the-year (r=0.5), helpers' contributions should meet the contribution level of parents in at least some helping roles to be considered as helpful helpers. Second, I ask: are there differences among individuals in the amount and type of help provided? Given the wide variation in helping contributions observed in other philopatric species, it is not possible to predict a priori if all helpers will help equally, and in which tasks. Finally, I ask: can we characterize patterns in helping behavior within giant otter families that could suggest underlying causes for the evolution of cooperative breeding? Here I suggest that there are at least three possible patterns or helping syndromes that could be observed in the field, as suggested from the literature on cooperative breeding and previous experience observing giant otter families. Each scenario carries specific implications for understanding the rise of cooperative breeding in the giant otter. I suggest that we might observe that helpers in giant otters behave as: 1) social climbers; 2) behavioral specialists; or, 3) slow learners. Alternatively, individual otters may make distinct dispersal choices that restrict the opportunity to observe family-level patterns.

Social Climbers, Behavioral Specialists and Slow Learners

"Social Climbers"

The first scenario I suggest is that helpers in giant otters may seek to be "social climbers" in a social hierarchy in which the expectation of inheriting the breeding position offers significant future rewards. This strategy would be particularly beneficial if juveniles depend upon acceptance by the breeding pair to stay on the territory through a "pay to stay" system, or are providing an honest signal of their ability as a collaborator on the territory (Balshine-Earn et al., 1997; Zahavi, 1995). Through heightened helping activity, "social climbers" extend the time they are tolerated on the natal territory, possibly also suppressing similar aspirations by same-sex siblings. In such a setting, I would expect helpers' relative contributions within the family to different helping behaviors to be positively correlated, because some helpers will contribute more in all categories of helping activities than will others. If one sex demonstrates greater philopatry, we would also expect members of that sex to dominate the "social climber" ranks, and for competitive interactions between these same-sex siblings to arise more frequently.

"Behavioral Specialists"

The second possibility I consider is that having multiple helpers in a family can allow for a division of labor within a family, via behavioral specialization (Clutton-Brock et al., 2003). Helpers here would assume particular helping tasks and avoid others. Preference for some behaviors over others could be related to sex. In this setting, an individual helpers' relative contribution to different helping behaviors would be negatively correlated, as different animals will be providing divergent services within the family (Clutton-Brock et al., 2003). Competition between siblings might be lower than in the "social climber" scenario, with limited or no hierarchical social structure observed.

"Slow Learners"

Finally, for an animal with a difficult feeding niche, such as top predators, size and skill acquisition can both be critical for survival and reproductive success, but slow to develop, as emphasized in the Slow Learning or Maturational Constraints hypotheses (Hawkes, 2006; Heinsohn, 1991; Johnson and Bock, 2004; van Noordwijk and van Schaik, 2005; van Schaik et al., 2006). If skill acquisition is slow, it is likely that all helping behaviors will not be performed at equal cost at all ages. Therefore, in "slow learners," at particular ages, animals may appear to be highly specialized for a given task, although the allocation of helping behaviors would change with age. Such an age-based polyethism can be considered a form of behavioral specialization, although some authors consider behavioral specialization to exist only when an animal continues to specialize in an individual task throughout its lifetime (Clutton-Brock et al., 2003). Here I consider the possibility of giant otters being "slow learners," as a third separate syndrome. Whereas the two previous syndromes could be differentiated by observing if individual helpers' relative contributions are positively or negatively correlated, a "slow learner" syndrome would be characterized by finding that skills and helping contributions accumulate or change allocation with age. Juveniles would not reach adult skill and helping levels by 1 y of age, when the juveniles of most other otter species disperse.

Significance of the Three Helping Scenarios

Because the first two possible helping scenarios ("social climbers" and " behavioral specialists") make opposite predictions about correlations between individual helpers' relative contributions, if either scenario operates at the family level, these two scenarioss should be clearly distinguished and mutually exclusive. The "slow learner" scenario does not exclude the possibilities that behavioral specialization or social climbing develops in giant otter families, but it does predict skill and helping gains with age, and that juveniles will be limited in developing specialized roles or higher social status until their skills match those of older siblings and adults. It is also possible that giant otter families harbor individuals with divergent helping and dispersal strategies, which would complicate the prediction of family-level patterns in the distribution of helping contributions.

Whether animals choose to be "social climbers" of a generalized nature, or "behavioral specialists" by virtue of choice or inherent learning constraints, differentiating between the three possible scenarios could inform our understanding of giant otter's cooperative breeding system as well as other aspects of their behavioral ecology. Evidence that giant otter juveniles engage in social climbing might suggest the possibility of a more hierarchical structure within giant otter families than has been believed to date. While potentially hard to observe in the field, such a hierarchical social structure could determine dispersal decisions that are little studied or understood. It would also suggest that a critical evolutionary constraint on giant otter behavior and reproduction is the difficulty of locating and defending quality breeding territories, as suggested by the Ecological Constraints hypothesis and Life History hypothesis. As decades of hunting and persecution have driven the giant otter to extinction throughout much of its original range, confirming the importance of territory saturation to otters' dispersal and reproductive choices might otherwise be difficult at most sites.

Evidence of behavioral specialization would primarily be of interest in describing giant otter social organization in greater detail, including how animals of different sexes, ages, and personalities organize themselves within the family structure to meet the needs of the family and of individuals at different stages of life. Since body size is correlated with slow brain development and extended adolescence, evidence of slow learning in giant otters would help explain via the Slow Learning or Maturational Constraints hypotheses why giant otters are alone among the 13 species of otters to engage in cooperative breeding. The extreme size difference observed between giant otters and other Lutrinae is just one of the predictions of the slow learning hypothesis that may fit the case of the giant otter (van Schaik et al., 2006).

METHODS

Study Area and Observation Periods

I conducted the study with two giant otter families that had permanent territories on Cocha Cashu and Cocha Salvador, two oxbow lakes of the Río Manú in Manú National Park, Perú. Chapter 2 provides a description of the ecology of oxbow lakes of the Manú and reports on fish, bird and caiman abundances on these two isolated, high-productivity lakes. In the Manú River, giant otters primarily breed on the 6 largest oxbow lakes in the park, but also use numerous smaller oxbow lakes, creeks, palm swamps, and backwater wetlands (Schenck, 1999). I followed the otter families only when resident on the study lakes.

To investigate basic demographic patterns in giant otters, I compiled data on the families at Cocha Cashu and Cocha Salvador over several years (Table 5.1). At Cocha Cashu, I began recording individuals' date of birth, sex, and dispersal date with the first appearance of the breeding pair Oz and Otto in 1997. Observations at Cocha Salvador commenced in 2001. My own observations are supplemented by information from other investigators at Cocha Cashu Biological Station and from annual censuses begun in 1999 by the Frankfurt Zoological Society, including the only other published account of an otter family, on Cocha Otorongo in Manú Biosphere Reserve (F. Hajek, J. Groenendijk, M. Kratt, G. Pieja, pers. comm.; Groenendijk and Hajek, 2006). Dispersal events were not always directly observed, but estimated in the following manner: if an animal was not directly observed living as a solitary or "floater" on the natal territory, I estimated dispersal age assuming wet season dispersal in January of the year the animal was first observed to be absent from the family group after reaching 1 y of age. Animals not observed in a second season were assumed to die before reaching 1 y of age.

I started intensive behavioral observations in February 2003, and involved a team of Peruvian students and foreign volunteers, most notably students of ichthyology from the Museo de Historia Natural in Lima. In 2003 I collected seasonal data on fish and fauna abundance (cf. Chapters 2, 3, 4) and on giant otter behavior and diet. Between 2004 - 2006, I collected only dry season data (July-October). Only my own behavioral observations are included in the data reported here, so observer bias is not present. In the context of this study, assistants' data were primarily used to document fauna abundance and diet, and to know the location of the family throughout the day.

At the start of the study, the Cocha Salvador group was already well-habituated to human observation, as it is subject to daily visits by tourist boats. The Cocha Cashu group took longer to habituate, but by 2004 were well accustomed to being followed by kayak. Behavioral data reported here include 2004-2006; I do not include 2003 data as habituation was incomplete on Cocha Cashu.

Behavioral Observations

I created a classification scheme for otter behaviors as shown in Table 5.2. I classified behaviors broadly into three categories of Cooperative behaviors, Non-cooperative behaviors, and Skills and Leadership behaviors. Cooperative behaviors included the two major categories of Assistance and Defense, each of which incorporated multiple observable behaviors. Assistance behaviors included Fish Share (sharing fish with beggars), Groom (grooming another family member), and various tasks related to caring for babies (combined into Baby Assist). Defensive behaviors of various sorts were also recorded, including snorts, periscopes, and bubble alarms (releasing a large bubble underwater below a caiman or the observer), caiman chases, Den Cruise (completing a circular cruise in the water in front of the den), and physical contact with a threat (biting or headbutting a caiman or parts of the observer's kayak). I also noted Non-cooperative behavior, which included only the behavior No Share – when begging resulted in either a refusal of the potential Donor to share with a Beggar, or a Steal by the Beggar from the Donor of the prey item. The final major category of behaviors I label Skill Acquisition and Leadership. This category includes Fish Catch, Begging, Handling time and Leadership, i.e. behaviors that help keep the group together by communication or action. Handling time proved not to differ between animals older than 1 y of age, so was removed from analyses.

I observed giant otters from a one-person, sit-on-top kayak, using Canon 12 x 36 image-stabilizing binoculars, an Olympus DS330 digital voice recorder with date/time stamp, and a Tungsten C Palm-pilot using a customized event recorder program (Lorch, 2002). Otters were followed by a single observer at a time, using continuous sampling (Martin and Bateson, 2007). Sampling shifts were organized into four 3-hour shifts per day: AM1 (6-9 am); AM2 (9-12pm); PM1 (12-3pm); and PM2 (3-6 pm). I attempted to distribute the observations throughout all 4 daily sessions, to capture the full range of daily activity in the dataset (Table 5.3). The number and identity of all otters in a party were also recorded for each session. Since Cocha Cashu was my home base, observations at that lake were more numerous, and spread out over a longer total period of time than at Cocha Salvador. At Cocha Salvador, I set up a field camp for a 10-14 day visit, and performed more intensive observations during each visit.

The event recorder software allowed me to register the start and end time of 18 categories of states or events. State variables that were tracked with the event recorder included location (presence in 1 of 4 equal-area regions of the lake; i.e., in Cocha Cashu: Northwest, Lobo Den, Center, EBCC regions); microhabitat (Log Zone, Grass Zone, Middle Zone); hunting intensity (Cruising, Low Diving, Medium Diving), and intra-group coordination (Low, Med, High). Individual events recorded included Fish Catch, Alarm, Beg, Share, and Groom. I also dictated any behavior of interest not recorded in the event recorder, noted the identity of otters involved in each event, and commented on any errors made in recording data in the event recorder. Finally, I dictated additional information on all prey captures including species or guild and size category (0-10cm, 10-20cm, 20-30cm, 30-40cm, or > 40cm).

I organized the behavioral data by first downloading the event recorder's start and end times for all behaviors in an Excel spreadsheet in chronological order. Next I interpolated all additional behavioral observations from the voice recorder, and added columns of information describing or counting information on prey items, behavioral interactions, and other observations in a format that allowed easy calculation of summary statistics per session (i.e. counts of behaviors, or cumulative time in a microhabitat). To assure independence of commonly repeated events such as Snorts and Periscopes or Leadership activities, only one instance of a given behavior was recorded for an individual until a change in the group's overall behavior or organization was observed. All behaviors by unknown animals were removed from the dataset. I report here only on data relevant to my questions on helping behavior.

In total, 163 3-h sessions were used in statistical tests - 103 in Cocha Cashu and 63 in Cocha Salvador. Not all 3-h sessions had equivalent minutes of direct contact-time with the otters, defined as time when otters were not resting, out of sight, or unobservable because of tourist boats or other disturbances that precluded observation. "Contact minutes" of each session were recorded and included in analyses. In total, 160 h of direct contact were obtained at Cocha Cashu in the 103 sessions there, and 123 h obtained from Cocha Salvador's 63 sessions (Table 5.2). Fish catches, by far the most common behavior recorded, totaled 2995 for the whole dataset.

Data Analysis

To test for differences in sex ratios of offspring from Cocha Cashu, Salvador and Otorongo, I applied an exact binomial test on all offspring of known sex by family. To test for differences in dispersal age between the sexes, I used the Exact Wilcoxon Rank Sum test (R 2.4.1) on the same dataset. Use of a Mann-Whitney U-test was precluded in this case due to the multiple ties in dispersal age estimates.

To analyze Question 1, if giant otter helpers provide help and attain skills comparable to adults, I compared the mean number of fish catches and behavioral events observed per animal per 3-h session for all family members including young-of-the-year where applicable (Figures 5.1 to 5.8).

To analyze Question 2, if differences exist among family members in skills and amount and type of helping contributions, I applied the non-parametric Kruskal-Wallis test for multiple comparisons in XLSTAT 2006 (Tables 5.4-5.6). Parents were included in this analysis, but young-of-the year excluded. If a significant difference was found among individuals at the family level, I checked pairwise comparisons using Dunn's procedure for multiple comparisons, including a Bonferroni correction to the test of significance (XLSTAT 2006).

To test Question 3, if a pattern of helping behavior at the family level could be described as indicative of social climbers, behavioral specialists, or slow learners, I used two methods. First, I calculated Spearman rank correlations on the percentage contribution of each helper (juveniles 1-4 y) to its family's total count of occurrences of a given behavior. I originally tested by family and year, and then combined Cocha Cashu and Cocha Salvador, to increase statistical power. I then calculated partial correlations on significant correlations to see if the results maintained significance when corrected for effects of age (pcor.test in R 2.4.1). Second, I further analyzed the effect of age on helpers' skill and helping contributions by constructing a mixed effects linear model for each skill and behavior, using Maximum Likelihood estimation (procedure lme in R 2.4.1). For each model, I used a summary statistic of each helper's mean count of a given behavior across all 3-hour sessions for each age at which the helper was observed. I included Age as a fixed effect, and Otter ID as a random effect, to incorporate patterns from each individual's repeated measures at different ages into the model. I only included data from helpers in age classes 1-4 y to construct the models, but present parents' summary statistics in graphics for comparison purposes.

RESULTS

Sex Ratios and Dispersal Ages

Demographic and dispersal data suggested that the families at Cocha Cashu and Cocha Salvador could be exhibiting distinctive family structures. Two notable features include differing sex ratios of offspring on the two lakes and the younger dispersal age of females at Cocha Cashu (Table 5.1).

While the number of male and female offspring are essentially equal at Cocha Cashu (8 males, 7 females, exact binomial p-value = 0.5) and Cocha Otorongo (4 males, 5 females, exact binomial p-value = 0.5), a statistically significant skew towards male offspring occurred on Cocha Salvador, with only 2 females and 10 males born that survived to 1 y of age (exact binomial p-value = 0.02).

At Cocha Cashu, females had notably younger dispersal ages than males, with most females dispersing just after 1 y of age. An Exact Wilcoxon Rank Sum test revealed that the mean age at dispersal on Cocha Cashu was significantly different between males and females (Mean dispersal age, Males = 3.4 y; Mean dispersal age, Females = 1.9 y; p = 0.03, W=36). Using a Mann-Whitney U-test, I found no significant difference at Cocha Salvador (Mean dispersal age, Males = 2.9 y.; Mean dispersal age, Females = 2.9 y; U=7.5; p = 0.93), but with such a low sample of females (2), the result is inconclusive. From observations of captive animals, sexual maturity is thought to occur around 2 y of age, so the average dispersal age on Cashu is surprisingly young (Sykes-Gatz, 2005). An exception to pattern of young female dispersal on Cashu was Olaf (a female with a male name), born 2002, who stayed on Cocha Cashu as a solitary even after the family disappeared in 2007.

To get further insight into whether the young dispersal age of females on Cocha Cashu situation was atypical, I also analyzed the only other published account of an otter family's demographics, from Cocha Otorongo, another large lake in Manú National Park (Groenendijk and Hajek, 2006). The age of dispersal of 4 males and 5 females failed to show a significant difference between males and females using an Exact Wilcoxon Rank Sum test ($p = 0.52$, $W=6.5$), although the trend was opposite the Cashu situation, with females at Otorongo dispersing at older ages than males (3.1 y for females vs. 2.8 y for males).

Q1: Do Giant Otter Helpers Help?

The first question I pose regarding giant otter helping behavior is whether or not offspring who delay dispersal and stay in the natal territory are in fact helping their parents to raise younger siblings. For all four behavioral categories defined as cooperative – Fish Share, Groom, Baby Assist, and Defense – visual inspection reveals that older helpers can meet or exceed the parents' rates of helping per 3-hour session (Figures 5.4-5.7). Rates of helping were variable and strongly influenced by age, otter identity, and skill level, the details of which I address in subsequent sections. Nevertheless, the overall conclusion is clear that giant otter helpers can and usually are contributing to the adults' efforts of raising their younger siblings through various forms of assistance.

Q2: Are There Differences Among Individuals in the Amount and Type of Help Provided?

The second question I pose concerns the variability in individual family members' skils and allocation of assistance. Overall, my results demonstrate that differences do exist among family members in skill development and helping contributions. Kruskal-Wallis statistics revealed repeatedly, in both families and in most years, that statistically significant differences among family members' exist in rates of helping, catching fish, and leadership (Tables 5.4-5.6). I report results by sub-categories of Skills and Leadership, Cooperative and Non-Cooperative Behaviors.

Skills and Leadership

Fish Catching

Kruskal-Wallis tests on catches of medium and large fishes revealed that Fish Catch skill differed significantly among individuals in both families and in most years, with the exception being Salvador in 2006 (Table 5.4 and Figure 5.1). The lack of significant differences among family members in Salvador, 2006 is probably due to two factors: 1) a lower sample size (number of sessions) collected in that year; and, 2) the lower number of helpers in the family that year, lowering the degrees of freedom in the test.

Results of the post-hoc pairwise comparisons between family members (Dunn's Procedure, XLSTAT 2006) are reported in the Appendix (Table A1), and notable features discussed below by lake.

Individuals' catch frequencies: Cocha Cashu

Post-hoc pairwise comparisons on Fish Catch ability provide groupings of animals with statistically significant differences (Table A1). From these tables and Figure 5.1, it is clear that the Cocha Cashu mother ("Ozstralia" or "Oz") had the highest catch-rate per 3-hour session in all years, although this was not always a statistically significant difference. For example, in 2004, Oz had a catch rate of 2.5 medium or large fish per session, well above the next most proficient otter, Orson, a 3 y old subadult (with a mean of 1.5 medium or large fish per session), but this difference was not significant. The father, Otto, had a surprisingly low catch rate of 0.9 medium and large fish per session. By 3 y of age, many offspring developed catch rates statistically indistinguishable from the mother and father. In addition to Orson in 2004, in 2005 Olaf (then aged 3 y), statistically tied Oz and the father in catching medium and large fish. By 2006, Oz was tied not only by the father and Olaf, but also by the 2 y Oswald, but not his same-aged brother, Osama.

Animals less than 1 y old were never seen to independently catch medium or large fish on Cocha Cashu during my observations. Once animals reached 1 y of age, catch rates were lower than for 2 and 3 y olds in all cases on Cocha Cashu, although the differences were not statistically significant from other helpers using these tests, except when compared to the high catch rates of Orson and Olaf (aged 3 or 4 y), who had attained adult proficiency.

Individuals' catch frequencies: Cocha Salvador

As in Cocha Cashu, the mother at Cocha Salvador, Cacao, consistently had high rates of fish catches, although hers was not the highest rate in all years. As both she and the Cocha Salvador father, Fantasma, were known to be > 14 y of age at the time of these observations, their skills may have been in decline. Fantasma's low catch rate was particularly notable, being comparable to juveniles of 1 y in all years. In 2004, Cacao did have the highest catch rate, and differed significantly from many family members including the father, the oldest helper (3 y old Diabolo), 2 y old Virute, and 1 y old Saggy. She did not, however, differ from the 1 y old Mars, who already had a high catch rate. In 2005, Cacao had the second highest catch-rate, after 2 y old Mars, but their catches were not significantly different from any but the 1 y old Ziggy and the father (Fantasma), who had the lowest catch-rates. In 2006, all Salvador otters had statistically indistinguishable catch-rates, perhaps because of the smaller family size and/or declining skills of the parents. Fantasma disappeared in 2007 at ~17 y, the oldest record of a giant otter known in the wild (Pieja and Kratt, pers. comm. and Groenendijk, pers. comm.). The mother appeared noticeably infirm in 2007 and commenced to beg rather than provide for other family members (cf. Chapter 6).

Among subadults at Cocha Salvador, the most notable feature is the difference between same-age brothers Mars and Saggy. While Mars by 1 y (2004) was clearly hunting independently, with a catch-rate indistinguishable from all other otters including the mother, Saggy continued to beg heavily and eschew independent hunting. Saggy performed relatively poorly in catching fish both in 2004 and 2005, compared even to younger siblings. Meanwhile, in 2005 Mars had the highest catch-rate in the family. Both dispersed in 2006 prior to the final set of observations reported here.

Begging

The Kruskal-Wallis test demonstrated differences in begging frequency in most years (Table 5.4 and A2, and Figure 5.2). Not surprisingly, the young-of-the-year and 1 y old helpers engaged in the most begging, and older helpers (2-4 y of age) rarely begged. Parents never begged in 2004-2006, although they occasionally received partial shares of large prey items that were shared among many individuals. In 2005 on Cocha Cashu, young cubs emerged from the den extremely late in the season (late September), so observations rarely included the young-of-the-year; differences between helpers were still apparent, however. In 2006, I did not find statistical differences between animals, which is probably a result of low sample size.

Some interesting comparisons in begging behavior arose among animals aged 1 y. For example, in Cocha Salvador, 2004, the 1 y old Saguarito (also known as Saggy) begged significantly more than his same-age brother Mars, and begged as frequently as the young-of-the-year. This difference mirrors their difference in fish catching described above. In 2006 on Salvador, one older offspring, Liana, was the sole survivor from a brood born early in the year, (estimated to have been born in February or March), but a second younger newborn, Caiman, probably born May-June, was also present by the time of my dry-season observations. The difference in begging between the two was already apparent, with Caiman's begging the most frequent of any animal observed on either lake in any year (note scale difference in Figure 5.2). By about 6-7 months of age, Liana still begged at similar rates to other young-of-the year in the dataset who were observed at younger ages (typically 1-2 months).

