JAGUAR (*PANTHERA ONCA*) POPULATION DYNAMICS, FEEDING ECOLOGY, HUMAN INDUCED MORTALITY, AND CONSERVATION IN THE VÁRZEA FLOODPLAIN FORESTS OF AMAZONIA

By

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To my mother and father

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The jaguar (*Panthera onca*) is the largest felid of the Americas, and its historical range has been drastically reduced in the last century to approximately 46% of its original size. This drastic reduction and continuing decline of jaguar populations has been associated with the compound effects of habitat loss, direct killing of jaguars, and depletion of prey populations. The Amazon Forest has been recognized as the most important region for the long-term survival of the jaguar. However, as human settlements, hunting pressure, and deforestation rates increase, the Amazon and jaguars may have their survival compromised. The Várzea Flooded Forest is an important ecosystem in the Amazonian Biome because of its rich soils and abundance of resources, but overexploitation makes it the most critically endangered environment in Amazonia. Studies previous to this one indicate that the Várzea can have high densities of jaguar for at least part of the year and also that they can be important breeding and weaning grounds for jaguars in Amazonia, but knowledge on jaguar ecology and the impact of people on jaguars in this environment are still very limited.

In the first chapter of this dissertation I make a thorough review of jaguar knowledge and conservation in Brazil, and apply the policy sciences approach to solving problems to understand why current jaguar conservation actions are not being effective in preventing jaguar population declines in Brazil. In the second chapter I estimate jaguar population density and survival in Mamirauá Sustainable Development Reserve using spatially explicit capture recapture models, and investigate if the co-existence of jaguars and people inside Mamirauá Reserve caused significant changes in jaguar population parameters over the course of six years of monitoring. In the third chapter I characterize the hunting of jaguars by local people in Mamirauá and Amanã Reserves, and estimate the total number of jaguars hunted in these two sites using closed population capture recaptures model and interviews. In the fourth and final chapter I investigate the feeding behavior of the jaguar in Mamirauá Reserve and compare it to other environments.

CHAPTER 1
THE JAGUAR CONSERVATION PROBLEM IN BRAZIL – A VALUES PROBLEM

The ecological and life history traits of large carnivores (e.g., low density, dietary needs, large home ranges, territoriality, and low fecundity) make them particularly prone to extinction, especially where intense conflict with humans for food and space result in direct persecution (Inskip & Zimmerman 2009). Understanding ecology and behavior has been the focus of most carnivore related studies in the last 2-3 decades but the need for ecological knowledge of many species in specific conservation contexts remains unfulfilled (Karanth & Chellam 2009). At the same time, there has been increasing support in the literature to the importance of understanding the human dimensions of carnivore conservation to improve the design of conservation policies (Weber & Rabinowitz 1996; Clark et al. 1996; Kellert 1996; Clark et al. 2001; Treves & Karanth 2003; Inskip & Zimmerman 2009; Treves 2009; Karanth & Chellam 2009).

Reflecting on diverse policy and management experiences Ludwig et al. (1993:36) concludes that “natural resource problems are not really environmental problems. They are human problems that we have created at many times and in many places, under a variety of political, social, and economic systems”. In the case of the large carnivore conservation problem, local human density has been found to be strongly associated with carnivore extinctions. Direct killing by humans has been identified as the most important cause of mortality in practically every large carnivore studied to date (inside and outside protected areas), and the sources of current threats are virtually all anthropogenic (Crawshaw 1995; Woodroffe & Ginsberg 1998; Woodroffe 2000; Cardillo et al. 2004; Andren et al. 2006; Adams et al. 2008; Obbard & Howe 2008; Robinson et al. 2008). This has led to the general realization that large carnivore conservation will only be successful if the human dimensions associated with the problem are carefully considered (Clark et al. 1996; Kellert 1996; Weber & Rabinowitz 1996; Clark et al. 2001; Treves & Karanth 2003; Inskip & Zimmerman 2009).

The jaguar (*Panthera onca*) is the largest felid of the Americas, the third largest felid in the world, and the only species of the genus Panthera in the New World. The historical range of the jaguar extended from Southwestern United States to Southern Argentina (Guggisberg 1975), but has been drastically reduced since European settlement to approximately 46% of its original size (Sanderson et al. 2002). This drastic reduction and continuing decline of populations in the last century have been associated with the compound effects of human actions: habitat loss, commercial hunting (for parts or trophy), retaliatory hunting, and depletion of prey populations (Figure 1-1; Doughty & Myers 1971; Smith 1976; Emmons 1987; Medellin et al. 2002; Sanderson et al. 2002; Caso et al. 2008).

Clark et al. (2001) describe the decision process surrounding jaguar conservation as highly fragmented, under-organized, complex and ineffective. The authors attribute these undesired characteristics to the lack of biological knowledge, the lack of a unified conservation strategy across the species range (i.e., stakeholders have different goals and problem definitions), understaffed, under-qualified, and bureaucratic government wildlife agencies susceptible to political change, and the difficulty of guaranteeing long-term funding. This scenario has arguably changed for the better with the increase in biological knowledge, efforts of researchers, non-governmental organizations, and government wildlife agencies to establish protected areas (PAs), and the proposal of national, regional, and range-wide strategies for the conservation of the jaguar

(Appendix 1-1; Quigley & Crawshaw 1992; Sanderson et al. 2002; Rabinowitz & Zeller 2010; Paula et al. 2011). Additionally, there has been general improvement of wildlife agencies, more stable economies, bans on commercial hunting and trade of jaguar and most prey species, and an increase of the number of PAs in Latin American countries (FAO, 2011). These improvements, however, have had limited success in stopping the decline of jaguar populations (Sanderson et al. 2002; Caso et al. 2008; Paula et al. 2011).

Brazil holds more than 50% of the jaguar's current range and, therefore, has a major role to play in the conservation of the jaguar (Sanderson et al. 2002). The country has stepped up to this responsibility, pioneering ecological research on the jaguar in the late 1970s (Schaller & Vasconcelos 1978; Schaller 1979), creating more PAs than any other country within the jaguar's range, and contributing in whole or part to >100 peer reviewed publications and book chapters on jaguars in the last 40 years, which represents ~39% of all research publications on the species (see Appendix for results and methodology of bibliography review methods).

Despite this relatively large number of publications, human dimensions aspects have only been approached in a few studies, and have been limited in analyzing local perceptions of people in relation to jaguars (Conforti & Azevedo 2003; Zimmermann et al. 2005; Santos et al. 2008). The jaguar conservation problem in Brazil is still being approached in a technical-rationalist way (Clark et al. 2001), "in which problems are assumed to be 'objective' entities that present themselves to the scientist or manager" where "it is assumed that only one rational understanding of the problem exists, which the problem solver must find and describe in an unbiased manner" (Clark et al. 1996).

Under this solution-oriented approach the jaguar conservation problem is defined by the main proximate ecological factors that are reducing populations and threatening the jaguar's survival: habitat loss, direct killing of jaguars, and depletion of prey populations. This definition, however, is inadequate because it only identifies symptoms whose origins are not analyzed and which will vary greatly according to ecological, political, cultural, social and economic characteristics (Figure 1-1). Solving the problem "demands that we clarify the nature of the problem and define it usefully before finalizing goals, identifying and choosing alternatives, committing resources, and implementing solutions" (Clark et al. 1996).

The policy sciences provide a means for researchers, policy makers, practitioners and other conservation professionals to understand and participate in the social and decision processes pertaining to natural resources realistically, comprehensively, practically, and constructively (Lasswell 1971; Clark et al. 2000). It provides the guidelines to create an "operational map" of the past and potential future of the policy system of interest, and a means to clarifying and achieving the common interest of stakeholders involved (Clark et al. 2000). This interdisciplinary problem-oriented approach to solving problems has already been demonstrated for large carnivores (Clark et al. 1996; Clark et al. 2000), but has never been used in jaguar conservation.

The objective of this paper is to define the jaguar conservation problem in Brazil using the policy sciences problem-oriented approach to solving problems (Lasswell 1971; Clark et al. 1996; Clark et al. 2000), to improve the understanding of the social context and decision making processes involved, to evaluate whether or not the current goal of the policy process is adequate in relation to the common interest of stakeholders, and to evaluate past, present and proposed conservation actions. Additionally, based on this analysis, I suggest strategies to improve jaguar conservation efforts in Brazil.

The Policy Sciences Method for Solving Problems

The policy sciences method of solving problems is a problem-oriented, contextual, comprehensive, and interdisciplinary approach that is applicable to any context where people interact (Lasswell & MacDougal 1992). The method provides a conceptual framework that has four dimensions: problem orientation, social process mapping, decision process mapping and observational standpoint (Lasswell 1971; Clark et al. 2000). Empirical data pertaining to each of these dimensions is collected, organized and analyzed to create a realistic model of the policy system of interest.

Problem orientation is a strategy to address problems and create solutions. It is comprised of five “intellectual tasks” (Lasswell 1971:39). The first is to clarify the goals of stakeholders and to define the goal of the policy process. The interests of participants will vary, and defining the goal must be inclusive and encompass as many views as possible. This task is usually addressed after an analysis of the social context of the problem (Clark et al. 2000). The second task is to describe the history and trends of the problem, using empirical data on the biophysical and cultural context of the problem, and any other relevant processes. It implies identifying the status of key elements of the problem in relation to the desired status of those elements, given the goal(s) identified in task one. The third task is a description of the physical, biological and social conditions that have influenced, permitted, or caused the trends. The fourth task is to predict future trends based on present and past conditions assuming that there are no new management interventions in present conditions. The fifth and final task is achieved by comparing the predicted future trends (task four) to the desired goals of the policy process (task one), and then creating, appraising and selecting alternative strategies to make up for the discrepancy between predicted and desired states.

The "social process is the interaction of people as they influence the actions, plans, or policies of other people, even if they are unaware of each other" (Clark & Wallace 1998). Social process mapping is a way of understanding any particular social context (Lasswell 1971). Policy sciences use conceptual categories to describe any social context (Table 1-1). The rationale is that each participant has a different perspective of the policy process and interacts with other participants in specific situations where they use their assets (or base values), through various strategies, to achieve desired outcomes (goals), which have specific effects over the policy process and over other participants. The resulting map of the social context clarifies which participants are being benefitted and which are being deprived of their desires under the current policy scenario, and provides a frame of reference to understand how management actions may influence participants in the future.

The decision-making process is concerned with who makes decisions and how natural resources are used. Decision process mapping is the analysis of the decision-making process that is part of any policy process. It consists of seven interlinked functions: intelligence, promotion, prescription, invocation, application, termination, and appraisal (Table 1-2; Lasswell 1971; Lasswell & MacDougal 1992). By understanding the decision process decision makers can maintain good practices and correct an ineffective process (Clark & Brunner 1996). The information for this work was gathered through a combination of interviews and personal interactions with stakeholders, as well as reports and publications from government agencies, newspaper articles, scientific literature, and publically accessible online databases.

To determine ones' observational standpoint is to clarify how a participant fits into the policy process. The standpoint is "an individual's value orientations and biases resulting from personality, disciplinary training, experiences, epistemological assumptions, and organizational allegiances" (Clark et al. 2000). I am a Brazilian biologist with a Master's degree in Ecology, and currently a PhD candidate in the Department of Wildlife Ecology and Conservation at the University of Florida. I have been involved in biological research and conservation of the jaguar since 2002, having specialized in the ecology of jaguars in the Várzea Floodplain Forests of Brazilian Amazonia. In my history as a jaguar researcher and conservationist, I have transitioned from an almost preservationist perspective, where I thought jaguars and humans should be separated in space for jaguars to have a chance of survival, to a human-based conservation perspective, where I can no longer see the survival of healthy natural jaguar populations without the involvement of stakeholders and consideration of their values and goals within this policy process. Although this background necessarily inserts some bias to my viewpoints, my intention is to analyze this process as an independent policy analyst.

My main motivation for this work is the possibility of contributing to the conservation of the beautiful, ecologically and culturally important, jaguar, and simultaneously achieving of the expectations of the stakeholders involved in this process. I believe jaguars have all of the features and historical conditions to be a model for the conservation of carnivores.

The Jaguar Conservation Problem in Brazil (Problem Orientation)

Definition of the Conservation Problem

In Brazil the jaguar has been classified as vulnerable to extinction in virtue of the steady decline of jaguar populations over the last century, despite large scale management actions to protect natural environments, the jaguar, and biodiversity in general, and the consistent increase of scientific knowledge on the jaguar (Machado et al. 2008; Paula et al. 2011; Appendix 1-1). Historically the jaguar occupied the entire extension of Brazil and occurred in all six major continental biomes of the country but today it is found only in five of the six Brazilian biomes and populations are severely reduced and isolated in at least three of these five biomes (Table 1-3; Figure 1-1). It is estimated that only 55% of the remaining natural areas are adequate to sustain jaguar populations (Ferraz et al. 2011). The main proximate causes of this decline have been habitat loss, commercial hunting, retaliatory hunting, and depletion of prey populations (Paula et al. 2011).

The more than one hundred scientific publications and book chapters published about jaguars in Brazil in the last four decades seem to have had limited effect on jaguar conservation (Appendix 1-1; Weber & Rabinowitz 1996; Sanderson et al. 2002; Rabinowitz & Zeller 2010; Caso et al. 2008; Paula et al. 2011). Even major national and international management actions such as the national ban on commercial hunting of wildlife in Brazil in 1967 (Brazilian Fauna Protection Law 5197/67), the international protected status of the jaguar since 1973 (CITES 1973), and the increase in the number of PAs (Rylands & Brandon 2005), have been unsuccessful in stopping the decline of jaguar populations in Brazil.

Current Goal of the Policy Process

The current goal of the policy process surrounding jaguar conservation in Brazil has been determined by a panel of researchers, non-governmental organizations and government wildlife agencies as: “to reverse the trend of decline of jaguar populations and reduce the jaguar’s threat status in all biomes of Brazil where the species still occurs in the next 10 years” (Paula et al. 2011).

Historical Trends and Conditions (Analysis of the Problem)

Our analysis of the jaguar conservation problem is organized in four parts that focus on the main proximate causes of jaguar decline: habitat loss, direct killing of jaguars, depredation of prey populations, and loss of population vigor. For each of these threats I identify how they influence jaguar population and what conditions have allowed these threats to persist or aggravate.

Habitat Loss

Habitat loss has been claimed to be responsible for major jaguar declines even in the most preserved natural areas of the most fragmented biomes of Brazil, such as the Atlantic forest (Leite et al. 2002; Mazzolli & Hammer 2008). As >37% of the natural habitats of the country have been converted to other land uses and the rate of habitat conversion is still high in all biomes (Table 1-4), habitat loss is arguably the most pressing issue in the conservation of the jaguar in Brazil. This loss of natural habitats is the compounded result of a myriad of human activities or of factors that have been created or exacerbated by human actions (Figure 1-2).

Brazil is divided into six continental biomes: Amazonia, the Atlantic Forest, the Caatinga, the Cerrado, the Pantanal, and the Pampa (Figure 1-1). Biomes, as defined by the Brazilian Institute of Geography and Statistics (IBGE), are groups of plants and animals constituted by continuous vegetation types identifiable at a regional scale, with similar geologic and climatic conditions, and shared history of change, resulting in a characteristic biological diversity. Until the 1900s the jaguar inhabited all biomes but a few decades ago it was extirpated from the Pampa biome (Fontana et al. 2003). The historical causes of habitat loss and the conditions that promoted it in each biome are distinct.

The Amazon forest is the largest tropical forest on our planet, covering 5,300,000 km² (Soares et al. 2006). It hosts approximately 25% of the world's terrestrial species (Dirzo & Raven 2003) and a fifth of the freshwater that runs from continents into the ocean (UNEP & ACTO 2008). More than 65% of the Amazon forest lay within Brazil's borders and constitutes the biome Amazonia. Amazonia remained practically intact to habitat loss until the early 1970s, but since then has experienced habitat loss at dramatic rates (Fearnside 2005). Most deforestation in this biome has been caused by large scale cattle farmers and soybean producers motivated by tax incentives, government-subsidized credit, inflation (i.e., deforestation enabled claim of land and land speculation, and cutting forest for cattle pasture was the cheapest way to do it), and growth in the international market for soybean and beef (Fearnside 2005). Government investment in infrastructure such as highways, railroads, and waterways, has also played its part, as it accelerates human migration to remote areas, increases clearing of established properties, and opens frontiers for investing timber profits in cattle ranches and soybean plantations (Fearnside 2005). Logging, including selective-logging, also increases the susceptibility of the forest to fire and further contributes to habitat loss (Nepstad et al. 2004). The large portion of Amazonia that remains, >82%, can be associated to the high logistical costs of exploring natural resources in this environment due to its large extension and intricate river system, to the large number and area of PAs, and more recently to efforts of the government to slow deforestation rates in the agricultural frontier areas to the south and east, known as the arch of deforestation (Figure 1-1). Additionally, in part to Brazil's forest code of 1965 (Law 4.771/65) which requires that 80% of rural private properties in this biome be maintained in its natural state.

The Pantanal is one of the largest continuous wetlands in the world covering >150,000 km^2 of the floodplain of the upper Rio Paraguay and its tributaries. The patchy landscape of this biome is a mix of grasslands (31%), woodlands (22%), bush savanna (14%), marshes (7%), semi-deciduous forests (4%), gallery forests (2.4%), and floating mats (2.4%; Harris et al. 2005). The main ecological factor influencing this environment is the flood pulse (Junk & Silva 1999; Oliveira & Calheiros 2000), which follows an annual, monomodal cycle with an amplitude of 2 to 5 m and duration of 3 to 6 months. The main human activity in this biome is cattle ranching and > 95% of the area is privately owned (Quigley & Crawshaw 1992; Soisalo & Cavalcanti 2006). Replacement of forest and savanna habitats by exotic grass species for cattle ranching, and burning to renew pastures, which often leads to uncontrolled fires, have resulted in most of the habitat loss in this biome (Harris et al. 2005; Alho 2008). Furthermore, cattle ranching is also becoming increasingly competitive, and intensive and irrigated agriculture spreading inside the floodplain are main factors of concern. Current PAs constitute less than 5% of the region and offer little help for conservation of the Pantanal (Table 1-4). The large area of natural habitat remaining in the Pantanal, >84%, is thought to be linked to the difficulties of implementing extensive agriculture in a seasonally flooded environment (Alho & Lacher 1991).

The Atlantic forest is one of the most highly threatened tropical forests in the world and is the Brazilian biome with the smallest portion (12%) of natural habitats remaining (Table 1-3), of which more than 70% is private property (Leite et al. 2002). Because of the human colonization path, the Atlantic forest has a much earlier history of habitat loss than other biomes, which probably explains its critical condition. The conversion of habitat in this biome has been closely related to the economic exploitation of different commodities throughout Brazil's history, such as Pau-Brasil tree (*Caesalpinia echinata*) in the 16th century, sugar cane in the 18th century, cattle ranching from colonization to present, coffee in the 19th and 20th centuries, and more recently, the expansion of urban areas and eucalyptus (*Eucalyptus* sp.) plantations (Dean 1997). Even today, despite severe legal restrictions on deforestation, the rate of forest loss is still high, approaching 0.25% or 350 km^2 per year (Fundação SOS Mata Atlântica and INPE 2011). As a consequence of this long history of degradation, the Atlantic forest is highly fragmented (Figure 1-1).

The Cerrado biome is the second largest biome of Brazil (Table 1-4). It covers most of Brazil's central plateau and is a combination of woodlands, savannas, grasslands, and gallery and dry forests (Eiten 1977; Ribeiro et al. 1981). The Cerrado is also the second most threatened biome of Brazil with >48% of its natural habitats lost and only 2.5% of its area inside PAs. The major causes of habitat loss in the Cerrado in the last three decades have been the expansion of the agricultural frontier and increment of the production of soy, maize, and beef (Klink & Moreira 2002; Klink &

Machado 2005). The production of charcoal is also a major contributor to habitat loss in this biome and the imminent expansion of sugar cane plantations is a clear threat (Carvalho et al. 2009). The growth of international markets for soybean and beef, associated with the small "legal reserve" requirements of the Brazilian Forest code for this biome have provided the right conditions for this trend. In the Cerrado, differently from Amazonia, land-owners are only required to maintain 20% of their properties in its natural state.

The Caatinga consists primarily of xeric shrubland and dry thorn forest that cover much of northeastern Brazil. It is the third most degraded and highly fragmented Brazilian biome with >45% of its natural habitats altered by human activities (Figure 1-1; Castelli et al. 2004). Habitat loss in the Caatinga also has a long history. The introduction of cattle and goats by Europeans in the early 1500s rapidly devastated the native plant species that lacked resistance to intensive grazing, and in the early sixteenth century most of the forests were destroyed for timber and for cattle ranching, leaving mostly open scrub forest (Coimbra-Filho & Câmara 1996; Leal et al. 2003). Current threats include slash-and-burn agriculture, which converts remnant vegetation to new and short-lived cropland, harvesting of firewood, and continuous depredation of the vegetation by cattle and goat herds, which are now estimated to number more than 10 million animals (Medeiros et al. 2000).

The Pampa is one of the smallest Brazilian biomes, occupying only 2.1% of the country. Grasslands, with sparse shrub and tree formations, are the dominant vegetation (Berreta 2001). Livestock production, mainly cattle and sheep, have been the main economic activity in the region. Habitat loss in the Pampa biome in the last 40 years has been the result of a strong expansion on agricultural activities, primarily due to the increase in production of corn, soybeans, wheat, and rice (Overbeck et al. 2007). The cultivation of exotic trees (e.g. for pulp production) has also increased and taken its portion of the biome as a result of incentives from both private industries and the government, and new projects will increase this area in the near future (Overbeck et al. 2007). Cultivated pastures and the introduction of exotic species of grass have also taken its toll of the natural grasslands of this biome.

Direct Killing of Jaguars

Commercial hunting was a critical issue for jaguar conservation in the 1960s due to an unfortunate trend in the fashion industry, which created a large demand for spotted-cat skins and transformed hunting of jaguars into a lucrative occupation for rural people (Doughty & Myers 1971; Smith 1976). Professional hunters were killing approximately 15,000 jaguars per year during that period in Brazilian Amazonia alone (Smith 1976). Back then, a jaguar was worth as much as US $130 to hunters and in the larger regional markets, such as Belem and Manaus, skins would sell for up to US $180 (Doughty & Myers 1971; Smith 1976). Updating these values to current buying power this would be equivalent to approximately US$ 505-976. The jaguar had an easily accessible, positive, economic value to stakeholders.

Today, despite their protected status (Brazilian Fauna Protection Law 5197/67, CITES 1973), illegal commercial hunting of jaguars still occurs due to market demand for hunting jaguars as trophy (i.e., there are people that want to hunt jaguars and are willing to pay large sums of money for it), buying jaguar parts as souvenirs (i.e. pelts, skull and teeth), meat for food, and raising cubs as pets. In 2010, a group of 11 people were arrested in the south of Brazil where they organized jaguar trophy hunts in three states, encompassing the Pantanal and Atlantic Forest biomes, including hunts inside Iguaçu National Park (R. Morato, personal comment). Their clients included hunters from Brazil, Europe and other Latin American countries and each hunt sold for US$ 1,500. Jaguar parts are also still collected as ornaments and trophies. It is common to find jaguar skulls and pelts on the walls of rural households in Amazonia and there is also a black market demand from urban centers (E. Ramalho, personal comment). Jaguar meat, although usually distributed among neighbors and family, may also be sold as bushmeat in local markets or within the hunter's community. For example, in Colombia jaguar meat is sold for about US $1.5/kg (Balaguera-Reina & Gonzalez-Maya 2008). The capture of cubs occurs occasionally, usually during hunting of game with dogs. The mother is either killed or chased off and the cubs are kept as pets by the hunter, given out to neighbors or sold. In Mamirauá Sustainable Development Reserve, for example, in 2004 a female jaguar cub was sold by a riverside tradesman for less than US $20 to a local farmer (E. Ramalho, unpublished data). This cub was raised into adulthood in the farmer's village inside a cage and was translocated to a zoo in 2008 at the age of five.

Cultural historical motives are also a large contributor to people killing jaguars. As the largest terrestrial predator in Brazil, capable of taking prey much larger than them, including humans, jaguars have historically been feared and killed by indigenous people and rural stakeholders. For indigenous people the jaguar has a multitude of cultural, cosmological and ecological meanings that are not negative, although they can be related to fear (Whitehead & Right 2004). For some indigenous people, however, this special relationship does not necessarily affect the decision of killing a jaguar if it is felt that the jaguar is threatening a tribe member, or to prevent future livestock depredation (P. Constantino, personal comment). It is difficult to assess the impact of indigenous communities on jaguar populations before colonization, but these communities probably exerted small hunting pressure on wild cats. Jaguars were occasionally killed for cultural rituals but were generally feared and respected (Smith 1976).

Despite the effort of colonizers to dissociate indigenous cultures to the jaguar, the perception and cultural importance of jaguars is unlikely to have changed (Fausto 2004). The jaguar has historically been revered by these cultures as symbols of power and beauty (Saunders 1998; Luna & Amaringo 1999; Whitehead & Right 2004). However, as indigenous communities evolve within the contemporary world and change their economic activities, it is expected that their impact on wildlife, including jaguars, may change. Livestock, for example, was not a subsistence activity for indigenous communities before colonization, who therefore had no motive to kill jaguars in retaliation for livestock losses. After the introduction of livestock, it is likely that indigenous farmers kill jaguars to prevent or retaliate for depredation in the same way that traditional livestock farmers do. Their impact on jaguars today will be associated with livestock depredation. Even after European settlers arrived, hunting pressure on jaguars and other spotted-cat populations in Amazonia was relatively small and concentrated around urban centers, agricultural frontiers, and small human settlements that were sparsely distributed along rivers in the Amazon basin (Smith 1976). Although there are no estimates of harvest rates for this period, the impact of hunting was likely small because demand for spotted-cat skins was relatively low and consequently there was no economic incentive to pursue these animals. Furthermore, human density was low and hunting was locally aggregated, leaving large portions of the jaguar population under little to no pressure. Consequently, there was a large source and few sinks.