Leadership

The final category of skill or development-related behaviors I measured were a number of behaviors that reflected leadership roles, including leading the pack during an activity (e.g., leading the hunting pack, changing direction of travel, entering or leaving the den first), and communicating through various loud ("waver scream") and soft ("suey-hum") contact calls with other animals to help keep the group together. Since few behaviors had high individual frequencies, I combined all observations into the one category of Leadership behavior for statistical analysis.

Kruskal-Wallis statistics demonstrated differences in Leadership among members of both families in all years (Table 5.4 and A3 and Figure 5.3). The parents clearly dominated the leadership role in both families, although it was shared increasingly with the helper Olaf as she grew older on Cocha Cashu, and in a lesser way by Saggy in the two years he was observed on Cocha Salvador. Statistically, Olaf matched the father's leadership by 2005 when she was 3, and she matched both parents by 2006 at the age of 4.

On Cocha Salvador, Saggy showed some precocity in leadership in spite of low skill ranking based on Fish Catch and Begging numbers. He began to match the mother's leadership role by 2005 when he was 2, primarily by being very active in communicating the loud and soft contact calls while the family was traveling. 3 y old Virute was also leading at the same level as the mother and Saggy in 2005. By 2006, these leaders had all dispersed, with no other helpers rising to take on significant leadership roles on Cocha Salvador that I observed. Interestingly, Ziggy, who acquired the breeding position in 2008 at the age of 4, did not show precocious leadership skills.

Differences Among Family Members: Helping

Of the four helping behaviors I analyzed, 3 behaviors – sharing fish, grooming, and defense – showed significant differences between family members in most years (Table 5.5, A4-A7, and Figures 5.4 - 5.7). The category Baby Assist did not show significant differences in most years, although a few Cashu animals did reveal some strong differences between a few individuals in 2005, 2006, discussed below.

Animals in different age groups differed in how they helped. Fish sharing was most common among the older animals, reflecting a positive correlation with age and fish catching ability as well as sharing, discussed further below. Also, the mothers at both Salvador and Cashu never failed to have the highest rate of sharing fish. Defense behavior was least common among the parents and young-of-the year, with very strong significant differences accruing to particular subadults. At Cocha Cashu, Olaf was the most active defender in all years, and at Cocha Salvador, Saggy was the most active defender at both 1 and 2 y of age, until he dispersed in 2006. On his departure, Saggy's defender's role was assumed in an impressive way by the 2 y old Rambo. Rambo engaged not only in the highest rates of defense, but also in the most aggressive forms of defense ever observed. Unlike most other defenders, who predominantly engaged potential threats with snorts, periscopes and bubble alarms that did not require direct contact, Rambo engaged in frequent headbutting and biting, and even pulling on handles on my kayak. Caimans and other perceived threats (e.g., birds, tourist catamaran, floating logs) were similarly harassed at high rates and intensities. Rambo's same-age sister Ziggy, however, did not engage in these intensive forms of defensive behaviors, and her frequency of defense did not differ significantly from the parents or younger offspring.

Grooming of other family members also showed significant differences among family members in most years, generally increasing modestly with age. On Cocha Salvador, it was less common that resting periods took place on logs where grooming could be observed rather than inside the den, so that data were sparser, especially in 2006. Therefore, only in 2004 did I uncover a significant difference between family members on Salvador, but suspect the lack of significance is largely a problem of sample size. The data show significantly greater frequency of grooming at older ages, with both parents and helpers >1 y engaging in frequent grooming of others.

Individuals' helping frequencies: Cocha Cashu

As well as being the most active defender of the Cocha Cashu group, Olaf also was the most likely to engage in a variety of Baby Assist behaviors, although the differences in assistance to babies were rarely large, and were not significantly different with all animals. In 2004, when she was 2 y of age, she had the highest rate of Baby Assist, but this help was not significantly different from any other family member. In 2005, she helped babies significantly more than Osama and Oswald, 2 of the 3 other helpers in the family that year. In 2006, she also helped significantly more than the father, Osama and Oswald, but not the mother nor Petunia, a 1 y old female. Of all the animals observed, Olaf seemed the most likely to be a "social climber" given her high contributions to many helping behaviors.

One unexpected feature of 2006 is that the father's helping seemed to decline both in Baby Assists and Fish Sharing, which was also reflected in an increase in non-cooperative behavior.

Individuals' helping frequencies: Cocha Salvador

In 2004, I observed one helper, the 3 y old male Diabolo, to have the highest grooming rate of all animals, which was significantly higher than all other animals besides the mother. He did not also help with high frequency in other helping behaviors, however. Similarly, in spite of Rambo's extraordinary effort expended as defender in 2006, he did not excel at any other helping behaviors.

Differences between Family Members: Non-cooperation

The final category of behavior I recorded was the non-cooperative behavior of refusing to share with a beggar (No Share). Frequency of refusing to share was evenly spread across all family members, and only few significant differences worth mentioning were found (Table 5.6 and A8, and Figure 5.8). Overall, a rise in refusing to share probably reflects differences in Fish Catch, as animals with higher rates of fish catch offer more opportunities for beggars to steal or simply be refused. On Cocha Cashu, 2005, the mother's No Share rate differed significantly from 2 1-y olds, Osama and Patty. Her elevated rate of Fish Catch probably determined this result. A more interesting result appeared in 2006, when the father appeared to genuinely refuse to share at a higher rate, in the same year that the lake was covered by the floating plant *Pistia stratiotes*, presumably lowering resource conditions.

Q3: Can we Characterize Patterns in Helping Behavior Within Giant Otter Families?

Correlation Analysis of Helping Behaviors

I found that correlations among relative helping contributions were weak and sporadic across years, with the exception of correlations with age (Table 5.7). Age correlated positively with Fish Catch, Leadership, Sharing and Grooming, and negatively with Begging. Begging and Sharing were negatively correlated in the 2004 data, but I found no negative correlations among helping behaviors that would indicate behavioral specialization at the family level. Of the positive correlations between helping behaviors that could indicate "social climbing," only a few retained significance after partialling out for the effect of age. Only one correlation between helping behaviors, that between Baby Assist and Leadership, held across more than 1 year. One other positive correlation between Leadership and Defense held in 2005 after correction for age. The other significant correlations that held after correcting for age in single years are between a skill measure and a helping behavior. These include a positive correlation between Fish Catch and No Share found in 2004, a positive correlation between Fish Catch and Baby Assist found in 2005, and a negative relationship between Begging and Fish Share found in 2004.

Mixed Effects Modeling of Age on Helping Behaviors

To better investigate the correlation with age on helping and skills, I also ran Maximum Likelihood linear mixed effects models for the data on helpers' behaviors. Figures 5.9-5.16 present the data graphically, with the finer, patterned lines connecting the repeated measures on the same helpers at different ages. Outlier animals are identified where instructive. Each mixed model determines a series of parallel lines for every individual helper in the model; helpers have equivalent slopes but unique y-intercepts. On Figures 5.9-5.16, I plotted the line representing the overall model fit to the helpers' data, and included parents' values assigned to Age Class 5 for comparison with the modeled trend based on the helpers' data. Table 5.8 reports statistics from the ANOVA call on each model, describing the significance of the fit of age with each behavior (Pinheiro and Bates, 2004), and Table 5.9 provides summary statistics for each model.

All models demonstrated that age is a strong predictor of skill or helping frequency, except for the model of Defense (ANOVA call on Age, p=0.45) and Baby Assist, which showed a positive trend with age that was just under statistical significance with a p-value at p=0.06 (Table 5.8). Removing the outlier value for Olaf caused the Baby Assist model to show a negative, rather than positive trend with age that was also non-significant (Figure 5.14 and Table 5.8).

Other models besides Baby Assist were also strongly affected by the inclusion of outliers, including Grooming and Defense. The exclusion of 3 y old Diabolo lowered the slope of Grooming (Figure 5.13). Similarly, removing Rambo and Olaf from Defense caused a positive trend with age to change to a negative trend with age.

Field Observations of Dominance and Territorial Disputes in Giant Otters

Because of the differing predictions of the 3 possible social syndromes with respect to sibling competition and hierarchies, it is important to share some additional anecdotal field observations I made on dominance and aggression interactions within my two study families. Most authors have agreed that no dominance hierarchy or aggression between family members structures behavior in giant otters (Duplaix, 1980; Laidler, 1984; but see Groenendijk and Hajek 2006). I feel, though, that this subject merits further study, as I did observe interactions between family members that suggested maintenance of dominance hierarchies, although at very low frequencies. I also observed some aggressive interactions between the resident family and dispersing offspring at Cocha Cashu that appeared to be severe.

In the first case, I observed a number of instances of the headshake display, in which family members who have been separated for a period, reunite and perform a fast headshake motion facing one another, so close as to almost be touching noses (Duplaix, 1980). I observed the headshake primarily being given to parents or older helpers by younger animals. I also observed one occasion where a 1 y helper offered a headshake to Olaf, the oldest helper at Cashu at the time, immediately followed by a rare, highly submissive behavior, in which the subordinate animal rolled over to expose its stomach to Olaf. Such displays of submissiveness are reminiscent of behaviors in primates and canids that maintain strict hierarchies, such as wolves (Mech, 1970; Mech and Boitani, 2003).

In addition, I occasionally observed play behaviors that at times seemed aggressive. The most notable perpetrator of “hard-core” play was Cacao, the mother at Salvador, who would appear to “waterboard” or mock-drown younger animals. Usually during play, any animal that is “attacked” quickly returns to the play area for more. However, on several occasions I noted that the juveniles the mother was “waterboarding” would escape from her vicinity and not return, suggesting that they were escaping an undesired or unwelcome situation.

In addition to aggressive and submissive displays within a family, I also observed aggressive interactions between the family and dispersing animals in coalitions with outsiders. In August 2005, I observed the formation of “The Gang of Four” at Cocha Cashu, consisting of two 1.5 y old female offspring (Stripe and Splotch) and two strangers, one of whom was an adult male born in 2002 on Cocha Salvador (Frita), and the other an adult female (Roto) born in 1999 on Cocha Otorongo (J. Calvimontes, pers. comm.). The Gang of Four would occasionally usurp the family territory during their absences, using the dens and latrines and hunting grounds while the family was away for periods of days or weeks. After one approximately 1-week absence from Cocha Cashu, the resident family returned while I was observing the Gang of Four at the main den. I first noticed the resident family in the middle of the lake, and on reaching a known campsite, they seemed to smell that the Gang of Four had been present there, and commenced waver-screaming, running around the area of the campsite, and heavily scent-marking surrounding vegetation. Throughout that day and the next, the family completed tours of the lake's perimeter, and at the den, other known campsites and latrines, the family repeated the screaming and scent-marking on multiple occasions.

Upon the family's arrival, I initially observed the Gang of Four to silently sneak away from the den, heading in the direction of the river, and I thought they had ceded the territory without incident. However, later in the afternoon, the Gang of Four precipitated a conflict by waver screaming at the family from the shore as the family swam by. The resident family chased the usurpers on land with more loud waver screaming, driving them further inland, and disappearing for several minutes. I saw no other direct conflicts, but Splotch and Stripe stayed with the Gang of Four, continuing to hunt with their new companions on the river, and on the lake in the family's absence. In the same period, I saw Splotch with a gash in her head that exposed a good portion of her skull, possibly from physical fighting that took place out of sight. A year later, Stripe and her same companions were still observed using the river in the vicinity of Cashu, but Splotch was no longer with them.

DISCUSSION

The results of this study provide the first quantitative data on the distribution of helping behaviors in giant otter families. To frame the study, I posed three questions regarding helpers in giant otters. First: do giant otter helpers help? Second: are there differences among individuals in the amount and type of help provided? Finally: can we characterize patterns in helping behavior within giant otter families that could suggest underlying causes for the evolution of cooperative breeding? And, of three possible helping scenarios, do patterns in helping contributions suggest giant otters behave as behavioral specialists, social climbers, or slow learners? The first two questions I can clearly answer in the affirmative from the results presented here. Juveniles can acquire adult levels of skills and helping contributions when they stay on the natal territory (Figures 5.1-5.8). Family members also clearly differ in the amount and type of help they provide. The third question, I suggest, is answered by the statement: "giant otters are slow learners in general, but they also vary in helping contribution by the individual otter, likely in response to social and environmental circumstances." Overall, a pattern of increased skill development and helping contribution with age is clear, best supporting the Slow Learning or Maturational Constraints Hypothesis for the evolution of cooperative breeding.

Answering the third question thoroughly requires considering not only the observed patterns in skill development and helping behavior, but also recognizing the role that "outlier" individuals play in demonstrating potentially important departures from those overall patterns. Recognizing variability within helpers' contributions can suggest polytheisms in helping behavior, as a result of environmental factors or phenotypic variation (Komdeur, 2006). I discuss my views on both the patterns I observed in skill development and helping behavior and the significance of outliers' behaviors. Finally, I discuss how data on demography and dispersal contribute to a larger understanding of variability in giant otters' helping contributions, and suggest how we can focus future studies.

Differences Among Family Members: Skill Acquisition and Leadership

Skill Acquisition

Skill development, as measured by ability in catching fish, showed a significant positive linear response with age class in the Fish Catch mixed model (Figure 5.9 and Tables 5.8-5.9). Non-parametric, post-hoc comparisons also indicated that fish catching skills continued improving in giant otter helpers as they age, and that helpers only approach adult capabilities between 2-3 y of age (with Mars on Salvador as a notable exception (Table A1)). The weaker contrast between parents and juveniles at Salvador, compared to Cashu, can probably be explained in part by the Salvador parents' advanced age at the time of these observations (around 14 y of age at the start of observations in 2004).

The second indicator of skill development among helpers, Begging, showed large variation in animals at 1 y of age, when new young-of-the-year are present, but begging declined precipitously for all animals by age 2 (Figure 5.10).

Two notable outliers in skill development include the same-age brothers on Salvador, Mars and Saggy, born 2003. Mars developed skills quickly and was a proficient hunter by just 1 y of age, matching even the mother in statistical comparisons (Figure 5.1 and Table A1). On the other hand, Saggy did not become proficient at hunting until well after 1 y of age, and engaged in extensive begging even when young-of-the-year (Rambo and Ziggy) arrived in 2004, matching their begging rates. Either natural ability or the use of alternative survival strategies may explain this variability in skill development among juvenile otters. Animals may choose to be "producers" or "scroungers" as alternative foraging strategies within the same family when begging for food is an option (Barnard and Sibly, 1981). Producers choose independent foraging, while scroungers attempt to cheat the system of food acquisition by prolonging their begging period well beyond the arrival of young-of-the-year. An extended scrounger strategy may have short-term benefits, however, as it also ensures that the scrounger loses opportunities to improve his/her own skills, which may be counter-productive in the long-term. An interesting follow-up study would be to determine the relative reproductive success of animals such as Mars and Saggy who exhibit differing skill development and/or foraging strategies at young ages.

Although comparable skill assessment for other otter species is not available, I would predict that in all the other species, where young disperse at 1 y of age, skill development reaches adult levels shortly before dispersal. In one comparative study of three species of gulls that varied in age at which adult plumage and initiation of breeding behavior was attained, the author showed that adult hunting skill level was achieved by the spring of the final year of adolescence, regardless of species (MacLean, 1986). The difficulty of obtaining highly mobile prey such as large schooling fish, as opposed to invertebrate prey used by many other otters, may help explain the longer learning curve experienced by giant otters, and the need for long-term philopatry (Heinsohn, 1991).

Leadership

Leadership behaviors tended to increase with age more slowly than fish catching skills or other helping behaviors, and unlike other behaviors, few helpers ever achieved adult levels of leadership (Figure 5.11 and Table A3). Opportunities to lead the family group do arise when parents are eating or hunting singly, but juveniles seemed to rarely assert themselves to direct group movements at such times. Since none of the leadership skills seem particularly rare, difficult or energy-demanding, it is interesting to ask why leadership behaviors seem to develop particularly slowly in giant otter helpers compared to other behaviors. The example of Olaf, the highest juvenile performer during all 3 years of observation in Leadership, Baby Assist and Defense, is perhaps most instructive. Her Leadership rate slowly but continuously increased up until her 4th year of age (Figure 5.11), and she was one of the few observed to lead group activities even when parents were traveling with the group

I suggest that Leadership may require the greatest "slow learning" lag of all the behaviors I measured. Successful leadership will depend on developing skills and knowledge that take time on the territory to accrue: skills such as knowing the spatial and temporal location of fish resources, deciding how to site and maintain a system of dens and campsites for year-round use, learning how to communicate desired activities and movements with others, and gaining respect from younger animals to follow directions. In the complex social and environmental settings experienced by giant otters, leadership skills may be one of the most challenging skills that otters develop in their early years of life, ultimately contributing to successful breeding attempts in the future. This idea may also be supported by the experience of zookeepers attempting to raise giant otters in captivity. Giant otters are notoriously difficult to breed in captivity, and most successful captive breeders are animals who were captured from the wild as established breeding pairs (G. Londroño, pers. comm.). Zookeepers also report that juveniles born in captivity but not allowed to live for extended periods with their parents rarely breed successfully, suggesting the importance of learning social and parenting skills over many years within a family (G. Londroño, pers. comm.).

Maternal Skills

Mothers generally demonstrated the highest skills and helping contributions of all family members, so it is useful to focus some discussion on their distinctive role in giant otter families. My finding that parents typically help at higher levels than non-breeders coincides with findings of Gilchrist and Russell (2007) for banded mongooses (*Mungo mungo*), but contrasts with the findings on meerkats (*Suricatta suricata*) by Clutton-Brock et al., 2004. One suggestion for these observations across taxa is that a more difficult feeding niche requires a more active role of parents in food supplementation. Giant otters take more large fish than related otter species (many of which take crustaceans or other invertebrates), and mongooses take prey such as snakes and small mammals, while meerkats are primarily insectivores.

Since giant otters do not develop a social hierarchy that determines access to prey, mother giant otters rarely benefit from prey catches of others. The fact that the mothers at both Cashu and Salvador had consistently high rates of fish catches in the dry season may confirm what others have suggested – that the mother's need to provide milk during a long weaning period (approx. 5 months; Sykes-Gatz, 2005) requires her to hunt more intensively than other family members (Staib, 2005). The mothers shared food at higher rates with young (Table A4), and therefore shoulder the greatest energy burden. Having many helpers may well facilitate the survival of larger litters than the mother could provide for alone, so long as helpers don't deplete local resources. The greater need to efficiently hunt throughout the day may also help explain why giant mother otters tend to be the most active leaders of group activities, as they have the greatest need to maintain productive fishing activity. Further analysis of demographic data could help determine if number of helpers in a family significantly raises juvenile survival.

Cooperative Behaviors: Helping

Not only skills, but also helping contributions increased with age, as reported both from correlation analysis, and from the mixed effects linear models. In Spearman correlation analyses, partialling out the effect of age removed significance from most of the correlations between helping behaviors (Table 5.7). As no consistent negative or positive correlations remained after correcting for age, I maintain that these results support the idea that of the three helping scenarios suggested, only the "slow learner" hypothesis received any support in this study.

I further investigated the effect of age on helping behaviors using mixed linear models (Figures 5.9-5.16; Tables 5.8-5.9). Here, all the helping behaviors studied revealed a significant positive effect of Age Class for helpers' contributions with the exception of Defense, which was non-significant, and Baby Assist, which had a positive trend, but a marginal p-value = 0.06. While non-linear models with asymptotic behavior at adult helping rates would conceptually fit many of the behaviors, linear models are considered more appropriate for data with only 4 age classes (J. Weiss, pers. comm..), but such non-linear refinements could also be considered if helpers older than 4 y are observed in the future.

For several behaviors, the strong effect of particular outlier animals potentially alters conclusions of the models. For Baby Assist, the effect of removing Olaf's extreme high values at ages 3 and 4 causes the positive response with age to become insignificant (Figure 5.14). For Grooming, removing Diabolo's extreme value at age 2 considerably lowers the slope of the response with Age for the model (Figure 5.13). For Defense, the only mixed model that did not find a likely positive trend with age, a (non-significant) positive trend is observed if the outliers Rambo and Olaf are included, but a negative trend observed (also non-significant) if the two are excluded (Figure 5.15). From long-term experience watching habituated and un-habituated otter families, I consider it relevant and interesting that this considerable variability exists within helpers, and particularly that at both Cocha Cashu and Cocha Salvador, a single individual appears to dominate the role of Defense. It is possible that giant otter families typically include an individual helper in the role as "family defender" but without leading to a family-level effect of behavioral specialization. Neither Rambo nor Olaf showed below-average performance on other helping behaviors, so the defense role may be taken on in addition to other helping roles, rather than through a division of labor, as expected in behavioral specialization.

The process of habituation should also be discussed in the context of Defense, given that many of the defensive observations I counted were directed toward the observer. Although the otters habituated to the kayak, and all individuals allowed observation from only a few meters by 2004, young-of-the-year are naïve about the observer at the start of every year, so that increased habituation (and lower defense against the observer) could be considered an alternative explanation to some of my observations. I suggest, however, that this is not the case, and that other factors are considerably stronger than each individual's accumulated habituation.

The primary factor I believe to dominate habituation levels of the family as a whole is the response of the mother to the observer, with *most* other family members taking their cues from her on how to respond to a potential threat. On Cocha Salvador, the mother, and the group as a whole, instantly accepted the observer in 2003, probably because the kayak was a tiny version of the large tourist catamaran to which they were already habituated for many years. In 2007, when the Salvador family was found with a new partner for Cacao after Fantasma's disappearance (presumed to have died of old age), her new partner FireCat was also instantly accepting of my kayak and observations (cf. Chapter 6). This immediate acceptance occurred in spite of Firecat having no previous experience with my kayak, and only comparatively short experience with tourist catamarans relative to other animals.

The mother on Cashu did not accept the observer/kayak until late in 2003 when 4 young cubs appeared (including Olaf), whose care seemed to drain her of any excess energy she could have put to defense. At that point, she seemed to finally and abruptly accept the kayak and observer as a non-threatening element, calming down in my presence, and generally ignoring me thereafter.

Individual helpers who were more or less likely to be on the alert and alarm at the observer continued to maintain similar Defense frequencies for most of their lives, or even increase dramatically later in life. Rambo on Cocha Salvador is the prime example of the latter case. I suspect an important factor contributing to the surge in his defensiveness at 2 y of age is the advent of sexual maturity, and an altered hormonal state. His same-age sister Ziggy did not suffer equally from the same "testosterone poisoning" or intensive displays of defensiveness. I conclude that the observations I made on Defense contribution were therefore measures reflecting valid differences in the choices of individuals in taking on the role of defense for the family.

Non-cooperative Behavior: No Share

The only non-cooperative behavior measured, No Share, provided an ambiguous story in this analysis. No Share was correlated with Fish Catch in 1 year (2004) of observations, even when corrected for the effect of age (Table 5.7). This result, though not consistent across years in my dataset, is perhaps to be expected as animals with high rates of Fish Catch will offer more opportunities for Beggars to initiate begging and be refused or to exact a steal. One unexpected result was the Cashu father's increase in No Sharing and decrease in Sharing (but not Fish Catch) in 2006. I speculate that this observation may have occurred because of food-stress brought on by the coverage of the lake in 2006 by the floating plant *Pistia stratiotes*. *Pistia* lowers oxygen levels, and limits phytoplankton and periphyton growth, leading to poor conditions for growth and survival of many fish species. Animals should meet their own needs before helping young-of-the-year, and Otto may have had marginal ability to share after meeting his own needs.

Reproductive Skew and Young Female Dispersal

The demographic data on Manú otters showed that more male offspring are produced than expected by chance on Cocha Salvador, and that females disperse at young ages compared to males on Cocha Cashu. Since females help more in some tasks (Leadership, BabyAssists) and are the more philopatric sex, dispersing shorter distances from the natal territory (Groenendijk and Hajek, 2006), these observations run counter to predictions of the "repayment model" of Emlen (Emlen et al., 1986). While the low production of female young on Cocha Salvador may be a random sampling anomaly, it may also suggest inbreeding depression in this small, isolated population. Because mammalian females' X-chromosomes are homozygous, accumulation of deleterious alleles on the X-chromosome could lower survival of female young (Senner, 1980). Further censuses and monitoring of giant otters in the Manú Biosphere Reserve are therefore warranted, to gain a better understanding of the genetic relatedness of Manú otters and to monitor the sex-ratio of offspring produced. Considering the low number of otters in the park, and the paucity of information on gene flow with otter populations outside the Manú Biosphere Reserve, conservation of the species in the park and Perú could be threatened if inbreeding depression and low female survival becomes the norm.

The lower dispersal age of Cocha Cashu females is also an intriguing demographic result, especially when viewed in the light of the behavior of the frequent "outlier" and eldest daughter there, Olaf. The lower dispersal age of females could reflect a choice by parents and/or older siblings, such as Olaf, to evict younger females, or it could reflect a choice by the younger females themselves to "float" and look for better reproductive opportunities off the natal territory. My behavioral observations included some indications of dominance and hierarchical structure in giant otter families, but with insufficient frequency to make strong conclusions in support of the suggestion that Olaf or her parents played a role in encouraging early dispersal of her younger sisters. An argument against Olaf playing a key role stems from the observation that 2 females (Ophelia and Odette) dispersed at young ages from Cashu before Olaf was born (Table 5.1). Therefore, while Olaf may well have stayed on the natal territory for ~5 years with the strategy to inherit the territory with a future mate, it is probably not fair to blame her presence and possible social dominance on the young dispersal of her female siblings.

Perhaps a more likely explanation for the young female dispersal on Cashu is an explanation based on territory quality, and low parental tolerance of “average” helpers on marginal habitat. Cashu is the smallest lake in the Manú to host long-term resident families (Schenck, 1999). Parents may be less tolerant of average helpers when resources on the territory are more limited, as their help may not sufficiently offset the expense of their use of scarce resources; parents should also value their own survival above that of any offspring (Ekman et al., 2001).   Olaf’s continued presence on the natal territory may therefore signal recognition by the parents of her relatively high contribution to helping relative to other helpers.

Alternatively, young female otters at Cocha Cashu may themselves recognize a stressed resource status, or low likelihood of outliving older female siblings’ ambitions to acquire the breeding position. Their dispersal choice would then favor early dispersal to seek out other reproductive opportunities. Given my limited ability to observe behaviors suggesting dominance and forced evictions on younger helpers, and the lack of a similar pattern observed on Cocha Salvador or other sites, it is clearly too early to draw conclusions about the forces determining age at dispersal in giant otters. However, an analysis of larger demographic datasets that include estimates of territory quality could illuminate if similar patterns arise in families with a long-term female helper, and compare across multiple families under different resource situations.

Conclusion: The Evolution of Cooperative Breeding in Giant Otters

The overarching question providing interest to this study is the question of how and why giant otters evolved their unique system of cooperative breeding. This study can not claim to provide the final answer to this question, but does offer some preliminary insights and guidance to future work.

The lack of consistent positive or negative correlations between helpers' contributions suggests that, at least at the aggregate family level, neither behavioral specialization nor social climbing is a strong organizing force in giant otter helping behavior. This contrasts with findings on meerkats (*Suricata suricatt)* in which cooperative activities were found to be strongly and positively correlated with each other (Clutton-Brock et al., 2003). This conclusion suggests that a possible benefit to group living from a division of labor in raising young is likely not a factor in giant otter philopatry. Similarly, I could not support the possibility that attaining a high social status is a critical feature in giant otters acquiring the breeding territory through analyses at the family level. The most important result of this study was the continuing improvement of skills and helping contributions with age even beyond the presumed age of reproductive maturity.

On the other hand, acknowledging that the behavior of "outlier" animals may be informative, multiple lines of reasoning suggest that Olaf, the most helpful female helper on Cocha Cashu, and the only animal observed to stay on her natal territory for over 4 years, may have been a single unique case of a social climber in my two study families. Cant and Field (2001) suggested an opposite effect: that subordinates should contribute less as they have greater likelihood of inheriting the breeding status. Again, the truth may lie in the fact that animals under different social and environmental constraints may behave distinctly (Komdeur, 2006). My suggestion regarding Olaf should therefore be considered an indicator that future studies should consider social climbing and territory acquisition as a potential feature of giant societies when additional datasets on giant otter demography can be compiled and analyzed. It is also likely that the acquisition of breeding territories is a limiting ecological constraint in an intact site such as Manú Biosphere Reserve. The possibly fatal inter-group interactions I observed on Cocha Cashu with the Gang of Four suggest that territories are sometimes violently disputed. The role of territory quality and the frequency of female inheritance of natal territories are still areas in need of comparative research.

In this study, I showed that skill acquisition and social leadership demonstrate long lags in development that are clearly important features of giant otters' life history overall, and suggest support for hypotheses such as the Skills Hypothesis and Maturational Constraints Hypothesis. As predicted by van Schaik et al., 2006, a variety of other behavioral traits are expected to accompany species limited by slow skill development or neurological and brain development. These can include greater avoidance of predation risk through grouping, vigilance behavior, and avoiding high-risk habitats. Additionally, the authors predict lower frequency of violent territorial disputes, complex social interactions including reciprocal altruism, and more tolerant social relationships with inexperienced young (van Schaik et al., 2006). Most of these predictions do coincide with the case of the giant otter, with the possible exception of the lower violence in territorial disputes. However, further comparative work across other otters and carnivore (esp. Mustelid) species is required for a final conclusion.

Helping in defense, grooming, babysitting and aiding of lost babies, leading the group, or a combination of some of these behaviors constitues an optimization problem for an otter who stays with the natal family as a helper, modified by abilities at all of these tasks as he/she ages. Young giant otters also may choose NOT to stay and help in their natal family beyond reproductive age, as I observed with females on Cocha Cashu. Final decisions on whether to disperse and how to contribute may depend on a number of factors including personality, resource status on the territory, make-up of fellow family members, including sex and skill sets of siblings present, and potentially other factors not yet understood. Distentangling the various contributing factors is a challenge that remains to understanding giant otter dispersal and helping decisions.

Given the remaining uncertainties in underlying causes of giant otters' cooperative breeding, it would be highly instructive to observe differences in helping behavior and dispersal choices in giant otters in very different habitats, such as low-productivity black-water river and swamps of the Guyanas. In lower productivity lakes or rivers, where resources are more evenly dispersed than on the oxbow lakes of the Manú, holding a delineated, high-quality territory may be of lower importance than on Manú oxbow lakes. One could predict that territories in such sites might be more fluid, and the need to be a social climber to inherit a good breeding territory less influential. Under such a scenario, animals such as Olaf who stay on the natal territory as helpers for many years beyond sexual maturity should be less common; animals that disperse upon reaching sexual maturity might be the norm for both sexes.

Finally, I suggest that a study on play interactions in giant otters could be fruitful, possibly providing better indicators of hierarchical relationships than we currently recognize.

In conclusion, I feel that giant otters offer a rich and complex social system that we are only beginning to fully appreciate. This is the first study to suggest that slow learning may be an important factor in the evolution of giant otter sociality and cooperative breeding, although it does not explain the variability in the helping behavior of individual helpers. It is also the first study to suggest that the role of "family defender" might be taken up by single individuals at a time in each family, a suggestion not known to me for other carnivore species. Because the giant otter is diurnal, gregarious, and easily habituated to observation, it continues to offer a unique opportunity to further study the causes and consequences of helping behaviors in a top carnivore's social system.

	Animal Name	Sex	Year Born[1]	Month/Year Seen as Floater	Dispersal Year	Estimated Age at Dispersal[2]
Cocha Cashu						
	Ozstralia	Mother	1994		2007? [3]	n/a
	Otto	Father	1994		2007? [3]	n/a
	Oscar	M	1997		2000	2.5
	Ophelia	F	1998		2000	1.5
	Odum	M	1998		2002	3.5
	Orlando	M	1999		2003	3.5
	Odette	F	2000	9/2001	2001	1.3
	Orbit	M	2000		2004	3.5
	Orson	M	2001		2005	3.5
	Oliver	M	2001	8/2005	2005	3.8
	Olaf	F	2002	8/2007	2007	4.8
	Stripe	F	2003	8/2005	2005	1.8
	Splotch	F	2003	8/2005	2005	1.8
	Patty	F	2004		2006	1.5
	Osama	M	2004		2007? [3]	
	Oswald	M	2004		2007? [3]	
	Petunia	F	2005	10/2006	2006	1.2
	Estrella	?	2006		? [3]	
	Escher	?	2006		? [3]	
Cocha Salvador						
	Cacao	Mother	1990		d. 2008	n/a
	Fantasma	Father	1990		d. 2007	n/a
	Saguaro	M	2001		2004	2.5
	Linnaeus	F	2001	9/2004	2004	3.3
	Diabolo	M	2001	9/2004	2004	3.3
	Frita	M	2002		2005 [5]	2.5
	Fantasmita	M	2002		2006	3.5
	Virute	M	2002		2006	3.5
	Saguarito (Saggy)	M	2003		2006	2.5
	Mars	M	2003		2006 [5]	2.5
	Ziggy [4]	F	2004		n/a	n/a
	Rambo	M	2004		2007	2.5
	Achilles	M	2005		n/a	n/a
	Caiman	M	2006		n/a	n/a

[1] Data previous to 1997 provided by Frankfurt Zoological Society Giant Otter Project or Gray Pieja/Martin Kratt.

[2] If not observed as a floater, I calculated dispersal age assuming dispersal in January of the last year observed.

[3] Only Olaf was seen in 2007 after the lake was covered in the floating plant *Pistia stratiotes*.

[4] Ziggy took over the female breeding position on Cocha Salvador in 2008.

[5] Frita and Mars also observed on Cocha Cashu as floaters. In 2008, Frita and 2 partners raised young there.

Table 5.1: Birth and Dispersal Dates of Giant Otters Surviving to 1 year on Cocha Cashu and Cocha Salvador. Data based on our own observations on both lakes, and from other sources where needed to determine birthdates. Floaters were typically observed living on the natal territory, but hunting and sleeping apart from the family.

- Cooperative
  - Assistance
    - FishShare
      - Share of a fish to a beggar
    - Groom
      - Grooming another family member
    - BabyAssist
      - Babysit (stay in den with babies while other adults hunting)
      - Accompany (associate with babies within the hunting party)
      - Recover Lost Baby (leave off hunting to retrieve baby separated from the group)
      - Communicate position (call back and forth to baby to give location)
      - Play (play with baby)
    - DenCleaning
      - Digging in den, or clearing away vegetation in front of den
  - Defense
    - Snort (explosive sound at a perceived threat)
    - Periscope (straining neck out of water to investigate, intimidate potential threat)
    - Bubble (release of a large air bubble beneath the observer or a caiman)
    - Chase (chasing off a potential threat, such as caiman, bird or monkey)
    - Bite (bite an object, such as a stationary caiman or observer's paddle/boat)
    - Headbutt (headbutt of an object such as caiman or observer)
    - DenCruise (perform a circular cruise in the water out in front of the den)
- Non-cooperative
  - No Share
    - Begging event that results in No Share or Steal event
- Skill Acquisition and Leadership
  - Fish
    - FishCatch
      - Catch of small, medium and large fish
    - Handle Time
      - Timing of prey consumption when observable on logs
    - Beg event
      - Vocal screams and "focal" begging at otter with prey, or physical chase to steal an item
  - Leadership Roles
    - Waver scream to give position
    - "Suey hum" call to unite
    - Lead activity (observation that an animal is in front of moving group, often accompanied by "suey hum" to keep group together)
    - Redistribute fish (taking prey item from one animal to give to another or to discard and move the group forward)
    - Headshake (participate in headshake greeting after separation)
      - Give or Receive

Table 5.2: Classification Scheme of Giant Otter Behaviors. Some cooperative and leadership behaviors used in the analysis combine a number of observed behaviors due to low sample sizes of individual behaviors. Non-cooperative behaviors observed were limited to the single NoShare category.

	Cashu			Salvador			
Session	2004	2005	2006	2004	2005	2006	***Total***
AM1	19	7	9	8	5	5	***53***
AM2	7	7	5	6	7	5	***37***
PM1	13	10	5	9	3	4	***44***
PM2	10	4	7	4	3	1	***29***
Grand Total	***49***	***28***	***26***	***27***	***18***	***15***	***163***

Table 5.3: Distribution of Observational Sessions on Cocha Cashu and Cocha Salvador, 2004-2006. Session designations are: AM1 = 6am - 9am; AM2 = 9am-12pm; AM3 = 12pm - 3pm; AM4 = 3pm - 6 pm.

	Fish Catch[1]			Begging			Leadership Events		
Year	K	df	p	K	df	p	K	df	p
Cocha Cashu									
2004	**31.3**	**6**	**<.0001**	**32.1**	**6**	**<0.0001**	**39.1**	**4**	**<0.0001**
2005	**27.1**	**5**	**<.0001**	**21.4**	**4**	**0.003**	**64.0**	**6**	**<0.0001**
2006	**13.9**	**5**	**0.02**	9.8	5	0.083	**36.4**	**5**	**<0.0001**
Cocha Salvador									
2004	**20.0**	**7**	**0.01**	**45.9**	**5**	**<0.0001**	**40.1**	**5**	**<0.0001**
2005	**18.1**	**7**	**0.01**	**50.7**	**6**	**<0.0001**	**41.3**	**7**	**<0.0001**
2006	3.6	4	0.47	**45.9**	**5**	**<0.0001**	**23.6**	**6**	**0.001**

[1] FishCatch of medium and large fish only

Table 5.4: Kruskal-Wallis Statistics for Differences in Family Members' Skill and Leadership Behaviors. Fish Catch and Begging are single-category behaviors while Leadership combines a number of distinct observed behaviors as detailed in Table 5.2. Values in bold are statistically significant at alpha = 0.05.

	Fish Share			Grooming			Baby Assist			Defense		
Year	K	df	p	K	df	p	K	df	p	K	df	p
Cocha Cashu												
2004	**42.1**	**6**	**< 0.0001**	**20.7**	**6**	**0.002**	5.0	6	0.54	**158.9**	**9**	**<0.0001**
2005	**18.0**	**5**	**0.003**	**27.4**	**5**	**< 0.0001**	**19.7**	**5**	**0.001**	**53.5**	**5**	**<0.0001**
2006	**12.3**	**5**	**0.03**	**11.4**	**5**	**0.05**	**13.5**	**5**	**0.02**	**91.5**	**7**	**<0.0001**
Cocha Salvador												
2004	**20.8**	**7**	**0.004**	**44**	**7**	**< 0.0001**	6.5	6	0.37	**40.9**	**9**	**<0.0001**
2005	**20.1**	**7**	**0.005**	8.2	4	0.08	2.2	4	0.7	**32.2**	**9**	**0.0002**
2006	8.5	4	0.08	18	3	0.39	9.5	5	0.9	**44.6**	**6**	**<0.0001**

Table 5.5: Kruskal-Wallis Statistics for Differences in Family Members' Helping Behaviors. Fish Share and Grooming are single-category behaviors while Baby Assist and Defense combine a number of distinct observed behaviors as detailed in Table 5.2. Values in bold are statistically significant at alpha = 0.05.

	No Share		
Year	K	df	p
Cocha Cashu			
2004	6.4	6	0.38
2005	**12.5**	**5**	**0.03**
2006	**14.3**	**5**	**0.01**
Cocha Salvador			
2004	**17.2**	**9**	**0.045**
2005	5.3	7	0.63
2006	6.5	4	0.17

Table 5.6: Kruskal-Wallis Statistics for Differences in Family Members' Non-Cooperative (non-sharing) Behavior. A No Share behavior is attributed to an otter receiving a beg when the begging event results in either a refusal to share or a Steal event. Values in bold are statistically significant at the alpha = 0.05 level.

2004

Variables	2004Age	FishCatch	Begging	FishNoShare	FishShare	Groom	BabyAssist	DenBuild	Leader	AllDefense
2004Age	**1.00**	0.23	**-0.85**	0.58	**0.75**	**0.91**	0.15	0.05	-0.11	-0.61
FishCatch	0.23	**1.00**	-0.36	**0.68 (0.70)**	-0.04	0.43	0.04	0.20	-0.10	0.15
Begging	**-0.85**	-0.36	**1.00**	-0.57	**-0.86 (-0.62)**	**-0.73**	0.20	-0.20	0.29	0.55
FishNoShare	0.58	**0.68 (0.70)**	-0.57	**1.00**	0.28	0.60	0.30	0.50	-0.15	-0.16
FishShare	**0.75**	-0.04	**-0.86 (-0.62)**	0.28	**1.00**	0.50	-0.08	0.00	-0.16	-0.51
Groom	**0.91**	0.43	**-0.73**	0.60	0.50	**1.00**	0.16	0.05	-0.13	-0.41
BabyAssist	0.15	0.04	0.20	0.30	-0.08	0.16	**1.00**	0.05	**0.62 (0.65)**	0.41
DenBuild	0.05	0.20	-0.20	0.50	0.00	0.05	0.05	**1.00**	-0.27	0.00
Leader	-0.11	-0.10	0.29	-0.15	-0.16	-0.13	**0.62 (0.65)**	-0.27	**1.00**	0.53
AllDefense	-0.61	0.15	0.55	-0.16	-0.51	-0.41	0.41	0.00	0.53	**1.00**

N=11

2005

Variables	2005Age	FishCatch	Begging	FishNoShare	FishShare	Groom	BabyAssist	DenBuild	Leader	AllDefense
2005Age	**1.00**	0.24	-0.36	0.39	**0.83**	**0.67**	0.36	-0.02	**0.71**	0.48
FishCatch	0.24	**1.00**	0.10	0.36	0.21	0.24	**0.78 (0.77)**	0.34	0.26	0.50
Begging	-0.36	0.10	**1.00**	**-0.68**	-0.19	-0.08	0.15	0.09	-0.52	-0.43
FishNoShare	0.39	0.36	**-0.68**	**1.00**	0.07	0.16	0.13	-0.14	0.46	**0.72**
FishShare	**0.83**	0.21	-0.19	0.07	**1.00**	**0.72**	0.31	0.19	0.59	0.30
Groom	**0.67**	0.24	-0.08	0.16	**0.72**	**1.00**	0.15	0.19	0.11	-0.06
BabyAssist	0.36	**0.78 (0.77)**	0.15	0.13	0.31	0.15	**1.00**	0.41	0.51	0.52
DenBuild	-0.02	0.34	0.09	-0.14	0.19	0.19	0.41	**1.00**	0.17	0.07
Leader	**0.71**	0.26	-0.52	0.46	0.59	0.11	0.51	0.17	**1.00**	**0.84 (0.81)**
AllDefense	0.48	0.50	-0.43	**0.72**	0.30	-0.06	0.52	0.07	**0.84 (0.81)**	**1.00**

N=10

2006

Variables	2006Age	FishCatch	Begging	FishNoShare	FishShare	Groom	BabyAssist	DenBuild	Leader	AllDefense
2006Age	**1**	**0.817**	-0.633	0.588	**0.753**	**0.730**	0.495	0.192	**0.764**	0.639
FishCatch	**0.817**	**1**	**-0.843**	0.554	**0.738**	0.711	0.455	-0.358	0.565	0.476
Begging	-0.633	**-0.843**	**1**	-0.268	**-0.807**	-0.366	-0.236	0.420	-0.236	-0.217
FishNoShare	0.588	0.554	-0.268	**1**	0.530	0.524	0.315	-0.071	0.665	0.675
FishShare	**0.753**	**0.738**	**-0.807**	0.530	**1**	0.590	-0.024	-0.243	0.258	0.333
Groom	**0.730**	0.711	-0.366	0.524	0.590	**1**	0.242	-0.116	0.460	0.566
BabyAssist	0.495	0.455	-0.236	0.315	-0.024	0.242	**1**	0.347	**0.82 (0.78)**	**0.755**
DenBuild	0.192	-0.358	0.420	-0.071	-0.243	-0.116	0.347	**1**	0.402	0.345
Leader	**0.764**	0.565	-0.236	0.665	0.258	0.460	**0.82 (0.78)**	0.402	**1**	**0.786**
AllDefense	0.639	0.476	-0.217	0.675	0.333	0.566	**0.755**	0.345	**0.786**	**1**

N=8

Table 5.7: Spearman Rank Correlation Coefficients of Cocha Cashu and Cocha Salvador Helpers by Behavior and Year. Numbers in bold are statistically significant at the alpha = 0.05 level. Numbers enclosed in boxes represent correlation coefficients that retain significance at the alpha = 0.05 level after correcting for the partial correlation with Age (corrected coefficient in parentheses).