The arrival of European settlers to the new world probably also brought along their deep-rooted fear of large carnivores and their cultural bias towards eliminating predators (Clark et al. 1996). Although jaguar attacks on people have been recorded in many areas throughout Brazil (CENAP, unpublished data) they are rare events and usually related to people approaching jaguars deliberately or by accident, mostly caused by animals cornered during hunting (Almeida 1976; Paula et al. 2008). The first official record of a predatory attack on a human occurred in June of 2008, in the Pantanal biome (Paula et al. 2008). In this case a fisherman was attacked and killed while sleeping in a tent in on the banks of the Paraná River, Mato Grosso state. His body was carried a couple hundred meters and he was partially eaten. Different from other large cats, there are no reported cases of jaguars that have developed man eating habits, but Paula et al. (2008) highlight that if habituation of jaguars to people (i.e., using baits for tourism) continues to occur, predatory attacks on humans may become an issue.

On top of this cultural import, contemporary rural stakeholders in general have a negative perception of the jaguar associated to real or perceived negative effects that jaguars may have on their livelihood, mainly: predatory attacks on people, economic losses due to depredation of livestock and dogs, and competition for game (Conforti & Azevedo 2003; Zimmerman et al. 2005; E. Ramalho, unpublished data). Negative symbolism associated with large carnivores in general, such as viciousness and ferociousness, also contribute to this perception (Leopold 1949; Kellert 1991; Kellert et al. 1996). These perceptions often lead to negative attitudes towards jaguars, where most of rural stakeholders do not support, or want no part, in jaguar conservation, and where the ultimate result is the persecution and deliberate killing of jaguars (Carvalho & Pezutti 2010; Hunting chapter). The overlap between the diet of the jaguar and that of subsistence hunters (Jorgenson & Redford 1993) and the consequent deduction that jaguars deplete prey populations also motivates rural stakeholders to kill jaguars. Jaguars are also killed for pleasure (trophy/sport hunting), status, or both, and bounties are still offered in most areas where jaguars kill livestock. This retaliatory killing of jaguars, as a form of control of depredation of domestic animals, is one of the main factors contributing to jaguar population decline in Brazil (Crawshaw 2003).

The perceived value of jaguars to stakeholders has been reported to be very distinct between biomes (Santos et al. 2008), age group, and rural and urban populations (E. Ramalho, unpublished data), and will also probably vary according to social, cultural, historical and economic factors. Regardless of the predominantly negative view of most rural stakeholders towards jaguars (Conforti & Azevedo 2003; Zimmerman et al. 2005), there has been increasing support from the general public to support the conservation of the jaguar. Positive perceptions and attitudes towards jaguars can be attributed to positive symbolism associated with large carnivores, such as beauty, strength, intelligence, courage, and endurance, or a general affection for nature, understanding of the ecological role of large predators, or moral and ethical beliefs, as observed by many authors (Leopold 1949; Lopez 1978; Rolston 1981; 1985; Kellert 1985, Kellert et al. 1996). These positive values, however, are difficult to quantify economically and are usually ignored or undervalued (Bishop 1978; Usher 1986;

Rasker & Hackman 1996), while negative values associated with livestock depredation are easily measured by stakeholders and therefore receive more attention.

The consumption of jaguar meat is not unusual among rural communities in Amazonia (E. Ramalho unpublished data) and the Atlantic Forest (Rocha-Mendes et al. 2005) biomes, and has been reported in the Colombian Chocó (Balaguera-Reina & Gonzalez-Maya 2008), but we found no recent records of these events in other Brazilian biomes. However, even in Amazonia, jaguars do not represent an important food resource and hunters will seldom, if ever, go out of their household with the intention of hunting a jaguar to eat. Because jaguars occur in low densities, are difficult to track, and are dangerous to hunters and dogs, actively hunting them for food is not cost-effective. The consumption of jaguar meat is usually associated with hunting of jaguars for other motives or during chance encounters (e.g., during fishing expeditions) and is driven by the protein needs of rural dwellers whose main source of protein is fish and game.

Decrease of Prey Populations

The jaguar is an opportunistic predator with a rather flexible feeding ecology, consuming over 85 different species of prey, from snakes to tapirs (*Tapirus terrestris*; Seymour 1989). However, in most environments studied to date, jaguar populations seem to depend on medium- to large-sized terrestrial mammals to survive (Novack et al. 2005). This dependence makes them vulnerable because medium and large-sized terrestrial mammals are less resilient to habitat loss, and because these animals are also the preferred game species of subsistence and commercial hunters (Jorgenson & Redford 1993; Robinson & Bennett 2000). Prey depletion by subsistence hunting has been pointed as a major threat to jaguar survival range-wide (Emmons 1987; Sanderson et al. 2002) including in Brazil (Guix 1997; Leite & Galvão 2002).

Subsistence hunting is a critical activity for indigenous and rural communities outside urban areas because wildlife is a major source of protein and fat. At the same time, subsistence hunting has been considered the main cause of wildlife population declines in Latin America (Redford 1992), and has increased in recent years as the result of human population growth, easier access to undisturbed natural habitats, improvement of hunting technology, and scarcity of alternative protein sources (Robinson et al. 1999). The increase of rural populations is usually followed by a decrease of game populations because the subsistence hunter's rationale is to maximize immediate harvest success instead of long-term conservation goals (Stephens & Krebs 1986; Robinson & Redford 1991; Alvard 1993). Commercial hunting, although presently illegal in Brazil, also contributes to defaunation, as there is demand for bushmeat inside communities and local markets, and law enforcement is scarce. Currently, one of the most important conservation issues for jaguars in Amazonia may be the implementation of the commercial harvest of black caiman (*Melanosuchus niger*), especially in the varzea floodplain forests where black caiman eggs constitute an important food source for jaguars (Ramalho 2006; Ramalho & Magnusson 2008, Silveira et al. 2010). The depletion of prey populations may also contribute to generating more conflicts between rural stakeholders and jaguars by increasing instances of livestock depredations (i.e., reducing availability of prey to jaguars may result in more livestock depredation and more direct killing of jaguars to protect livestock.

Jaguar Population Vigor

Analyses of the genetic structure of the jaguar have concluded that there has been historical connectivity between jaguar populations across broad geographical areas, with few barriers to gene flow on a continental scale (i.e., the Amazon river, the Andean mountain chain, and a apparent barrier in Central America; Eizirik et al. 2001; Ruiz-Garcia et al. 2006).

However, reduction and isolation of jaguar populations as a consequence of all the threats described in the previous sections contributes to the decrease of genetic diversity of subpopulations within biomes, as well as drift induced differentiation among local fragments, as shown by Haag et al. (2010) for the Atlantic Forest biome. This reduction of genetic diversity due to inbreeding depression, has been shown to have harmful effects on development, survival and growth rate of species in captivity and in the wild, and may leave small jaguar populations at the mercy of stochastic forces that lead to extinction: demographic, genetic, environmental and catastrophes (Schaffer 1983).

Future Projections

If the current conditions persist jaguar populations will continue to decrease in Brazil, and the jaguar will eventually become extinct in more Brazilian biomes. The most threatened jaguar populations are in the Atlantic forest and Caatinga, where subpopulations are small (in both biomes subpopulations average less than 40 individuals, and total population is less than 200 individuals – Table 1-3), isolated (i.e., biomes are largely fragmented), and poorly protected (not enough parks and inefficient law enforcement). The causes of this decline will continue to be habitat loss, retaliatory hunting, and depletion of prey populations.

The Social Context

We have identified six major groups of stakeholders directly involved in the jaguar conservation problem in Brazil (Table 1-5). Small- to medium-sized farmers and traditional communities (SFTC) include people that live in rural areas with properties

<900 ha, and <500 heads of cattle or other livestock herd (this is the classification used by IBGE – www.ibge.gov.br). They may be single families, a community of families, or a tribe. They are usually poor and live inside or in the vicinity of jaguar habitat. Their livelihoods may be directly affected by a jaguar (i.e., depredation of livestock, attack or perceived threat of attack on humans), and/or their livelihoods depend on jaguar habitat (i.e., extractivist activities, converting natural habitats for pasture or plantations) and/or prey. Large scale farmers (LSF) include livestock farmers and crop producers with properties >900 ha and/or >500 heads of cattle or other livestock herd (this is the classification used by IBGE). These stakeholders are usually wealthy and/or politically powerful agricultural businessman, and national or international corporations (i.e., Monsanto). Non-governmental organizations, research institutions, and universities (NRU) include researchers, conservationists and their funders. Government wildlife agencies (GWA) represent the Brazilian government environmental agencies directly involved in the jaguar policy process: ICMBIO, CENAP and IBAMA. The general public (GP) includes the national and international urban populations that do not interact with jaguars on a daily basis or never interact. Trophy hunters and outfitters (THO) are all sport hunters and outfitters, and any other individual or organization, involved in the activity of hunting animals for sport. They are currently prohibited by law to exercise this activity in Brazil, with the exception of a few private properties in the south of the country which have obtained special permits to hunt specific game species, but not the jaguar.

By mapping the social milieu of jaguar conservation in Brazil (Table 1-5), I observed that stakeholders can be further grouped into two categories: direct interaction stakeholders (DIS), and indirect interaction stakeholders (IIS). DIS are people whose livelihoods involve, or depend, on the direct interaction with jaguars, their natural habitat, and their prey. Three stakeholder groups fit these attributes: SFTC, LSF, and THO. Their goals involve improving their livelihoods of at least three of these four base values: wealth, well-being, power, and respect. As strategies to achieve their goals SFTC and LSF kill jaguars to prevent future loses of livestock (wealth – less economic losses to depredation equals more profits) and/or potential jaguar attacks on local people (well-being – people feel safer). They also hunt legally for subsistence (well-being – wildlife is an important source of protein for many SFTC), or illegally, for commercial or recreational purposes (wealth and well-being – some people profit economically from selling wildlife, which is most cases is complementary subsistence activity for SFTC; others hunt for leisure), and convert natural habitats to pasture and croplands, legally, and illegally, to increase agricultural profits (wealth). They use their political power to pressure the government for more management rights over natural resources (power and respect – they demand legal rights to hunt wildlife commercially and to be able to convert larger areas of natural habitat within their properties). The goal of THO is to have the right to hunt wildlife (power), including the jaguar, because it is an activity that gives them pleasure (well-being), and develop hunting enterprises, because they can generate profit (wealth). Because none of these activities are currently allowed by law, some of them hunt or promote hunting illegally in their property or in state lands, taking advantage of the incapability of the government to enforce the law. The strategies of DIS (i.e., converting natural habitats to pasture or croplands, illegal killing of jaguars, and over-exploiting or illegal hunting of prey populations) are considered to be the main proximate causes of the declining trend of jaguar populations, habitat, and prey populations.

IIS are stakeholders whose livelihoods do not generally involve, or depend, on the direct interaction with the jaguar, their habitat, or their prey. The other three stakeholder groups fit these attributes: NRIU, GWA, and GP. Their main goal is to reverse the current trend of decline of the jaguar population of Brazil. Most of these stakeholders have pleasure in knowing jaguars still exist, that they are protected in the wild, and will be around for the next generations to appreciate (well-being). And some of them, mainly NRIU and GWA, also understand the ecological and cultural importance of the jaguar. Their strategies, however, are mainly coercive, restricting management rights of natural resources for DIS (i.e., ban on hunting of jaguars and wildlife, creation of reserves, restricting the portion natural areas within private properties that can be converted to other land uses) without giving stakeholders alternatives to compensate restrictions. These strategies are guided by a technical-rationalist biological rationale that does not take into consideration the goals and value demands of DIS.

This discrepancy between the goals of DIS (who are assumed to be responsible for a large part of the jaguar conservation problem) and the strategies of IIS seem to be a central obstacle for the effective solution of the problem, since the strategies of DIS only benefit DIS, and the strategies of IIS only benefit IIS, both depriving the other stakeholders group of achieving their goals. The question is now: who is going to be the bigger man and change strategies to encompass other stakeholder goals and value demands?

The Decision Process

Research and Planning (Intelligence Function)

In Brazil, the collection, analysis, and distribution of information about the jaguar's biology and conservation have been the responsibility of NRU and GWA. Since the 1970s, when the first field studies on jaguar ecology were conducted in the Pantanal biome (Schaller & Vasconcelos 1978), considerable advances have been made with regards to scientific information on the jaguar. Our review of jaguar scientific literature in Brazil resulted in 145 research publications, including peer-reviewed publications, thesis and dissertations, books, and book chapters (see Appendix 1-1 for details on literature review methods). Nonetheless, important scientific information to guide management decisions is lacking in all biomes.

The ecology and behavior of the jaguar is still poorly understood in Brazil. Diet has been the ecological aspect most studied to date, being the subject of research on 17 (48.6%) of the 35 studies on jaguar ecology and behavior. But research on jaguar feeding habits has been concentrated in the Atlantic forest and Pantanal biomes, and is scant in the other three biomes. Scientific information on movement, home-range size, and habitat use, and on populations parameters and structure are have only been conducted to some extent in the Pantanal and the Atlantic forest. In the other biomes home-range sizes are unknown and jaguar density has only been estimated in one or two sites per biome, being difficult to estimate population sizes.

Most studies that involve jaguar conservation propose actions to improve the status of jaguar populations (15; 55.6%), but there are no studies in any of the five biomes that have actually empirically tested a conservation strategy proposed. Status and distribution studies are abundant in the Atlantic forest biome (7; 25.9%) but are practically non-existent everywhere else. And, despite the drastic impact of habitat loss on jaguar populations, only two studies involve evaluating the impact of habitat loss on jaguars in Amazonia and the Atlantic forest biomes.

The conflict between human and jaguars has also received smaller attention than expected based on the impact of this interaction on the jaguar (22; 20.2%). The impact of jaguar livestock depredation has concentrated in the Atlantic forest and Pantanal biomes (4 studies in each), but has also been studied in Amazonia and the Cerrrado. These studies however use different methods and units, which make them hard to compare. Direct hunting of jaguar is another crucial, yet neglected topic. To this day there is only one study which has actually tried to estimate the number of jaguars killed by local people, and that was in Amazonia (Carvalho & Pezutti 2010). The human dimensions of the jaguar conservation problem have only been approached in three publications, all of which looked at local perceptions about the jaguar (Conforti & Azevedo 2003; Zimmerman et al. 2005; Santos et al. 2008), but not at their goals, values demands, or interactions with other stakeholders.

Planning activities have been realized at a national level by NRIU and GWA. In 2007, NGO Jaguar Conservation Fund (JCF) organized the first national meeting of jaguar researchers in Brazil and in 2009, the Brazilian government initiated a jaguar conservation planning effort with the “Workshop for the conservation of the jaguar”. This meeting, organized by the Brazilian government agency CENAP (National Center of Research and Conservation of Mammalian Carnivores)/ICMBIO (Chico Mendes Institute of Conservation of Biodiversity) in partnership with NGO Panthera, and supported by NGO Instituto Pró-Carnívoros, IUCN’s (International Union for

Conservation of Nature) Cat Specialist Group and the Conservation Breeding Specialist Group (CBSG), brought together 37 researchers and policy makers that study or have studied jaguars in Brazil with the objective of evaluating the current status and trend of jaguar populations in the country, and the production of a National Action Plan for the conservation of the species.

Recommending and Debating Policies (Promotion Function)

Recommending and debating policies related to jaguars has only been done at local scales (i.e., inside a few protected areas), but has never been done at regional or national scale. I am aware that it is unrealistic to imagine a meeting of all groups of stakeholders identified, from all biomes, at one location, at one point in time, to discuss and decide on alternative policies to solve the jaguar conservation problem in Brazil. But what I have shown by mapping the social context is that the goals, values demands, strategies, and interactions of stakeholders involved can, at least initially, be represented by information from scientific literature or professional experience, giving a much clearer view of how different policies will affect stakeholders and the policy process as a whole. Although this social map is a model, it improves the decision process and provides a frame of reference for adapting to more specific situations where policies to recuperate jaguar populations need to be implemented.

Creating, Implementing and Enforcing Rules (Prescription, Invocation and Application Functions)

Creating rules at regional and national scales (i.e., laws) is a task of the government and its wildlife agencies, but this function has been historically limited by a lack of scientific knowledge on important aspects of jaguar ecology in all biomes, as show in the intelligence function section. Until very recently, almost all management actions that contributed to the conservation of the jaguar in Brazil had not been specifically designed for the conservation of the jaguar. The only formal management action that was created, implemented and enforced specifically designed for jaguars was the international ban on hunting and trade of jaguars, enacted by the inclusion of the jaguar in appendix 1 of CITES (1973). Interestingly, this action was created and implemented before any solid scientific information on jaguars was available in Brazil or anywhere else.

The National Action Plan for the conservation of the jaguar in Brazil (Paula et al. 2011) is the first recovery plan designed for the jaguar in Brazil. The action plan contains a valuable and unprecedented compilation of information on the status, trends and threats to the jaguar, its habitats, and its prey, in all 5 biomes where the species exists in Brazil. It also compiles a prioritized list of conservation actions proposed by the participants to revert the declining trend of jaguar populations in each Brazilian biome.

Building corridors to connect jaguar sub-populations, and a formal recognition of the jaguar as a natural symbol of Brazil by the Brazilian government, are the only two current conservation actions that are being formally undertaken by the GWA and NRIU to specifically address the conservation of the jaguar in Brazil. Corridors are under implementation in the Atlantic Forest biome and the Caatinga biomes in Brazil, led by the NGO Institute of Ecological Research (IPÊ) and CENAP (R. Morato, personal comment). In both cases implementers have involved local stakeholders through public meetings, and have taken into consideration their goals and value demands to improve the chances of success of the corridors. In all these cases, however, stakeholders are consulted after the conservation action has already been decided by GWA and NRIU.

Meetings only have the function of adapting the strategy to the demands of local stakeholders.

Evaluation and Termination of Rules (Appraisal and Termination Functions)

Although it is commonly accepted that protected areas, and the bans on hunting and trade of wildlife, have had a positive impact on the conservation of jaguars, natural habitats, and prey populations, there has been no quantitative evaluation of the impact, or other measure of success, of these strategies on jaguar populations. How many jaguar where killed before the ban on hunting versus how many jaguar are killed today? Have protected areas had a positive impact on jaguar and prey populations? What is the impact of subsistence hunting and illegal hunting on jaguar and prey populations inside and outside protected areas?

Because evaluation of conservation measures have not been promoted it is difficult to determine which rules to terminate.

Current Solutions, Recommended Solutions, and Alternative Solutions

Bans on Hunting and Trade of Jaguars and Prey

Bans on hunting of wildlife in Brazil in 1967 (Brazilian Fauna Protection Law 5197/67) and the inclusion of the jaguar in appendix 1 of CITES, banning hunting and international trade of jaguar parts in 1973 (CITES 1973), have had a substantial impact on commercial hunting of jaguars in Brazil, and are thought to have reduced the number of jaguars killed in Brazilian Amazonia by half (Smith 1976). However, it is naïve to believe that these bans can effectively protect jaguars in Brazil given that GWA do not have enough staff or financial resources to regulate direct killing of jaguars for commercial or other motives. Additionally, the diversity of municipal, state, and federal competencies of GWA, under different economic, social, and political pressures throughout Brazil, make it even harder to enforce these bans (Crawshaw 2003).

Although these strategies helped address the killing of jaguars for commercial reasons, the ban on hunting also reduced the jaguar to a zero or negative social-economic value to rural stakeholders (SFTC and LSF) because they cannot profit from the commercial harvest of jaguars anymore; however, at the same time, they still feel threatened physically by jaguars and have a financial burden from livestock losses from jaguar depredation. Today, this negative social-economic value associated with the jaguar is the most frequent motivation of SFTC and LSF for killing jaguars in Brazil and other countries, wherever livestock farmers and jaguars coexist (CENAP, unpublished data; Sanderson et al. 2002). This negative social-economic value is created by the proximity of jaguars and people, associated with anthropogenic imbalances in the environment (i.e. habitat loss, decrease of prey populations), lack of information about the species, natural variations in prey availability, and poor management of livestock (especially calves), all of which usually lead to jaguars approaching properties and killing livestock. This negative value is easily estimated by the stakeholder (i.e., the value of the livestock), and because stakeholders have to cope with the loss themselves, they choose the cheapest and fastest solution to stop and prevent depredation future depredation, which is to kill the jaguar.

The ban on hunting of wildlife also decreased the pressure on jaguar prey populations, but outside PAs animals are hunted almost indiscriminately, and often inside PAs too (Leite & Galvão 2002), due to the limitations of GWA in enforcing the law. The impact of subsistence hunting on wildlife is also of major concern and it is still highly controversial if subsistence hunting is sustainable or not (see section on depletion of prey populations).

Protected Areas

So far, the main strategy of the Brazilian government to mitigate habitat and biodiversity loss has been the creation of PAs (Peres 2005; Silva et al. 2005). PAs in Brazil have functioned as effective barriers to habitat loss (Silva 2005), and remain a corner stone of conservation worldwide, being credited with saving wildlife populations from regional and range-wide extinction (Terborgh et al. 2002; Woodroffe & Ginsburg 1998), despite deficiencies in management and implementation, and criticism for imposing societal goals on local people (West & Brockington 2006). Indigenous territories (IT) have also contributed to the conservation of natural habitats, especially in Amazonia, where they encompass over a fourth of the biome's area (Table 1-4). Unfortunately, this relative success has not been enough to protect natural habitats, jaguars, and prey population because many PAs only exist on paper and most have inadequate law enforcement. Additionally, PAs do not protect large portions of most biomes (Table 1-4), and most habitat loss is expected to occur in private properties outside PAs (Soares et al. 2006). Furthermore, the actual success of this strategy in protecting jaguar and prey populations is controversial (Chapter 3), although local people and researchers frequently report higher abundances of both inside PAs (E. Ramalho, personal comment).

To prevent unnecessary and unwanted habitat conversion outside PAs, the Brazilian government created the Brazilian forest code (Law 4.771/65) in 1965, a federal law that determines the extent and specific areas of a private property that must be maintained in natural state. These areas are denominated permanent protected areas

(APPs). The extent of a private property that must be assigned as an APP varies from 20% in the Cerrado, to 80% in Amazonia. Riparian areas along waterways must be protected, independently of biome, but with varying extents relative to the width of the waterway (e.g., 30 m for streams narrower than 10 m). This legislation has also been successful to some extent, but compliance with minimum legal requirements are highly variable (Resque et al. 2004) and difficult to enforce due to poor land titles management.

Of great concern for jaguar conservation is the current proposal of Senator Aldo Rebelo, representative of agricultural producers, to change the Brazilian forest code. The core of his proposal contends giving amnesty to landowners that have destroyed natural habitats illegally (i.e., over the allowed limits as explained in the previous paragraph), and establishes new, less restrictive, rules for determining APPs. His proposal has already been approved in the House of Representatives by a great majority of deputies and is soon to be voted on in the Senate. While it has been acknowledged by all sides of this debate that the forest code needs to be updated, it is imperative that this legislation is not changed to allow larger portions of private properties to be converted to other land uses, as this would result in a accelerated reduction of natural habitats in all biomes, and may seal the fate of small jaguar populations in the most fragmented biomes of Brazil: Atlantic forest, Cerrado, and Caatinga.

Better Management of Livestock

Improvement of livestock management practices has been cited in numerous publications as an effective and inexpensive way to reduce livestock depredation by jaguars, and, consequently, human-jaguar conflict (Quigley & Crawshaw 1992;

Crawshaw & Quigley 2002; Hoogesteijn et al. 2002; Azevedo & Murray 2007). Suggestions include concentrating births in a shorter period of time to allow better management and protection of calves, and maintain more vulnerable age classes away from areas of higher predator occurrence (Crawshaw 2004); moving cattle herds away from jaguar core areas (Azevedo & Murray 2007).

Improving livestock management practices has been shown to be a successful strategy to reduce livestock depredation by jaguars and it is even suggested that private farms, with adequate management, could be successful wildlife sanctuaries (Hoogesteijn & Chapman 1997; Hoogesteijn et al. 2002). It is also cheaper than other methods of reducing livestock depredation, like the techniques for adverse conditioning of predators described below. But the issue is that being cheaper does not mean that livestock owners will agree to do it, or comply to do it. The number of farmers actually willing to change their management practices to prevent depredation is, unfortunately, very small. The simple reason is that it is even cheaper, less time and energy demanding to kill jaguars than it is to change management practices. We can understand this very easily by making an analogy to urban stakeholders. What is the reaction of most people from larger cities when they are asked to not use their car because of global warming? Even if you give the people a reasonable alternative public transportation system, it still implies leaving your house earlier, having to walk to the station, stay in line, buy a ticket … And bottom line, not many people are willing to do it if they have the option of driving.

Techniques for Adverse Conditioning of Predators

Different methods for reducing the frequency of livestock depredation through adverse conditioning have been tested in Brazil, such as electric fences, nauseating substances put in carcasses of depredated livestock, toxic collars, electronic devices with strong lights and loud sounds, dogs and llamas to guard sheep, and fireworks, but the high cost of most of these have been prohibiting to most livestock owners (Crawshaw 2004).

Corridors

The solution that is in vogue for jaguar conservation at national (Leite et el. 2002; Cullen 2006; Haag et al. 2010) and range wide scales (Rabinowitz & Zeller 2010) is the creation of corridor of habitat to connect jaguar subpopulations. This strategy has been was proposed by IBAMA in 1996 (Ayres et al. 1997), but only recently has it started to be applied specifically for jaguar conservation. Corridors are currently under implementation in the Atlantic Forest and the Caatinga biomes in Brazil, led by the NGO Institute of Ecological Research (IPÊ) and CENAP, respectively, and in Central and South America by NGO Panthera.

Theoretically, corridors allow the exchange of individuals between patches of natural habitat, facilitate gene flow between subpopulations and reduce chances of stochastic extinction (Fahrig & Merriam 1994), as well as the potential for deleterious genetic effects resulting of inbreeding depression (Brown et al. 2004). However, not only the effectiveness of corridors in facilitating animal movement between habitat patches remains controversial (Rosenberg et al. 1997; Beier & Noss 1998; Bennett 2003), but the financial, political, and logistical viability of using corridors as a single species conservation strategy over large scales, such as Brazil, or continental and multinational scales, such as Latin America, has never been evaluated for large carnivores. In fact, Cullen et al. (2005), in simulations of the viability of jaguar subpopulations in the Atlantic forest biome, show that corridors may have a negative effect on connected subpopulations if these subpopulations are not effectively protected. This is worrisome since most PAs in Brazil are ineffectively protected (Soares et al. 2006).