Models with All Datapoints

Fish Catch

	df1	df2	F-value	p-value
Intercept	1	17	209.20	<0.0001
Age	1	9	10.10	0.011

Begging

	df1	df2	F-value	p-value
Intercept	1	17	23.50	<0.001
Age	1	9	17.27	0.003

Leadership

	df1	df2	F-value	p-value
Intercept	1	17	9.64	0.006
Age	1	9	6.80	0.028

Sharing

	df1	df2	F-value	p-value
Intercept	1	17	113.20	<0.0001
Age	1	9	31.50	<0.001

Grooming

	df1	df2	F-value	p-value
Intercept	1	17	20.90	<0.001
Age	1	9	10.09	0.011

Baby Assists

	df1	df2	F-value	p-value
Intercept	1	17	15.60	0.001
Age	1	9	4.87	0.055

Defense

	df1	df2	F-value	p-value
Intercept	1	17	15.08	0.001
Age	1	9	0.63	0.449

No Shares

	df1	df2	F-value	p-value
Intercept	1	17	145.50	<0.0001
Age	1	9	15.01	0.004

Models with Outliers Removed

Grooming

	df1	df2	F-value	p-value
Intercept	1	16	33.50	<0.0001
Age	1	9	10.70	0.001

Baby Assists

	df1	df2	F-value	p-value
Intercept	1	16	24.49	<0.001
Age	1	7	0.25	0.630

Defense

	df1	df2	F-value	p-value
Intercept	1	15	34.40	<0.0001
Age	1	6	1.39	0.283

Table 5.8: ANOVA Results on Linear Mixed Effects Models. Effect of Age on different skill and helping behaviors from Mixed Effects Models. Models in the left column incorporate all datapoints, while models in the right column have outliers removed. See text for details.

	Fish Catch	Begging	Leadership	Sharing	Grooming	Defense	BabyAssists	No Share
Intercept	0.54	0.75	-0.05	-0.04	-0.10	0.63	0.01	0.20
Age	0.21	-0.26	0.08	0.27	0.19	0.21	0.08	0.14
AIC	17.29	15.06	-28.02	-0.96	11.65	96.45	-11.53	-16.30
logLik	-4.65	-3.53	18.01	4.48	-1.83	-44.22	9.77	12.15
level-1 R^2	0.38	0.39	0.23	0.60	-0.08	0.01	0.28	0.50
% variance from Random Effects	0.34	0.01	0.43	<<0.001	0.53	0.43	0.44	0.33

Table 5.9: Summary Statistics on Mixed Effects Models. Effect of Age on different skill and helping behaviors from Linear Mixed Effects Models.

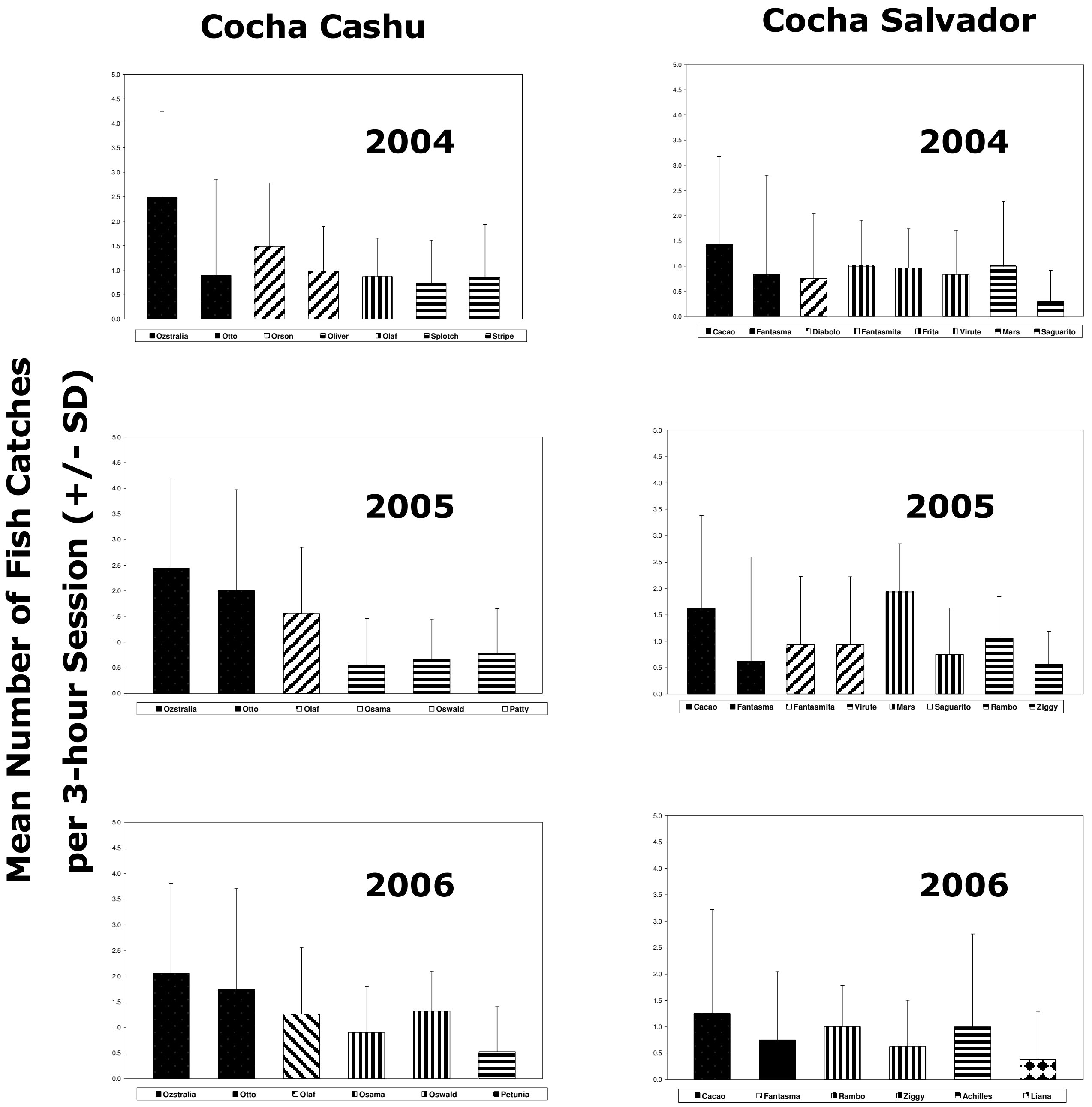

Figure 5.1: **Mean Number of Fish Catches per 3-hour Session.** Medium (20-30cm) and large (>30cm) fish size classes combined for giant otter family members by lake and year. Filled rectangles are parents; left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds, and diamond-patterned <1yr. old.

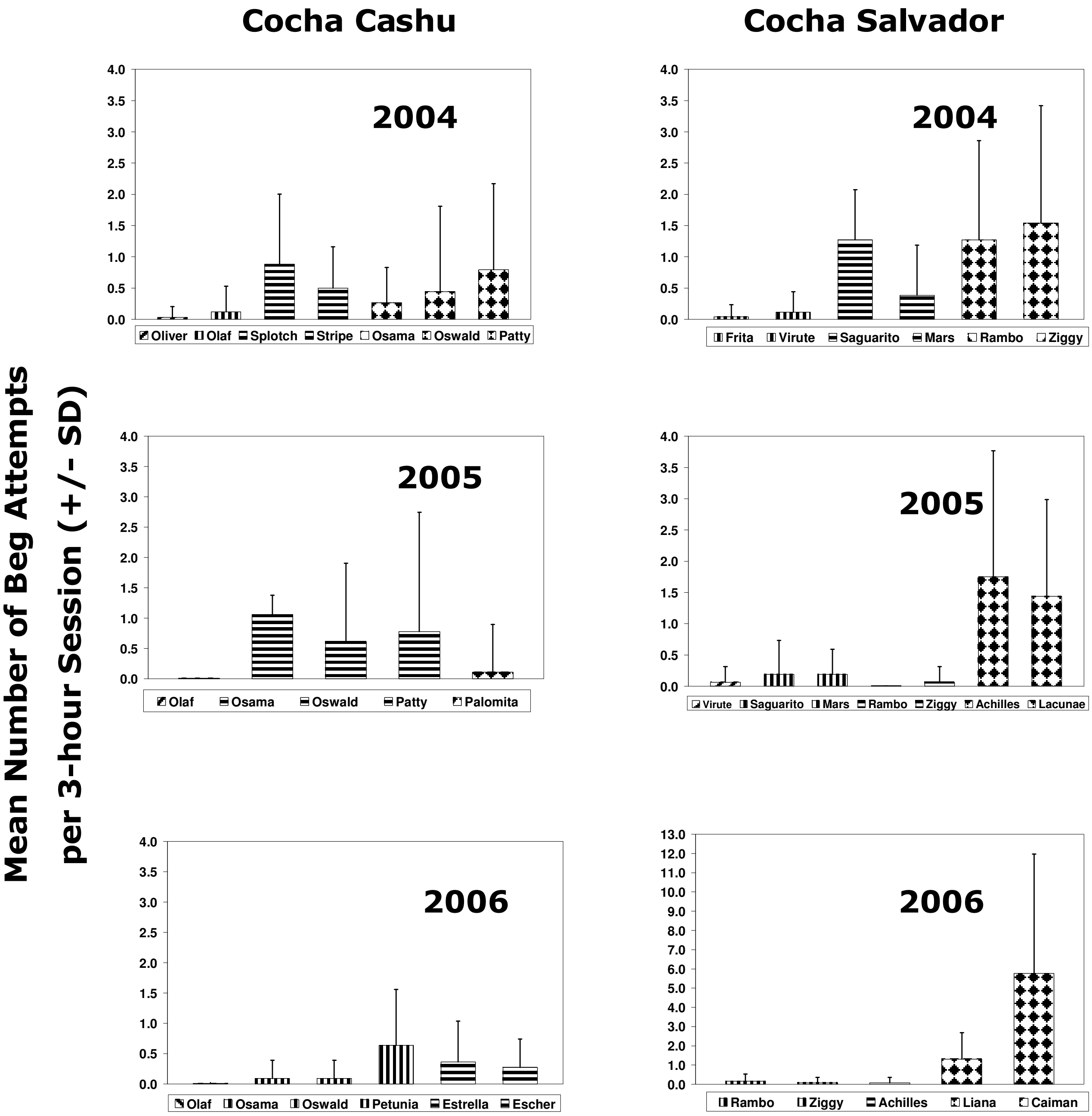

Figure 5.2: **Mean Number of Beg Attempts per 3-hour Session.** Helpers and young-of-year only by lake and year. Unknowns removed. Left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds, and diamond-patterned <1yr. old. (Note different scale on Salvador 2006 from others).

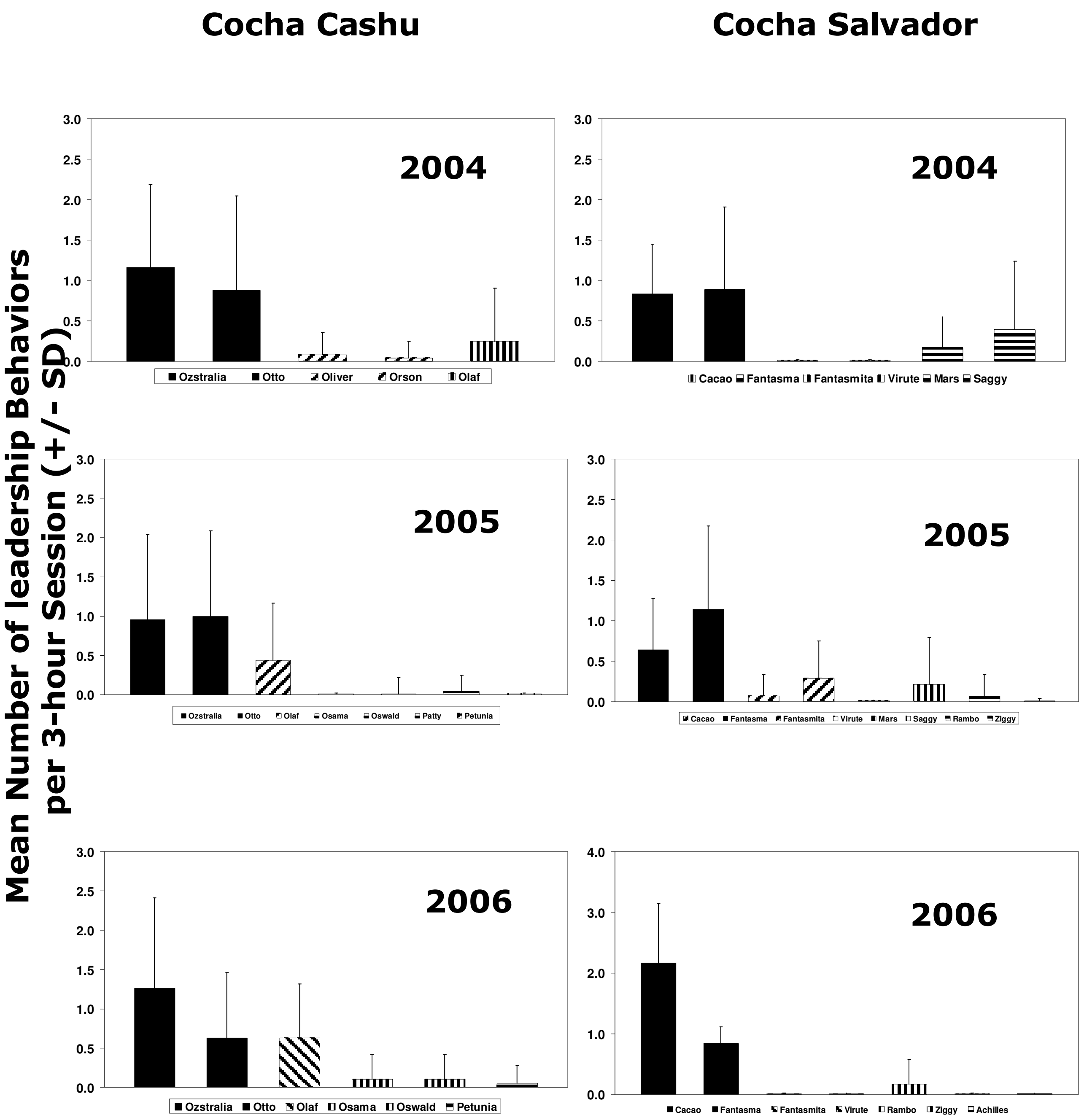

Figure 5.3: **Mean Number of Leadership Acts per 3-hour Session.** Parents and helpers only by lake and year. Unknowns removed. Left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds, and diamond-patterned <1yr. old. (Note different scale on Salvador 2006 from others).

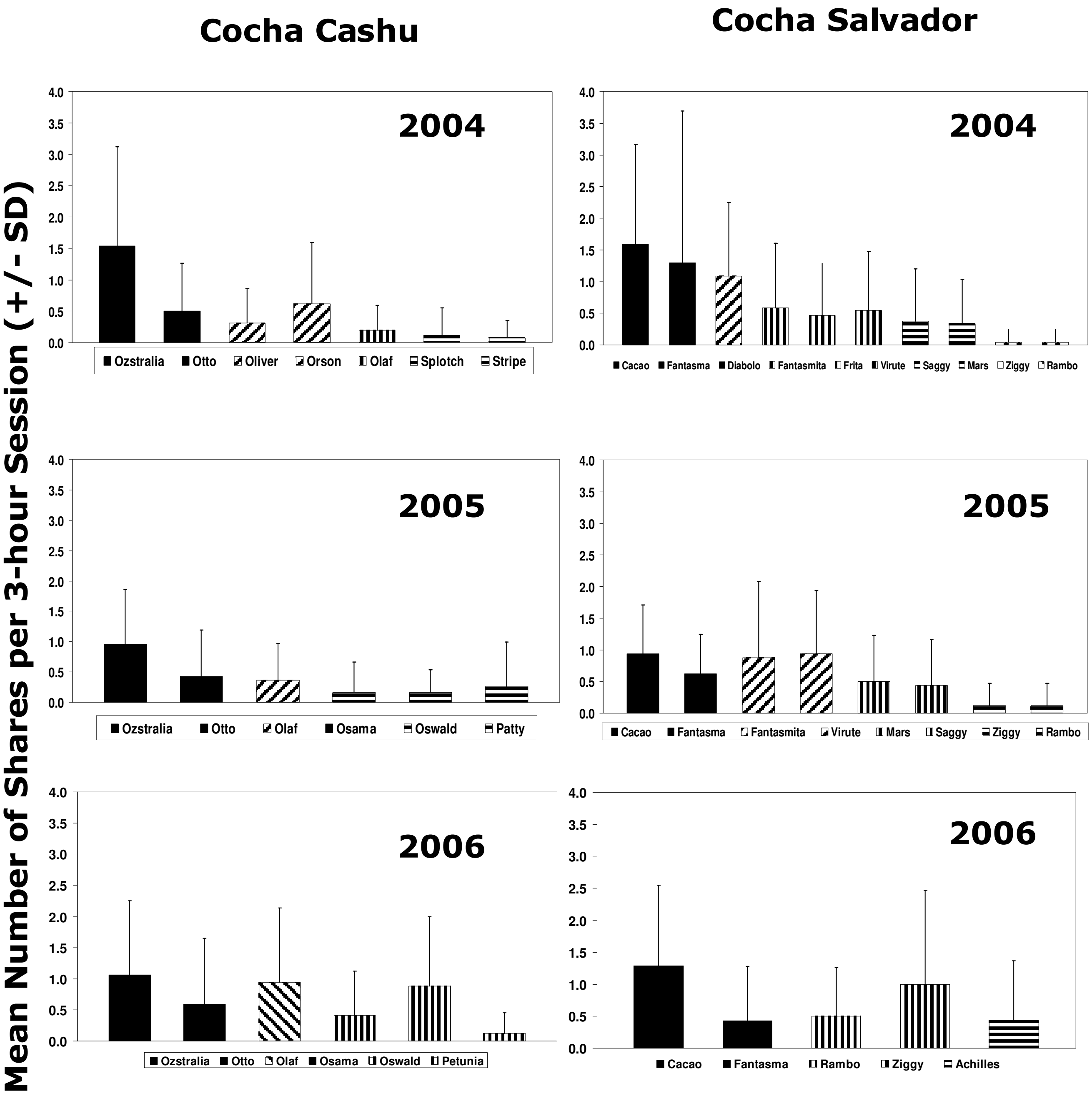

Figure 5.4: **Mean Number of Shares per 3-hour Session.** All parents and helpers, and young-of-year where appropriate, by lake and year. Unknowns removed. Solid rectangles are the parents; left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds, and diamond-patterned <1yr. old.

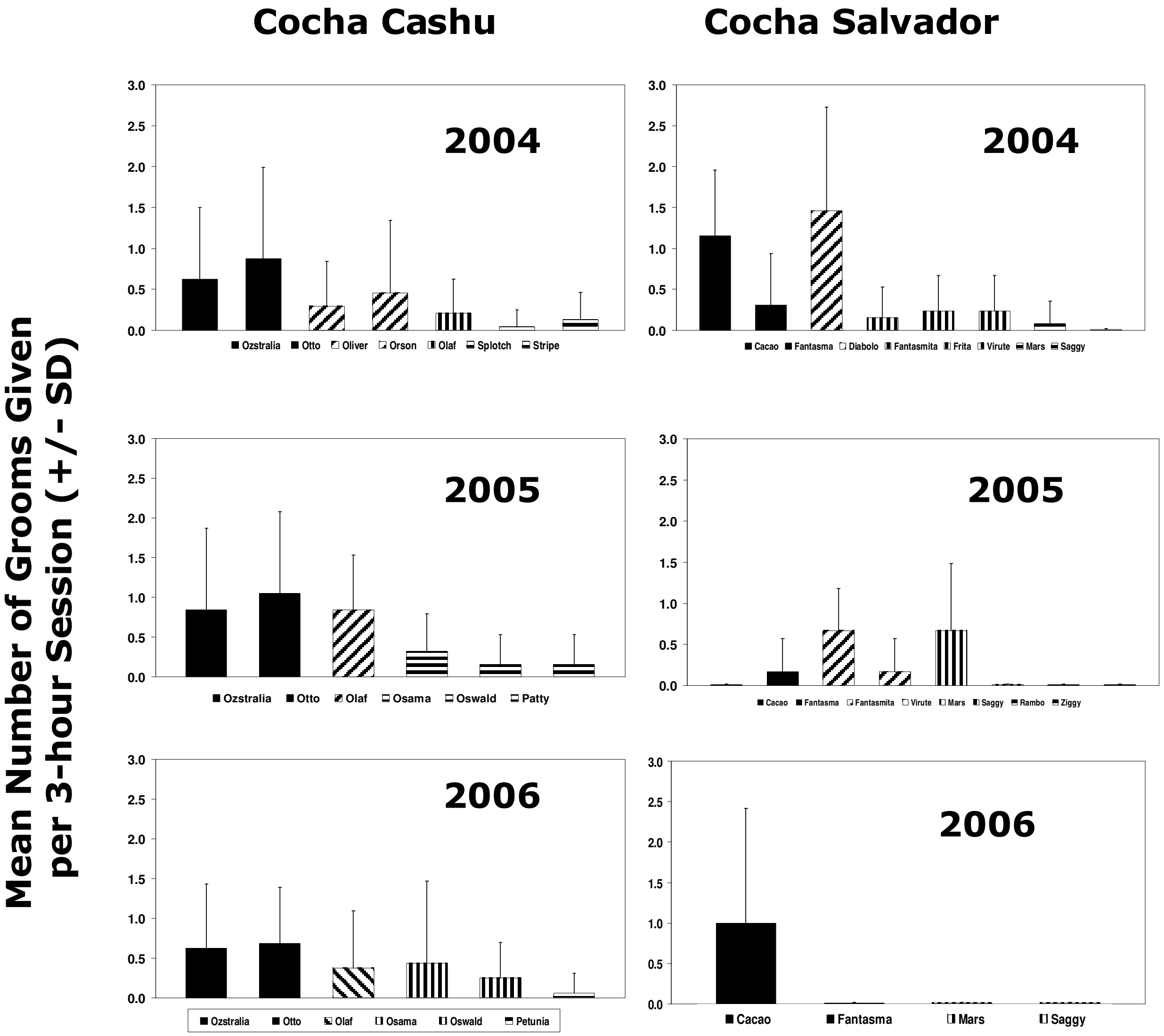

Figure 5.5: **Mean Number of Grooms per 3-hour Session.** All family members observed, by lake and year, unknowns removed. Solid rectangles are the parents; left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds, and diamond-patterned are <1yr. old.