Translocations

Translocation of jaguars serves the same purpose of corridors, that is, to facilitate gene flow between subpopulations and reduce chances of stochastic extinction (Fahrig & Merriam 1994), as well as the potential for deleterious genetic effects resulting of inbreeding depression (Brown et al. 2004). The few cases of jaguar translocation described in literature have reported translocated individuals being killed shortly after release (Rabinowitz, 1986; Crawshaw, 1995). Other attempts in Brazil have been inconclusive due to inadequate monitoring after release (Crawshaw, 2003). On the other hand, experiments with pumas (*Puma concolor*) in the United States indicate that translocations may be successful with sub-adult individuals in dispersion age, as these animals have a higher probability of remaining at target site if conditions are favorable (Crawshaw, 2003).

Compensation Schemes

Compensation schemes have been applied unsystematically, and informally, in a few locations in Brazil, namely in the Pantanal and Cerrado biomes. The rationale of this strategy is that by compensating rural people from losing livestock from jaguar depredation that these stakeholders will agree, and comply, with not killing jaguars. To a certain extent this line of thought is adequate in relation to some human values. When rural people lose livestock they lose wealth, and by financially compensating them for their loss you give them back the wealth they lost, and they go back to the status quo, as if there was no jaguar attack. Therefore, there is no more reason to kill jaguars. In none of these cases was there was any scientific evaluation of the effectiveness of this strategy, but its discontinuity in Brazil and lack of scientific support indicate inefficiency or inadequacy as a strategy to reduce conflicts between SFTC and LSF, and jaguars.

Farmers consulted by Crawshaw (2003), when asked about solutions to the livestock problem, cite financial compensation for losses as one of the preferred methods to deal with livestock depredation by jaguars. This is a logical and understandable preference, since stakeholders do not have to do anything (i.e., don’t have to spend more money, more time, or more energy) in order to avoid economic losses. However, Crawshaw (2003) points to a few caveats related to this strategy. First, if the strategy is implemented by the government at a local level it will generate a justified dissatisfaction of other stakeholders in similar situations in other areas, which could implicate in more antipathy for jaguar conservation and continuation or increase of illegal control of jaguars. Second, funding to cope with compensations must be self-sustainable or it will be inevitably doomed to failure. Finally, there must be a multi-institutional technical body to attest the veracity of declared depredations and application of compensations that, given the size of continental dimensions of Brazil and the small staff of GWA, seems like an unattainable task.

Ecotourism

Dalponte (2002) suggests a program that integrates research, education and tourism. The main obstacle for jaguar related ecotourism is the sightings themselves, which are have only been shown to be frequent enough to allow tourism in some areas of the Pantanal. Studies have to be conducted to evaluate the viability of tourism. Does it generate enough profit to compensate depredation losses, change livestock management practices, or change stakeholder activities from livestock farming to ecotourism?

Sports Hunting

Hunting large carnivores as a strategy to maintain populations at target levels, reduce losses to local stakeholders, and build public support for carnivore conservation has been found to be largely lacking in support from scientific data (Treves 2009). There are also numerous arguments against hunting of large carnivores based on ethical, functional and economic grounds (Rutberg 2001; Knight 2003; Peterson 2004; Campbell & Mackay 2009). There have been, however, non-experimental attempts to use research captures as means of generating funds for research and conservation, although these are undocumented.

Crawshaw (2003) mentions that a frequent solution proposed by farmers in Brazil to deal with the depredation of livestock is the sports hunting of “problem animals” (animals that have acquired the habit of eating livestock). Despite the inevitable vociferous opposition from a large part of society (i.e., WGOs and GP) he believes that his option should not be discarded without well controlled experiments of its efficacy, as there is plenty of scientific support showing the efficiency of sport hunting as a tool to manage wildlife.

Hunting of prey, on the other hand, has been used with success, as conservation strategy for jaguars in Mexico (Rosas-Rosas & Valdez 2010). Their strategy involved the creation of an economic alternative for local farmers, in this case the commercial sports hunting of white-tailed deer (*Odocoileus virginianus*), in exchange for the support of the farmers in not killing jaguars in retaliation for livestock losses.

Environmental Education

Environmental education has also been proposed as a conservation action in many publications (Crawhaw 1995; Dalponte 2002;) but the success of this action is seldom measured.

Discussion

Because jaguars are large and ecologically sensitive predators with extensive area requirements, it is unlikely that PAs will be enough to conserve viable jaguar populations in the long run, unless jaguars can move and survive outside the boundaries of PAs (Soulé & Noss 1998). Hoogesteijn et al. (2002) suggest that informal protection, stakeholders accepting jaguar within their properties, may be the most important factor in jaguar conservation. Through a distinct approach, I come to a similar conclusion.

The comprehensive problem oriented approach used in my analysis of the jaguar conservation problem in Brazil allowed me to observe that there is a disconnect between the goals of DIS and the actions proposed, and rules prescribed by GWA and NRIU. I contend that this is the result of a traditional technical-rationalist approach to conservation that only views the conservation problem through its proximate causes, but pays little attention to the social context and the decision process of the problem. In the case of the jaguar, although researchers and managers generally acknowledge the importance of DIS in the conservation of jaguars, they usually view DIS as a means to an end, rather than integral participants of the policy process, having goals and value demands that should be accounted for. I believe that, to a large extent, this is the reason why jaguar conservation in Brazil has been ineffective.

As a first step to improve the jaguar policy process in Brazil, I suggest a more comprehensive goal, one that would appeal to all stakeholders instead of just a portion of them. The current goal, as defined by Paula et al. (2011), does not take into consideration the goals and values of the DIS, who are responsible for most habitat loss, illegal killing of jaguars, and depletion of prey populations. It is no surprise, but rather an expected human behavior, that they do not want to participate or collaborate with stakeholders responsible for management, NRIU and GWA, in the conservation of the jaguar. Policy makers must understand that it is not enough to acknowledge that DIS must participate in jaguar conservation, as has been done extensively in literature (Weber & Rabinowitz 1996). If jaguars are to survive in the long run it is imperative that managers genuinely understand that their goals and values are as valid as any of the other stakeholders, and should be incorporated into management knowledge before policy makers define goals, suggest actions, and prescribe rules. Based on this rationale I suggest an alternative goal for this policy process: to reverse the trend of decline of jaguar populations and reduce the jaguar's threat status in all biomes of Brazil where the species still occurs, and, at the same time, reduce and/or compensate economic losses and threats of attacks to stakeholders who interact with jaguars on a daily basis, and empirically evaluate competitive alternative economic uses of natural resources (i.e., habitat and wildlife) to substitute inappropriate natural habitat conversion or retaliatory killing of jaguars.

The policy process for jaguar conservation is still incipient, and, more importantly, knowledge deficient. Our analysis of jaguar literature in Brazil shows that jaguar ecology is poorly understood, there have been no management experiments to evaluate proposed conservations actions, or strategies already implemented. There needs to be more research in all biomes aimed at filling gaps in knowledge necessary for the decision process. The National Plan for the conservation of the jaguar is an important step in gathering this information and orienting future research, but it remains to be seen if goals will be completed and orientations will be followed. Evaluation of conservation actions need to be put into practice as soon as new actions are implemented and current efforts to create corridors should be carefully monitored in relation to economic and time costs, versus effectiveness. Also, other alternatives should be evaluated, especially those that include the goals of DISs, and not only those of IIS.

Strategies are being proposed for large scales without trial runs. After a proposal of strategies, it is the duty of those that have proposed it to test it, before making it a large scale prescription.

It is not fair for society to demand from SFTC and LSF to cope with losses due to depredation by jaguar on their own (Crawshaw 2003), and if we do that we cannot criticize the strategies they use to deal with those losses. There is increasing understanding among DIS of the importance of conserving jaguars and the will to support it as long as the damage caused by jaguars is solved or at least reduced (Crawshaw 2003). It is up to conservationists to take this opportunity, if not for the sake of all stakeholders, for the sake of jaguars.

I conclude that the jaguar conservation problem is, first of all, a values problem and that the process can be greatly improved if strategies are designed to improve the livelihood off all stakeholders, instead of looking at the problem from a biased biological perspective.

Table 1-1. The conceptual framework of the social process (adapted from: Lasswell, 1971; Clark & Wallace, 1998)

Categories	Definition
Participants	All individuals, groups, or institutions that can affect and/or be affected by the policy process. The analyst of the process should include participants that he/she feels should be involved in the policy process but that are not currently involved.
Perspectives	The way participants view the policy process (demands, expectations and identifications) and the direction they want the process to go (their desired goals). What does each participant want?
Situations	The situations, events, where participants interact (e.g., meetings, workplace, etc.).
Base values	The assets that participants use to achieve their desired goals. Lasswell (1971) identifies 8 base values that can be used in any social process: 1) power - to be able to make and carry out decisions 2) enlightenment - to have knowledge 3) wealth - to have money or its equivalent 4) well-being - to have health, physical and psychic 5) skill - to have special abilities 6) affection - to have family, friends, and warm community relationships 7) respect - to show and receive deference 8) rectitude - to have ethical standards
Strategies	The strategies participants use to achieve their desired goals.
Outcomes	The outcomes achieved under the current policy process. Which participants are achieving their desired goals and which are not?
Effects	The effect the current policy process has on the participants desired outcomes.

Table 1-2. The seven decision functions that constitute a policy process (adapted from: Lasswell, 1971; Clark & Wallace, 1998)

Decision function	Definition
Intelligence (research and planning)	Information relevant to decision making is collected, analyzed, and distributed. Planning and prediction take place. Goals are clarified.
Promotion (debating and recommending)	Active advocacy debate about what to do. Recommendations are made and alternatives are debated based on desired goals of participants.
Prescription (creating rules)	Policies or guidelines are formulated and enacted. Demands are crystallized. These rules must be specified, communicated, and approved by participants.
Invocation (implementation of rules)	Rules are put into practice and applied in actual cases.
Application (dispute resolution)	Deviations from the rules are resolved and implementation continues. There must be enforcement as well as continuous approval, or disapproval of behavior.
Appraisal (review)	An assessment of performance. Efforts are evaluated and responsibility for success or failure is determined.
Termination	Terminating rules that are not having the desired outcome, or that have already achieved their goal, and compensating participants who are adversely affected by termination.

Table 1-3. Number of known jaguar subpopulations per biome, average size of subpopulations per biome, and estimated total population of jaguars per biome. Numbers in parenthesis represent subpopulation estimates that may be considered partially disconnected from the main population of Amazonia

Biome	# subpopulations	Avg. sub-pop. size	Pop. size
Amazonia	1 (4)	>10000 (473)	>10000
Atlantic Forest	8	21	169
Caatinga	5	35	178
Cerrado	11	86	949
Pantanal	1	>5000	>5000

Source: Paula et al. 2011.

Table 1-4. Biome's original area, percentage of Brazil's area in each biome, area and percentage of habitat lost, area and percentage of biome remaining, total number of protected areas (conservation units (CUs) and indigenous territories (ITs)), area and percentage of biome protected

Biome	Amazonia	Cerrado	Atlantic Forest	Caatinga	Pampa	Pantanal	Total
Original area [1] (km²)	4,196,943	2,036,448	1,110,182	844,453	176,496	150,355	8,514,877
Pertecentage of Brazil (%)	49.3	23.9	13.0	9.9	2.1	1.8	100
Habitat lost [2,3] (km²)	744,584	986,247	977,172	383,297	95,308	22,969	3,209,577
Perc. of habitat lost (%)	17.7	48.4	88.0	45.4	54.0	15.3	37.7
Area of biome remaining (km²)	3,452,359	1,050,201	133,010	443,182	81,188	127,386	5,287,326
Perc. of biome remaining (%)	82.3	51.6	12.0	52.5	46.0	84.7	62.1
Number of CUs [1]	219	189	418	75	13	7	867
Area inside CUs (km²) [1]	1,070,061	165,227	101,762	62,631	5,851	4,400	1,409,932
Perc. inside CUs (%)	25.5	8.1	9.2	7.4	3.3	2.9	16.6
Number of ITs	409	NI	NI	36	NI	NI	NI
Area inside ITs (km²) [4]	991,951	85,388	5,104	2,185	24	2,561	1,087,213
Perc. inside TIs (%)	23.65	4.20	0.46	0.26	0.01	1.71	12.8
Area inside protected areas (CUs + ITs) (km²)	2,062,012	250,615	106,866	64,816	5,875	6,961	2,497,145
Perc. inside protected areas (CUs + ITs)(%)	49.1	12.3	9.6	7.7	3.3	4.6	29.3

[1] source: Ministério do Meio Ambiente (MMA) http://www.mma.gov.br/estruturas/sbf_dap_cnuc2/_arquivos/uc_por_biomacnuc_02junho2011_119_1.pdf; [2] habitat loss in Amazonia up to 2010, source: <http://www.obt.inpe.br/prodes/prodes_1988_2010.htm>; [3] habitat loss in all other biomes up to 2008, source: <http://siscom.ibama.gov.br/monitorabiomas/>; 4 Miranda et al. 2008.

Table 1-5. The social context of the jaguar conservation problem in Brazil. It includes the groups of participants: small farmers and traditional communities (SFTC); large scale farmers (LSF); NGOs, research institutes, and universities (NRIU); government and wildlife agencies (GWA); the general public (GP); and trophy hunters and outfitters (THO). And their goals within the policy process, their strategies to achieve their goals, the outcomes of their strategies, and the effects that their actions have on other participants. Goals, strategies, outcomes and effects refer to the use, gain, or loss of the eight base human values as defined by Lasswell (1971) - power, enlightenment, wealth, well-being, skill, affection, respect, and rectitude

	Goals (What are the participants goals?)	Strategies (actions) & Assets (How do participants use their assets, or base values, to achieve their goals?)	Outcomes (What are the outcomes of the participants actions?)	Effects (How do outcomes affect participants and the policy process?)
Small farmers and traditional communities (SFTC)	(1) to stop losing livestock to depredation by jaguars (wealth and well-being). (2) to be safe from potential jaguar attacks (well-being). (3) to maintain their legal right to hunt game species for subsistence within their properties (power, well-being, respect). (4) if corridors are implemented in their properties, or in the vicinities of their properties, they want to their region to be formally recognized by the government as a jaguar conservation region. (respect, wealth, and well-being).	(a) They kill jaguars (power) to prevent, or retaliate, depredation (1), and when they feel physically threatned (2). (b) They hunt game species (power) for subsistence. (c) They use their crucial role (power) in the establishment of corridors to guarantee their recognition (i.e., a green stamp on their produce)(4).	Outcomes of (a): Jaguar populations may support the harvest and remain stable, decrease, or go extinct depending on jaguar population size, connectivity, and intensity of persecution. And/or move away from properties and communities. Depredation decreases locally or regionally, temporarily or for a long period, or ceases. People encounter jaguars and their signs less often, or never. Outcomes of (b): Game populations may support harvest, decrease, or go extinct, depending on population size, connectivity, and harvest rates. And/or move away from properties and communities. Game species become harder to encounter.	Effects of outcomes of (a): SFTC are benefited because economic losses are reduced and they feel safer. They gain wealth and well-being. NRIU, GWA, and GP are contrary to the illegal killing of jaguars by SFTC. To the majority of these participants the killing is unjustified. They lose respect and well-being. Effects of outcomes of (b): If game population decrease and/or become harder to encounter SFTC that depend on meat for protein may starve, switch to secondary game species, switch to alternative subsistence activities, or move to another rural location or urban areas. They lose well-being and wealth.

Table 1-5. Continued

	Goals (What are the participants goals?)	Strategies (actions) & Assets (How do participants use their assets, or base values, to achieve their goals?)	Outcomes (What are the outcomes of the participants actions?)	Effects (How do outcomes affect participants and the policy process?)
			Depredation of livestock by jaguars may increase if prey populations are negatively affected by subsistence hunting. Outcomes of (c): GWA formally recognizes SFTC in the region where corridors are created as jaguar conservation agricultural properties	If jaguar depredation on livestock increases as a result of the decrease of natural prey SFTC loose wealth and well-being, and more conflict may lead to more killing of jaguars. Effects of outcomes of (c): SFTC feel that they are part of the conservation process and that their demands are being taken into account. They gain respect, and their formal recognition by the government may help selling their product and increase wealth and well-being.
Large scale farmers (LSF)	(1) to stop losing livestock to depredation by jaguars (wealth).	(a) They kill jaguars (power) to prevent, or retaliate, depredation (1). (b) They destroy natural vegetation and transform it into pasture and crop land (2) (power and wealth).	Outcomes of (a): Jaguar populations may support the harvest and remain stable, decrease, or go extinct depending on jaguar population size, connectivity, and intensity of persecution. And/or move away from properties and communities.	Effects of outcomes of (a): LSF are benefited because economic losses are reduced. They gain wealth and well-being. Effects of outcomes of (b): Reduction and fragmentation

Table 1-5. Continued

	Goals (What are the participants goals?)	Strategies (actions) & Assets (How do participants use their assets, or base values, to achieve their goals?)	Outcomes (What are the outcomes of the participants actions?)	Effects (How do outcomes affect participants and the policy process?)
	(2) to have legal rights to remove a larger percentage of the natural vegetation of their properties to expand pasture and crop land (power, wealth, and well-being). (3) if corridors are implemented in their properties, or in the vicinities of their properties, they want to their region to be formally recognized by the government as a jaguar conservation region. (respect, wealth, and well-being).	(c) They use their crucial role (power) in the establishment of corridors to guarantee their recognition (i.e., a green stamp on their produce)(4).	Depredation decreases locally or regionally, temporarily or for a long period, or ceases. Outcomes of (b): Natural habitats are reduced and become fragmented. Jaguar and prey populations decrease or go extinct. Outcomes of (c): GWA formally recognizes LSF in the region where corridors are created as jaguar conservation agricultural properties.	of natural habitats may increase depredation of livestock by jaguars. LSF loose wealth and more jaguars are killed. Effects of outcomes of (a) and (b): NRIU, GWA, and GP are contrary to the illegal killing of jaguars and the destruction of natural habitats by LSF. To the majority of these participants the killing and the destruction of natural habitat is unjustified. They lose respect and well-being. Effects of outcomes of (c): LSF feel that they are part of the conservation process and that their demands are being taken into account. They gain respect, and their formal recognition by the government may help selling their product and increase wealth and well-being.

Table 1-5. Continued

	Goals (What are the participants goals?)	Strategies (actions) & Assets (How do participants use their assets, or base values, to achieve their goals?)	Outcomes (What are the outcomes of the participants actions?)	Effects (How do outcomes affect participants and the policy process?)
Trophy hunters and outfitters (THO)	(1) to have legal rights to hunt jaguars and other wildlife for sport (well-being). (2) to have legal rights to keep jaguar, and other wildlife parts as suveniers (well-being). (3) to be able to profit from trophy hunting (wealth and well-being).	(a) They hunt illegally (1)(2)(power and wealth). (b) They create illegal hunting enterprises (3)(power, wealth, and skill).	Outcomes of (a) and (b): Jaguar and prey populations may support the harvest and remain stable, decrease, or go extinct depending on population size, connectivity, and intensity of persecution. And/or move away from properties.	Effects of outcomes of (a) and (b): NRIU, GWA, and GP are contrary to the illegal killing of jaguars by SFTC. To the majority of these participants the killing is unjustified. They lose respect and well-being. Hunters are able to hunt. They gain well-being. And outfitters profit from the illegal hunting. They gain wealth and well-being.
NGOs, research institutions and universities (NRIU)	(1) to reverse the trend of decline of jaguar populations and reduce the jaguar's threat status in all biomes of Brazil where the species still occurs in the next 10 years (well-being).	(a) They conduct research and workshops (skill and wealth) to gather information on jaguar biology and conservation (enlightment). (b) They write scientific and non-scientific publications and reports (skill) to share information on jaguar biology and conservation with other	Outcomes of (a): More and better information is available for the scientific community and policy makers. Outcomes of (b): Other participants are better informed of jaguar biology and conservation. Outcomes of (c): Some management actions implemented or proposed by GWA reflect NRIUs perspective of the policy process.	Effects of outcomes of (a): NRIU gain scientific knowledge to plan future research and propose better management actions. They gain enlightment. Effects of outcomes of (b): GWA have more information on which to base management actions. They gain enlightment. Management actions have a

Table 1-5. Continued

	Goals (What are the participants goals?)	Strategies (actions) & Assets (How do participants use their assets, or base values, to achieve their goals?)	Outcomes (What are the outcomes of the participants actions?)	Effects (How do outcomes affect participants and the policy process?)
		participants (enlightment). (c) They use their knowledge (enlightment), technical abilities (skill), resources (wealth), recognizement as serious and ethical institutions (respect and rectitude), to pressure the government to implement management actions to revert the decline of jaguar and prey populations, and their habitat.		higher potential of being successful. SFTC and LSF usually have no access to this information or find it of little use to achieve their goals. The GP receives most of this information, usually through media outlets (i.e., TV, internet, newspapers). The GP gains enlightment and well-being. SFTC gain little enlightment and rarely well and a portion of these participants feels pleasure (well-being) for receiving information about the jaguar biology, research and conservation. Effects of outcomes of (c): Management actions proposed and implemented do not take into consideration the goals of SFTC, LSF and THO. They cannot hunt jaguars or their prey without approval of GWA (power), jaguars depredation continues to cause them economic losses and jaguars cannot be used for commercial purposes (wealth and well-being), THO are deprived of their pleasure of hunting and

Table 1-5. Continued

	Goals (What are the participants goals?)	Strategies (actions) & Assets (How do participants use their assets, or base values, to achieve their goals?)	Outcomes (What are the outcomes of the participants actions?)	Effects (How do outcomes affect participants and the policy process?)
				revenue (well-being and wealth), SFTC remain concerned about jaguar attacks (well-being), and SFTC feel disrespect for being deprived of rights over their natural resources without their consent (respect).
Government and Wildlife Agencies (GWA)	(1) to reverse the trend of decline of jaguar populations and reduce the jaguar's threat status in all biomes of Brazil where the species still occurs in the next 10 years (well-being).	a)(b)(c): same as NRIU (d) They created a law (power) that protects natural areas within private properties, the permanent protected areas (APPs). (e) They banned hunting of the jaguar and trade of jaguar parts (power). (f) They banned commercial hunting and trade of wildlife (power). (g) They created and implemented protected areas (power, wealth, and skill).	Outcomes of (a)(b)(c): same as NRIU Outcomes of (d) and (g): More natural areas are protected inside and outside private properties. More populations of jaguar and prey are protected. Outcome of (e): Commercial hunting of jaguars and trade of jaguar parts decreased. Hunting pressure over jaguar populations decreases. Outcomes of (f): Commercial hunting and trade of wildlife decreases. Hunting pressure over game populations decreases.	Effects of outcomes of (a)(b)(c): same as NRIU Effects of outcomes of (d): Mainly LSF, but to some extent SFTC, lose decision right over a portion of their property where they cannot modify the natural habitat for pasture or crops. They lose power, wealth and respect. Effects of outcomes of (e)(f): Commercial hunting of jaguar and other wildlife is no longer a viable economic activity for SFTC. They lose power.

Table 1-5. Continued

	Goals (What are the participants goals?)	Strategies (actions) & Assets (How do participants use their assets, or base values, to achieve their goals?)	Outcomes (What are the outcomes of the participants actions?)	Effects (How do outcomes affect participants and the policy process?)
		(h) They use GIS methods to monitor deforestation (skill and wealth). (i) They establish corridors to link subpopulations (power, wealth, skill). (j) They created compensation schemes to refund livestock farmers for livestock lost to depredation by jaguars (wealth and skill).	Outcomes of (h): Deforestation can be monitored and participants responsible for deforestation can be held accountable. Outcomes of (i): Viability of small subpopulations may increase. Outcomes of (j): Retaliatory hunting of jaguars decreases and/or more cattle depredations are reported. Deaths that are not jaguar related be reported as jaguar depredation.	Effects of outcomes of (g): The livelihood of SFTC living inside protected areas improved because wildlife is more abundant. They gain power, wealth, respect, and well-being. Effects of outcomes of (g) and (h): Deforestation rates decreased. LSC lose power and wealth. Effects of outcomes of (i): GWA's chances of effectively implementing corridors increases. Effects of outcomes of (j): SFTC and LSF receive compensation. They gain wealth.
General public (GP)	(1) jaguars to be protected and available for future generations (well-being).	(a) Pressure the government to take action to protect the jaguar (power). (b) Donate resources (wealth) to NRIU to enable research and conservation actions.	Outcomes of (a): May lead to implementation of management action or law enforcement efforts. Outcomes of (b): More resources are available for research and conservation.	Effects of outcomes of (a): GWA is pressured to act, but also gains political support. GWA gains power. Effects of outcomes of (b): NRIU has more resources for research and conservation actions. They gain power and wealth.

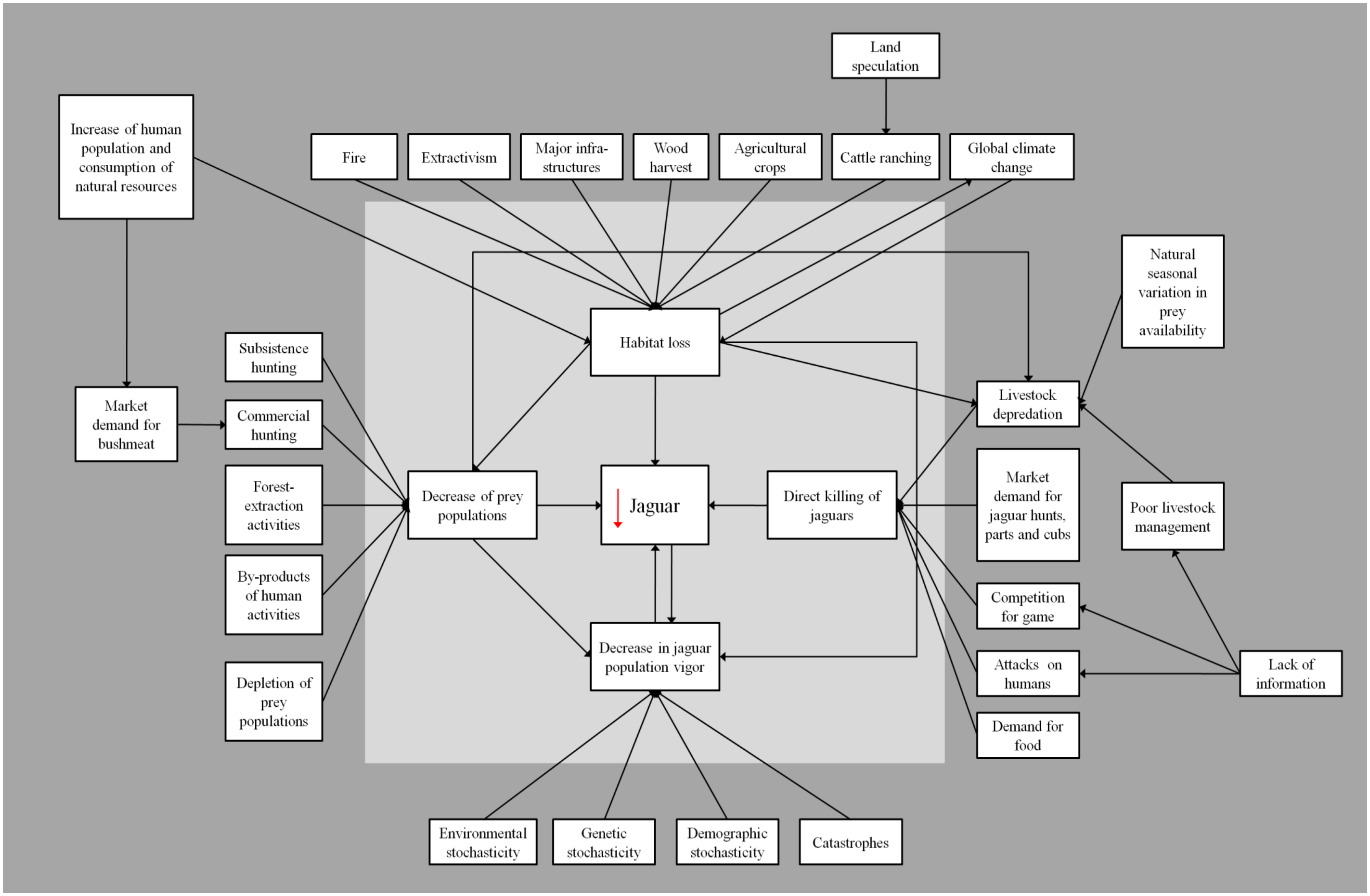

Figure 1-1. Flowchart representing proximate causes of jaguar population decline in Brazil (light grey area) and the factors that contribute to the aggravation of these causes (darker grey area)

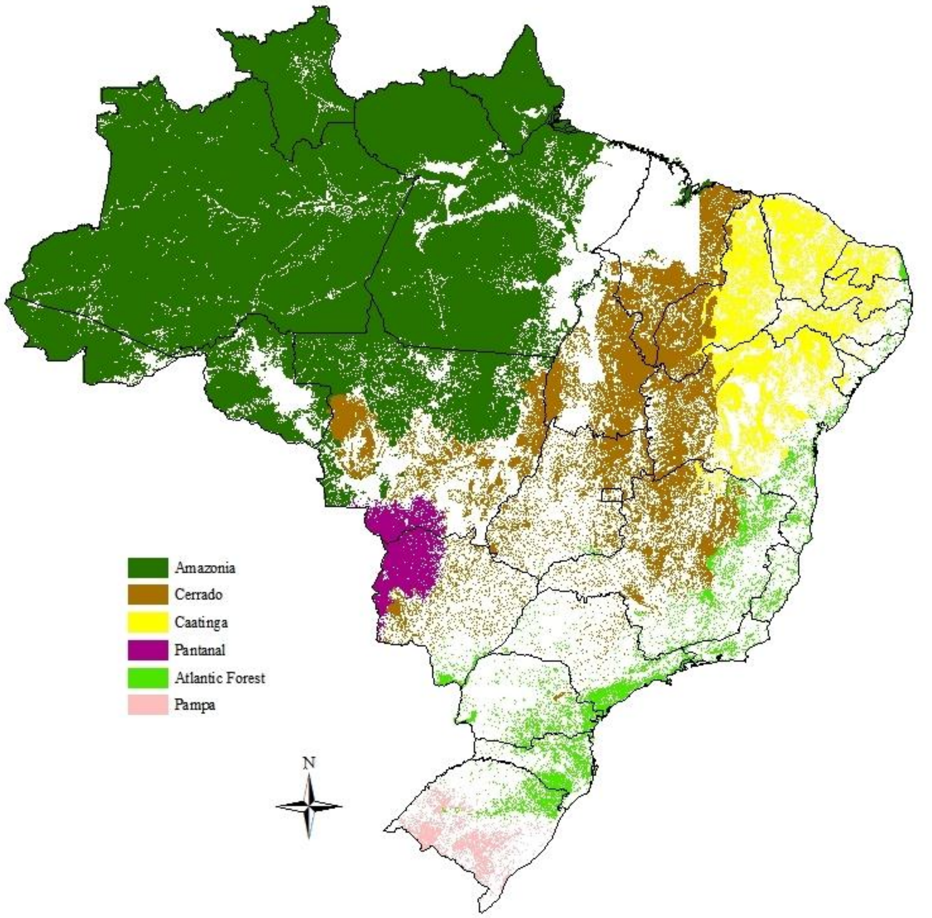

Figure 1-2. Remaining original vegetation of Brazilian biomes in 2008. Data source: MMA, INPE and IBGE

CHAPTER 2
JAGUAR (*PANTHERA ONCA*) POPULATION DYNAMICS AND ACTIVITY PATTERNS IN A SUSTAINABLE USE RESERVE IN THE VÁRZEA FLOODPLAIN FORESTS OF BRAZILIAN AMAZONIA

Estimates of abundance and other demographic parameters are crucial in determining trends in population dynamics and identifying parameters responsible for those trends. Demographic information is desired in the decision-making process of conservation and management of wildlife, but is still limited or non-existent for most species including many endangered ones (IUCN 2011). This shortage of demographic information is mainly due to the logistical and financial constraints associated with sampling animal populations at the required spatial and temporal scales (e.g., monitoring the jaguar (*Panthera onca*) population of Amazonia), and the inability of current sampling methods to detect all individuals even within a limited survey area (i.e., imperfect detection; Williams et al. 2002). Demographic parameters are particularly difficult to estimate for large felids because they occur at relatively low densities, have large home ranges, and are typically difficult to detect due to their elusive and cryptic nature. The management of large felids, and inference on population dynamics, are thus often hindered by limited or unavailable information on demographic parameters.

The lack of demographic information for large felids started to change after Karanth (1995) proposed the use of camera-traps associated with closed population capture-recapture (CR) models as a method to estimate abundance and density of tigers (*Panthera tigris*) and showed its potential use for other individually marked species (method further developed in Karanth & Nichols 1998, 2000, 2002). Since then, there has been wide use of this methodology to estimate density of many carnivores (Trolle & Kéry 2003, 2005; Maffei et al. 2005; Di Bitetti et al. 2006, 2008; Jackson et al.

2006; Dillon & Kelly 2007, 2008; Kelly et al. 2008; Cuéllar et al. 2006). More recently this methodology was applied under the “robust design” capture-recapture approach (Pollock 1982, Pollock et al. 1990) to estimate other population parameters such as survival, growth rates, and recruitment, and to make better inference about population dynamics (Karanth & Nichols 2006). The methodology developed by Karanth (1995) became particularly popular for estimating density of jaguar populations and has been used in over 83 surveys in at least 50 different locations since 2003 (Wallace et al. 2003; Maffei et al. 2011). These surveys, however, only cover a small portion of the 137 Ecoregions[1] of the jaguar’s current range, are not available for most of Amazonia (Fig. 2-1) which is thought to be the most important area for the conservation of the jaguar (Sanderson et al. 2002, Caso et al. 2008, Paula et al. 2011), and the majority of surveys have not been conducted over sufficiently long enough periods of time to observe population dynamics and allow estimation of other population parameters.

The closed population capture-recapture method so far used to obtain jaguar abundance and density estimates has relevant weaknesses. Wide-ranging animals like the jaguar have large home ranges and are highly mobile, which means that jaguars occurring in the border regions of trap arrays will move in and out of the survey area during the survey, even when we restrain the survey to a short period of time, thereby violating the critical assumption of population closure. This movement of individuals can be viewed as a form of temporary emigration and it leads to heterogeneity in capture probabilities (i.e., individuals with center of activity in the vicinity of the trap array will have lower exposure to trapping compared with individuals whose center of activity is

[1] Ecoregions are defined by Olson et al. (2001) as relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change.

located inside the trap array), negatively biasing detection probability and positively biasing abundance estimates (Kendall et al. 1997, Kendall 1999). To convert abundance estimates to density it is necessary to calculate the effective trapping area (ETA) of the survey. Traditionally, this has been achieved using *ad hoc* approaches based on estimates of boundary strip width, usually half or the full mean maximum distance moved (MMDM) by individuals captured during the survey (Karanth & Nichols 1998, 2002). The MMDM is used as a surrogate of the home-range size radius, which is added as a buffer to the trap array to estimate ETA. This is viewed as the weak link in this methodology because this approach has no theoretical mechanism to link abundance with the survey area to estimate density (William et al. 2002), and ETA may vary with different methods, yielding different density estimates for the same abundance estimate (Soisalo & Cavalcanti 2006; O'Brien 2011).

To deal with these issues formal model-based procedures have been developed to estimate density directly from capture history data and the auxiliary spatial information from the location where individuals are captured (Efford 2004; Borchers & Efford 2008; Royle & Young 2008; Royle et al. 2009). These procedures have been developed under likelihood (Borchers & Efford 2008; Efford et al. 2009a) and Bayesian analysis frameworks (Royle & Young 2008; Royle et al. 2009a, b) and use hierarchical models to condition the encounter history data to an underlying point-process that describes the distribution of individuals in space (Efford 2004; Royle & Young 2008; Borchers & Efford 2008; Royle et al. 2009a). Recently, it has been shown that density estimates for jaguars and other species were consistently overestimated by the MMDM method when compared to model-based spatially explicit capture-recapture (SECR) methods (Gerber et al. 2011; Noss et al. 2012).

In this study we used a SECR approach under a Bayesian analysis framework to estimate jaguar density from 2005-2009 in Mamirauá Sustainable Development Reserve, a Várzea Floodplain Forest site in the Brazilian Amazon with a relatively high human density (1.55 people/km²) and high human induced mortality of jaguars (Ramalho 2012 – Chapter 3). We also estimate jaguar survival for the period and test the prediction that jaguar survival and density are stable in Mamirauá Reserve despite high human induced mortality because of the large number of immigrants and abundance of prey. Additionally we describe jaguar activity patterns in the study area.

Methods

Study Site

Várzea Floodplain Forests

Floodplains can be briefly defined as wetlands that periodically transition between terrestrial and aquatic phases, or, ecologically, as "areas that are periodically inundated by the lateral overflow of rivers or lakes and/or by direct precipitation or groundwater; the resulting physico-chemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations and produces characteristic community structures" (Junk et al. 1989). In Amazonia floodplains fringe the Amazon River and its large tributaries along most of their course, with the exception of the estuary, covering an area of approximately 300,000 km² (Junk 1997). These river floodplains are seasonally inundated by the large and predictable monomodal flood-pulse of the Amazon River and its tributaries (e.g., the average annual amplitude of the flood-pulse in Mamirauá Sustainable Development Reserve is

>10 m, Ramalho et al. 2009). Amazonian floodplains have been categorized as two main types based on their hydrological characteristics. When inundated by alluvial (muddy) white-water rivers, which are nutrient and sediment rich (e.g., Amazon River), they are called Várzea. When inundated by black-water rivers (e.g., Rio Negro), which are nutrient and sediment poor, they are called Igapó.

Várzea forests cover approximately 180,000 km^2 (2.6%) of the Amazon basin (Fig. 2-2) and are crucially important to Amazonia due to the abundance of fish, and their role as breeding grounds for many species of fish, birds, mammals and reptiles (Bayley & Petrere 1989; Goulding 1996; Thorbjarnarson & Da Silveira 2000). These areas are also very fertile due to the constant renewal of soil nutrients caused by annual flooding, which makes Várzea forests the most productive environments of Amazonia (Morán, 1990). These attributes and the proximity to rivers (the main transport routes for local people) have historically favored human occupation of the Várzea forests by people, resulting in the most densely human populated environment in Amazonia (Ayres 1993).

In the Várzea floodplain forests, as in other floodplain environments, the variation in the water level dictates most ecological processes. As the water level rises, the nutrient rich waters invade the floodplains, replenishing the soil with nutrients, restricting the terrestrial habitat, and expanding the aquatic habitat. Fish and other aquatic organisms reproduce during flooding, taking advantage of the lower density of predators, which have migrated or are confined to small islands of dry land, and the abundance of food, such as seeds from dispersing trees. The trees of the Várzea forests also take advantage of the high water level to disperse their seeds using water and fish as dispersal agents. When the water recedes the aquatic organisms become restricted and concentrated in lakes, channels, and other water bodies, or migrate into the main course of the larger rivers. In this low water season, Várzea forests become accessible to the terrestrial fauna, and attractive to predators, which find an abundance of prey concentrated in small water ways. It is in the areas surrounding these bodies of water, in the interface between the aquatic and terrestrial environment, that most predator-prey interactions occur (Junk 1993). Most terrestrial animals and predators reproduce during this period in which food is abundant to them. This cycle allows for a great variety of organisms to occur in the same area, but demands that plants and animals have a large range of morphological, anatomical, physiological and ethological adaptations, to survive (Junk 1993).

Mamirauá Sustainable Development Reserve

This study was conducted in Mamirauá Sustainable Development Reserve (hereafter, Mamirauá Reserve), located in the western portion of Brazilian Amazonia, approximately 30 km northwest from the city of Tefé, in Amazonas state (1°49'-3°09'S, 64°45'-67°23'W)(Fig. 2-3). Mamirauá Reserve is delimited by the Japurá and Amazon Rivers, and the Auati-paranã channel, and encompasses an area of 11,240 km² of Várzea forests (6.25% of the total area of the Várzea ecosystem in Amazonia). It is the largest protected area exclusively dedicated to protecting this type of environment. The climate in the region is tropical humid with average annual precipitation of 2,373 mm (Ayres 1993).

Mamirauá Reserve was originally created as an Ecological Station in 1984 by the Brazilian Environmental Agency (SEMA) and in 1990 its administration was transferred to Amazonas state government (decree nº 12,836 of March 9th 1990). Mamirauá

Ecological Station was created mainly in response to a proposal from biologist José Márcio Ayres to create a protected area of approximately 2,500 km², primarily to protect the endangered white uakari monkey (*Cacajao calvus calvus*; Fig. 2-4) and its habitat (Queiroz 2005). However, the area ultimately designated for conservation was 11,240 km², almost five times larger than that requested, due to the environmentally favorable national political climate in Brazil in the late 1980s and the increasing world-wide concern about global warming and loss of biodiversity (Esterci & Ramalho 2007).

This rare and paradoxical circumstance, where a government creates a protected area that is actually much larger than solicited, although often welcome and at first view positive, resulted in a caveat. The objective of an Ecological Station is to preserve nature and to be a pristine natural area for the realization of research and educational activities (Brasil 2000). People are not allowed to live in, visit, or use natural resources from inside an Ecological Station. However, Mamirauá Ecological Station encompassed a crucial system of Várzea forest lakes and other water ways with fishery stocks that supplied hundreds of thousands of people in the region, and also contained the households and subsistence territories of approximately 5,000 local people distributed over 60 villages, whose livelihoods were completely dependent upon the natural resources of the area. The creation of such a large Ecological Station was clearly inappropriate given the socio-economic characteristics of the region and the function of this type of protected area (Esterci & Ramalho 2007). Facing this dilemma, Ayres and other researchers proposed the creation of a sustainable development reserve, a new category of protected area that they judged more adequate and viable for the area. This type of reserve was based on the sustainable use model of protected areas that was rapidly gaining popularity over the fortress conservation model, and was based on the rationale that for effective conservation to occur local people had to participate in the management of the protected areas and benefit from the conservation of the natural resources within it.

Mamirauá Reserve was the first sustainable development reserve to be created in Brazil (Queiroz 2005; Esterci & Ramalho 2007). Sustainable development reserves are defined in the Brazilian National System of Conservation Units (SNUC) as natural areas inhabited by traditional human populations whose existence is based in sustainable systems of natural resource exploitation, developed through generations and adapted to the local ecological conditions, and that play a fundamental role in the protection of nature and maintenance of biological diversity. The objective of this category of protected area is to promote the conservation of biodiversity, and, at the same time, to secure the conditions and means necessary for reproduction, improvement of quality of life, and sustainable exploitation of natural resources by traditional local people, as well as to value, conserve and improve upon the knowledge and natural resource management techniques developed by these populations.

The environment and the ecology of animals and plants in Mamirauá Reserve, as in other Várzea forest areas, are largely determined by the flood-pulse, as the water level of the Amazon River and its tributaries in the region of Mamirauá Reserve can fluctuate >13 m in a year, with an average annual fluctuation of >10 m (Fig. 2-5; Ramalho et al. 2009). The variation of altitude of the terrain within the Várzea forests of Mamirauá Reserve, and the consequent difference in level and period of flooding of the area, created distinct terrestrial environments with characteristic vegetation structure and composition. Ayres (1993) identifies three main types of environment and defines them as follows. The High Restinga (HR) represents the higher elevation terrain that is flooded for up to 4 months per year by a water column of up to 2.5 m. These areas, although structurally similar to Terra Firme forests (upland forests) have a distinctive tree community. Most frequently encountered botanic families reported by Ayres were Annonaceae (16.4%), Euphorbiaceae (10.5%), Leguminosae (7.8%), Apocynaceae (7.4%), Lecythidaceae (6.0%), and Lauaraceae (5.2%). Some of the largest tree species in Amazonia, such as the samaumeira (*Ceiba pentandra*) and the assacu (*Hura crepitans*), are found in this environment. The Low Restinga (LR) represents intermediate elevation terrain with a generally open understory. This environment covers most of Mamirauá Reserve and can be flooded for up to 6 months by a water column of up to 5 m. In the LR, Euphorbiaceae is the most frequent botanical family (18.8%) followed by Leguminosae (16.0%), Lecythidaceae (7.0%), Myrtaceae (5.8%), and Annonaceae (5.5%). Some of the most frequent tree species found by Ayres in this environment were the mututi branco (*Pterocarpus amazonicus*), the matá-matá (*Eschweilera albiflora*), and the piranheira (*Piranhea trifoliate*). Palms are rare in both of the restingas. The Chavascal (CH) is the lowest terrestrial environment in the Várzea forests of Mamirauá Reserve. The CH is a swampy environment with low vegetation and a dense understory, and can be flooded for up to 8 months per year by a water column of 7 m or more. The most abundant plants in the CH are the bamboos called tabocas (*Bambusa* spp.), the munguba (*Pseudombax munguba*), the piranheira, the imbaúbas (*Cecropia* sp.), and apuí species (*Ficus* spp.). The palm jauari (*Astrocaryum jauari*) is also frequently found.

Because Mamirauá Reserve is a seasonally inundated island in the middle of two large rivers, animals that live inside it have to be well adapted to swimming and/or climbing trees, and to survive the steep annual fluctuation in resource availability caused by flooding. These peculiar environmental characteristics are responsible for the presence of some endemic species, but also to a lower density and diversity of terrestrial species in general. Primate diversity is lower than in the surrounding Terra Firme forest, but Mamirauá Reserve encompasses most of the distribution of the white bald-headed uakari monkey and the entire distribution of the endemic blacked-headed squirrel-monkey (*Saimiri vanzolinii*). Threatened and charismatic top predators such as the jaguar, the black caiman (*Melanosuchus niger*), the pirarucu (*Arapaima gigas*), and the Amazon river dolphin (*Inia geoffrensis*) are abundant. Mamirauá Reserve also holds a diverse fish and bird fauna with at least 340 species of each group (Queiroz & Peralta 2011).

The human population of Mamirauá Reserve lives primarily along the margins of the main Rivers (e.g., Amazon River and Japurá River), on smaller channels, and along the margins of some lakes. The main economic and subsistence activities of local people are agriculture, hunting, fisheries, and harvesting of wood and other non-timber products. The main source of protein comes from fishing. The human population of Mamirauá Reserve is estimated at 9,733 people (0.87 people/km^2), distributed in 1684 households over 181 villages (MSDI 2011).

This study was conducted during 2005-2010 in an area of ~566 km^2 around Mamirauá Lake, a well-protected area of Mamirauá Reserve where jaguar prey populations are abundant and have been protected since the creation of the Reserve in the 1990's. In this area, some of the main prey of jaguars are abundant. Caiman populations are estimated to be concentrated at 230 individuals/km of margin (Da Silveira 2002), brown-throated three-toed sloth (*Bradypus variegatus*) density is estimated to be over 200 individuals/km² (Queiroz 1995), and red howler (*Allouata seniculus*) occur at 35 individuals/km² (F. Pain unpublished data). This area receives regular human activity from local fisherman and tourists from the Uakari ecotourism lodge.

Field Methods

Camera-trap surveys

Jaguars were surveyed with camera traps in the low water season of years 2005-2008 in a total of four surveys (Table 2-1). The low water season in Mamirauá Reserve extends from September to December, after which the water starts to rise (Ramalho et al. 2009). Camera traps were installed along trails created by humans and wildlife, near the margin of lakes, and in other locations that maximized the probability of jaguars being photo-captured (Karanth & Nichols 2002). Selection of camera-trap locations was based on signs of jaguar presence (e.g., tracks, scats, carcasses of prey, and scratches on trees), and my own experience or that of local people in identifying jaguar travel paths in the study site. At each location two camera traps were set on opposite sides of the target path, separated by 3-5 m. Each camera-trap pair composed a camera-trap station. Camera traps were programmed to take photographs 24 h per day with a 30 sec interval between photos, and to record date and time on each photograph. Camera traps were inspected for malfunction, batteries and film at 3-7 day intervals. Both digital and conventional film cameras were used and included the following models: Camtrakker® (Cam Trak South Inc., GA. USA) models Original (film) and Environmental unit (film), Bushnell® (Bushnell Corp., KS, USA) model Trail Master (digital), Tigrinus® (Tigrinus lnc., SC, Brazil) models Convencional (film) and Digital (digital). In total four camera-trap surveys were conducted at approximately yearly intervals (Table 2-1).

Each camera-trap station was also equipped with a homemade lure of sardine and eggs which was placed in a small container in the center of the station at equal distance from the two camera-traps. The objectives of using the lure were to increase the chances of a jaguar being photographed, and to position jaguars at a central position between the camera traps for a longer period of time to improve the quality of pictures and chances of identification of individuals. Although there is little information on the effect of lures on jaguar camera trap surveys, this homemade lure worked well to draw jaguars and other felids to a central position in camera-trap stations in preliminary surveys at the study site (Ramalho 2006; Fig. 2-6). Additionally all supplies to make the lure were easily accessible in local markets and the cost of equipping stations with the lure were minimal, approximately $ 0.05 USD per station-night. In using lures, however, I made two important assumptions. First I assumed that the lure was only effective at a small range (i.e., <100 m) and therefore did not cause animals to displace their home ranges (i.e., the lure did not draw animals from outside the effective sampling area). In a survey conducted by Gerber et al. (2011) the use of lure did not affect permanent immigration or emigration, abundance and density estimation, maximum movement distances, or temporal activity patterns of Malagasy civets (*Fossa fossana*), but did provide more precise population estimates by increasing the number of recaptures. Second, although the odor of the lure changed with time I assumed that its effectiveness in attracting the interest of jaguars did not change over the 3-7 day period within which lures were not replaced.

The number of camera-trap stations used in each survey varied from 5 to 17, and effort varied between 735 and 2,695 trap-nights (Table 2-1). Trap polygon area varied between 3.6 and 81 km^2 (Table 2-1). In surveys conducted in 2007 and 2008 cameras were moved every 30 days in blocks. Camera trap stations were placed between 0.7 and 1.4 km apart. It is also important to reiterate that surveys were conducted in the low water season, when terrestrial habitats are extensively available, and that density is likely to change during the high water season (May-August; Ramalho et al. 2009) when virtually all terrestrial habitats of Mamirauá Reserve are under water.

Foot snare live captures

Jaguars we also physically captured with foot snares also during the low water season, from October to December, in years 2008-2010 (Table 2-1). Assistance in captures was provided by local knowledge and a professional trapper (D. Simpson, www.wildlifecaptureinternational.com). Foot snares followed the design described by Frank et al. (2003) for African lion (*Panthera leo*) with minor modifications. Snares consisted of an approximately 1-m long and 5- mm diameter stainless steel aircraft cable with ~5 cm loops at both ends made with swaged aluminum ferrules and a 19 mm angle iron lock used to keep the snare tight on the foot of the animal after the snare was sprung. Snares were fired using a modified Aldrich spring-powered throw arm and were anchored to the ground or to a tree.

Captured jaguars were immobilized with Telazol (tiletamine-zolazepan, Fort Dodge do Brasil), or a combination of Telazol and ketamine hydrochloride. Telazol was administered via an intramuscular shot using a 3 ml Daninject dart propelled by a CO_2

rifle, an air rifle, or a blowpipe. Additional Ketamine was administered also via an intramuscular shot using a syringe. Dosage for Telazol was 6 mg/kg, and for ketamine 1 mg/kg. After immobilization individuals were fitted with a VHF or GPS/ARGOS telemetry collar made by Telonics, USA® (Mesa, AZ) or Telemetry Solution (Concord, CA) and released. GPS locations where collected by the Telonics GPS/ARGOS collar every 5 hours. VHF collars were monitored on the ground for 5 day periods, at 7 day intervals, and a one hour search was conducted by plane every two months to find collared animals that could not be found on ground searches. All GPS collars produced by Telemetry Solutions (n = 6) stopped operating properly shortly after deployment or in the lab.