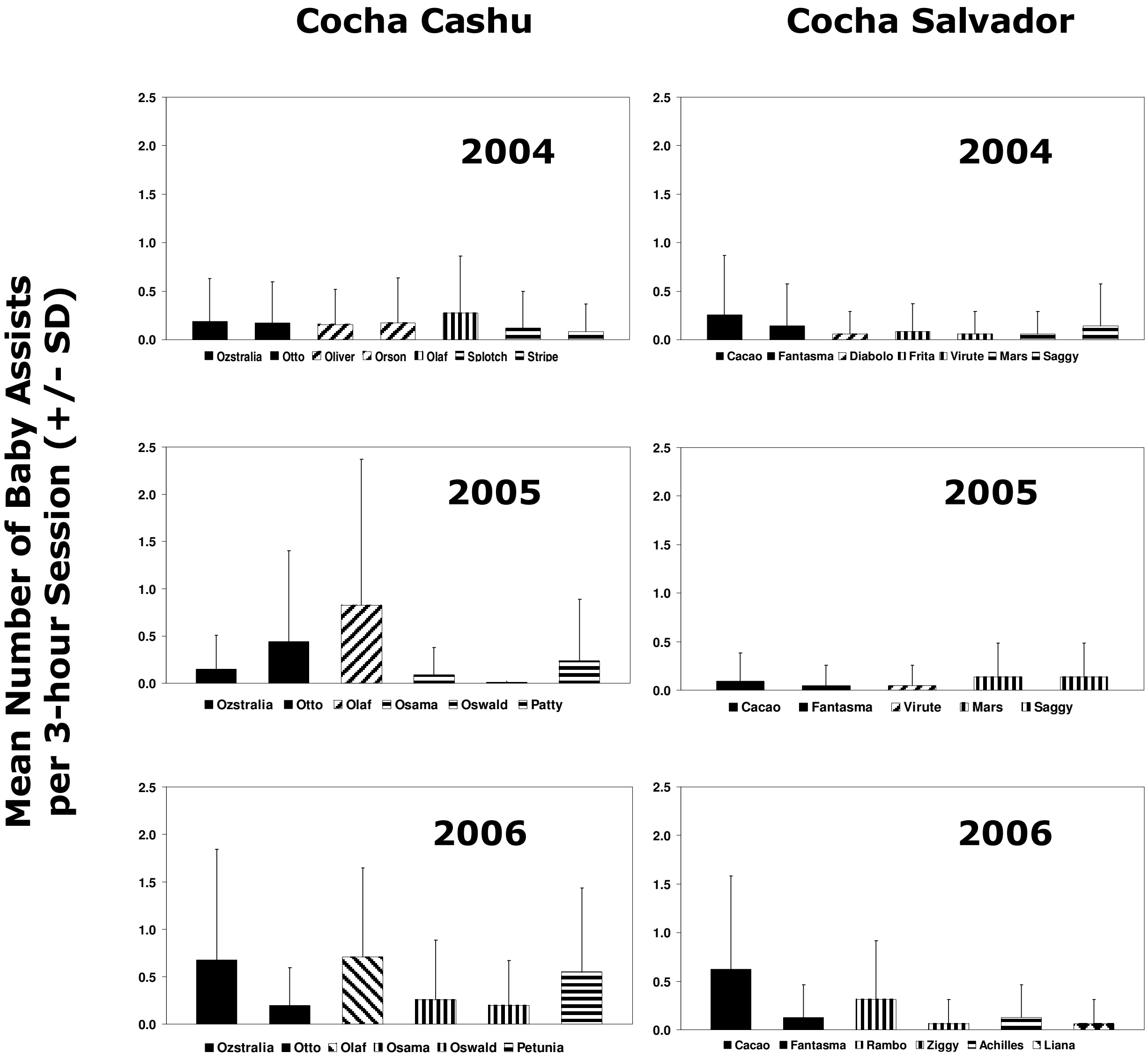

Figure 5.6: **Mean Number of Baby Assists per 3-hour Session.** Parents and helpers, by lake and year, unknowns removed. Solid rectangles are the parents; left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds.

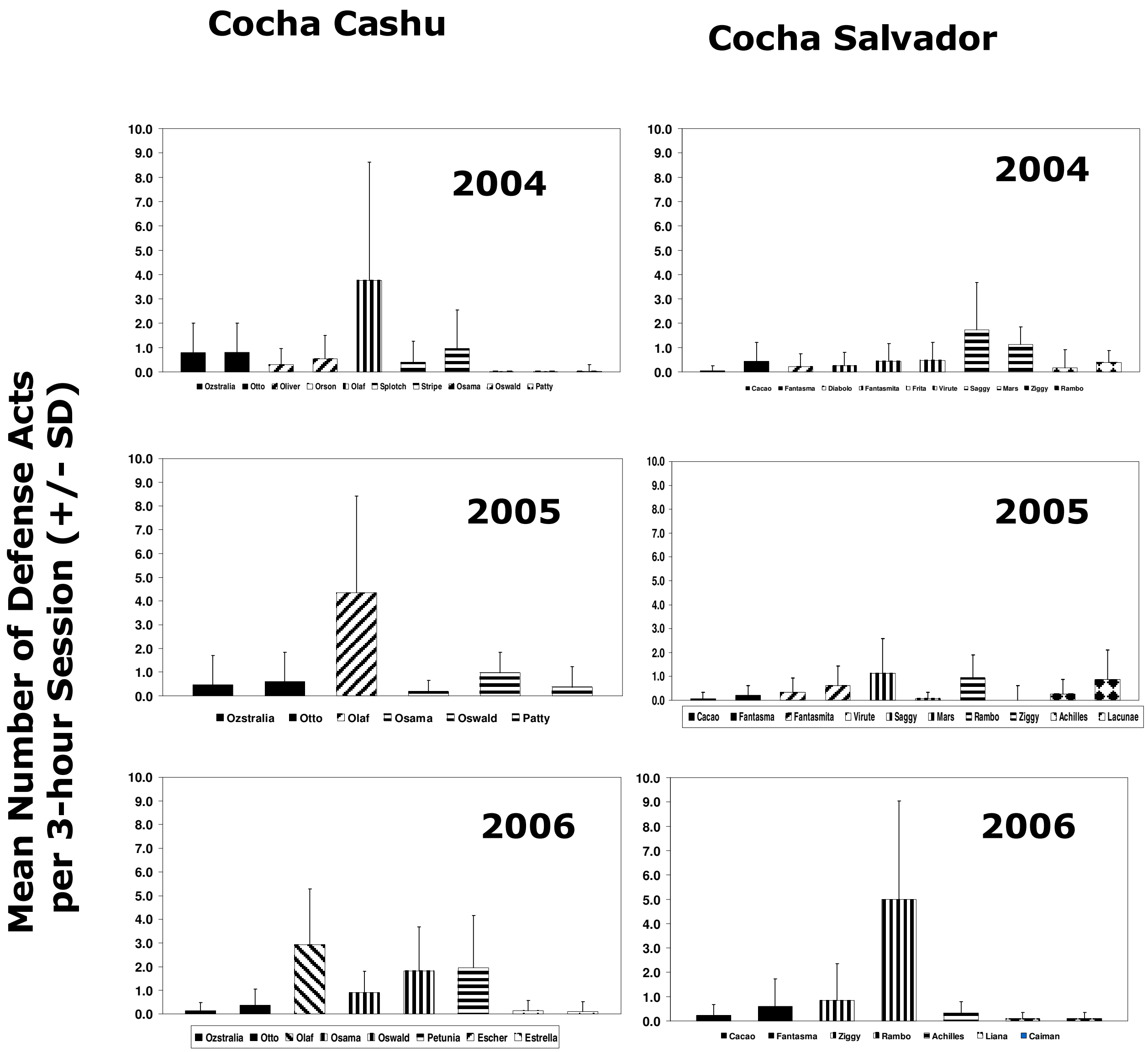

Figure 5.7: **Mean Number of Defense Acts per 3-hour Session.** All family members, by lake and year, unknowns removed. Solid rectangles are the parents; left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds, and diamond-patterned are <1yr. old.

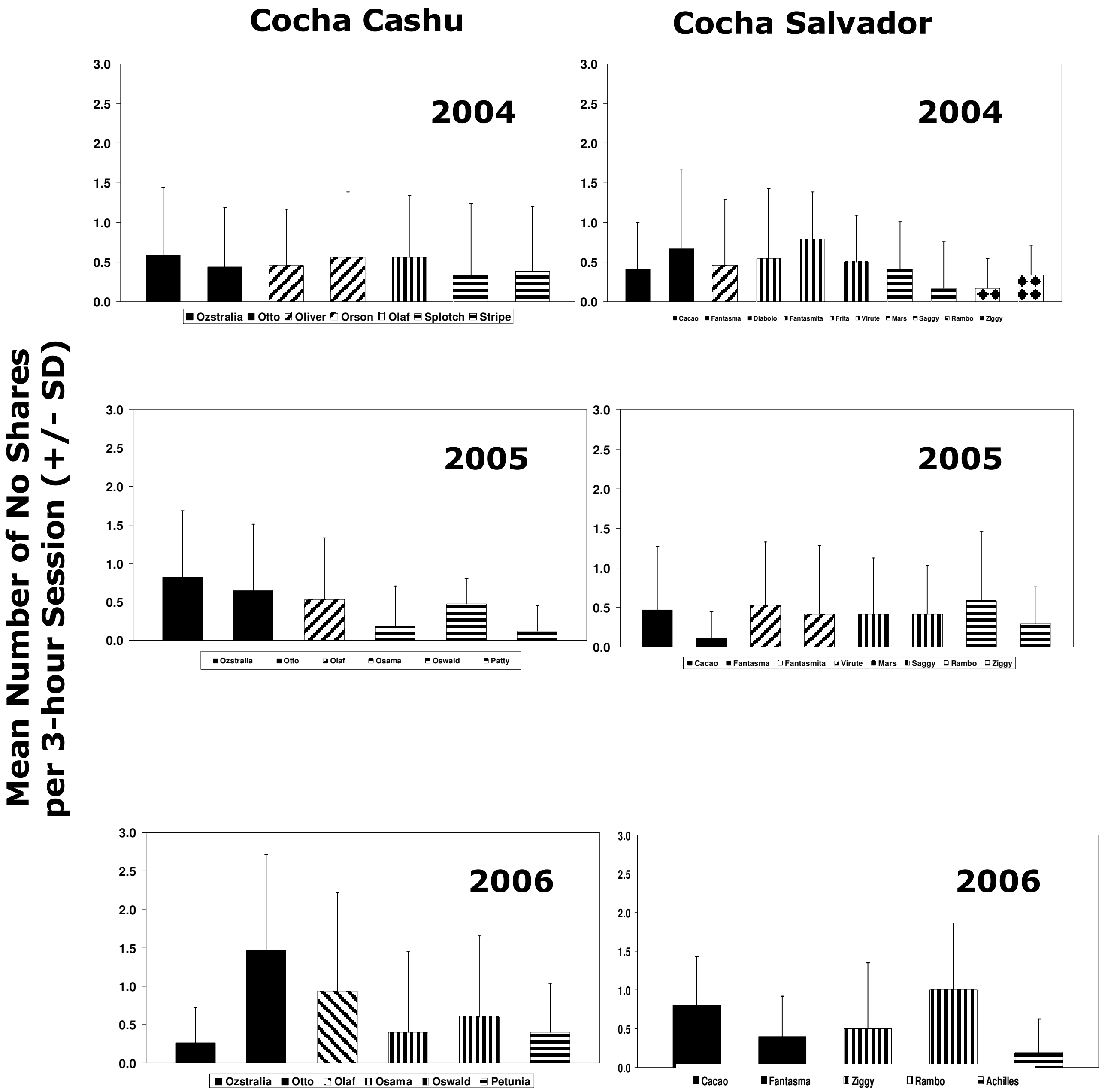

Figure 5.8: **Mean Number of No Shares per 3-hour Session.** Based on sum of begs received resulting in a refusal to share or a steal. All family members, including young-of-year where applicable, by lake and year. Solid rectanbles are the parents; Left-handed diagonal stripes 4 yr-olds; right-handed diagonals 3 yr-olds; vertical stripes 2 yr-olds, horizontal stripes 1 yr-olds, and diamond-patterned <1yr. old.

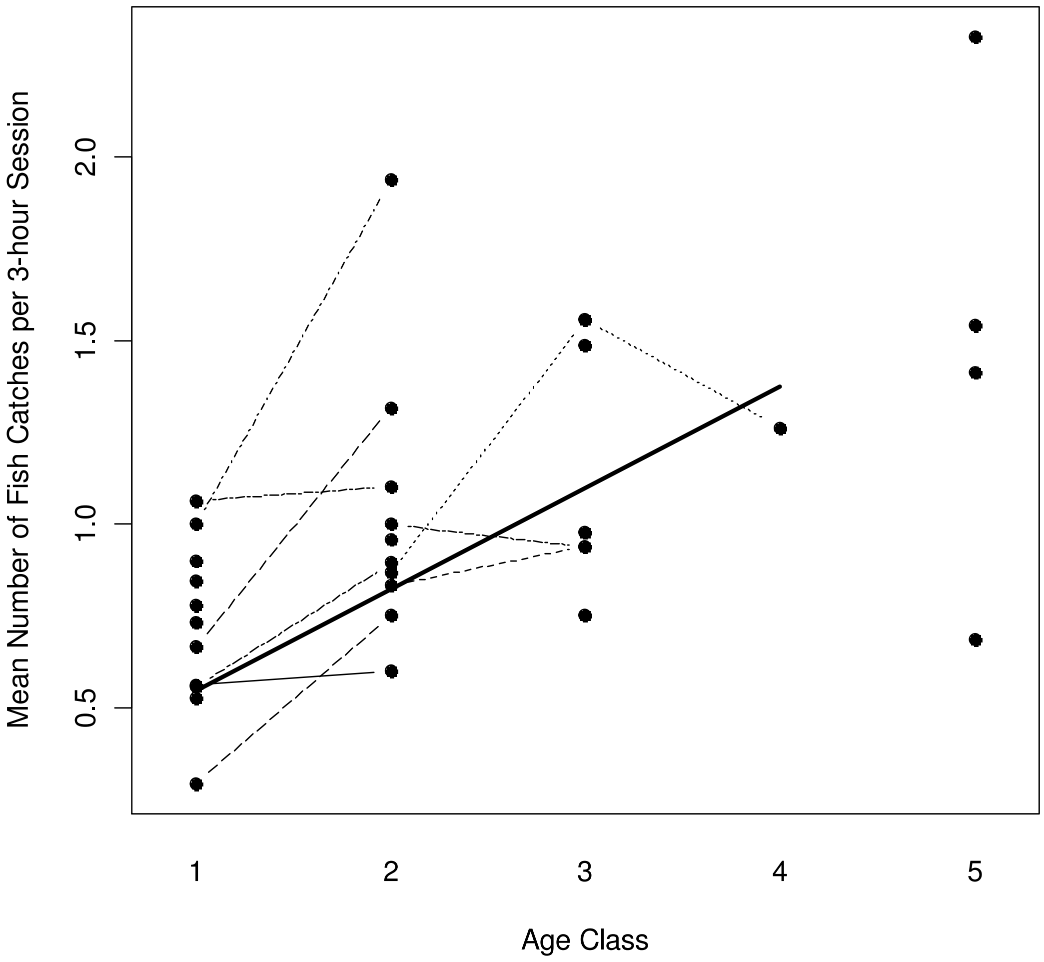

Figure 5.9: Linear Mixed Effects Model on Fish Catch Rate. Random intercept model overlaid on raw data of Otters' Mean rate of Fish Catch per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid line represents the final model fit between Age Classes 1-4. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

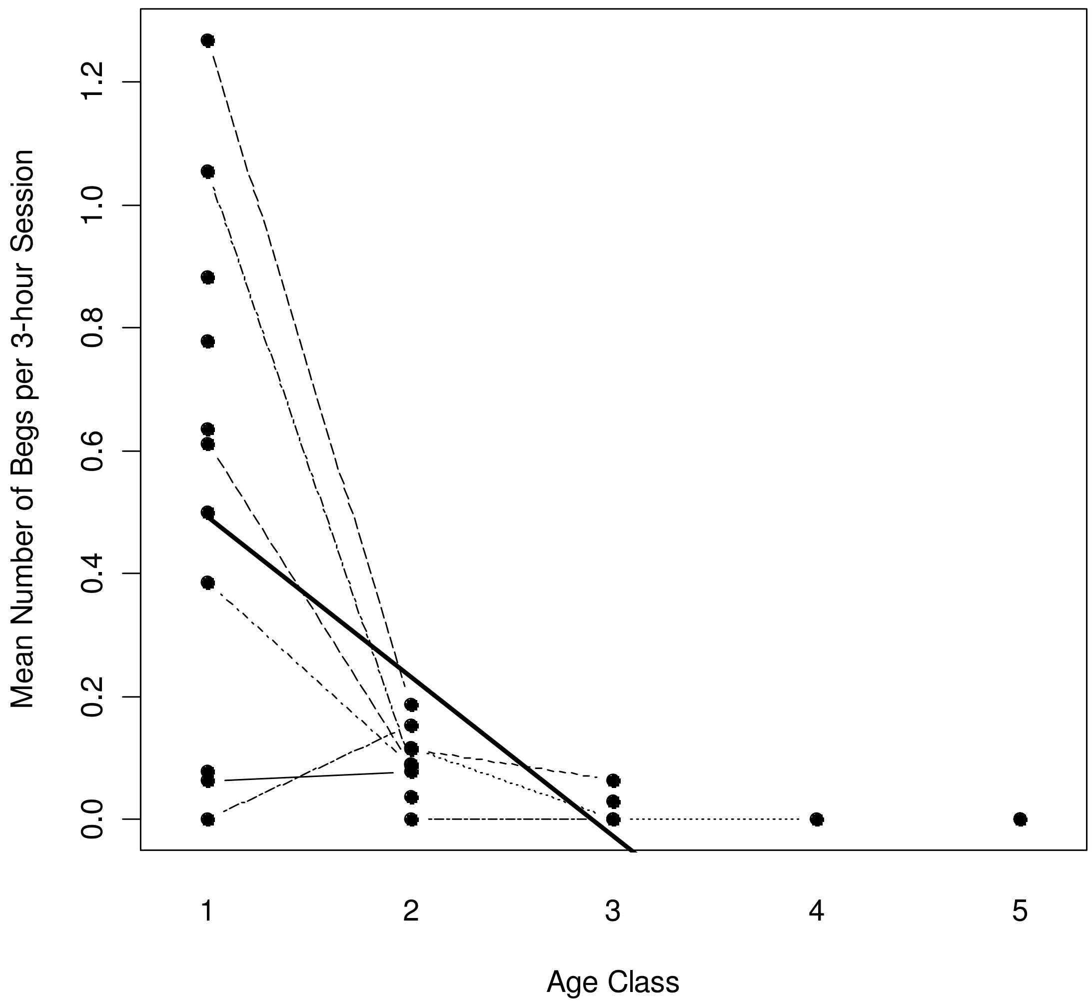

Figure 5.10: Linear Mixed Effects Model on Begging Rate. Random intercept model overlaid on raw data of Otters' Mean rate of Begging per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid line represents the final model fit between Age Classes 1-4. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

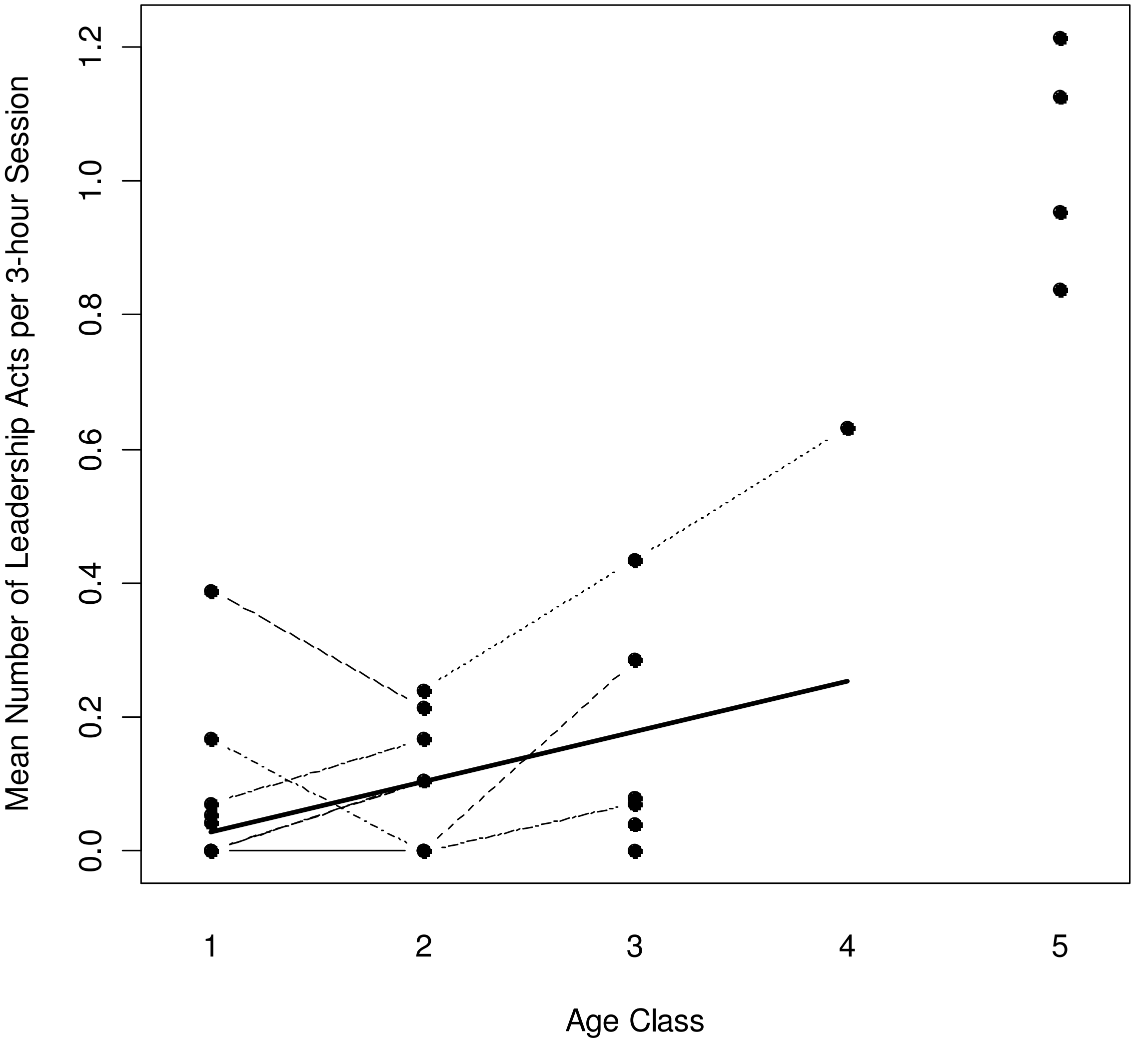

Figure 5.11: Linear Mixed Effects Model on Leadership Rate. Random intercept model overlaid on raw data of Otters' Mean rate of Leadership per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid line represents the final model fit between Age Classes 1-4. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