Data Analysis

Population density

Historically, the estimation of abundance and density of carnivores in camera trapping studies has been done using ad hoc or heuristic methods based on closed-population capture-recapture estimators of population size applied to individual encounter histories. Although this approach is adequate for estimating the population size exposed to sampling, the effective sample area of the trapping array is unknown because conventional methods used to estimate effective sample area are not formally linked to the observed encounter history data.

To address this issue, spatial capture-recapture models have been developed by conditioning the encounter history data to an underlying point-process that describes the distribution of individuals in space in the context of a multinomial observation model where each individual can only be captured in one trap per sampling occasion (Efford 2004; Royle & Young 2008; Borchers & Efford 2008; Royle et al. 2009a). Royle et al

(2009b) describe a hierarchical modeling framework for inference from spatial capture-recapture data for methods wherein the traps function independently of one another, allowing individuals to be captured multiple times within a sampling occasion.

To estimate the density of jaguars in this study I used the R software package SPACECAP 1.0 (Singh et al. 2010), which was specifically developed for estimating animal densities from camera trap surveys using the spatial capture-recapture models developed by Royle et al. (2009b). The models used in SPACECAP are based on point process models where it is supposed that, in a population of N individuals, each individual has a center of activity si = (s1j, s2j; i = 1, 2, ..., N), over which their movements are concentrated. It is assumed that these activity centers are independent, uniformly distributed over some region S, the state-space of a binomial point process, and that the location of activity centers does not change during the survey. S is defined as an area large enough to contain the trap array and also assure that all individuals outside S have a zero probability of being captured in the trap array. The basic inference problem is to estimate the number of activity centers per unit area of S, which is equivalent to estimating N under the point process model. This uniform point process model represents a prior distribution for individual activity centers.

To model the overlap of activity centers with the trap array, it is assumed that the trap array is represented by J traps having locations xj (j = 1, 2, …, J). Traps are assumed to work independently so that individuals can be encountered by more than one trap within a sampling occasion. It is also assumed that the probability of an individual i being encountered by trap j (i.e., the juxtaposition of si and xj) is a decreasing function of the distance between the trap and the individuals activity center, plus one or more parameters that will be estimated. The distance between individual i 's activity center and trap j is represented by $d_{ij} = || s_i - x_j ||$.

Because the location and number of activity centers is unknown, the method of data augmentation is used to define the parameter space (Royle & Dorazio 2008). Data augmentation is the physical augmentation of the n observed encounter histories with some large number of "all-zero" histories to form a list of M pseudo-individuals that includes the actual N individuals as a subset. M must be large enough so as not to truncate the posterior of N. The result is that the model for the augmented data is a zero-inflated version of the model when N is known. In this model N is replaced by $1 - \Psi$, where Ψ is the probability that an individual pertaining to M is a member of the population of size N that was exposed to sampling by the trap array.

To implement these models, SPACECAP requires three input files: potential home-range centers, trap deployment details, and animal capture details. The potential home-range centers file contains spatial information of a grid of equally spaced points generated to encompass the whole extent of the trap array plus an additional area surrounding it, where the researcher believes all individuals potentially detectable by the trap array are contained. Each point in this grid is a potential home-range center and the area covered by the grid is the state-space (S). The trap deployment details file contains spatial information on the location of each trap plus information on the operational status of each trap (i.e., if a trap was operational or not) at each sampling occasion. The animal capture details file consists of each individual's capture history plus the location of each capture.

For this study, S was defined as the area covered by the trap array plus a 15 km buffer around it (Fig. 2.7), with a total area of 1,079 km^2 (i.e., excluding non-habitat). Each potential home-range center within that area was spaced 250 m apart, a 0.0625 km^2 pixel. In defining the model for the analysis, we considered the possibility of trap response to capture, used the spatial capture-recapture model with a half-normal detection function, and the Bernoulli's encounter model. In the setting of the analysis we used 10,000 iterations with 1,000 initial burn-in values, thinning rate of 1, and data augmentation of 300.

Survival and recapture probabilities

The primary interest in this section of the study was to estimate annual apparent survival (ϕ) and recapture rates (p) and to assess if there was evidence of variation in ϕ and p throughout the study (2005-2010). During this period there were no obvious anthropogenic or environmental events (e.g., increase in the number of jaguars killed by local people, or decline in abundance of main prey) in the study site that that would indicate significant changes in jaguar survival (i.e., no apparent reason to believe that ϕ and p would be different between years). However, an unusually high flood in 2009, the largest flood in over 50 years, could have affected ϕ by forcing more individuals to leave the Várzea in search of higher ground in the neighboring Terra Firme forests. Every year the terrestrial habitat of Mamirauá Reserve is severely reduced by flooding, but in 2009 all terrestrial habitat was flooded. To evaluate this hypothesis, I included the level of flooding as a factor influencing ϕ. Flooding was included in models in two ways: as a categorical variable indicating normal flooding and high flooding (low-high Flood) and as a continuous variable in meters above sea level (Flood).

I was also interested in assessing whether there was significant difference in ϕ and p between males and females. I hypothesized that females would have higher ϕ for two main reasons. The first is based on the theory of sexual segregation, which predicts that female behavior will always have the objective of increasing the chances of survival of offspring, while males will behave in a manner that favors their chances of reproducing, even when such behaviors increase personal risk (Main 2008). Under this rationale, females would stay in the Várzea during annual flooding periods, raising their cubs in a semi-arboreal-aquatic lifestyle for a portion of the year, while males would migrate out of the Várzea during flooding to avoid the scarcity of food and terrestrial habitat and maintain their physical condition in preparation for the next reproductive period. The second is that males are well-known for having larger ranges than females, which increases the likelihood of encounters with people which could lead to higher mortality. This notion is corroborated by the higher number of male jaguars killed by local people in comparison to females in the study site (Ramalho 2012 – Chapter 3).

To estimate apparent survival and recapture rates we used Cormack-Jolly-Seber (CJS) CR models (Cormack 1964; Jolly 1965; Seber 1970) implemented in program MARK 6.2 (White & Burnham 1999). To test our hypotheses we used a set of candidate models that represented the effect of time (i.e., sampling year), flood level (i.e., highest level of flooding during the year of the survey), and sex, on survival; and the effect of sampling method (i.e., camera traps or snares), and sampling effort on recapture probability. Akaike's information criterion, corrected for small sample size (AICc), was used as an objective means of model selection (Burnham & Anderson 2002). Goodness-of-fit was assessed on a fully time-dependent model using program

RELEASE from within MARK (White & Burnham 1999). Survival and recapture probabilities were model averaged using Akaike weights (wi) to include model uncertainty in the estimates of parameter precision (Buckland et al. 1997).

We also incorporated the presence of transients in our models given that 13 (54.2%) of the 24 individuals captured in our surveys were only captured once. As defined by Pradel et al. (1997), a transient is “an individual that is marked, released, and which then permanently emigrates from the sample, such that it is no longer available for encounter in the future”. As our analysis produces estimates of apparent survival and not true survival, individuals that emigrate permanently will appear to have died, and thus lower estimates of apparent survival of resident animals which are available for recapture in subsequent surveys. To account for the presence of transients we used a class of models referred to as ‘time since marking’, or TSM models, which estimate the survival of residents and transients separately.

Activity patterns

As cameras operate intermittently throughout the surveys and 24 h per day it is usually assumed that the number of photographic captures by time period reflects an animal’s activity pattern (e.g., Cuellar et al. 2006; Di Bitetti et al. 2006; Maffei et al. 2004). To quantify the activity patterns of jaguars in Mamirauá Reserve we counted the number of pictures of jaguars per hour period of the day, and by separating the day into four time periods: dawn, day, dusk, night. Dawn and dusk were comprised of two hour periods with centers around sunrise and sunset respectively. Day was comprised of an 11-hour period and night of a 9-hour period. To evaluate if jaguars were more likely to be photo-captured during any of these periods, I used a contingency test using the chi-squared statistic (Zar 1984). To increase the sample size for this analysis, I used photographs from a survey conducted in the study site during the dry season of 2011, which was not used for the estimation of density and survival.

Results

The combined effort using cameras and snares was 10,668 trap-nights for the six years of study in Lake Mamirauá. The surveys yielded 94 observations of jaguars and allowed identification of 24 adult jaguars, of which 10 were male and 14 were female for a male:female sex ratio of 1:1.4. In total, camera traps identified 22 individuals and foot snares identified an additional 2 individuals out of a total of 9 captures, all of which were adult jaguars (Table 2-2). The combined rate of capture during this study was one jaguar per 113 trap-nights of effort, and cameras were more effective in detecting jaguars than were snares. Cameras recorded one jaguar per 98 trap-nights, whereas snares captured one jaguar per 227 trap-nights (Table 2-2).

Density

The estimated number of jaguars within the 1,079 km² state-space area considering only appropriate habitat (Fig. 2-7) varied between 125 ± 48.96 and 252 ± 47.83 jaguars (estimated mean $\pm$ posterior SD) with an estimated abundance of 193 (Table 2-3). Population density in the surveyed area was high compared to most published reports, and varied between 11.60 ± 4.54 and 23.37 ± 4.43 jaguars/100 km² with an average density of 17.84 jaguars/100 km² (Table 2-3; Fig. 2-8). In the five intervals between surveys conducted in years 2005 and 2010, the population decreased during 2005-2007, had a sharp increase between 2007 and 2008, and then maintained densities intermediate to these two time frames during 2009 and 2010 (Table 2-3). The posterior mean of ψ (the data augmentation parameter that represents the ratio of the number of animals actually present within S to the maximum allowable number set by us during analysis) was lower than 1 for all years (Table 2-3), indicating the data augmentation number M = 300 was adequate and did not truncate our estimates of population size and density.

Survival and Recapture Probabilities

The saturated model (group structure (males and females) and time-variant ϕ and p) fitted the data reasonably well, yielding a $\hat{c}$ = 1.29, and we adjusted the AIC scores by this measure of over-dispersion (White & Burnham 1999). The most parsimonious model in our candidate model set was {ϕ(M2,low/high-flood) p(effort)}, where transients and level of flooding influenced apparent survival, and effort affected recapture probabilities (Table 2-4). This model was substantially better than the other 39 models in the candidate set (AICc weight = 0.34). I formally tested our hypotheses by comparing more general models with reduced models using the likelihood ratio test (LRT). I found no evidence of variation in survival associated with gender or time (Table 2-5). I did however find support for variation in survival dependent upon flood level (χ^2 = 6.126, df = 2, P = 0.047), and also for differences in survival rates between residents and transients (χ^2 = 4,864, df = 1, P = 0.027; Table 2-5). I did not find evidence of time or sampling method variation in recapture probabilities (Table 2-5), but found strong support for the influence of sampling effort (χ^2 = 4.496, df = 1, P = 0.034).

I obtained estimates of survival and recapture probabilities for residents and transients for each sampling period by model averaging the estimates of the best ranked models in our candidate data set (i.e. models with QAICc weight > 0.05)(Table 2-6). For model averaging, I also excluded models that were failing to estimate parameters (i.e., models with singular values because of parameters estimated at the boundary). Model averaged survival estimates for resident jaguars varied between 0.59 ± 0.21 and 0.78 ± 0.20 with an average of 0.66 over the entire study (Table 2-7). The highest survival rate for residents was observed between 2008-2009 surveys, which was the period when flooding was highest during the study (Fig. 2-5). For transients survival estimates were much lower, varying between 0.34 ± 0.26 and 0.40 ± 0.17, with an average of 0.38 over the entire study (Table 2-7). Flooding appeared to have a negative effect on survival of transients, but large variance in survival estimates give weak inference to this conclusion (Table 2-7; Fig. 2-9).

Population Structure and Reproduction

Evidence of transients in the population of jaguars in Mamirauá Reserve was inferred from the high number of adult animals that were captured during only one survey period (e.g. Pradel et al. 1997). The mean proportion of residents to transients was roughly 1:1 (i.e., 51.5% of the 24 adult jaguars observed were transients), which was estimated by dividing the average survival of animals identified as transients by the average survival of residents (for details see Pradel et al. 1997). A similar proportion was observed in the raw data, with 11 individuals captured in surveys during more than one year, and 13 individuals captured during only one survey. Assuming individuals caught in only one year were transients, the sex ratio of residents and transients was quite different. For residents, the male:female ratio was 1:2.7 (3 males and 8 females), whereas for transients it was 1:0.9 (7 males and 6 females).

Fourteen individual female jaguars were photographed or physically captured during this study. At least 5 of these females, 4 of which were residents, were pregnant or with small cubs. This indicates that jaguars are reproducing and rearing their cubs in the Várzea Forests of Mamirauá Reserve. Furthermore, one female was photographed or physically captured during multiple years and provided evidence of producing multiple litters during the study period. This jaguar was documented as pregnant with one cub at heel in 2006, was not observed pregnant or with a cub in 2007 and 2008, was not captured on film during 2009, and then was physically captured in December 2010 and determined pregnant. Upon capture, this female was outfitted with a GPS telemetry collar and monitored for 12 months until December 2011, a period during which she is believed to have successfully raised her cub. During the year she was monitored with GPS telemetry she remained in Mamirauá during the entire year, including during the flooded season. It is also relevant to report that she was captured in the same area over all years. This female, therefore, demonstrated strong site fidelity. Her cub (also a female) also demonstrated strong site fidelity and established a home range in the same area as her mother, where she was observed in 2007, 2008, and 2010.

Activity Patterns

Jaguars were photographed during all hours of the day and night, characterizing a cathemeral behavior, but were most active during daylight hours (63.1% of observations). The distribution of activity observed reflected a bimodal pattern of behavior with peaks of crepuscular activity during early morning (between 5:00 and 8:00 hr), and during midday (between 12:00 and 16:00 hr). Jaguar were observed more frequently than expected during the day and dawn, and less than expected in dawn as dusk (chi-squared = 7.78, df = 3, p-value = 0.05; Fig. 2-11).

Discussion

The results of this study reveal that, at 17.84 jaguars/100 km², jaguars can live in very high densities in the Várzea Floodplain Forests of Amazonia during the low water season. Densities of more than 12 jaguars/100 km² have never been reported prior to this study (Maffei et al. 2011). High density of jaguars are thought to be associated with high density of prey (Nuñez 2012), a flexible cat social system (Harmsen et al. 2009), and/or mutual avoidance (Nuñez 2006). The high density of jaguars observed in this study may be made possible by the abundance, concentration, and accessibility of prey in Mamirauá Reserve during the low water season. Mamirauá Reserve has one of the largest densities of caiman in Amazonia, and also has high densities of brown-throated three-toed sloth and red howler monkeys, all of which are important prey for jaguars in Mamirauá (Ramalho 2012 – Chapter 4). The relationship between prey abundance and large carnivore abundance has also been demonstrated for the tiger in India (Sunquist et al. 1999; Karanth et al. 2004). Evidence of a flexible social structure is supported by the high degree of overlap indicated by the large number of jaguars captured in our relatively small sample area.

The high density of jaguars, however, seems unlikely to be maintained during one whole year. As water rises in the Várzea a large portion of the jaguars may migrate, crossing the Amazon or Japurá Rivers in search of higher dry ground. This lateral migration and changes in density with flooding are observed in many animal populations living in the Várzea (Junk et al.1989). However, the single adult female that was monitored via a GPS collar did remain in the Várzea throughout both the low- and high-water periods. This female had a cub at the beginning of the high-water period and large rivers such as the Amazon may present a formidable obstacle to migrating with a cub. Therefore, females with offspring may remain resident and survive by living a semi-arboreal existence during high water periods. This is consistent with sexual segregation theory, which predicts females will sacrifice foraging opportunities in lieu of security for offspring (Main et al. 1996, Main 2008). However, in the absence of a larger sample size and information on male migratory patterns, it is not possible to make conclusive statements regarding migratory patterns of male and female jaguars in response to seasonal flooding in the Várzea.

Density and survival did not show clear trends over the period of this study and suggest the jaguar population in the study area remains fairly stable (Table 2-3) despite high levels of human activity and human induced mortality (Ramalho 2012 – Chapter 3). Estimates of average apparent survival revealed survival rates among resident jaguars to be approximately 66%, but survival rates of transient jaguars were considerably lower and ranged between ~30-40% (Fig. 2-9). There was no evidence of variance in survival related to gender, despite reports of higher numbers of male jaguars being killed by people in the study area (Ramalho 2012 – Chapter 3). These data support the idea that large felid populations may be able to withstand high human induced mortality if prey populations are adequate (Karanth & Stith 1999). However, the relatively high percentage of transients in the population (~50 %), indicates that there is a large number of new individuals coming into the population every year and suggests that immigrants may play an important role in maintaining the jaguar population of Mamirauá Reserve. Approximately 73 jaguars are killed by people every year in Mamirauá Reserve (Ramalho 2012 – Chapter 3), and immigrant jaguars may play an important role in replacing this source of mortality.

The social organization of jaguars is similar to that of other large cats with males occupying larger home ranges than females, and male home ranges overlapping with those of multiple females (Sunquist & Sunquist 2002). In areas where ranges of individuals of the same sex overlap, they tend to avoid each other by not using the same area at the same time (Nuñez 2006). Having said that, home ranges may overlap extensively even among individuals of the same sex. This is particularly true during the reproductive season when multiple male jaguars have been observed to accompany one female at the same time (Almeida 1976; Hoogesteijn & Mondolfi 1992). This behavior has also been reported by several local people in Mamirauá Reserve (E. Ramalho, unpublished data). The observations made in this study corroborate the social organization and land tenure system expected for jaguars and confirms that jaguars are reproducing in the Várzea during the low water season, which would explain the temporary tolerance of a high density of individuals.

The activity pattern of the jaguar in Mamirauá Reserve was cathemeral, but mostly diurnal, with peaks of activity at dawn and around 13:00 h. Higher activity of the jaguar has been found to coincide with periods of higher activity of their main prey (Harmsen et al. 2011), when prey are thought to be more vulnerable. The jaguar has four main prey species in Mamirauá: the spectacled caiman, the three-toed sloth, the lesser tamandua (Tamandua tetradactyla), and the red howler monkey (Ramalho 2012 – Chapter 4). The activity patterns of jaguars may match periods of higher activity of sloths and red howlers. However, the lack of information on the activity pattern of these species in the study area makes it hard to establish this relationship. Three toed sloths have been found to be highly active during the day in some sites (Sunquist & Montogomery 1973) but not in others (Castro-Vásquez et al. 2010). The lesser tamandua is more active during the night, which could explain part of their activity during the night. Establishing these relationships between activity of prey and predators is further confounded by the fact that camera traps were located on trails, which may be good foraging areas for the arboreal prey, but may not represent foraging for spectacled caiman.

This study has demonstrated that Várzea floodplain forests are breeding and rearing grounds for jaguars in Amazonia and as such the protection of these areas should be a conservation priority. This demonstrated also that high jaguar densities may be maintained in the Várzea despite high levels of human activity and human induced mortality of jaguars if prey populations are abundant and there is a stable source of immigrants. The abundance of prey is likely due in part to the fact that none of the most important prey species of the jaguar in Mamirauá Reserve are intensively used by local people as a protein source (Ramalho – Chapter 4). Although reproduction was confirmed during this study, information is not available on reproductive success for this population and, consequently, it is not known whether annual reproduction replaces adult mortality and if population densities of jaguars would remain stable without a steady influx of immigrants. However, under current scenarios, our data suggest jaguar populations are relatively stable in Mamirauá Reserve, despite the ineffectiveness of protected areas in preventing human induced mortality of jaguars (Carvalho & Pezzuti 2010; Ramalho 2012 – Chapter 3).

Table 2-1. Survey years, periods, field method used (camera trap or foot snare), area covered by trap array, and effort (reported as trap-nights)

Year	Period	Method	Trap polygon (km^2)	Effort (trap-night)
2005	8 July 2005 – 20 October 2005	Camera trap	53.9	2352
2006	16 July 2006 – 5 December 2006	Camera trap	3.6	735
2007	19 July 2007 – 28 January 2008	Camera trap	81.9	2583
2008	25 July 2008 – 9 December 2008	Camera trap and foot snare	16.6	2695
2009	12 September 2009 – 29 November 2009	Foot snare	11.3	1778
2010	10 November 2010 – 10 December 2010	Foot snare	8.4	525

Table 2-2. Effort and capture rates per method and combined

	Camera	Snare	Camera + Snare
Total effort (trap-nights)	8146	2522	10668
Effort per capture (trap-nights)	98	229	113
Capture per trap*night	0.010	0.004	0.009
Capture per 100 trap*night	1.02	0.44	0.88
Individuals captured	22	9	24

Table 2-3. Posterior summaries of model parameters for the jaguar surveys in Mamirauá Reserve based on data from 24 jaguars. N is the number of jaguar exposed to sampling and D is the density per 100 km², σ is the scale parameter of a bivariate normal encounter function, λ_0 is the baseline detectability for an individual whose activity center is located precisely at a trap, and Ψ is the data augmentation parameter

	Year of survey													
	2005		2006		2007		2008		2009		2010		Average	
Parameter	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
N	181.161	73.692	161.931	68.946	125.118	48.963	252.182	47.829	214.658	74.520	219.873	65.880	193.000	87.170
D	16.790	6.830	15.008	6.390	11.596	4.538	23.372	4.433	19.894	6.906	20.390	6.110	17.887	8.079
σ	0.694	0.222	1.023	0.243	0.377	0.094	0.255	0.122	0.297	0.268	0.568	0.316	-	-
λ_0	0.003	0.002	0.008	0.005	0.029	0.013	0.739	1.560	0.040	0.039	0.017	0.170	-	-
Ψ	0.591	0.241	0.522	0.222	0.404	0.159	0.807	0.154	0.070	0.244	0.720	0.215	-	-

Table 2-4. Model selection statistics for the full set of candidate models

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Model Likelihood	Num. parameters	Deviance
ϕ (M2,low/high-flood) p(effort)* **	83.889	0.000	0.336	1.000	6	27.862
ϕ (M2,low/high-flood) p(.)* **	85.921	2.032	0.122	0.362	5	32.358
ϕ (M2,low/high-flood) p(method)* **	86.920	3.030	0.074	0.220	6	30.892
ϕ (M2,flood) p(.)	86.977	3.087	0.072	0.214	5	33.414
ϕ (M2,low/high-flood) p(method,effort)* **	87.232	3.342	0.063	0.188	8	25.990
ϕ (M2) p(.)	87.377	3.487	0.059	0.175	3	38.484
ϕ (M2,flood) p(effort)*	87.903	4.014	0.045	0.134	6	31.876
ϕ (low/high-flood) p(method)* **	88.414	4.525	0.035	0.104	3	39.521
ϕ (.) p(effort)*	89.088	5.199	0.025	0.074	3	40.195
ϕ (flood) p(effort)*	89.165	5.275	0.024	0.072	4	37.978
ϕ (M2) p(t)	89.700	5.811	0.018	0.055	7	31.115
ϕ (.) p(.)	90.027	6.138	0.016	0.047	2	43.348
ϕ (low/high-flood) p(effort)*	90.301	6.412	0.014	0.041	4	39.115
ϕ (flood) p(method)*	90.602	6.712	0.012	0.035	4	39.415
ϕ (.) p(method)*	90.776	6.887	0.011	0.032	3	41.883
ϕ (flood) p(method,effort)* **	90.847	6.958	0.010	0.031	6	34.820
ϕ (low/high-flood) p(method,effort)* **	90.978	7.089	0.010	0.029	6	34.951
ϕ (M2,g) p(.)	91.133	7.244	0.009	0.027	5	37.570
ϕ (.) p(method,effort)* **	91.616	7.726	0.007	0.021	5	38.053
ϕ (low/high-flood) p(.)	91.683	7.794	0.007	0.020	3	42.790
ϕ (flood) p(.)*	91.840	7.950	0.006	0.019	3	42.946
ϕ (g) p(.)	92.155	8.266	0.005	0.016	3	43.262
ϕ (.) p(g)	92.237	8.347	0.005	0.015	3	43.343
ϕ (.) p(g,effort)	93.224	9.335	0.003	0.009	5	39.661
ϕ (g) p(method.effort)* **	94.024	10.135	0.002	0.006	6	37.996
ϕ (.) p(t)* **	94.080	10.190	0.002	0.006	6	38.052
ϕ (g) p(g)	94.407	10.518	0.002	0.005	4	43.221
ϕ (g,low/high-flood) p(effort)*	94.497	10.608	0.002	0.005	6	38.470
ϕ (.) p(g,method)*	94.960	11.071	0.001	0.004	5	41.397
ϕ (g,low/high-flood) p(method)* **	95.183	11.294	0.001	0.004	6	39.155
ϕ (t) p(t)*, **	95.833	11.943	0.001	0.003	9	31.831
ϕ (M2, .,t) p(.)	96.049	12.160	0.001	0.002	10	29.177
ϕ (g) p(t)*, **	96.582	12.692	0.001	0.002	7	37.996
ϕ (t) p(.)	97.288	13.398	0.000	0.001	6	41.260
ϕ (M2, g,t) p(g,.)	98.654	14.764	0.000	0.001	12	25.682
ϕ (g,flood) p(.)*	99.961	16.072	0.000	0.000	5	46.398
ϕ (g,flood) p(g)*	101.174	17.285	0.000	0.000	6	45.146
ϕ (g,flood) p(g,method,effort)*	104.748	20.859	0.000	0.000	12	31.776
ϕ (M2, g,t) p(.)	118.380	34.491	0.000	0.000	17	27.676
ϕ (g,t) p(g,t)*, **	123.725	39.835	0.000	0.000	18	28.967

* Models where we applied an alternative optimization procedure based on simulated annealing.

** Models where confidence intervals were derived using profile likelihood.

Table 2-5. Results of likelihood ratio tests used to test hypotheses related to survival and recapture probabilities. Model parameters are transients (M2), gender (g), level of flooding (low/high-flooding), time (t), constant (.)