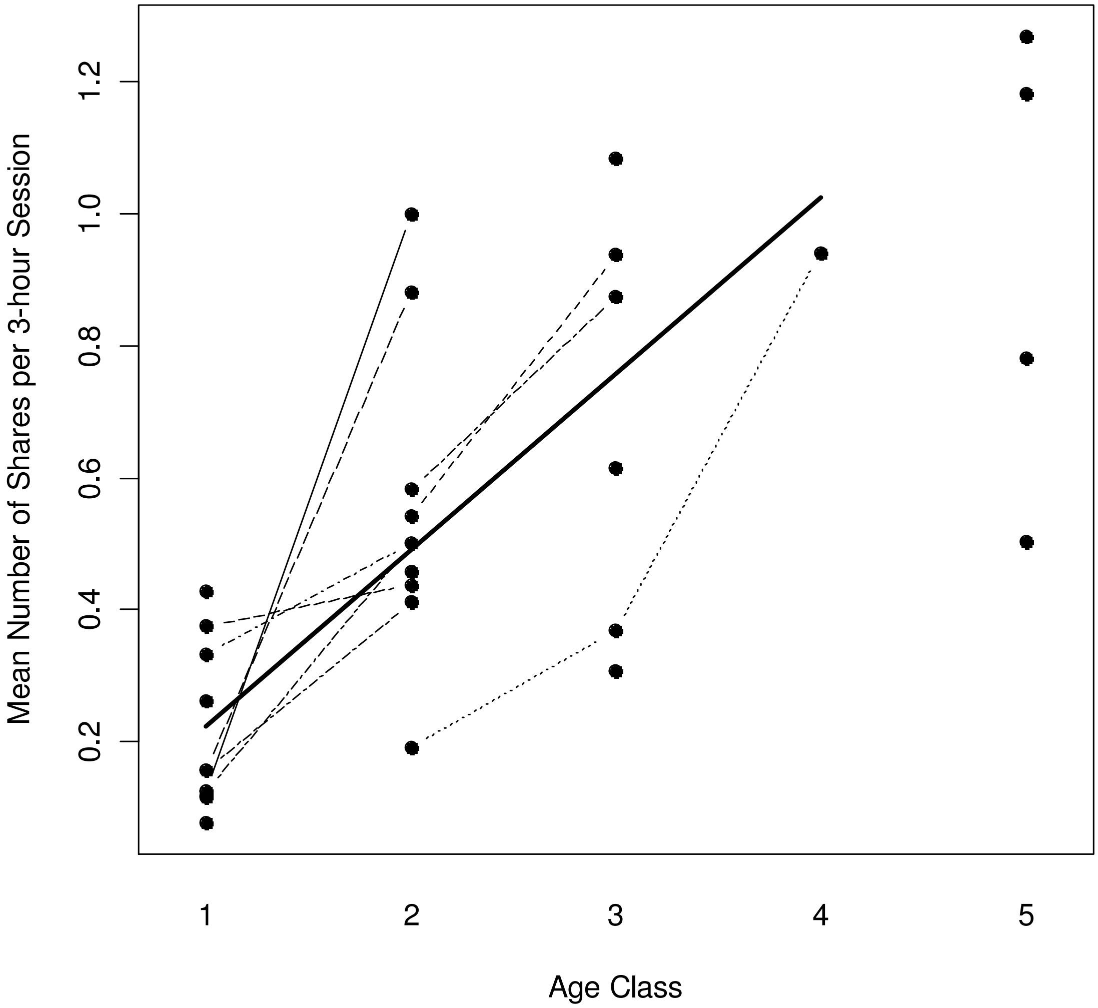

Figure 5.12: Linear Mixed Effects Model on Sharing Rate. Random intercept model overlaid on raw data of Otters' Mean rate of Sharing per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid line represents the final model fit between Age Classes 1-4. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

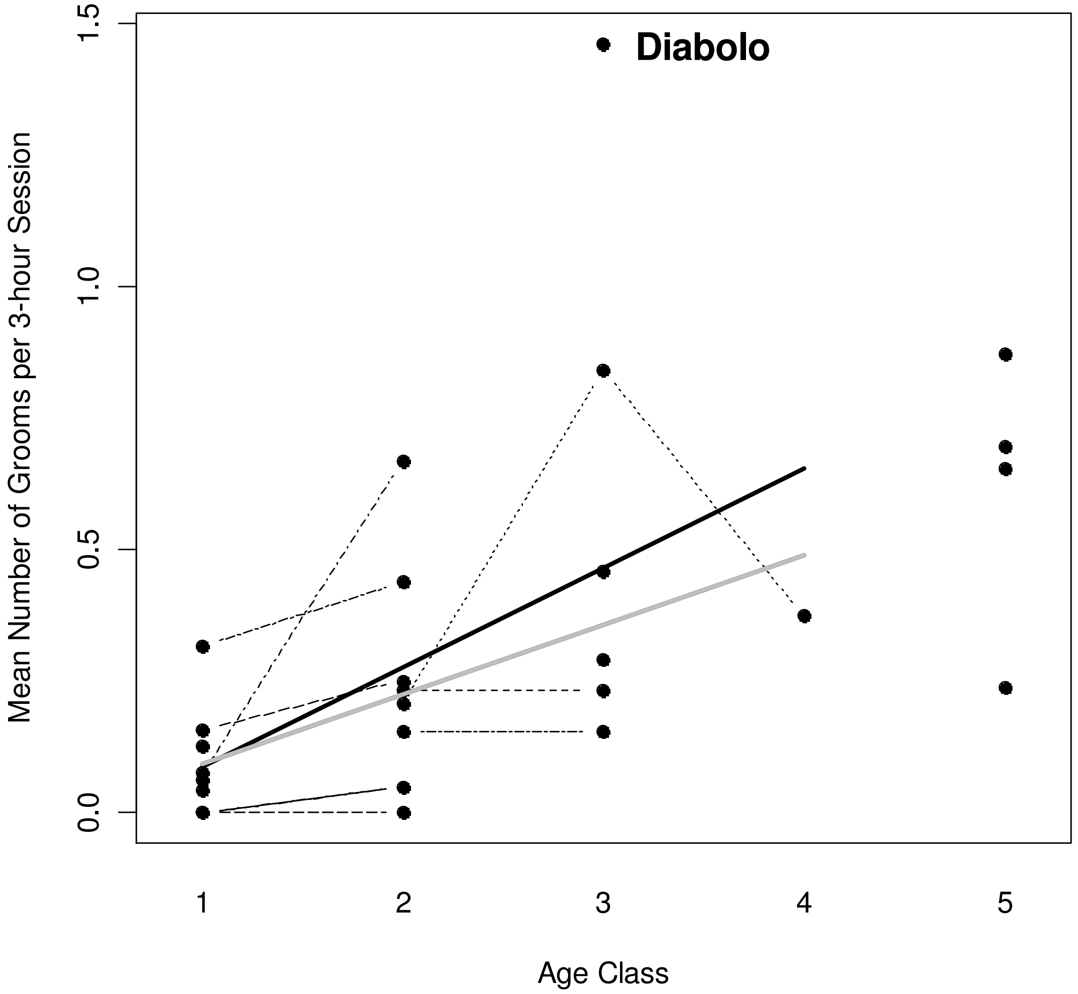

Figure 5.13: Linear Mixed Effects Model on Grooming Rate. Random intercept model overlaid on raw data of Otters' Mean rate of Grooming per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid black line represents the final model fit between Age Classes 1-4. The solid gray line represents the model with the outlier Diabolo removed. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

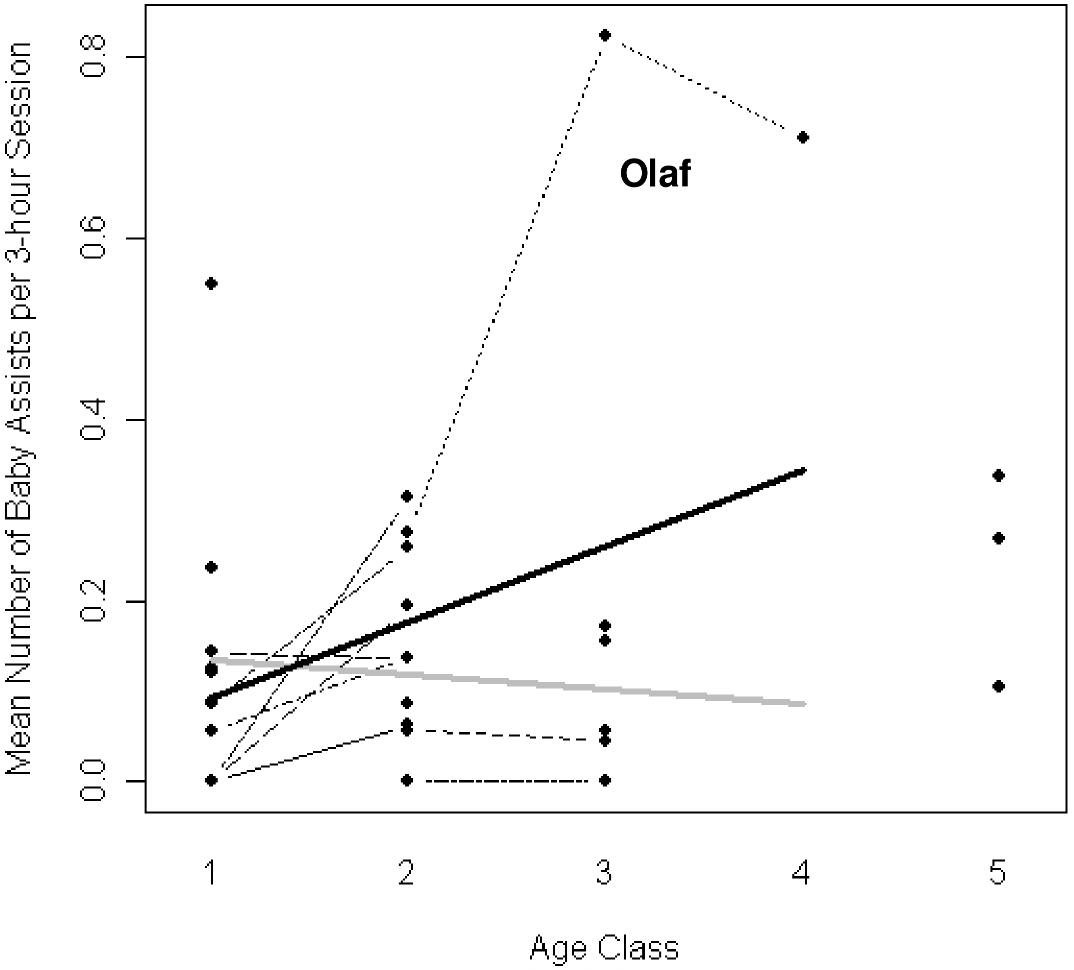

Figure 5.14: Linear Mixed Effects Model on Baby Assist Rate. Random intercept model overlaid on raw data of Otters' Mean rate of Baby Assist per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid black line represents the final model fit between Age Classes 1-4. The solid gray line represents the model with the outlier Olaf removed. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

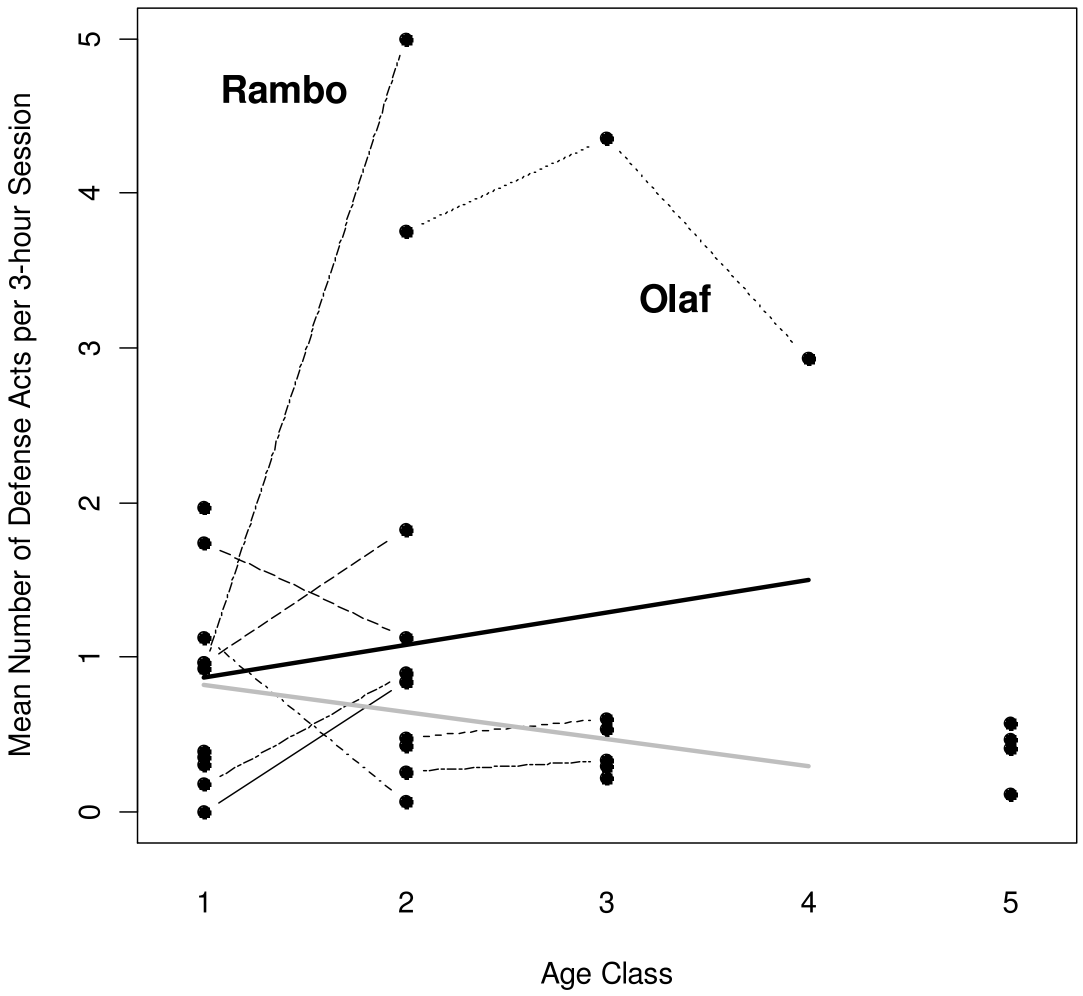

Figure 5.15: Linear Mixed Effects Model on Defense Rate. Random intercept model overlaid on raw data of Otters' Mean rate of Baby Assist per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid black line represents the final model fit between Age Classes 1-4. The solid gray line represents the model with the outliers Olaf and Rambo removed. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

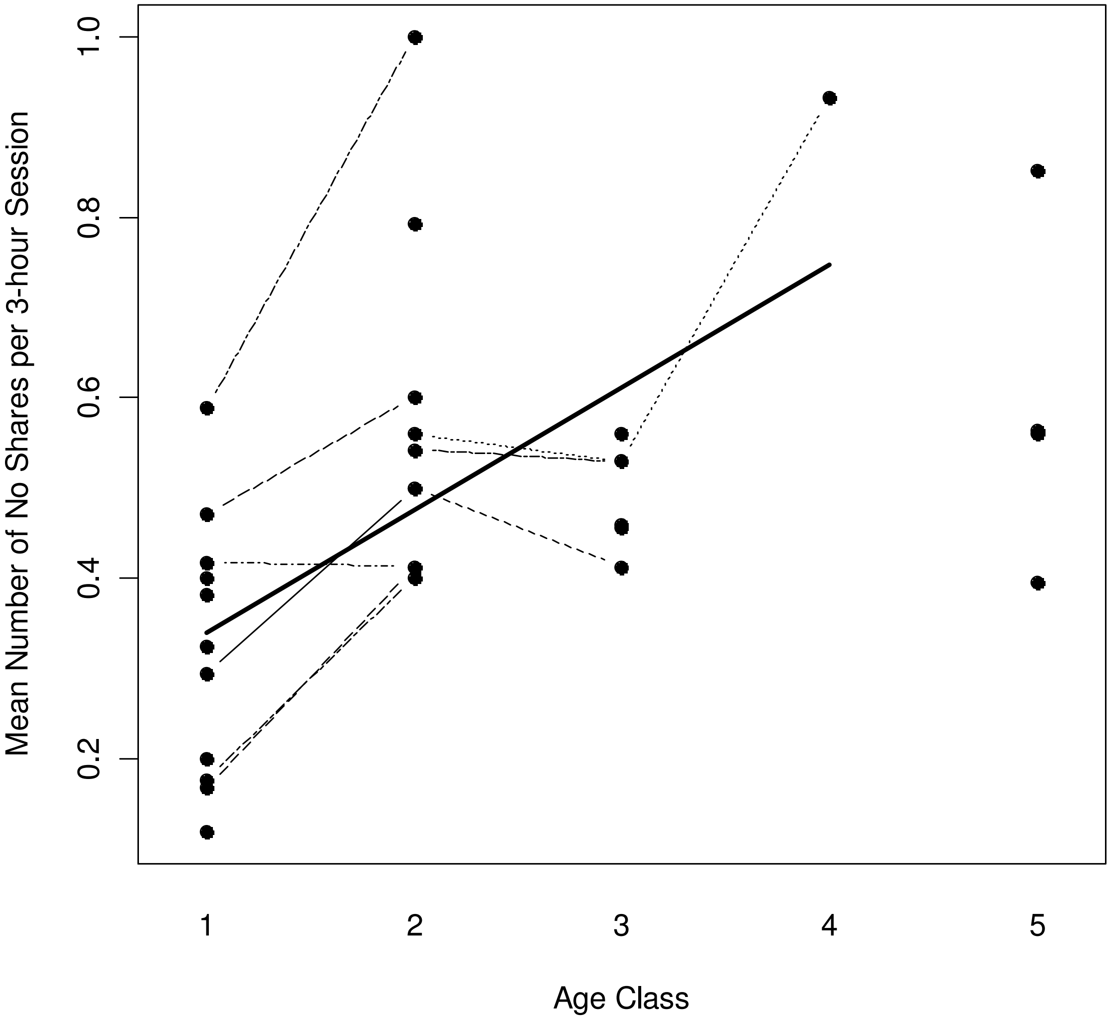

Figure 5.16: Linear Mixed Effects Model on No Share Rate. Random intercept model overlaid on raw data of Otters' Mean rate of No Share per 3-hour session. Dashed lines connect individual otters' repeated measures across years, and the solid line represents the final model fit between Age Classes 1-4. The model was fit to helpers in Age Classes 1-4. Parents' Data assigned to Age Class 5 for comparison.

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CHAPTER 6 FROM PROVIDER TO BEGGAR: SUPPLEMENTAL FEEDING OF AN AGED MATRIARCH IN THE GIANT OTTER (*PTERONURA BRASILIENSIS*)

ABSTRACT

Care and feeding of elderly family members is a human trait rarely reported to be found in other animals, but which I observed in a wild family of giant otters. My observations demonstrate a role-reversal in a >11 y old mother, in which she switched from being a provider of large prey items to a beggar from her partner and offspring during the first year she was observed without any offspring. In 2007, during an 8-day observation period, she initiated 43 begging bouts, which resulted in 11 shares. These 11 shares were distributed evenly among 3 of the 4 other family members, with only the oldest male offspring failing to share with her. Both non-adaptive and adaptive hypotheses could explain the family members' aid to the elderly mother. Family members may help the aging mother without any expectation of future benefits because they redirect helping behavior normally provided to young of the year, or because helpers are trained to follow their mother as the dominant leader of the family. Family members may also help the aging mother under the expectation that she will provide ongoing benefits in spite of her aged condition in keeping with the "Grandmother Hypothesis" of adaptive menopause.

INTRODUCTION

Investigators of human behavior in the social sciences continue to hold assumptions of human uniqueness over animals on topics such as cooperation and social interactions, in spite of the fact that many behaviors once thought to occur exlusively in humans have subsequently been shown to occur in other animals (de Waal, 2007). For example, primates and birds use tools, and cultural traditions spread among cetaceans, chimpanzees, *Cebus* monkeys, orangutans, and coral reef fishes (Nishida, 1980; Rendell and Whitehead, 2001; Struhsaker and Leland, 1977; van Schaik et al., 2003; Warner, 1988; Weir et al., 2002; Wright, 1972).

Another human trait that is rarely reported for animals other than humans is the care and feeding of elderly family members. I observed feeding assistance to be given regularly to a > 11 y old female giant otter during approximately 8 days of continuous observation, suggesting that helping behavior in cooperatively breeding giant otters can extend to the aged and infirm.

Helping of elderly family members is rarely documented in wild animals, but a few anecdotal reports suggest the possibility of observing it among social animals. Perhaps the most similar behavior reported to date is the tolerance shown by African wild dogs (*Lycaon pictus*) towards sick or injured family members who are allowed to feed at group kills (Malcolm, 1980). Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are also reported to assist injured family members (Monterey Bay Aquarium, 2008). Among captive animals, bonobos (*Pan paniscus*) frequently aid other group members. One example at the Milwaukee County Zoo is the response of group members to Kidogo, an elderly bonobo who suffered from a serious heart condition. He received assistance from multiple members of his group, while others tried to take advantage of his condition (de Waal, 1997). To my knowledge, however, no other study has reported detailed food sharing data with a family elder in a wild group of animals under observation.

The Giant Otter

The giant otter is unique among the 13 extant species of otters in breeding cooperatively. The mated pair remains together year-round throughout their reproductive history, and young are born approximately annually, with occasional reports of multiple litters in a year (G. Londroño, pers. comm.; Duplaix, 1980; Groenendijk, pers. comm.). Juveniles stay with the family in which they were born for 1.5 to 4 y, and family groups can consist of 10-13 individuals (pers. obs.). Mortality of young in the first year of life is about 35%, but after reaching 1 y of age, most animals survive until dispersal (Groenendijk and Hajek, 2006). Reproductive maturity occurs around 2 y of age (Sykes-Gatz, 2005). All family members appear to assist young-of-the-year through various tasks such as defense, grooming, and sharing prey (Duplaix, 1980).

Although certain behaviors, such as greeting headshakes, wrestling, and play may indicate means of maintaining dominance relationships among family members (pers. obs.; cf. Chapter 5), giant otters do not have a dominance hierarchy that determines access to food, such as is seen in some canids and primates (Duplaix, 1980; Harrington et al., 1983; Mech and Boitani, 2003; Silk, 1986). Instead, nearly every prey item is either eaten by the otter that catches it or it is wholly or partially shared with beggars. Beggars are typically <1 y old offspring, although yearlings and adult helpers also receive shares when a very large prey item is available to be shared among family members.

The Cocha Salvador Giant Otter Family

This report is based on my observations of one of the two habituated families of wild giant otters with whom I worked on oxbow lakes in the Manú National Park and Biosphere Reserve (MBR), Peru. Feeding and behavioral observations have been ongoing since 2001 for the resident otter families of Cocha Cashu and Cocha Salvador, with this report focusing on events occurring in the Cocha Salvador family during 2004-2007.

The female Cacao is known from annual censuses by the Frankfurt Zoological Society Giant Otter Project (FZS) to have been the breeding female on Cocha Salvador since at least 1999 (J. Groenendijk and F. Hajek, pers. comm.). Cacao and her first partner, Fantasma, produced litters of 1-4 cubs annually until 2006. In September 2007, Fantasma was absent from the Cocha Salvador group, presumably having died after I last observed him in October 2006. FZS researchers have never seen a female younger than 3 years with a litter, so a minimum age for Cacao during 2007 observations is 11 y (Groenendijk, pers. comm.). Photographic evidence indicates that Fantasma was born in 1991 (M. Kratt and G. Pieja, pers. comm.), thus disappearing when 15 y of age. Cacao had acquired a new partner, Firecat, by the time of September 2007 observations, although no young were present. Firecat's age is unknown, but presumably is a minimum of 3 y.

Three juveniles remained with Cacao and Firecat in 2007, including one reproductive-age female (Ziggy, born 2004) and two younger males (Achilles, born 2005 and Caiman, born 2006). The other young born in 2006 (Liana, sex unknown) was absent, presumably not surviving to 1 y, and a 3 y male (Rambo) last seen in October

2006 was also absent, presumably having dispersed. Although no newborns appeared with the family in 2007, the family's behavior otherwise seemed normal. The new male was well-integrated into the family group and he both groomed and shared prey with all other family members.

Cacao did not appear sick or injured, but it appeared that her eyesight and mobility were somehow compromised. She frequently became separated from the family group and she had lower hunting success than in previous years. She begged from other family members, a behavior rarely observed for parents either at Cocha Cashu or at Cocha Salvador. In this report I compare her behavior in 2007 to other years and describe the response to her begging by her family members.

METHODS

Study Site and Observation Methods

The Manú Biosphere Reserve (MBR) protects the entire watershed of the Río Manú and a variety of upland and lowland forest habitats (cf. Chapter 2). Cocha Cashu Biological Station, within the MBR, is a lowland tropical moist forest site, with elevation ~400 m and annual rainfall ~ 200 cm (Terborgh, 1983). The Río Manú is a "whitewater" river, signifying that it carries abundant sediment from the nearby Andes (Barthem et al., 2003). Periodic channel avulsion creates numerous isolated oxbow lakes, such as Cocha Cashu and nearby Cocha Salvador, that are the preferred habitats of giant otters (Schenck, 1999). By nature of their isolation from the main river, and high allocthonous nutrient input from surrounding vegetation, oxbow lakes are highly productive habitats. Giant otter families maintain smaller territtories on Manú oxbow lakes than those using lower productivity sites (Duplaix 1980; Laidler, 1984). Cocha Salvador, the largest lake in the MBR, is approximately 6.6 km long and 175m wide, and constitutes the entirety of the Salvador otter family's observed territory. The family was present on the lake every day I visited during both wet and dry seasons.

Thanks in part to this small, isolated territory, the Cocha Salvador otters are easily followed by personal kayak for all-day follows. They are also habituated to human observation because of tourist groups that habituated the otters to observation from a large catamaran. The Cocha Salvador family instantly accepted my kayak-based observations at a distance of only a few meters when I began observations in 2001. Observations reported here were conducted in intensive periods of 1-2 weeks in 2004-2007 during the dry season, the season in which newborns tend to emerge from the dens (Schenck, 1999). The 2007 observations at Cocha Salvador took place during 11-19 September. During 2004-2007, I observed the otters alone (2004-2006) or with one assistant (2007), amounting to 86, 45, 34, and 41 contact-hours, respectively. Contact-hours include time following the otters in any activity other than resting in and around the den. As giant otters are individually recognizable throughout their lives by distinctive white markings on their necks, no capture or marking was required.

A single observer followed the otters in a sit-on-top kayak, with observers alternating in 3-hour shifts beginning at 6AM or whenever the otters first left their den. Giant otters are diurnal, maintain one or two sleeping dens, and also use satellite latrines and campsites during daylight hours (Duplaix, 1980; Schenck, 1999). A family may move newborns between sleeping dens periodically, probably to avoid the build-up of faeces and parasites (Schenck, 1999). When multiple dens were in use, evening observations continued until nightfall, to determine their location for the next morning's observation.

Observers recorded continuously on a palm pilot running customized event recorder software on a PocketC compiler (Lorch, 2002; Martin and Bateson, 2007). Behavioral events that were recorded included: Alarm, Fish Catch, Beg, Share, No Share, and Steal. The identity of individual otters responsible for each event was dictated into a voice recorder, as were the size-classes (0-10cm, 10-20cm, 20-30cm, >30cm) and species of all fish caught during observations. Additional behavioral observations such as leadership of the family's movements, participation in grooming, playing, and defense (usually against caiman or the observer) were also dictated into the voice recorder.

Data Classification and Analysis

I scored each begging bout as resulting in a Share, No Share, or a Steal. I identified both the potential Donor and the Beggar wherever possible. Unknown Donors were usually animals observed in open water that shared small items with young before re-submerging quickly, making identification difficult. If more than one animal begged for the same prey item, the result for only the winning Beggar is reported here, so as not to inflate the rate of No Shares of any Donor.

Many shares to a Beggar are obvious donations of whole or partial prey items, initiated by the Donor and clearly shared with the Donor's intent. At times, however, separating Steals from Shares was difficult. A transfer of a prey item is commonly preceded by a period of defensive growling and avoidance of the Beggar, and consumption by the Donor of a large portion of the prey item. A Beggar frequently approached a family member with a prey item, usually making vocalizations typically used in the context of begging, and snatched the item from the Donor's mouth. However, most transfered items seemed to eventually be handed over without resistance. Steals were therefore recorded only rarely, and only if the Donor seemed to turn away as if to escape from the Beggar just before the item was transferred. Even then, I never observed possession of a stolen item to be contested subsequently and retrieved. In 2007, I observed only one transfer that might have been a Steal under these guidelines, and I conservatively classified it as a Share.

Data processing and analysis involved downloading data from the event recorder into an Excel spreadsheet and interpolating voice recordings in chronological order. All data are reported as raw counts and percentages of events observed.

RESULTS

Fish Catches, Begging, and Sharing

Individual otters caught different numbers of large (>30 cm), with an individual's percentage of the total caught typically increasing with age (Table 6.1; cf. Chapter 5). Donors (the animals to whom begging was directed) also shared and refused to share, at different rates, based on age and fish catching ability (Table 6.2 and 6.3). Table 6.3 lists all begging bouts observed in 2007, identifying both the Beggar and the Donor for each bout.

In 2004-2006 observations, Cacao consistently caught the highest number of large (>30 cm) fishes, and was the most generous Donor. However, in 2007, I did not observe Cacao to catch any large fish, and she was the most active Beggar, and the least active Donor.

When the family was with young-of-the-year in 2004-2006, rates of sharing were high across the entire family. Including unknown Donors, begging bouts ending in a share constituted 63% (229/362), 65% (109/168), and 70% (81/116) of observations in 2004, 2005, and 2006 (Table 6.2). Considering Shares from known Donors only, Cacao had the highest willingness-to-share, with 79% (38/48), 65% (15/23), and 69% (18/26) of begs to her ending in a share in those years (Table 6.2). Before 2007, Cacao received food from others only once in 2004, and once in 2006, both occasions when extra-large prey items were caught by others and shared around the family.

Behavioral Changes in Cacao, 2007

Besides changes in hunting and sharing rates, I also observed a number of relevant changes in Cacao's interactions with other family members. She frequently became separated from the group when they engaged in fast chases after a school of fish. On these occasions, she had to employ the loud "waver scream" (Duplaix, 1980) to locate the others. In contrast to young otters who vocalize loudly and continuously before grabbing for or receiving food, she typically waited quietly in front of a family member in possession of a large prey item, squinting and staring at the other otter for many minutes. While waiting for a share, she vocalized infrequently or just immediately prior to approaching the Donor to acquire the remainder of the prey item.

Family Assistance to Cacao

Cacao begged for prey items 43 times during my observations (Table 6.3). Her success rate of 26% (11/43) was considerably lower than for begging by young-of-the-year in 2004-2006. Individuals that shared with Cacao included her new partner, Firecat, and all juveniles but Achilles. Achilles, a 2 y old male, refused to share with Cacao all 7 times he was solicited by her, but shared with Caiman and Firecat on a single occasion each. Ziggy, the oldest offspring, received the most begs (19) as a result of her high rate of captures, and she never solicited begs. Although Ziggy did share with multiple family members including Cacao, the percent of begs from Cacao for which she shared was low at 19% (3/16 begs from Cacao), compared to 27% (3/11 begs from Cacao) for Caiman, and 57% (4/7 begs from Cacao) for Firecat (Table 6.3).

Family members also assisted Cacao in a second context. When Cacao became separated from the group and called to others using the waver-scream, other otters assisted her to rejoin the group, either by returning the waver-scream or by swimming to her and leading her back to the group. This type of assistance was also frequently observed with young-of-the-year, who become separated from the group when handling prey items for extended periods. Those who offered Cacao this assistance were Caiman, Firecat, and Achilles.

DISCUSSION

Cacao’s failure to catch large fish, frequent begging, and need for assistance in staying with the group are observations that contrast dramatically with her role as provider and leader in previous years. That her family members assisted her and shared prey items with her is a new observation for the species. It is particularly interesting because assistance to the elderly is so seldom reported for wild animals.

Importance of Sharing to Cacao

Most of the items Cacao received as shares were substantial portions of large prey. For example, she received from Firecat most of a >50 cm corvina (*Plagioscion* *squamossissimus*), the consumption of which she monopolized for nearly 7 minutes before handing off the remainder to Caiman, the youngest family member. She therefore appeared to be receiving considerable nutrition by begging, and at negligible energetic cost. Nevertheless, the number of observed shares with Cacao (11 over 8 days), when considered as daily intake (1.4 shares per day) clearly was not sufficient to meet her daily nutritional needs. Shares to Cacao supplemented her own hunting efforts, as she caught small and medium fish in numbers comparable to other family members. Aid to her, therefore, primarily compensated for her low success at catching large prey items.

When young are present, giant otters distinguish between individual beggars, and selectively share with young-of-the-year over yearlings (pers. obs.). As a consequence, yearlings suffer a period of parent-offspring conflict when new young emerge, during which time begging success declines and they must accelerate self-provisioning (Trivers, 1974). Hunting skills are still developing in most yearlings, so that in this period, they may use less-preferred, but easy-to-catch prey items such as stingrays, armored catfish, and turtles (pers. obs.). Sharing rates with beggars may be extremely low for these animals still transitioning to adult competence levels, but rise with age and hunting skill. By 2 y of age, juveniles in the Cocha Salvador and Cocha Cashu families matched and even exceeded adult sharing rates, although significantly, mothers nearly always had the highest rates of sharing of all family members until these 2007 observations (cf. Chapter 5).

Although other social carnivores allocate food according to a dominance hierarchy (e.g. chimpanzees: Goodall, 1986; wolves: Harringon et al., 1983, Mech and Boitani, 2003), with young occasionally forced to give food over to more dominant and older animals, this is not true of giant otters, where no dominance hierarchy has been observed to control affect access to food, and most food transfers are from older to younger animals. The Cocha Salvador family's situation in 2007 therefore appears to constitute a role-reversal in which the majority of prey transfers within the family were from young-to-old rather than from old-to-young. Cacao's low begging success rate (26%) compared to young-of-the-year is probably explained by the low intensity of her begging behavior compared to that of young-of-the-year.

Why Share with the Matriarch?

The willingness of Cacao's family to provide her with supplemental food raises the question of what benefits might accrue to the family members from helping their aged matriarch. Some general features of giant otters' social behavior make aiding and sharing food with aged adults likely, and specific conditions for the Cocha Salavdor family are also likely to be relevant.

Non-Adaptive Explanations

One possible explanation for family members' aid to Cacao is that assistance to her replaced behavior that would normally be directed toward young-of-the-year. Since yearlings are still begging when new young arrive, helpers are accustomed to year-round food sharing. In the absence of young-of-the-year in the Salvador 2007 family, helping that would normally have been provided to young-of-the-year could instead be directed to the new begging behavior of the mother. No future direct benefits to the Donor are accrued by sharing in this interpretation.

I consider this interpretation unlikely, however, for a number of reasons. First, most shares to Cacao were significant portions of large prey items, and so represent a considerable cost for Donors to bear with no expectation of reciprocation or other direct or indirect gain. Second, given the strong differences in the cues provided by Cacao and young giant otters, it seems unlikely that sharing with the mother is merely a non-adaptive, habitual response to begging. In a study of African wild dogs, the suggestion that regurgitating food to pups only occurred in response to begging behavior was similarly rejected (van Lawick and van Lawick-Goodall, 1971). Giant otters know their family members, and make choices to share or not that should reflect a cost/benefit decision-making framework.

A second possible explanation is that helpers may be driven to share when solicited by particularly dominant individuals such as the mother, or simply because of the strong bond established between offspring and the mother. In chimpanzees, members of both sexes are observed to readily come to the aid of their mother, even when well into adulthood and no longer in need of her protection (Goodall, 1986). In giant otters, the mother is typically the main leader of group movements and activities, so other family members may be accustomed to acquiescing to her demands (cf. Chapter 5). The main argument against this hypothesis is the current belief that no dominance hierarchy structures giant otters' social interactions. On the other hand, future research may reveal stronger social hierarchies to operate in giant otters' society based on studies of play and dispersal patterns (cf. Chapter 5). This hypothesis also can not explain Firecat's high willingness to share, as he had limited previous experience with Cacao as leader of the family.

Finally, as Cacao and Firecat appeared to be newly partnered, Firecat's assistance to Cacao could be considered courtship feeding. Almost nothing is known about the development of pair-bonds in giant otters in the wild, but courtship feeding has never before been reported either in the wild or in captivity. It is therefore also unlikely that this would explain Firecat's high rate of sharing, and also fails to explain the sharing by juveniles.

Adaptive Explanations

Alternatively, family members may share to realize either future foraging benefits if she recovers, or important non-food benefits provided by her regardless of her hunting skill and reproductive status. In elephants, the matriarch plays a central role in organizing social interactions within a family, and with other elephant herds (McComb et al., 2001; Poole et al., 1988). In giant otters, the matriarch also takes on several roles that assist the family beyond providing food, such as leading group movements, knowing the territory's diverse and seasonally-changing food resources, defending the group from predators, babysitting young in the den while others forage, accompanying the slow-swimming babies during hunting bouts, and teaching slow-learning young about threats and fishing techniques (Chapters 4 & 5). Of these roles, knowledge of resources, defense from predators, and leadership in directing movements are the only forms of assistance that could accrue direct benefits to other family members present in 2007. All other roles benefit survival of young-of-the-year, with indirect (kinship) benefits accruing to their siblings. Since predator defense and leadership roles are also undertaken by fathers and older offspring, it is potentially conceivable that sharing food with Cacao in 2007 was provided on behalf of future siblings, assuming Cacao were to remain as either breeder or as a "grandparent helper" to a daughter in future years (Richardson et al., 2007).

Support for this conjecture is available from observations on both wild and captive giant otters that suggest that menopause may be a feature of giant otter life history, beginning around 11-12 y of age (G. Londroño, pers. comm..; Groenendijk and

Hajek, 2006; Londroño et al., 2006; Sykes-Gatz, 2005). Future benefits from maintaining a matriarch on the territory could be explained via the "Grandmother Hypothesis" of adaptive menopause (Diamond, 1998; Hawkes et al., 1998; Hill and Hurtado, 1991; Packer et al., 1998; Richardson et al., 2007; Sherman 1998). Under this hypothesis, females in long-lived species may gain greater fitness as their risk of mortality from reproduction increases with age by aiding survival of their daughters' offspring rather than continuing to reproduce themselves.

Evidence of menopause and "grandmother helpers" in giant otters comes from both wild and captive giant otters. The only other published account of a long-term demographic study in giant otters comes from Cocha Otorongo, also in the Manú Biosphere Reserve (Groenedijk and Hayek, 2006). These authors describe multiple cases of sisters or daughters of the previous breeding female acquiring the breeding position with immigrant males, with the previous breeding female assisting as helper (Groenendijk and Hajek, 2006). Of particular note, in 2001 at Cocha Otorongo, the breeding female Isla stopped reproducing at age 10 after 3 years with a new male, after which her daughter Microbio took over the breeding spot with her step-father. The 10 y old Isla stayed with the family, but specifics of her helping behaviors as a grandmother were not obtained. This precedent suggests the possibility of a similar turnover of the breeding position by Cacao's daughter Ziggy occurring on Cocha Salvador, and Cacao's status changing to Grandmother and helper.

Evidence from captive breeding also suggests the likelihood that menopause may limit reproduction in female giant otters several years prior to their death (G. Londroño, pers. comm.; Sykes-Gatz, pers. comm.). In one case at the Zoo in Cali, Columbia, the breeding female produced nine litters between 1999 and 2004, and then stopped producing litters at 12 y of age after a period of increasingly infrequent estrus and mating periods (Londroño et al., 2006). As of this writing (2008), she was still alive in the colony, but non-reproductive (G. Londroño, pers. comm.).

Two further examples of ~10 y old females ending reproduction are reported from Hagenbeck Tierpark and Dortmund Zoo, where both breeding females had difficult pregnancies and slowing estrus cycles prior to stopping litter production (Sykes-Gatz, 2005). Captive males, on the other hand, have successfully bred twice in captivity up to 14 y of age, and the oldest recorded age in captivity was for a female who lived to 19 y. (Sykes-Gatz, 2005). While it is obviously not possible to determine if Cacao's failure to produce a litter in 2007 was due to menopause, the concordance of her age and the above cases suggests it as a possibility.

In 2007, I observed grooming and sharing between Firecat and Cacao to be greater than between Firecat and the 3 y old female Ziggy (the only candidate for a future female breeder from the Salvador family), so that it appeared that a pair-bond existed between Firecat and Cacao rather than Firecat and Ziggy. It is nevertheless conceivable that Ziggy might rise to the position of breeding female with her step-father if Cacao's apparent infirmity also limits her reproductive capacity. If Cacao were to change her position from that of breeding female to matriarch-helper, and her varied helping roles improved survival of offspring, indirect inclusive fitness benefits from sharing would accrue to all family-members. Supplemental aid to Cacao would therefore be adaptive, and ought to continue. On the other hand, the family might choose to end aid to Cacao either because begging by young is more effective, or because supplementing Cacao's nutritional needs would put her into competition for food with young-of-the-year, and exceed the value of her compensatory help. In the latter case, ending aid to Cacao could be adaptive.

Although the future roles of Cacao, her partner Firecat, and her 3 y old daughter Ziggy are yet to be realized, my multi-year observations of the Cocha Salvador family offer the possibility that the Grandmother Hypothesis could explain care of an elderly matriarch in giant otters. If confirmed in future observations on the Salvador family or other giant otter families, it would be an important contribution to understanding behavior and social organization of these top carnivores.

Although the Grandmother Hypothesis has been evoked to explain the life history of a few mammals and at least one bird species, I am not aware of any case where the species was concurrently reported to help such a grandmother to survive (Packer et al., 1998; Robertson et al., 2007). Here I have documented an unequivocal role reversal for a wild mother giant otter from provider to aged dependent, and have shown how most of her family willingly cooperated in subsidizing her nutrition. These observations are rare and fortuitous, given the longevity of giant otters in the wild, and the scarcity of family groups under continuous study for demography and behavior. It will be particularly interesting to see if the matriarch Cacao survives to the next breeding season within this family, so that we can again observe her roles within this surprisingly complex family, perhaps not as a breeding mother, but as matriarch, grandmother, and helper.

	Year Born	2004 Catches (contact hours: 86)		2005 Catches (contact hours: 45)		2006 Catches (contact hours: 34)		2007 Catches (contact hours: 41)	
Cacao	~1996	18	23%	9	18%	5	26%	0	0%
Fantasma	1991	11	14%	5	10%	3	16%	-	-
Firecat	~2004?	-	-	-	-	-	-	7	25%
Diabolo	2001	8	10%	-	-	-	-	-	-
Frita	2001	9	11%	-	-	-	-	-	-
Virute	2002	11	14%	6	12%	-	-	-	-
Fantasmita	2002	10	13%	2	4%	-	-	-	-
Mars	2003	9	11%	9	18%	-	-	-	-
Saguarito	2003	3	4%	7	14%	-	-	-	-
Rambo	2004	0	0%	6	12%	4	21%	-	-
Ziggy	2004	0	0%	4	8%	4	21%	9	32%
Achilles	2005	-	-	1	2%	3	16%	8	29%
Lacunae	2005	-	-	0	0%	-	-	-	-
Liana	2006	-	-	-	-	0	0%	-	-
Caiman	2006	-	-	-	-	0	0%	4	14%
Total		*79*		*49*		*19*		*28*	

Table 6.1: Large (>30 cm) Fish Catches for Cocha Salvador family members, 2004-2007. Cacao and Fantasma are the original breeding pair, with Firecat replacing Fantasma in 2007. All others are offspring of Cacao and Fantasma.

		Donor												
Year	Beg Result	Cacao	Fantasma	Rambo	Ziggy	Achilles	unk	Diabolo	Frita	Virute	Fantasmita	Mars	Saguarito	Grand Total
2004	Share event	38	31	1	1	-	90	13	11	13	14	8	9	229
	No Share	8	13	4	4	-	12	10	15	7	11	10	4	98
	Steal event	2	3	0	4	-	14	1	4	5	2	0	0	35
2004 Total		***48***	***47***	***5***	***9***	***-***	***116***	***24***	***30***	***25***	***27***	***18***	***13***	***362***
2005	Share event	15	10	2	2	1	35	-	-	15	14	8	7	109
	No Share	7	2	9	5	0	3	-	-	5	7	6	7	51
	Steal event	1	0	0	0	0	2	-	-	2	2	1	0	8
2005 Total		***23***	***12***	***11***	***7***	***1***	***40***	***-***	***-***	***22***	***23***	***15***	***14***	***168***
2006	Share event	18	6	7	14	6	30	-	-	-	-	-	-	81
	No Share	8	4	9	5	2	5	-	-	-	-	-	-	33
	Steal event	0	0	1	0	0	1	-	-	-	-	-	-	2
2006 Total		***26***	***10***	***17***	***19***	***8***	***36***	***-***	***-***	***-***	***-***	***-***	***-***	***116***

Table 6.2: Share, No Share and Stealing Results of Begging Bouts to Individual Donors Observed on Cocha Salvador, 2004-2006. Animals to the right of the “unk” Donor column are juveniles who dispersed before the 2006 field season.