Hypotheses	Reduced model	General model	χ^2	df	p-value
Survival					
Gender influences survival rates	ϕ (M2) p(.)	ϕ (M2,g) p(.)	0.913	2	0.633
There is no time variation in survival during this study	ϕ (.) p(t)	ϕ (t) p(t)	6.221	3	0.101
High floods will influences survival	ϕ (M2) p(.)	ϕ (M2,low/high-flood) p(.)	6.126	2	0.047*
Transients are present and have different survival than residents	ϕ (.) p(.)	ϕ (M2) p(.)	4.864	1	0.027*
Recapture probability					
No time variation in recapture probabilities	ϕ (M2) p(.)	ϕ (M2) p(t)	7.369	4	0.117
Sampling effort affects recapture probabilities	ϕ (M2,low/high-flood) p(.)	ϕ (M2,low/high-flood) p(effort)	4.496	1	0.034*
Sampling method affects recapture probabilities	ϕ (M2,low/high-flood) p(.)	ϕ (M2,low/high-flood) p(method)	1.466	1	0.226

* Significant results at a nominal $\alpha = 0.05$

Table 2-6. Model ranking of CJS mark-recapture models used to estimate apparent survival (ϕ) and recapture probability (p) for jaguars in Mamirauá Reserve from 2005-2010. Only models used in model averaging with more than 0.05 QAICc weight and fully estimable parameters (i.e., no singular values) were used for model averaging. Model selection statistics presented are: quasi-likelihood adjusted Akaike's information criteria (QAICc), delta QAICc (ΔQAIC), QAIC weight, model likelihood, number of parameters, and deviance

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Model Likelihood	Num. Par	Deviance
ϕ (M2,flood) p(.)	86.977	0.000	0.283	1.000	5	33.414
ϕ (M2) p(.)	87.377	0.400	0.231	0.819	3	38.484
ϕ (M2,flood) p(effort)*	87.903	0.927	0.178	0.629	6	31.876
ϕ (.) p(effort)*	89.088	2.111	0.098	0.348	3	40.195
ϕ (flood) p(effort)*	89.165	2.188	0.095	0.335	4	37.978
ϕ (.) p(.)	90.027	3.050	0.062	0.218	2	43.348
ϕ (low/high-flood) p(effort)*	90.301	3.324	0.054	0.190	4	39.115

* Models where we applied an alternative optimization procedure based on simulated annealing was applied

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Table 2-7. Estimated model averaged survival (ϕ) and recapture probabilities (p) for resident and transient jaguars between sampling periods. Values shown are weighted average estimates, with standard error (SE), lower (LCI) and upper (UCI) 95% confidence intervals

		2005-2006				2006-2007				2007-2008				2008-2009				2009-2010			
		Estimate	SE	LCI	UCI	Estimate	SE	LCI	UCI	Estimate	SE	LCI	UCI	Estimate	SE	LCI	UCI	Estimate	SE	LCI	UCI
Residents	ϕ	-	-	-	-	0.59	0.21	0.21	0.89	0.61	0.19	0.25	0.88	0.78	0.20	0.26	0.97	0.67	0.17	0.31	0.90
	p	-	-	-	-	0.85	0.11	0.50	0.97	0.85	0.11	0.51	0.97	0.78	0.10	0.53	0.92	0.66	0.20	0.25	0.92
Transients	ϕ	0.40	0.17	0.14	0.73	0.38	0.15	0.15	0.68	0.39	0.15	0.16	0.68	0.34	0.26	0.05	0.83	0.40	0.18	0.13	0.75
	p	0.72	0.16	0.35	0.92	0.91	0.10	0.49	0.99	0.91	0.10	0.51	0.99	0.79	0.11	0.50	0.93	0.62	0.23	0.20	0.92

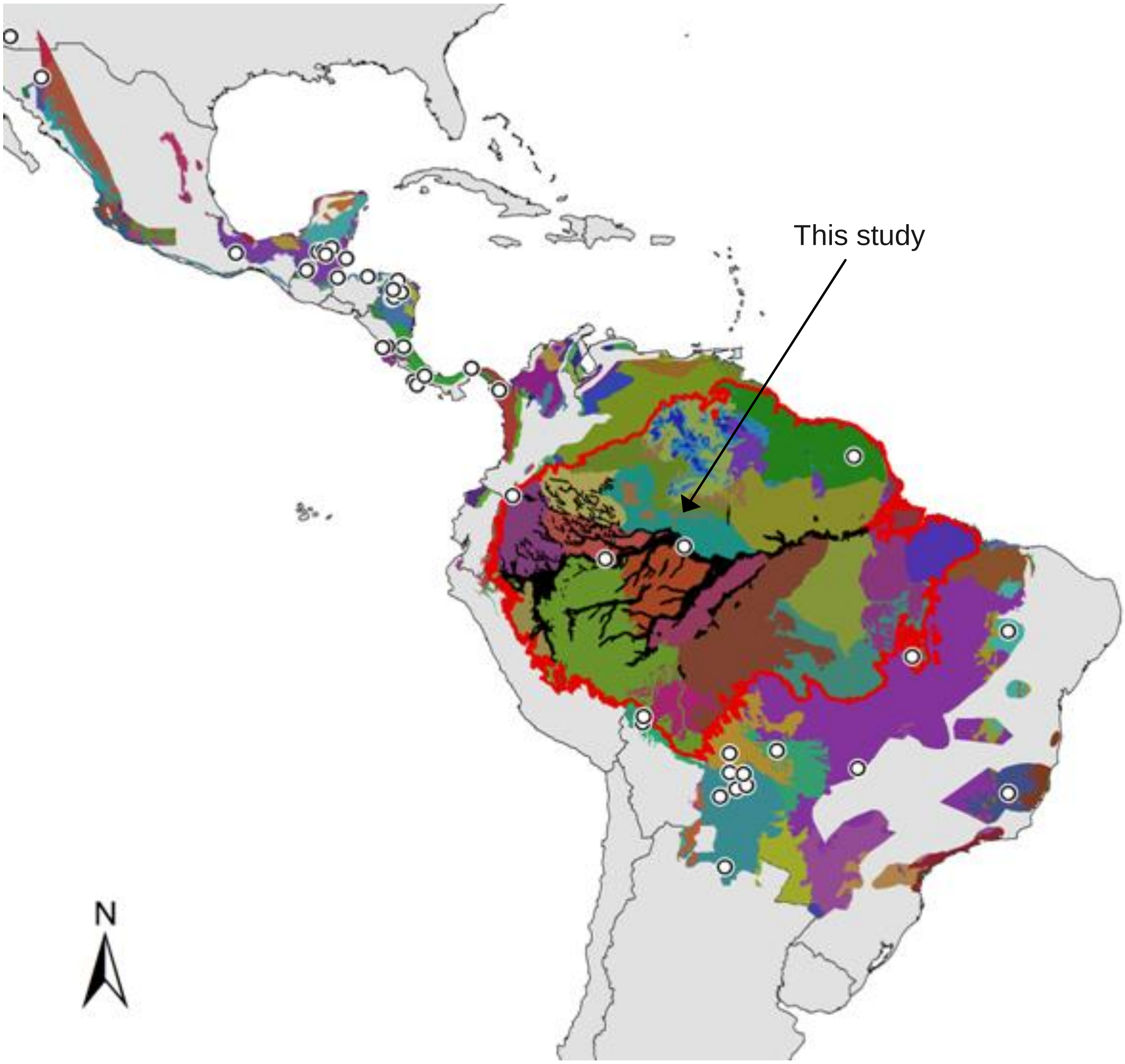

Figure 2-1. Location of all camera-trap surveys conducted to date to estimate jaguar density (white circles), Ecoregions within the jaguar present distribution (other colors), and extent of Amazonia (red line)

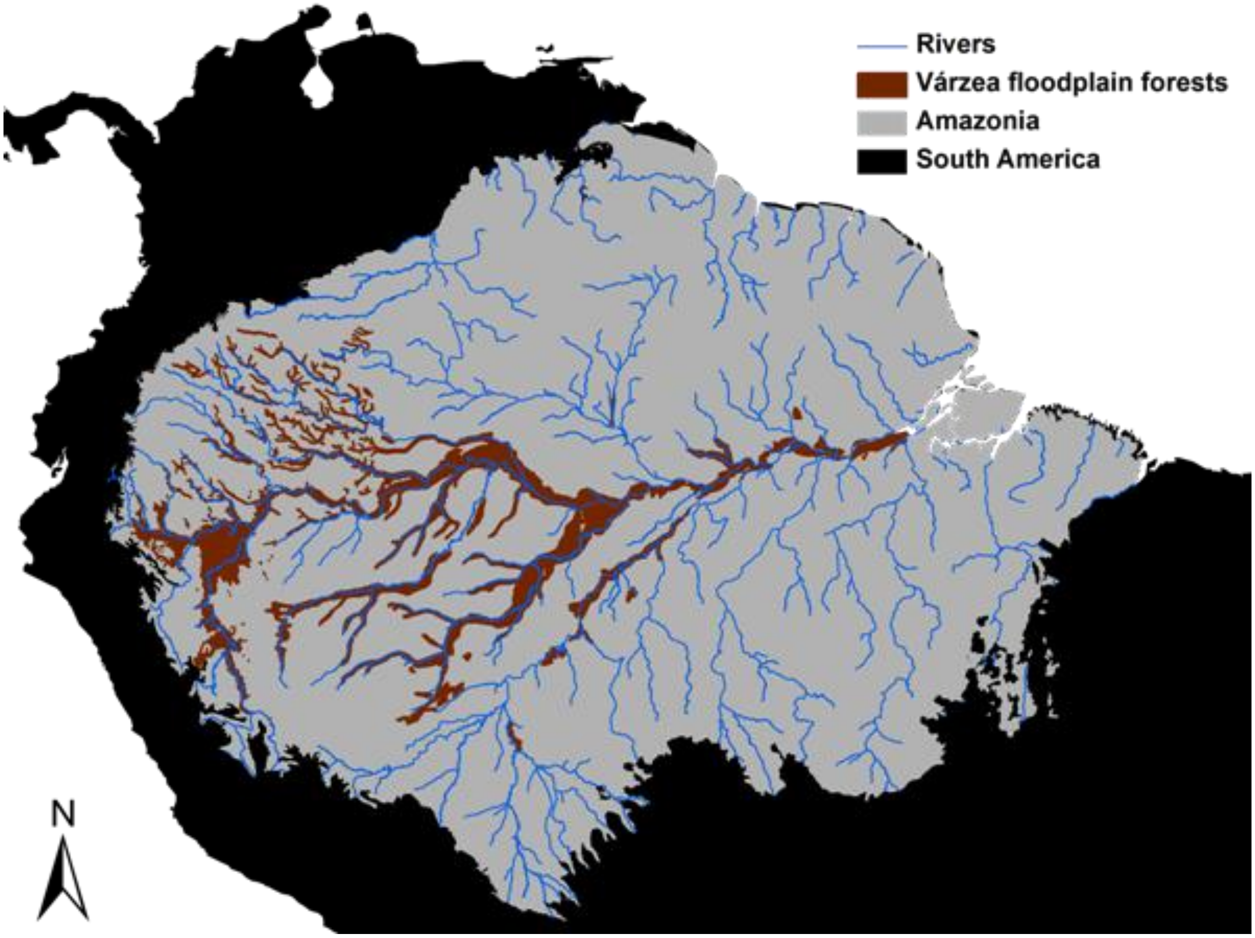

Figure 2-2. Location and extent of the Várzea floodplain forests of Amazonia

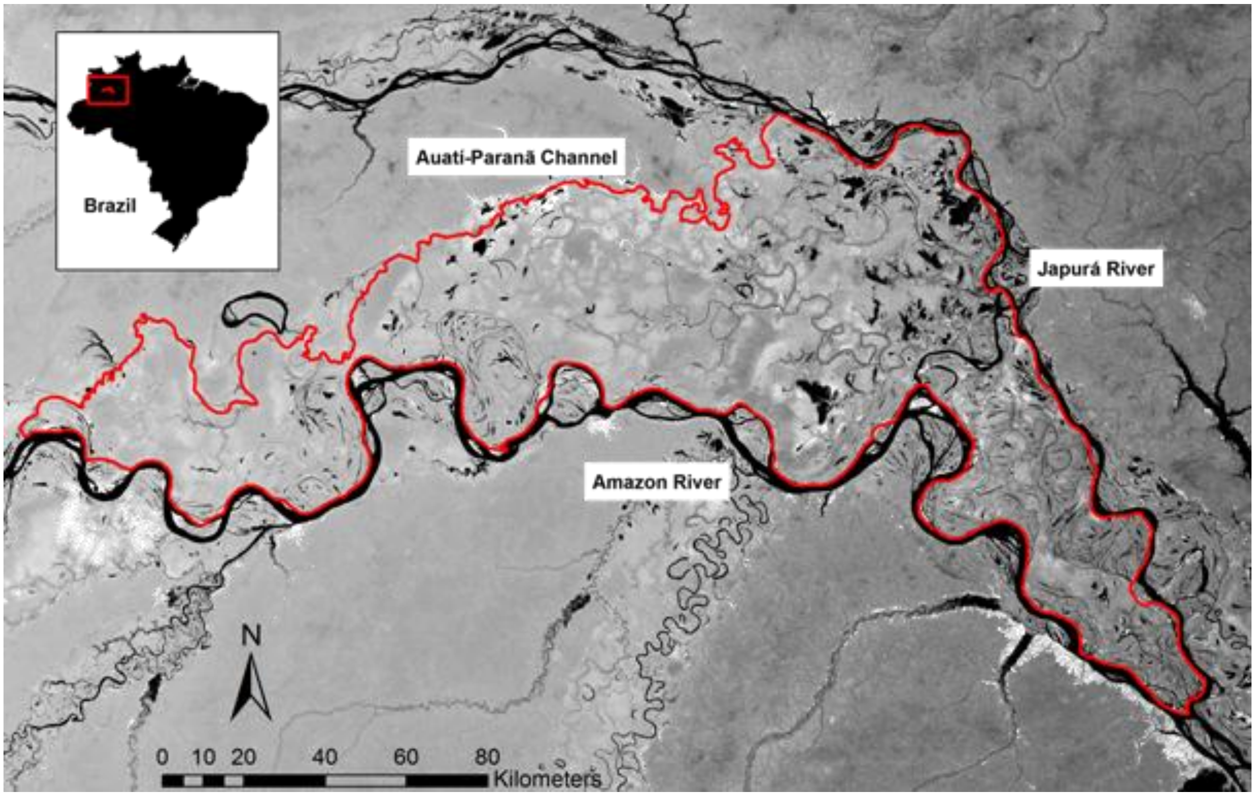

Figure 2-3. Smaller frame shows location of Mamirauá Sustainable Development Reserve within Brazil. In larger frame red line represents the limits of the Reserve


Figure 2-4. White uakari monkey. photo: Luiz Claudio Marigo

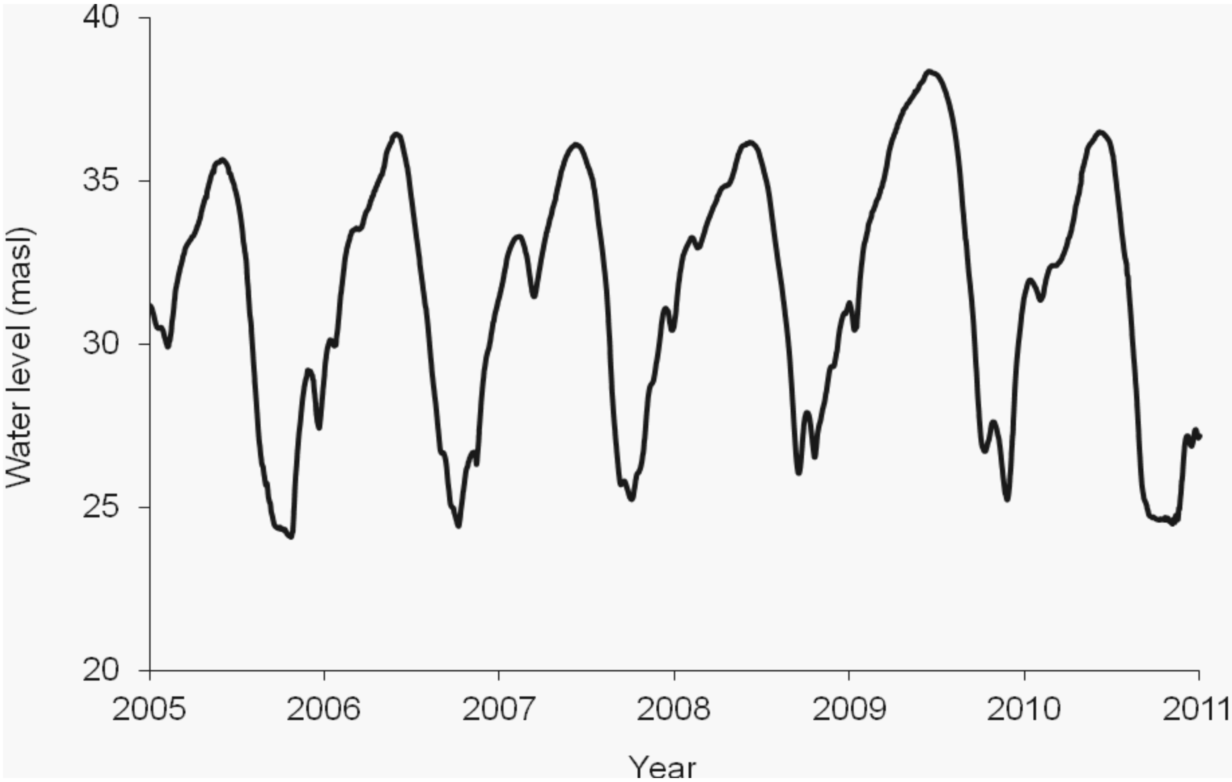

Figure 2-5. Water level dynamics during the period of this study. Water level is presented in meters above sea level (masl)

Figure 2-6. Felids sniffing the homemade lure used in this study during a preliminary camera-trap survey in the study site. Panthera onca (A), Leopardus pardalis (B), and Leopardus wiedii (C)

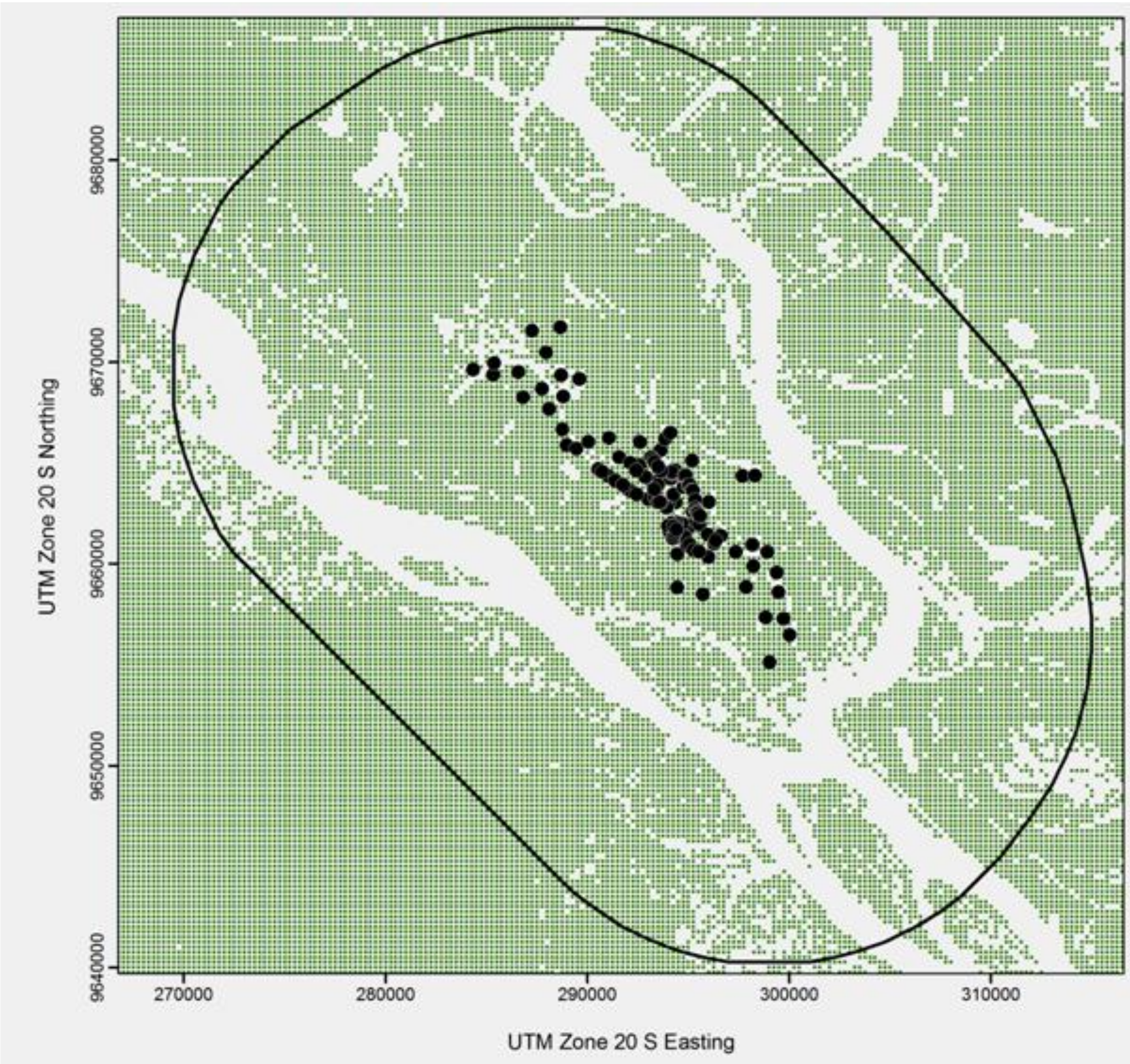

Figure 2-7. State-space area of 1,079 km² determined by a 15 km buffer (black line) around the trap array used to survey the jaguar population of Mamirauá Reserve (black circles), potential home-range centers (green pixels). White areas represent non-habitat

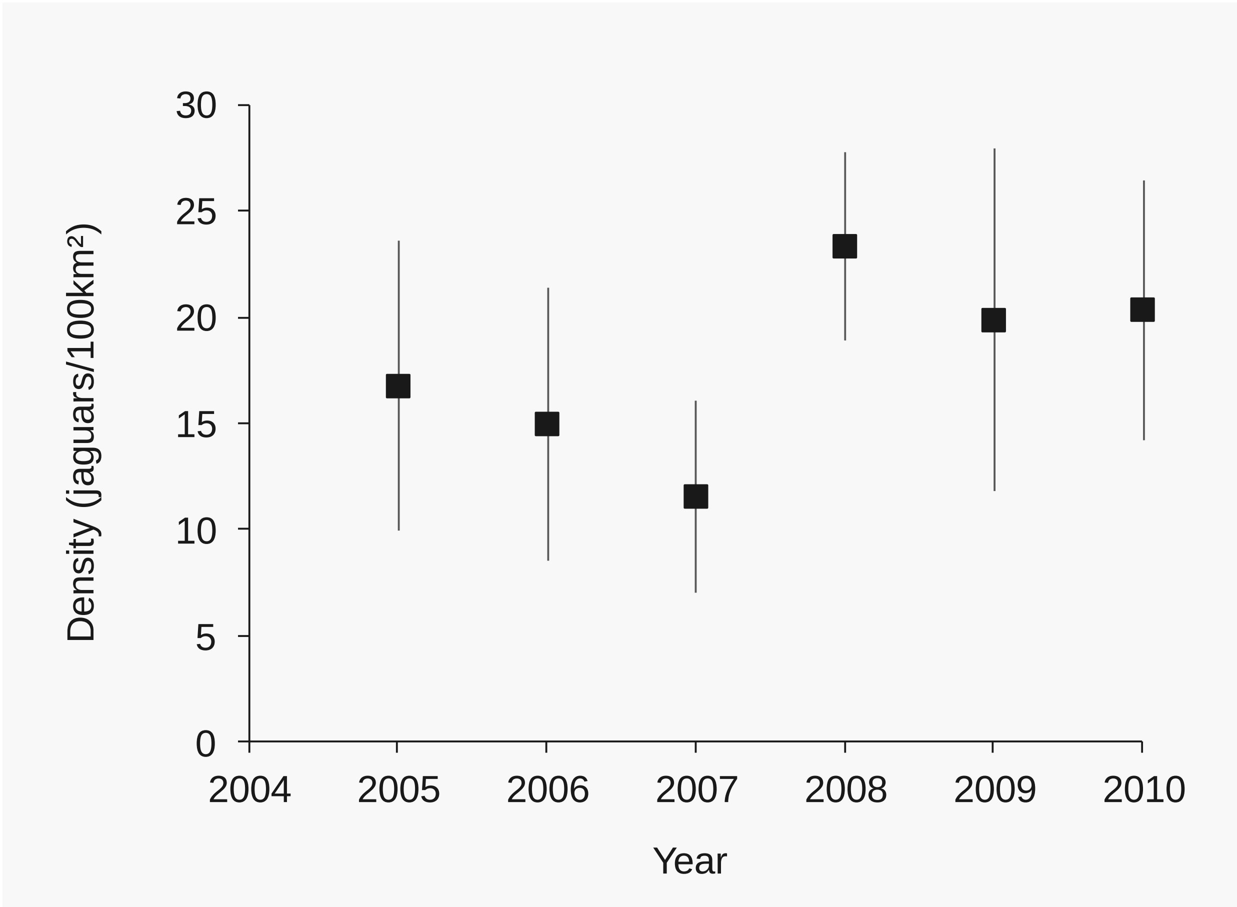

Figure 2-8. Jaguar density per year with SD of the posterior

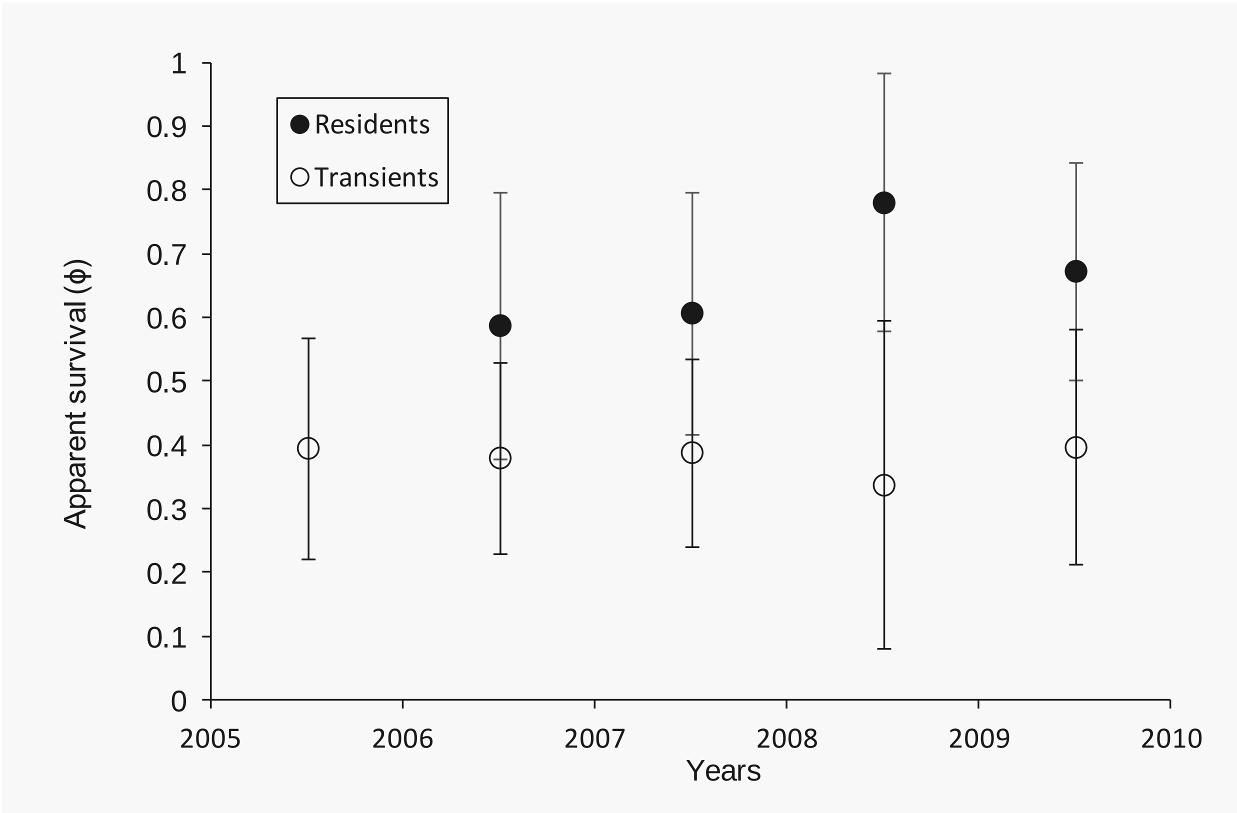

Figure 2-9. Apparent survival rates of resident (black circles) and transient (white circles) jaguars

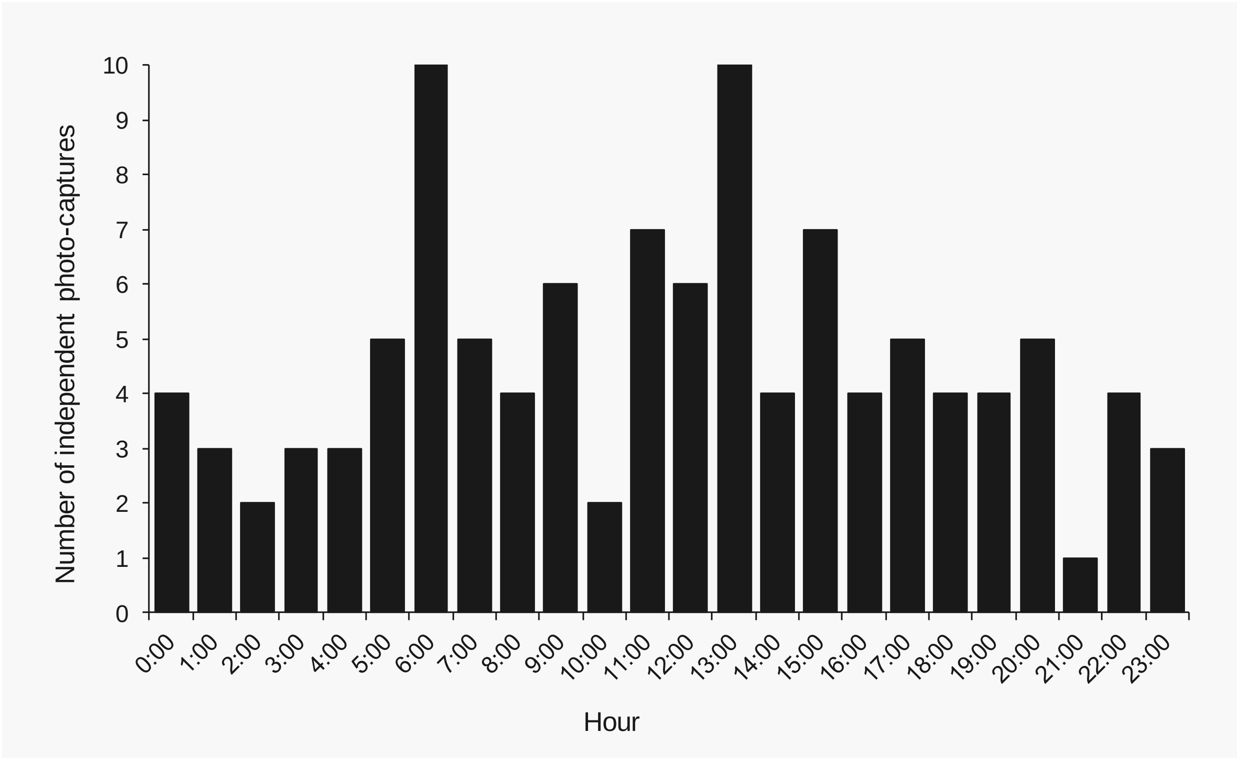

Figure 2-10. Activity patterns of jaguars in Mamirauá Reserve according to the number of independent photo-captures recorded per one hour period of the day (n=111)

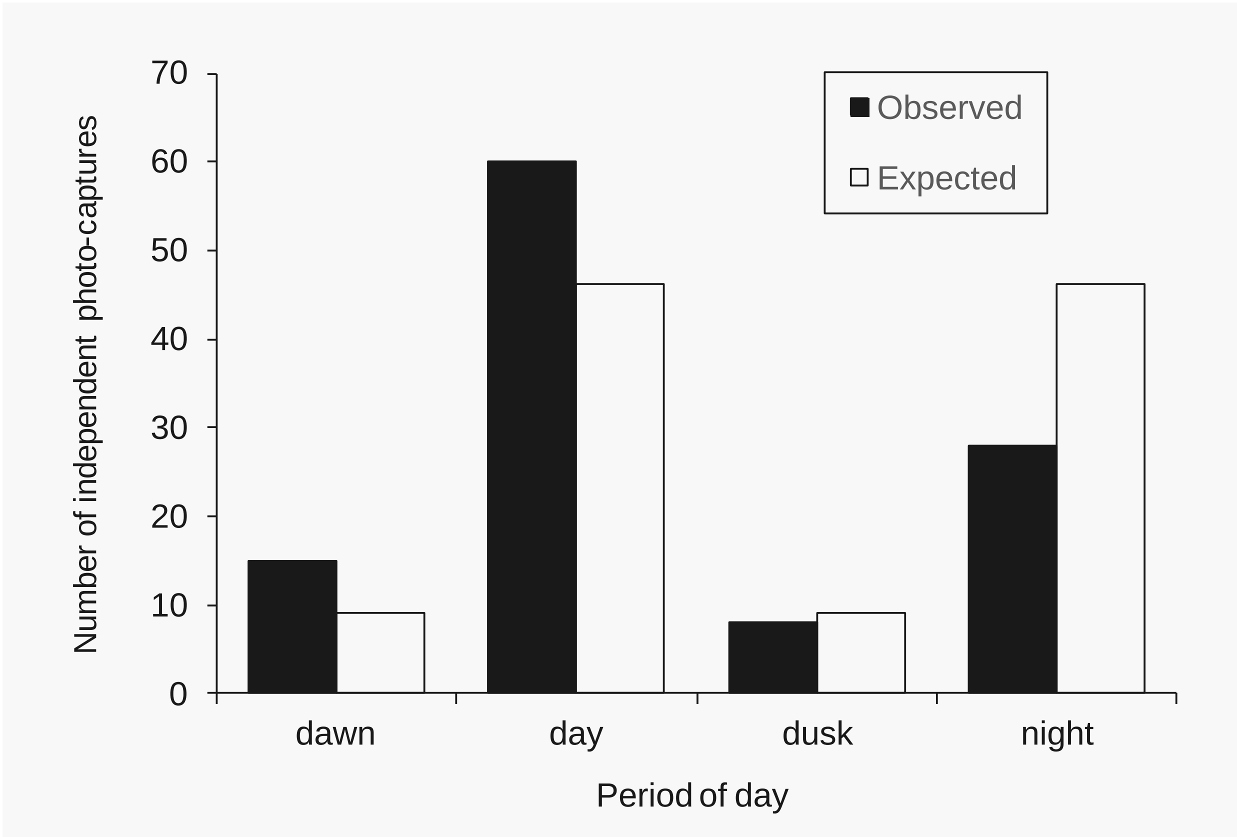

Figure 2-11. Number of observed independent photo-captures recorded per period of the day (black bars) and expected number of captures based on availability (n=111). Chi-squared = 7.78, df = 3, p-value = 0.05

CHAPTER 3
ESTIMATING LARGE CARNIVORE MORTALITY FROM HUNTING USING CAPTURE-RECAPTURE MODELS: THE CASE OF JAGUARS IN THE AMAZON FLOODPLAIN FORESTS

Hunting - here defined as the legal or illegal pursuit and/or trapping of animals by humans with the intent of killing them for food, management, sport, or trade - has been reported to be the greatest source of mortality for many large carnivore species, and has caused the decline of large carnivore populations inside and outside protected areas worldwide (Noss et al. 1996; Woodroffe & Ginsburg 1998; Woodroffe 2001; Andren et al. 2006; Adams et al. 2008; Obbard & Howe 2008; Robinson et al. 2008). Hunting accounted for 53% (28 individuals) of total mortality of radio-collared pumas (*Puma concolor*) in two populations in Washington State, USA (Cooley et al. 2009). Gray wolf (*Canis lupus*) populations have been consistently reduced by hunting in eastern Asia (Reading et al. 1998), Europe (Sidorovich et al. 2003) and the USA (Carbyn 1987). Between 77 and 85% of 99 radio-collared grizzly bears (*Ursus arctos*) were killed by people in the interior mountains of Northwestern USA (McLellan et al. 1999). Poaching accounted for 75% of radio-collared Amur tigers monitored in the province of Primorski Krai, in Russia, between 1976 and 2005 (Goodrich et al. 2008). In Laikipia, Kenya, 17 out of 18 monitored lions (*Panthera leo*) were killed in retaliation for livestock depredation, with an estimated population decrease of 4% per year (Woodroffe & Frank 2005). In Western South Africa 60% of recorded leopard (*Panthera pardus*) deaths resulted from hunting (Balme et al. 2009). Hunting is thus a critical issue in the conservation of large carnivores.

The jaguar (*Panthera onca*) is the third largest felid in the world, and the only representative of the genus Panthera in the American continent. The jaguar is currently classified as Near Threatened by the International Union for Conservation of Nature (IUCN) due to the declining trend of most jaguar populations and extensive reduction of the jaguar's historical range in the last century (Sanderson et al. 2002; Caso et al. 2008). Despite the international ban on trade and export of jaguar parts that resulted from the inclusion of the jaguar in Appendix 1 of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1973 and national bans on hunting of jaguars in most countries after the 1960s, the declining trend of jaguar populations and continuing contraction of its range have persisted (Sanderson et al. 2002; Caso et al. 2008; Paula et al. 2011).

Hunting is recognized as one of the most important threats to the survival of the jaguar (Ojeda & Mares 1982; Brown1983; Melquist 1984; Swank & Teer 1989; Sanderson et al. 2002; Caso et al. 2008; Paula et al. 2011). Commercial motivation for hunting in the 1960s and 1970s, due to the high international demand for jaguar skins, promoted the overexploitation of jaguar populations range wide. In the late 1960s a high quality jaguar coat could be sold for as much as US $20,000 in New York, and 31,105 jaguar skins were imported into the United States from 1968 to 1970 (Myers 1973). During the early 1970s, approximately 15,000 jaguars were killed every year in Brazilian Amazonia alone to support the international skin trade (Smith 1976; Fitzgerald 1989). Hunting related to fur trade was also an important mortality factor in Argentina until the country joined CITES in 1980 (Altrichter et al. 2006), and overhunting is considered the main factor responsible for the decline and decimation of jaguar populations in Venezuela (Hoogesteijn & Mondolfi 1987).

The national bans on jaguar hunting in most countries where jaguars occur and the international ban on trade of jaguar body parts are thought to have considerably reduced the number of jaguars killed for commercial motives (Smith 1976). Hunting, however, continues to be one of the main causes of decline of jaguar populations. Hunting is a major source of jaguar mortality in Iguaçu National Park in Southern Brazil, where at least 70 jaguars were killed by hunters between 1995 and 2002 (Crawshaw 1995, 2002; Conforti & Azevedo 2003) and also in Northern Misiones, in Argentina (Paviolo et al. 2008). In the semi-arid Chaco of Argentina, high mortality from hunting is motivated by a desire to exterminate jaguars even where jaguars don't attack livestock (Altrichter et al. 2006). In Brazil, hunting continues to be one of the main causes of decline of jaguar populations in all biomes of the country (Paula et al. 2011). In Amazonia, jaguars are hunted for subsistence and illegal trade, given that law enforcement is difficult in isolated rural villages, which are consequently not subject to control (Reina and Gonzalez-Maya 2008), and in Mamirauá and Amanã Sustainable Development Reserves, hunting of jaguars occurs regularly (Valsecchi, 2005). Despite the evidence that hunting can have a major impact on jaguar populations, few studies have estimated jaguar mortality from hunting or characterized the hunting events to determine when, where, how and why people hunt jaguars.

Mortality of jaguars from hunting has been estimated by the number of radio collared animals killed by hunters (e.g., Crawshaw 1995) or through interviews with local people (e.g., Michalski & Peres 2006). The first method is logistically complex, time consuming and financially prohibitive for most research budgets. The second only allows researchers to access the minimum number of jaguars killed because interviewees may forget, have no knowledge of, or consciously omit the occurrence of jaguar hunting events due to the illegality of this activity and the association of researchers to law enforcement. The minimum number of jaguars reported killed is an unknown fraction of the total number of jaguars killed and thus has limited application, serving only to set a minimum boundary on the real number of jaguars killed.

Carvalho and Pezzuti (2010) were the first to use a statistical approach to go beyond the minimum number reported in interviews and attempt to estimate the true number of jaguars killed. Using a first-order jackknife (Manly 1997), they obtained an estimate of mortality of jaguars from hunting that was almost twice the minimum number of jaguars reported killed in their interviews. Their method, however, does not allow estimation of the uncertainty associated with their estimates, nor does it allow the use of different models that take into account different detection probabilities assumptions.

Fortunately, the problem of estimating the number of jaguars killed is very similar to the methodological challenge of estimating the size of wildlife populations. In both cases a survey method yields a count statistic (e.g., minimum number of jaguars killed reported in interviews, or minimum number of jaguars identified during a camera-trap survey) which represents an unknown fraction (p) of the population of interest. In the case of jaguar mortality from hunting, the estimate represents an unknown fraction of the total number of jaguars killed. For these count statistics to be useful it is necessary to estimate p so that the real parameter of interest can be estimated (i.e., total number of jaguars killed or abundance). Capture-recapture (CR) models were specifically designed for estimating p and, subsequently, the real parameter of interest, abundance (or in the case of this study the total number of jaguars killed). This methodology is robust, well developed and tested, and has shown to be effective for estimating abundance and density of large cats in many environments (Karanth 1995; Karanth & Nichols 1998, 2000; Silver et al. 2004; Maffei et al. 2004; Soisalo & Cavalcanti 2006; Maffei et al. 2011). The similarities in the methodological challenge of estimating abundance using field surveys and estimating total number of jaguars killed using interviews suggests that CR models may also allow estimation of p for the case of mortality from hunting.

The objectives of this study were to characterize jaguar and puma hunting events, to estimate jaguar mortality from hunting using CR methodology in two Sustainable Development Reserves located in the Western portion of Brazilian Amazonia, and to evaluate the effectiveness of sustainable development reserves in controlling hunting of jaguars. In characterizing jaguar and puma hunting events I tested the following hypotheses:

- Hunting of large cats has a seasonal variation in its distribution and occurs more frequently during months and season when the water level is higher and terrestrial habitat is less available (i.e., the flood season, months of May-July).
- The jaguar is hunted more frequently than pumas because jaguars occur at high density in the Várzea flooded forest (Chapter 2) and are known for outcompeting and excluding pumas from areas closer to water bodies in areas where they co-occur.
- Male jaguars and pumas are hunted more frequently than females because male large cats usually have larger home ranges and disperse greater distances.
- Most hunting events will be opportunistic because killing of jaguars is often associated with livestock depredation and chance encounters near margins of lakes, streams and other water bodies where both humans and large cats search for food.

Methods

Study Sites

This study was conducted in two neighboring Sustainable Development Reserves (SDRs) in the Western portion of Brazilian Amazonia, Mamirauá and Amanã SDRs (Fig. 3-1). SDRs are defined in the Brazilian National System of Conservation Units (SNUC) as natural areas inhabited by traditional human populations whose existence is dependent upon sustainable systems of natural resource exploitation and that play a fundamental role in the protection of nature and maintenance of biological diversity. The objective of this category of protected area is to promote the conservation of biodiversity and secure and improve the quality of life of traditional human populations (Brazil 2000).

The climate in the region is tropical humid with a stable average monthly temperature around 26°C and an average annual precipitation of 2,373 mm (Ayres 1993) with 64% of the annual precipitation occurring during December-May. The flood pulse of the Amazon River causes river levels in the region to fluctuate an average of 10.6 meters annually (Ramalho et al. 2009). The flooding caused by this fluctuation may inundate the entirety of Mamirauá Reserve and also the western portion of Amanã Reserve.

Mamirauá is located at the confluence of the Japurá and Amazon Rivers, but entirely encompassed within the Amazon River floodplain (Fig. 3-1) (2°56'S, 65°25'W). Created in 1990 Mamirauá was the first SDR to be created in Brazil (Queiroz 2005, Esterci & Ramalho 2007). The Reserve covers an area of 11,240 km^2, and is the only official protected area in Brazil exclusively protecting the Várzea ecosystem.

The Várzea is a wetland that is seasonally inundated by the large and predictable monomodal flood-pulse of the Amazon River and its tributaries (e.g., the average annual amplitude of the flood-pulse in Mamirauá Sustainable Development Reserve is >10 m, Ramalho et al. 2009). Inundation forces the Várzea to periodically transition between terrestrial and aquatic phases, resulting in a biota that has morphological, anatomical, physiological, phenological, and/or ethological adaptations to this flooding regime (Junk et al. 1989). Most frequently encountered botanic families are Annonaceae, Euphorbiaceae, and Leguminosae (Ayres 1993). Some of the most frequent tree species found are Pterocarpus amazonicus, Eschweilera albiflora, and Piranhea trifoliate.

Because Mamirauá is a seasonally inundated island in the middle of two large rivers, animals that live inside the Reserve have to be well adapted to swimming and/or climbing trees and able to survive the steep annual fluctuation in resource availability caused by flooding. These peculiar environmental characteristics are responsible for the presence of some endemic species but also for a lower density and diversity of terrestrial species in general. Primate diversity is lower than in the surrounding Terra Firme, but Mamirauá Reserve encompasses most of the distribution of the white bald-headed uakari monkey (*Cacajao calvus calvus*) and the entire distribution of the endemic blacked-headed squirrel-monkey (*Saimiri vanzolinii*). Threatened and charismatic top predators such as the jaguar, the black caiman (*Melanosuchus niger*), the pirarucu (*Arapaima gigas*), and the Amazon river dolphin (*Inia geoffrensis*) are abundant. Mamirauá Reserve also holds a diverse fish and bird fauna with at least 340 species of each group (Queiroz & Peralta, 2011).

Amanã is located between the black, nutrient-poor, waters of the Negro River and the white, nutrient-rich, alluvial waters of the Amazon River, also near the confluence of the Japurá and Amazon Rivers (Fig. 3-1) (2°21'S, 64°16'W). It was created in 1998 and covers a mosaic of three main ecosystems – Terra Firme, Igapó, and Várzea – covering an area of 23,500 km² (for a detailed description of forest types see Prance 1978, 1980). The Terra Firme ecosystem encompasses all non-floodable areas of the Amazon Forest and is the predominant ecosystem in Amanã covering approximately 84% of the Reserve. The diversity and density of tree species is higher in the Terra Firme in comparison to the Igapó and the Várzea. The most abundant tree species in the Terra Firme environments of Amanã are Eschweleira coreacea, Iryanthera paraensis, Virola calophylla, Iryanthera sp., and Iryanthera juruensis (Souza 2006). Igapó, like the Várzea, is a seasonally inundated environment. The difference is that the Igapó is flooded by black-water rivers, while the Várzea is flooded by white-water rivers (Ayres, 1993). Igapós cover 9% of Amanã and 6% of Várzea.

The mosaic of forest types found in Amanã make it one of the most bio-diverse forests in the world (Sears & Marín 2001), but detailed information on the fauna of the Reserve is still lacking. However, many charismatic, endangered, and ecologically important species are common in Amanã, including the lowland tapir (*Tapirus terrestris*), Amazonian manatee (*Trichechus inunguis*), the harpy eagle (*Harpyia harpija*), black-faced uakari (*Cacajao melanocephalus*), giant river otter (*Pteronura brasiliensis*), pink river dolphin (*Inia geoffrensis*), and both the jaguar and the puma.

The human populations of Mamirauá and Amanã live primarily along the margins of the main Rivers, on smaller channels, and along the margins of Lake Amanã (Fig. 3-1). The main economic and subsistence activities of local people in both Reserves are agriculture, hunting, fisheries, and harvesting of wood and other non-timber products.

But the intensity of these activities is markedly different. In Mamirauá the principle source of protein comes from fishing, whereas hunting is the major source of protein in Amanã. The human population in Mamirauá is 9,733 people (0.87 people/km²), distributed in 1684 households over 181 villages. In Amanã there are 3,653 people (0.15 people/km²), distributed in 612 households over 84 villages (MSDI 2011). This study covered only a portion of both Reserves and was conducted in areas with the largest concentration of villages (Fig. 3-1).

Characterizing Hunting Events

To characterize large cat hunting events, I interviewed local people using a semi-structured interview in which I recorded information on the hunting event and on the large cats killed. Villages visited were selected based on a logistically viable route through the study areas that would allow us to survey the largest number of settlements during the survey. Households were selected at random and people from the same household were not interviewed. The first step I took after approaching a household was to explain the purpose of the study, to assure every interviewee that all information provided would only be used for the objectives of this study and that anonymity would be preserved for all participants. I started the interview asking subjects if they knew of any large cat events or stories. Events and stories could be a hunting event, but could also be a sighting, a depredation of livestock event, an attack on a person, a scat found, or an animal calling. The idea of this first question was to get the interviewee more comfortable with the questionnaire and with the interviewer.

During the interviews, for each hunting event I recorded the date (or month, or season, when interviewee could not remember date), name of location (e.g., Lake Mamirauá, Amazon River, near a village or someone’s house), major environment (i.e., Várzea, Terra Firme, Igapó, or river), whether the event occurred during day or night, the activity of the hunter at the moment of the event, method used in the hunt, motivation/reason to hunt, if hunter was a livestock owner, if meat was consumed, and if parts were collected. The name of the hunter was obtained whenever possible but ideally it was given spontaneously by the interviewee. Although giving the name of the hunter was delicate information given the illegality of killing a large cat, this information was often key in identifying animals during analysis. For each large cat reported killed, I recorded the species, whether the animal was melanistic or not, sex, age class (i.e., cub, sub-adult, adult), and reproductive state (pregnant or lactating). I also recorded any other information regarding the event that could facilitate the identification of that event and its distinction from other events (e.g., a jaguar was killed on the same day as the soccer tournament). Information provided also enabled me to determine whether the hunt was opportunistic (i.e., the hunter's activity was not specifically related to hunting a large cat), intentional (i.e., the hunter's primary objective was to hunt a large cat), or accidental (i.e., the hunter killed a large cat involuntarily, such as might occur by mistaking a large cat for another species when hunting).

To evaluate if hunting events had a seasonal distribution I compared the observed number of hunting events reported for each season with the expected number of hunting events based on the number of months within each season. For example, flood season lasts three months (25% of the year), and if season of the year had no effect on hunting events I would expect 25% of hunting events to occur within this season. To determine if there was a significant difference between observed and expected values I used Pearson's Chi-squared test (Zar 1984). I also used Pearson's Chi-squared test to compare frequencies of hunting events for jaguar and puma, for males and females, and for opportunistic and intentional hunts.

Estimating Total Number of Jaguars Killed using CR Methodology

Capture-recapture methodology (CR) was originally designed to allow estimation of population size because the imperfect detection provided by available field survey methods did not allow a total count of animals in the population of interest (Karanth 1995; Karanth & Nichols 1998, 2002). In this study, my field survey method is represented by the interviews, and instead of abundance I am interested in the total number of jaguars killed.

Like most field survey methods used to count the number of animals in a population (e.g., line transects, point counts, camera-traps, etc.) interviews used in this study to estimate the total number of jaguars killed are unlikely to detect all animals that were in fact killed (i.e., the probability of detection is less than one). Consequently, interviews yield an imperfect count, or a count statistic, that represents an unknown fraction of the total number of jaguars killed during hunting events. As in the estimation of abundance, to estimate the true number of animals hunted it is necessary to estimate this unknown proportion, the detection probability (p).