		Donor						
	Beggar	Achilles	Cacao	Caiman	Firecat	Ziggy	unk	**TOTAL**
Share	Achilles	-	0	0	0	0	0	**0**
	Cacao	0	-	3	4	3	1	**11**
	Caiman	1	1	-	1	1	2	**6**
	Firecat	1	0	0	-	1	0	**2**
	Ziggy	0	0	0	0	-	0	**0**
	TOTAL Shares	***2***	***1***	***3***	***5***	***5***	***3***	***19***
No Share	Achilles	-	0	0	1	0	0	**1**
	Cacao	7	-	8	3	13	1	**32**
	Caiman	0	0	-	0	1	0	**1**
	Firecat	1	0	0	-	0	0	**1**
	Ziggy	0	0	0	0	-	0	**0**
	TOTAL No Shares	***8***	***0***	***8***	***4***	***14***	***1***	***35***
	TOTAL Begs Received	***10***	***1***	***11***	***9***	***19***	***4***	***54***

Table 6.3: Matrix of Donor and Beggar identifications observed in September 2007 begging bouts on Cocha Salvador.

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CHAPTER 7 SUMMARY AND CONCLUSIONS

SUMMARY

The original objectives of this research were to investigate if oxbow lakes maintain random or predictable fish and faunal communities after annual flooding, observe seasonal and annual patterns in diet of giant otters on phytoplankton-dominated oxbow lakes, and quantify helping behaviors in giant otters, with a view to assess if behavioral specialization, social climbing, or slow learning characterizes the roles of different helpers in a family. Results brought some surprises, as well as confirmations of what I expected to find from previous experience at the field site.

In Chapter 2, I looked at bird, caiman and fish communities on two different lake types, Type 1: isolated, phytoplankton-dominated lakes, and Type 2: connected, macrophyte-dominated lakes. I found that oxbow lake bird communities were predictable from year to year, with the strongest predictor the individual lake sampled. Indicator Analysis of bird species responsible for the distinction between Type 1 and Type 2 lakes demonstrated that piscivorous fish most strongly associated with Type 1 lakes, while herbivorous and snail-eating birds were associated with Type 2 lakes. Overall, bird communities were sensitive to lake type, and to individual lake characteristics, regardless of yearly changes, including a heavy flooding event in 2003.

Like birds, caiman were sensitive to lake type, regardless of year, and in spite of the heavy floods of 2003 that reduced their population significantly on Cocha Cashu.

The smallest size class of caiman was the most variable between lake types, suggesting that breeding success, or even attempting breeding, was highest on Type 1 lakes.

Fish communities were more varied in their response to flooding and Lake Type than bird and caiman data. The 2003 flood had a strong effect on fish communities, homogenizing the fish communities in the oxbow lakes in that year. Subsequently, Type 1 lake samples demonstrated greater community similarities than Type 2 lakes, which showed widely divergent communities from one sampling event to the next.

I conclude that the Lake Types I identified based on connectivity and chlorophyll concentrations can provide predictive power across multiple years for Manú oxbow lake fauna, and especially for bird and caiman communities. Fish communities were more changeable, especially in the Type 2 lakes that maintain connectivity to the main river year-round. As a follow-up study, I am embarking on a collaboration to look at migratory patterns of fishes in Manú oxbow lakes, directly sampling in channels that connect the lakes and the river.

Chapters 3 and 4 report on shifts in the diet of giant otters during different seasons, and compare families hunting with and without young cubs in the dry season. Using visual observations, rather than scat analysis, allowed me to report with confidence where and when different types prey were taken, and confirm the large effect that hunting with young cubs has on giant otter prey selection and habitat use. Although early studies based on scat seemed to indicate the giant otter was a specialized predator on a few species of fish (considered to be because these fish were slower and easier to catch; Schenck, 1999), my results suggest that the otters use fish resources of oxbow lakes more broadly. In part due to my lack of repeat data in the wet season, questions that still remain include the role of fish such as gymnotids as potential keystone resources during high water, and whether the specialization of giant otters on Cichlid prey in the dry season is specific to certain types of oxbow lakes. In addition, the issue of benefits and risks of hunting where caiman are most common when with young cubs could be clarified with comparative studies on lakes with lower densities of caiman. Finally, understanding niche overlap between *Lontra* and *Pteronura* is a potentially interesting avenue for comparative study between the Manú and other lowland habitats where they co-occur.

My investigation of giant otter helping behavior provided the first quantitative data in the literature. I suggest that giant otters both are constrained from dispersal by slow skill development, and that individuals may choose alternative dispersal and helping strategies as their individual skills, situations, environment and personalities allow. Particularly slow to develop are complex social and communication skills that allow helpers to lead the group and assist young cubs in need. Yet I also observed particular individuals who appeared to help disproportionately, and others who specialized in defense of the family without contributing in excess to other helping roles at the same time. Unlike in other animals with sentinels, it appears that a single individual takes on the sentinel role exclusively, with little rotation for the responsibility. The overall conclusion is that individuals choose to stay and help in giant otter family using different criteria, which may be related to resource abundance, numbers and behaviors of siblings, and personality differences that arise from a young age. Many more families of giant otters could be observed to confirm if these suggestions hold across families with varying composition and in diverse habitats.

CONSERVATION IMPLICATIONS

I did not conduct this study with the specific goal of learning information that would affect conservation efforts on behalf of the giant otter. Conditions outside the Manú Biosphere Reserve will have greater impacts on the future of giant otters in Southeastern Perú than the already favorable conditions inside the park. However, given the endangered status of the giant otter, and the paucity of information on its use of habitat and fish resources, I hope that some of the information generated by this research is useful to better understanding the otters' conservation needs. One obvious result is their dependence on high productivity oxbow lake habitats, which are threatened by resource extraction, conversion, and proposed channelization throughout much of Amazonia. Although now recovering from a population bottleneck, giant otters are slowly recolonizing into areas from where they were extirpated. An effort to maintain the fish and water quality conditions they depend upon, and to halt illegal persecution of the otters by local people will be important efforts to the survival of the species, and the reconnection of genetically isolated populations. I also recommend continued monitoring of sex ratio of young surviving to 1 y, to ensure that low female survival, a possible effect of inbreeding depression, doesn't depress population numbers within the park in the future.

A positive conservation message regarding human/otter conflict is also apparent from the results of this study. Giant otters are often despised by local fisherman for allegedly depressing populations of desirable fish species. While otters do eat several kilos of fish per day, I documented considerable dietary flexibility of the otters, including heavy use of very small Cichlid prey when raising babies. These small Cichlids are not targets of local fishermen in the Manú and surrounding areas. On Cocha Cashu, I observed the greatest reliance on "Open Water Detritivores," which include species desired by fishermen such as *Prochilodus*, but their dependence on them was highest in the year when fish populations were already depressed by the presence of the floating plant *Pistia stratiotes*. The populations of most migratory fish eaten by giant otters may well be more dependent on favorable conditions for feeding and growth, than on top-down regulation by the giant otters themselves. Much is left to be learned about the needs of fishes at different stages of life in their movements between lake and river systems in Amazonia, but it seems clear that efforts to conserve fish resources in Amazonia will likely depend more on intelligent regulation of human extraction and pollution of freshwater resources than on ill-advised removal of fish-eating predators such as the giant otter.

APPENDIX 1:

Post-Hoc Pairwise Comparisons of Family Members' Skills and Helping Behaviors

Cashu

2004

Sample	Mean of ranks	Groups		
Splotch	134.300	A		
Otto	139.689	A		
Stripe	142.178	A		
Oliver	144.878	A	B	
Olaf	148.989	A	B	
Orson	181.211		B	C
Ozstralia	214.756			C

Bonferroni corrected significance level: 0.0024

2005

Sample	Mean of ranks	Groups		
Osama	36.972	A		
Oswald	39.917	A		
Patty	44.139	A	B	
Olaf	63.500		B	C
Otto	65.250			C
Ozstralia	77.222			C

Bonferroni corrected significance level: 0.0033

2006

Sample	Mean of ranks	Groups	
Petunia	39.711	A	
Osama	47.789	A	
Oswald	58.053	A	B
Olaf	59.158	A	B
Otto	69.132		B
Ozstralia	71.158		B

Bonferroni corrected significance level: 0.0033

Salvador

2004

Sample	Mean of ranks	Groups		
Saguarito	66.438	A		
Diabolo	84.458	A	B	
Virute	89.646	A	B	
Fantasma	93.667	A	B	
Mars	101.083		B	C
Frita	103.104		B	C
Fantasmita	106.625		B	C
Cacao	126.979			C

Bonferroni corrected significance level: 0.0018

2005

Sample	Mean of ranks	Groups		
Ziggy	49.625	A		
Fantasma	52.375	A		
Saguarito	56.188	A	B	
Rambo	61.000	A	B	
Virute	61.813	A	B	
Fantasmita	63.563	A	B	
Cacao	81.375		B	C
Mars	90.063			C

Bonferroni corrected significance level: 0.0018

2006

Sample	Mean of ranks	Groups
Fantasma	20.900	A
Ziggy	22.250	A
Achilles	25.950	A
Rambo	27.350	A
Cacao	31.050	A

Bonferroni corrected significance level: 0.005

Table A1: Post-hoc pairwise comparisons on Otters' Fish Catch Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.

Cashu

2004

Sample	Mean of ranks	Groups		
Oliver	91.147	A		
Olaf	98.235	A		
Osama	111.618	A	B	
Oswald	116.794	A	B	C
Patty	133.294		B	C
Stripe	136.294		B	C
Splotch	149.118			C

Bonferroni corrected significance level: 0.0024

2005

Sample	Mean of ranks	Groups	
Olaf	31.500	A	
Palomita	36.000	A	
Oswald	47.194	A	B
Patty	53.944		B
Osama	58.861		B

Bonferroni corrected significance level: 0.005

2006

Sample	Mean of ranks	Groups
Olaf	27.000	A
Osama	29.909	A
Oswald	29.909	A
Escher	35.727	A
Estrella	36.273	A
Petunia	42.182	A

Bonferroni corrected significance level: 0.0033

Salvador

2004

Sample	Mean of ranks	Groups	
Frita	50.981	A	
Virute	55.942	A	
Mars	66.115	A	
Rambo	98.038		B
Ziggy	99.365		B
Saguarito	100.558		B

Bonferroni corrected significance level: 0.0033

2005

Sample	Mean of ranks	Groups	
Rambo	41.500	A	
Virute	44.625	A	
Ziggy	44.625	A	
Saguarito	48.438	A	
Mars	50.875	A	
Lacunae	78.406		B
Achilles	87.031		B

Bonferroni corrected significance level: 0.0024

2006

Sample	Mean of ranks	Groups		
Ziggy	21.462	A		
Achilles	21.462	A		
Rambo	23.423	A		
Liana	41.731		B	
Caiman	56.923			C

Bonferroni corrected significance level: 0.005

Table A2: Post-hoc pairwise comparisons on Otters' Begging Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.

Cashu

2004

Sample	Mean of ranks	Groups	
Orson	47.180	A	
Oliver	49.360	A	
Olaf	54.600	A	
Otto	75.680		B
Ozstralia	88.180		B

Bonferroni corrected significance level: 0.005

2005

Sample	Mean of ranks	Groups		
Osama	63.000	A		
Oswald	63.000	A		
Petunia	63.000	A		
Patty	66.174	A		
Olaf	87.239	A	B	
Otto	109.957		B	C
Ozstralia	114.630			C

Bonferroni corrected significance level: 0.0024

2006

Sample	Mean of ranks	Groups	
Petunia	41.237	A	
Osama	43.974	A	
Oswald	43.974	A	
Otto	65.158		B
Olaf	67.658		B
Ozstralia	83.000		B

Bonferroni corrected significance level: 0.0033

Salvador

2004

Sample	Mean of ranks	Groups	
Fantasmita	39.000	A	
Virute	39.000	A	
Mars	47.417	A	
Saggy	52.000	A	
Fantasma	72.500		B
Cacao	77.083		B

Bonferroni corrected significance level: 0.0033

2005

Sample	Mean of ranks	Groups		
Mars	43.500	A		
Ziggy	43.500	A		
Fantasmita	47.286	A		
Rambo	47.286	A		
Saggy	51.929	A	B	
Virute	58.643	A	B	
Cacao	74.643		B	C
Fantasma	85.214			C

Bonferroni corrected significance level: 0.0018

2006

Sample	Mean of ranks	Groups	
Fantasmita	17.000	A	
Virute	17.000	A	
Achilles	17.000	A	
Ziggy	17.000	A	
Rambo	20.000	A	
Fantasma	27.333	A	B
Cacao	35.167		B

Bonferroni corrected significance level: 0.0024

Table A3: Post-hoc pairwise comparisons on Otters' Leadership Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.

Cashu

2004

Sample	lean of rank	Groups		
Stripe	70.769	A		
Splotch	71.673	A	B	
Olaf	80.173	A	B	
Oliver	87.346	A	B	
Otto	96.327	A	B	
Orson	99.846		B	
Ozstralia	134.365			C

Bonferroni corrected significance level: 0.0024

2005

Sample	lean of rank	Groups	
Osama	48.184	A	
Oswald	50.132	A	
Patty	51.184	A	
Otto	57.842	A	B
Olaf	59.026	A	B
Ozstralia	78.632		B

Bonferroni corrected significance level: 0.0033

2006

Sample	lean of rank	Groups	
Petunia	36.000	A	
Osama	45.559	A	B
Otto	48.618	A	B
Oswald	58.176		B
Olaf	58.559		B
Ozstralia	62.088		B

Bonferroni corrected significance level: 0.0033

Salvador

2004

Sample	Mean of ranks	Groups	
Saggy	75.604	A	
Mars	76.542	A	
Frita	81.563	A	
Virute	83.604	A	
Fantasmita	85.875	A	
Fantasma	99.917	A	B
Diabolo	109.458	A	B
Cacao	120.917		B

Bonferroni corrected significance level: 0.0018

2005

Sample	Mean of ranks	Groups	
Rambo	45.875	A	
Ziggy	45.875	A	
Saggy	59.125	A	B
Mars	62.563	A	B
Fantasmita	70.625	A	B
Fantasma	71.406	A	B
Virute	77.844		B
Cacao	82.688		B

Bonferroni corrected significance level: 0.0018

2006

Sample	Mean of ranks	Groups	
Achilles	29.143	A	
Fantasma	30.429	A	
Rambo	32.929	A	B
Ziggy	38.857	A	B
Cacao	46.143		B

Bonferroni corrected significance level: 0.005

Table A4: Post-hoc pairwise comparisons on Otters' Sharing Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.

Cashu

2004

Sample	Mean of ranks	Groups		
Splotch	65.708	A		
Stripe	72.125	A	B	
Olaf	78.542	A	B	
Oliver	82.604	A	B	C
Orson	89.333	A	B	C
Ozstralia	96.500		B	C
Otto	106.688			C

Bonferroni corrected significance level: 0.0024

2005

Sample	Mean of ranks	Groups		
Oswald	40.105	A		
Patty	41.632	A		
Osama	49.763	A	B	
Ozstralia	66.237		B	C
Olaf	72.289			C
Otto	74.974			C

Bonferroni corrected significance level: 0.0033

2006

Sample	Mean of ranks	Groups	
Petunia	36.750	A	
Oswald	45.000	A	B
Osama	46.125	A	B
Olaf	46.750	A	B
Ozstralia	55.875	A	B
Otto	60.500		B

Bonferroni corrected significance level: 0.0033

Salvador

2004

Sample	Mean of ranks	Groups	
Saggy	36.000	A	
Mars	39.654	A	
Fantasmita	43.308	A	
Frita	46.962	A	
Virute	46.962	A	
Fantasma	48.077	A	
Diabolo	79.192		B
Cacao	79.846		B

Bonferroni corrected significance level: 0.0018

2005

Sample	Mean of ranks	Groups
Saggy	11.000	A
Fantasma	13.417	A
Virute	13.417	A
Mars	19.000	A
Fantasmita	20.667	A

Bonferroni corrected significance level: 0.005

2006

Sample	Mean of ranks	Groups
Fantasma	4.000	A
Mars	4.000	A
Saggy	4.000	A
Cacao	6.000	A

Bonferroni corrected significance level: 0.0083

Table A5: Post-hoc pairwise comparisons on Otters' Grooming Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.

Cashu

2004

Sample	Mean of ranks	Groups		
Splotch	65.708	A		
Stripe	72.125	A	B	
Olaf	78.542	A	B	
Oliver	82.604	A	B	C
Orson	89.333	A	B	C
Ozstralia	96.500		B	C
Otto	106.688			C

Bonferroni corrected significance level: 0.0024

2005

Sample	Mean of ranks	Groups		
Oswald	40.105	A		
Patty	41.632	A		
Osama	49.763	A	B	
Ozstralia	66.237		B	C
Olaf	72.289			C
Otto	74.974			C

Bonferroni corrected significance level: 0.0033

2006

Sample	Mean of ranks	Groups	
Petunia	36.750	A	
Oswald	45.000	A	B
Osama	46.125	A	B
Olaf	46.750	A	B
Ozstralia	55.875	A	B
Otto	60.500		B

Bonferroni corrected significance level: 0.0033

Salvador

2004

Sample	Mean of ranks	Groups	
Saggy	36.000	A	
Mars	39.654	A	
Fantasmita	43.308	A	
Frita	46.962	A	
Virute	46.962	A	
Fantasma	48.077	A	
Diabolo	79.192		B
Cacao	79.846		B

Bonferroni corrected significance level: 0.0018

2005

Sample	Mean of ranks	Groups
Saggy	11.000	A
Fantasma	13.417	A
Virute	13.417	A
Mars	19.000	A
Fantasmita	20.667	A

Bonferroni corrected significance level: 0.005

2006

Sample	Mean of ranks	Groups
Fantasma	4.000	A
Mars	4.000	A
Saggy	4.000	A
Cacao	6.000	A

Bonferroni corrected significance level: 0.0083

Table A6: Post-hoc pairwise comparisons on Otters' Grooming Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.

Cashu

2004

Sample	Mean of ranks	Groups			
Osama	196.000	A			
Oswald	196.000	A			
Patty	201.093	A			
Oliver	246.185	A	B		
Splotch	249.685	A	B	C	
Orson	278.852		B	C	
Stripe	299.315		B	C	
Ozstralia	305.796			C	
Otto	306.963			C	
Olaf	425.111				D

Bonferroni corrected significance level: 0.0011

2005

Sample	Mean of ranks	Groups	
Osama	61.875	A	
Patty	67.893	A	
Ozstralia	77.321	A	
Otto	78.500	A	
Oswald	85.964	A	
Olaf	135.446		B

Bonferroni corrected significance level: 0.0033

2006

Sample	Mean of ranks	Groups			
Estrella	74.121	A			
Escher	77.121	A			
Ozstralia	79.000	A			
Otto	95.759	A	B		
Osama	127.603		B	C	
Petunia	146.621			C	D
Oswald	152.621			C	D
Olaf	179.155				D

Bonferroni corrected significance level: 0.0018

Salvador

2004

Sample	Mean of ranks	Groups		
Cacao	86.326	A		
Ziggy	96.130	A		
Diabolo	100.457	A		
Fantasmita	104.783	A	B	
Rambo	107.652	A	B	
Fantasma	115.152	A	B	
Frita	115.152	A	B	
Virute	120.065	A	B	
Mars	141.978		B	C
Saggy	167.304			C

Bonferroni corrected significance level: 0.0011

2005

Sample	Mean of ranks	Groups			
Ziggy	54.000	A			
Cacao	58.533	A	B		
Mars	58.533	A	B		
Fantasma	67.600	A	B	C	
Achilles	68.800	A	B	C	
Fantasmita	73.333	A	B	C	D
Virute	87.300		B	C	D
Lacunae	90.300			C	D
Saggy	96.633			C	D
Rambo	99.967				D

Bonferroni corrected significance level: 0.0011

2006

Sample	Mean of ranks	Groups	
Liana	32.962	A	
Caiman	32.962	A	
Cacao	38.885	A	
Achilles	41.846	A	
Fantasma	46.000	A	
Ziggy	47.115	A	
Rambo	82.231		B

Bonferroni corrected significance level: 0.0024

Table A7: Post-hoc pairwise comparisons on Otters' Defense Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.

Cashu

2004

Sample	Mean of ranks	Groups
Splotch	103.412	A
Stripe	108.824	A
Otto	116.471	A
Oliver	119.742	A
Orson	127.618	A
Olaf	128.309	A
Ozstralia	128.647	A

Bonferroni corrected significance level: 0.0024

2005

Sample	Mean of ranks	Groups	
Patty	40.353	A	
Osama	41.265	A	
Oswald	51.118	A	B
Olaf	53.794	A	B
Otto	58.529	A	B
Ozstralia	63.941		B

Bonferroni corrected significance level: 0.0033

2006

Sample	Mean of ranks	Groups	
Osama	36.633	A	
Ozstralia	37.633	A	
Petunia	41.133	A	
Oswald	44.233	A	
Olaf	50.000	A	B
Otto	63.367		B

Bonferroni corrected significance level: 0.0033

Salvador

2004

Sample	Mean of ranks	Groups	
Rambo	99.167	A	
Saggy	99.167	A	
Ziggy	107.229	A	
Mars	117.417	A	B
Diabolo	117.854	A	B
Cacao	123.417	A	B
Fantasmita	123.938	A	B
Virute	132.500	A	B
Fantasma	133.125	A	B
Frita	151.188		B

Bonferroni corrected significance level: 0.0011

2005

Sample	Mean of ranks	Groups
Fantasma	54.971	A
Virute	64.941	A
Ziggy	66.176	A
Mars	68.412	A
Saggy	71.029	A
Cacao	71.294	A
Fantasmita	75.029	A
Rambo	76.147	A

Bonferroni corrected significance level: 0.0018

2006

Sample	Mean of ranks	Groups
Achilles	19.000	A
Ziggy	23.350	A
Fantasma	23.500	A
Rambo	30.350	A
Cacao	31.300	A

Bonferroni corrected significance level: 0.005

Table A8: Post-hoc pairwise comparisons on Otters' No Share Rate per 3-hour Session, based on Dunn's Procedure (XLSTAT 2006). Groups assigned to overalapping categories are not distinguishable statistically.