When the count statistics of the survey method yield numbers of marked (captured) and unmarked (not captured) individuals, such as those resulting from camera-trap surveys, abundance can be estimated through closed population CR models. The resulting data of a camera-trap survey is made of individual capture histories for each animal photographed, where 1's represent occasions when the individual was captured, and 0's represent occasions when the individual was not captured. For example, if animal #1 has a capture history of 00101, it means that it was photo-captured in the third and fifth sampling occasions, but was not photo-captured in the first, second and forth sampling occasions. Each capture history allows estimation of the probability of observing that capture history based on p (Karanth & Nichols 1998).

In this study, I was interested in estimating the total number of jaguars that were killed. Therefore, a jaguar was considered ‘captured’ once it was reported by an interviewee as having been killed. I also replaced sampling occasions in the columns of capture histories, by interviewees. Therefore in my adapted capture histories, if a hunted jaguar had a capture history of 00101, it means that it was not detected in the interviews with interviewees 1, 2, and 4, but was detected in the interviews with interviewees 3 and 5. Setting up the data this way allows the estimation of p much the same way that it would be done in a study designed to estimate abundance.

To estimate the parameter of interest p from the individual capture histories I used software Capture (Otis et al. 1978; Rexstad & Burnham 1991). The software calculates p under different models that reflect different assumptions for p. There are two basic steps to this process. The first step is to create a model that states the probability of the data observed based on the parameter(s) of interest (i.e., p), which is a product of the probabilities of all capture histories recorded. The second step is to select the estimate of the parameter that maximizes the likelihood function. Both steps are done by Capture.

The software calculates abundance, or in this case number of jaguars killed during hunting events, for each model and ranks them indicating the one that best suites the data set. Available methods include: Mo, no variation of p between individuals or sampling occasions; Mh, different p for each individual but constant over time (i.e.

interviewee); Mb, difference in p between captured and not-captured individuals; Mt, difference in p between sampling occasions (Karanth & Nichols 1998). Capture can also compute estimates of abundance under models that allow two sources of variation in p (Karanth & Nichols 1998). In this study I assumed that hunting events have different capture probabilities because they have different characteristics which make them more or less likely to be detected (e.g., a jaguar shot while depredating livestock near a village may have higher detectability than a jaguar shot in the forest). Therefore Mh is the most logical model to be use for estimates of the number of jaguars killed. Additionally, Otis et al. (1978) showed in simulations that when p varies by individual that Mo provides estimates of abundance that are significantly negatively biased. So even when Mo or another model was selected I also used Mh when both models were adequate for the data.

For the analysis of the data I considered each interviewee a capture occasion and each group of 48 interviewees as a survey block, with a total of three blocks. These blocks were combined to form one final matrix with all identified jaguars killed making up the rows and the combined 48 sampling occasions making up the columns (Karanth & Nichols 2002). Interviewees of the three blocks were combined so that the first interviewee (i.e., sampling occasion) in all blocks formed sampling occasion number one, the second interviewee in all blocks combined formed sampling occasion two, and so forth.

To estimate the area covered by this survey (i.e., area from which jaguars were harvested) I used the area defined by villages as their area of use within the Reserves plus a 9 km buffer around villages (Fig. 3-1, Fig 3-2). This 9 km distance is suggested to be the furthest away from a village local people will explore non-timber forest products in Amazonia (Peres & Lake 2003).

Important Assumptions for Estimation of Total Number of Jaguars Killed

Surveys that use closed population CR models must adhere to several important assumptions for the analysis to be valid. Since I adapted the CR methodology for estimating jaguar mortality from hunting using an interview survey, I adapted CR assumptions accordingly.

Assumption 1, and perhaps the most important assumption, is that I was able to accurately identify recaptures of the same individual from the information provided by interviewees. To guarantee this assumption was met I considered that a recapture occurred only when two or more events reported by different interviewees had matching information on most of the following characteristics of the hunting event: (1) species killed, (2) age class, sex, and whether the animal killed was melanistic, (3) name of hunter, (4) date (month, year, season) of event, (5) location and environment where event occurred, (6) method of hunt, motive for the hunt, activity of the hunter, and whether the meat was consumed. Additional information given by the interviewee was also used to match events. Given the relative rarity of jaguar hunting events at any one location, the local fuss created by most jaguar hunting events, and the method of matching information described above, I believe that this assumption was well met in this study.

Assumption 2 is that interviewees provided accurate information about hunting events to the best of their knowledge and did not make up jaguar hunting events that did not exist. Because hunting of jaguars is illegal in Brazil, It would be unexpected that a person would describe a jaguar hunting event that did not occur and that could the interviewee himself and/or a neighbor. The omission of information may have affect this assumption, but the error associated with the omission of information was presumably minimized by interviewing multiple individuals from the same village.

Assumption 3 was of population closure, that is, no jaguars were killed during the period used to calculate the estimates of number of jaguars hunted. Although information characterizing hunting events included dates previous to January 2009, estimating jaguar mortality from hunting using CR methodology required defining a discrete sampling period that met the above assumption of a closed population. This assumption was met by defining an 18-month period (January 2009 to mid-July 2010) that ended on the day of the first interview, which ensured that no jaguars killed during the interview period were included in the sample population.

Results

The survey was conducted over a 12-day period from the 15th to the 26th of July of 2010 and included 53 villages in Mamirauá and Amanã Reserves (Fig. 3-2). A total of 144 people were interviewed and information on 257 large cat hunting events was reported. Of these events 239 were reported as confirmed kills and 18 events that a jaguar was wounded but escaped. Events dated from the 1960s to 2010, with most of reported events occurring during 2009 for both species (Fig. 3-3). Most hunting events were reported as happening during the day (80%, n=243) (Table 3-1). Parts of dead animals (e.g., pelt, skull, teeth, claws, or fat) were collected as souvenirs, for medicinal purposes, or illegally traded in 130 events (61%, n=214).

Distribution of Hunting Events among Environments

Hunting events were reported in three types of environment: Várzea, Terra Firme, and river. Most events reported occurred in the Várzea (56%, n=247), followed by Terra

Firme, (43%) (Table 3-2). Events in which the large cat killed was in a river were rare, only being reported three times. In all three cases that a large cat was killed in a river the species hunted was a jaguar, and in the two events where sex was identified individuals killed were females. One was killed in the Japurá River and the other in the Amazon River.

Seasonality of Hunting Events

Distribution of reported jaguar hunting events throughout the year had a marked seasonal distribution, being more frequent in the first two months of the flood season (May and June; Fig. 3-4), which represented 45.6% of the total number of events where month was identified (n=79). Seasonality was also observed when events were grouped into seasons (Table 3-1; Fig. 3-5). The number of events reported in each season (i.e., observed events) was significantly different from expected under a null hypothesis of no seasonal variation ($\chi^2 = 22.52$, df = 3, $p < 0.01$). Jaguar hunting events occurred almost twice as often as expected during the flood season indicating a concentration of events during this season. On the other hand, the frequency of events was almost half of the expected during the rising season. Hunting events during drought and lowering season occurred at approximately the same frequency as expected.

Seasonality in the distribution of puma hunting events was not observed in the analysis by month, probably due to the small number of events recorded during this survey (Fig. 3-6). When grouped into seasons, the distribution of puma hunting events was similar to that of the jaguar (Fig. 3-7), with events occurring more than expected during the flood season and less than expected during the rising season. However, differences between observed and expected number of events per season was not significant ($\chi^2 = 5.78$, df = 3, p = 0.12)

Hunting Pressure on Jaguars and Pumas

Jaguars were reported hunted significantly more frequently than pumas ($\chi^2 = 60.66$, df = 1, $p < 0.01$). Of all events, 83% were related to the jaguar and only 17% to the puma (n=257). Most jaguars were killed in the Várzea (63.6%, n = 206), while pumas were killed more frequently in the Terra Firme (80.5%, n = 41). This pattern was consistent throughout all seasons, with the exception of the lowering season when jaguars and pumas were killed in approximately the same proportion in the Terra Firme and the Várzea (Fig. 3-8).

Hunting Pressure on Males and Females

Males from both species were killed more often than females, with an overall ratio of 1.7:1.0 (Table 3-1). Males and females were killed in similar proportions for both species, but the ratio of males to females killed was slightly higher for pumas, 1.9:1.0, than for jaguar, 1.7:1.0. Males were hunted more frequently than females in the Várzea and Terra Firme, but the ratio of males to females hunted was higher in the Várzea, 2.1:1.0, when compared to the Terra Firme, 1.4:1.0. This pattern was maintained when jaguar were analyzed alone, but not for pumas. Pumas where hunted in the Várzea only five times, and all individuals killed were males.

Opportunistic Versus Intentional Hunting

The majority of reported events was identified as opportunistic (57.7%, n = 234), intentional hunting events accounted for 96 events (41%), and events which occurred by accident were reported only three times. Most hunting events of both species were opportunistic, but the proportion of intentional hunts was higher for jaguars, 45.1%, than for pumas, 20.5%. Opportunistic events were more common in the Várzea, but proportions were similar between Várzea and Terra Firme.

Hunting Method

Shotguns were the most common method used to kill large cats, and were used in almost 80% of all reported hunts (Table 3-1). Shotgun events were associated with hunting dogs in 67 cases (35.1%, n = 191). The second most frequently used method was a harpoon in association with another weapon (usually a large club), which accounted for 13.6% of all kills. Although both species were killed with shotguns, only jaguars were killed with harpoons (Table 3-1). Harpoons are used by local people to fish and consist of a wood or bamboo spear with a metal tip that is attached to the spear by a fine rope, and that comes off once the harpoon hits its target but remaining attached to the spear by the rope. When people harpoon a jaguar, they usually throw one or more harpoons at the jaguar (which is usually in the water) and tie the spear to a tree, reducing the jaguar's mobility. They then hit the animal in the head with a long stick or other weapon.

Shotguns were the most common weapon used to kill large cats in the Várzea and Terra Firme, but harpoons were rarely used in the Terra Firme. Shotgun traps and other methods (e.g., callback) were also rarely used.

Motive of Hunt

The main reported motive for hunting large cats in the Várzea and the Terra Firme was depredation of livestock, which was reported for 120 events (47.1%)(Table 3-1). Of these events, the most frequently predated species of livestock was the pig, 62 events (57.7%), followed by cattle, 21 events (17.5%), chicken, 14 events (11.7%), dog, 13 events (10.8%), sheep, 8 events (6.7%), duck, 5 events (4.2%), and buffalo, 2 events

(1.7%). The second most frequent answer to the motivation of hunts was ‘not identified’, which was reported for 111 times (43.5%). This category of answer encompasses cases in which the hunter had no apparent reason for hunting the animal, but also cases where the interviewee did not know or did not want to say the motive of the hunt. Unfortunately, these two cases cannot be separated. Other motives reported were attacks on humans, commerce (i.e., illegal trade of meat or body parts), and others (e.g., medicinal purposes).

Depredation was the most frequent motive for hunting jaguars and pumas. Most frequently depredated livestock species, however, differed between jaguars and pumas. Jaguars depredated on pigs in 58% (n=100) of cases, followed by cattle, 18%, while pumas were divided between chicken, 35.7%, sheep, 28.6%, and pigs, 28.6% (N=14).

Activity of the Hunter

The most frequent activity of the hunter at the time of the hunt was hunting large cats, reported in 87 cases (39.5%, n=220), followed by subsistence hunting of other animals, 56 cases (25.5%), fishing, 45 cases (20.5%), and other activities (e.g. traveling, herding, resting at home), 32 cases (14.5%). Hunting large cats was the most frequent activity of hunters in both environments, followed by subsistence hunting in the Terra Firme and fishing in the Várzea. Hunter activity differed between events relating to jaguars and pumas. While in most jaguar related cases hunters where out specifically to hunt jaguars (43.8%), in puma hunts in most cases hunters where hunting other species for subsistence when the event occurred (60%).

Consumption of Meat

The meat of large cats killed was consumed and/or sold for consumption in 96 cases (43.05%, N=223). Consumption of large cat meat was reported in a relatively high proportion of cases for both species, but jaguar meat was consumed more often than puma meat (44.3% and 37.5%, respectively). Given that people don't like to mention that they eat this kind of meat, it is likely that meat of large cats is actually consumed more than reported.

Estimates of Total Number of Jaguars Killed

To estimate the number of jaguars killed, I used data from January 1st 2009 to July 14th 2010 to guarantee population closure and more accurate estimates, since detection rates were expected to decrease with time. When I analyzed that for this whole period, 18.5 months, model Mh, where capture probabilities are heterogeneous between jaguars killed, was selected by Capture as the best model for the data. The statistical test in program Capture confirmed population closure (z=-1.144, P=0.126) and the estimated number of jaguars killed was 108 (SE=16.85; p-hat = 0.021), with a 95% confidence interval of between 86 and 154 individuals (Table 3-3). In the analysis of year 2009 only, model Mh was also selected and population closure was also confirmed (z=-0.217, P=0.414). The number of jaguars estimated to have been killed in 2009 was 73 (SE=15.55, p-hat=0.018), with a 95% confidence interval of between 54 and 118 individuals (Table 3-3). In the analysis of the portion of 2010 that was surveyed, model Mo was selected by Capture. However, given the characteristics of hunting events Mh is a more appropriate model for the data of this study because hunting events have different capture probabilities depending on their characteristics. This was also a reasonable step given that the model criteria should only a small difference in AIC between these two models. For data from 2010 Capture indicated lack of population closure (z=-1.875, P=0.030). The number of jaguars estimated to have been killed in 2010 was 29 and 33, with Mo and Mh respectively (SE=3.28 and 5.03, p-hat = 0.035), with a 95% confidence interval of between 25 and 38 individuals for Mo and between 27 and 48 for Mh (Table 3-3).

The minimum number of jaguars killed in 2009 and 2010 was respectively 38 and 24, and the minimum number for the period was 62 animals (Table 3-3). These represent 52.1%, 72.1%, and 57.1%, of the total number of jaguars killed estimated using CR models.

Discussion

Amazonia is recognized as the most important biome for the long-term conservation of Neotropical felids (Oliveira 1994) due to its large area, connectivity, preservation status, low human density, and proportion of area inside reserves. These attributes help maintain wild cat populations, but do not impede hunting, especially in the Várzea (e.g., Mamirauá Reserve) and it’s bordering Terra Firme forests (e.g., Amanã Reserve), where most of the human population of Amazonia is concentrated (Goulding et al. 1996).

Both jaguars and pumas are frequently hunted by local people in the Várzea floodplain forests and neighboring Terra Firme forests of central Brazilian Amazonia. However, hunting pressure on the jaguar is of particular concern since the hunting events involving the jaguar represented 82.8% of all events reported, 4.8 times more than pumas. This finding is corroborated by the data from the community-based Fauna Use Monitoring System of Mamirauá Sustainable Development Institute, which found similar results for the same period and the same area (J. Valsecchi, unpublished data). This large difference in the number of jaguars versus pumas killed by local people, however, does not necessarily indicate preference, or higher dislike, of hunters for jaguars but is most likely a result of the larger abundance of jaguars in the floodplain and its transition zone with the neighboring Terra Firme (Chapter 2), and consequently a higher encounter rate of jaguars and people, higher frequency of conflicting interactions, hence larger number of jaguars killed. The higher encounter rate can be exemplified by the camera trap surveys conducted in Mamirauá Reserve, which have recorded over 100 pictures of jaguars in the last six years, but only one of puma (Emiliano Ramalho, unpublished data). At the same time, the only preference that was mentioned by interviewees was that puma meat tasted better than that of jaguars, so that if there was preference it would be to hunt pumas. This higher abundance of jaguars in the floodplain is also corroborated by other studies which have reported that jaguars tend to exclude or reduce abundance of pumas in area closer to water bodies (Crawshaw & Quigley 1991). In summary, jaguars are hunted more frequently because they are in conflict with people more frequently.

Jaguar hunting events were markedly seasonal, not only when observed by the number of events per month, but also when comparing number of events per season, corroborating hypothesis 1. The seasonality of hunting events observed, with most hunting events occurring during the flood season, may be explained by the large variation of the water level in the region due to the flood pulse regime of the Amazon River and its tributaries, which causes the flooding of large extents of forest including virtually the whole area of Mamirauá Reserve. Flooding reduces the terrestrial habitat and forces the lateral migration of terrestrial animals to higher ground (Junk 1989). Flooding also causes a natural seasonal variation in prey availability because spectacled caiman (*Caiman crocodiles*) are scattered in the growing aquatic habitat, eggs of black caiman (*Melanosuchus niger*) spectacled caiman are not available, and access to other important prey, such as the sloth, becomes limited because area for foraging is restricted by flooding. This may force at least a portion of the jaguar population to migrate from the Várzea to the Terra Firme in search of dry ground and prey. This lateral migration also causes them to cross paths with people and their livestock. This finding has great importance in directing future conservation actions in Amazonia and optimizing resource allocation, since optimal efforts to reduce conflict, hence number of jaguars killed, should be focused in the flood season when most jaguars are killed.

The higher frequency of males killed is most likely the result of higher encounter rates between jaguars and people. Males are expected to move larger distances than females throughout the year and this may include lateral migration from the Várzea to the Terra Firme during flooding. This would also be consistent with sexual segregation theory, which predicts that males in polygynous species use areas during non-breeding periods where they can maximize body condition in preparation to compete for mates, whereas females select areas that maximize offspring security (Main et al. 1996, Main 2008). Female jaguars have been documented raising offspring in the Várzea (Chapter 2), and have been documented to remain in the Várzea during flooding (E. Ramalho, unpublished data), which likely restricts their movement patterns during flooding and reduces encounter rates with people.

Hunts were opportunistic in almost 60% of cases, which indicates that most hunting events were not directly related to a depredation event but rather were carried out as a preventive measure against depredation of livestock, attacks on people, for food, and/or status. On the other hand, the main motivation for killing large cats was depredation of livestock. Pigs, cattle, chicken and dogs being the most often predated livestock species. Poor management of livestock is common in Amazonia, and improving management of at least pigs and cattle could have a significant impact on the number of jaguars killed. Although none of the interviewees identified subsistence hunting as a motivation for hunting large cats, the meat of kills was consumed in over 40% of reported events. This contradicts other studies which have indicated that jaguars and pumas are rarely killed by subsistence hunters (Yanez et al. 1986, Cunningham et al. 1995, Hoogesteijn et al. 1996, Novack et al. 2005). It also indicates that large cat meat is considered by many local people as an opportunistic source of protein.

The estimate of total number of jaguars killed from January 2009 to mid-July 2010 (n = 108, 95% CI: 86-154) raises questions about the effectiveness of current conservation measures in protecting large cats in Brazilian Amazonia. The first issue worth noting is the fact that all hunting events were recorded inside two of Brazil's most well guarded Amazonian protected areas, Mamirauá and Amanã SDRs. Under the co-management of Mamirauá Sustainable Development Institute and the Amazonas State Government, these Reserves have one of the largest law enforcement budgets and logistical support of any protected area in Amazonia. Mamirauá Institute has also implemented various capacity building and environmental education actions with the local people during the last 15 years since the creation of the Reserves, and local people have had the chance to interact with researchers and participate in research. It is therefore clear that sustainable use protected areas, under current models of management, are not effective at preventing the hunting of jaguars.

On perhaps more positive notes, females were killed less frequently than males, and the density of jaguars in the Várzea portion of the study area has been maintained in the last five years, despite the heavy hunting pressure. Hunting may be shifting the male to female ratio in the Várzea, which is relatively low in Mamirauá, 0.79:1.0 (Chapter 2), but does not seem to be influencing population size. This may be explained by the compensatory mortality theory which predicts that the more frequent harvest of adult males, which comprised more than 60% of all hunting events recorded in this study, will reduce intra-specific competition and trigger positive density-dependent responses in reproduction and survival of offspring and females (Connell 1978).

Although SDRs have the goal of maintaining wildlife populations, they were not designed to reduce hunting of jaguars, and consequently are not effective for that goal. Other mechanisms have been put in place for that purpose. The national ban on hunting of jaguars in Brazil is a coercive measure; it prohibits people from hunting jaguars because the Federal government believes it is important to conserve jaguar populations. This measure was effective at reducing commercial hunting of jaguars because it was associated with another coercive measure, the international ban on trade of jaguar parts. Commercial hunting of jaguars was thus effectively controlled in Brazil, not only because it became nationally illegal, but also because market demand was drastically reduced, hence economic motivation for hunters to pursue jaguars was also reduced. However, as shown by the large number of jaguars killed in two well protected Reserves, these measures have little effect on the current motivations for killing jaguars in the Brazilian portion of Amazonia.

The national ban on hunting of wildlife in Brazil since 1967, and the inclusion of the jaguar in Appendix 1 of CITES in 1973 are also ineffective towards contemporary hunting of jaguars in Amazonia. Although they have had an important role in stopping commercial hunting and trade (Smith 1976) in the past, and are still effective today, they are inadequate against current hunting of jaguars, simply because the main motivations for hunting these large cats have changed. When these two conservation actions were created and implemented, the main motivation for killing jaguars was commercial, meaning that people went out of their way and actively searched for jaguars to kill and make a profit. Today, the main motivations for killing jaguars in Amazonia are the economic loss imposed on local people by livestock depredations. Also, fear of jaguars, which are culturally portrayed as dangerous, treacherous and powerful animals, may also play a role as suggested by large number of opportunistic hunting events that had no clear motivation. Other conservation actions, such as payment of local people by the Amazonas State Government for environmental services (e.g., Bolsa Floresta), which started in September of 2007, also have little chance to affect hunting since there is no accountability from local people on their performance in conservation, including whether they killed jaguars or not.

Of even greater concern should be the possibility of increased hunting pressure on jaguar populations associated with the proposed changes in the forest code of Brazil, which are currently being voted in congress and may reduce the amount of protected areas in Amazonia considerably, which itself is a threat to large carnivores. Most hunting of jaguars today seems to occur in the Várzea floodplain forests and neighboring Terra Firme forests, where most of the human population of Amazonia is concentrated. And the only reason that hunting pressure has not caused the extinction of jaguars in these areas seems to be the input of individuals from the continuous inhabited Terra Firme forests, and probably increased survival of females due to their ecology. If roads are built and affect these sources and if prey in the Várzea decreases and influences females' behavior this may have catastrophic impacts in the jaguar populations of Amazonia.

Conclusions

The use of CR models to estimate total number of animals killed is a promising method to obtain estimates of mortality from hunting on endangered charismatic species like jaguars and pumas. Careful attention should be taken, however, in guaranteeing that assumptions are met, especially in the identification and matching of hunting events reported by different interviewees. Using such models provide an objective and robust method for estimating the extent of mortality from hunting and identifying the need for conservation strategies to address such losses.

It is clear to me that jaguars and pumas are ineffectively protected from hunting in Brazilian Amazonia, despite protected areas, the national ban on hunting, the international ban on trade, environmental education, and payment for ecosystem services. New conservation measures that take into account the current motives for killing jaguars and pumas must be designed and implemented if hunting pressure on these large cats is to be reduced along the Amazon River floodplain forests and neighboring Terra Firme. In doing so, it is imperative that the human values of stakeholders involved, especially those that interact with jaguars and pumas directly (i.e., local people), be taken into consideration and that all stakeholder groups participate as wholly as possible in the conservation process (Chapter 1). Their participation and consideration of how this conservation process influences their human values is indispensable to the success of new conservation actions.

Table 3-1. Characterization of all reported hunting events, and by species

	All events		*P. onca*		*P. concolor*	
	N	%	N	%	N	%
Total	256		212	82.8	44	17.2
Environment	247		206		41	
Várzea	139	56.3	131	63.6	8	19.5
Terra Firme	105	42.5	72	35.0	33	80.5
River	3	1.2	3	1.5	-	-
Season	225		187		38	
Drought	52	23.1	42	22.5	10	26.3
Rising	51	22.7	44	23.5	7	18.4
Flood	102	45.3	88	47.1	14	36.8
Lowering	20	8.9	13	7.0	7	18.4
Sex	190		159		31	
Male	119	62.6	99	61.1	20	64.5
Female	71	37.4	60	37.0	11	35.5
Male:Female ratio	1.7		1.7		1.8	
Method of hunt	241		200		41	
shotgun	124	51.5	100	50.0	24	58.5
shotgun and dogs	66	27.4	52	26.0	14	34.1
harpoon	33	13.7	33	16.5	0	0.0
shotgun trap	9	3.7	9	4.5	0	0.0
bush knife	5	2.1	4	2.0	1	2.4
other	4	1.7	2	1.0	2	4.9
Type of hunt	233		195		38	
opportunistic	134	57.5	106	54.4	28	73.7
intentional	96	41.2	88	45.1	8	21.1
accidental	3	1.3	1	0.5	2	5.3
Motive of hunt	254		211		43	
depredation	120	47.2	104	49.3	16	37.2
attack on human	13	5.1	10	4.7	3	7.0
commerce	8	3.1	8	3.8	-	0.0
other	3	1.2	3	1.4	-	0.0
not identified	110	43.3	86	40.8	24	55.8
Activity of hunter	219		185		34	
hunting large cats	87	39.7	81	43.8	6	17.6
subsistence hunting	55	25.1	35	18.9	20	58.8
fishing	45	20.5	41	22.2	4	11.8
other	32	14.6	28	15.1	4	11.8

Table 3-1. Continued

	All events		*P. onca*		*P. concolor*	
	N	%	N	%	N	%
Meat consumed	222		183		39	
yes	96	43.2	81	44.3	15	38.5
no	126	56.8	102	55.7	24	61.5

Table 3-2. Characteristics of hunting events by environment type

	Várzea		Terra Firme		River	
	N	%	N	%	N	%
	139	56.3	105	42.5	3	1.2
Species	139		105		3	
P. onca	131	94.2	72	68.6	3	100.0
P. concolor	8	5.8	33	31.4	-	-
Season	131		87		3	
Drought	27	20.6	22	25.3	2	66.7
Rising	30	22.9	19	21.8	-	-
Flood	64	48.9	36	41.4	1	33.3
Lowering	10	7.6	10	11.5	-	-
Sex	105		73		2	
Male	71	67.6	42	57.5	-	-
Female	34	32.4	31	42.5	2	100.0
Male:Female ratio	2.1		1.4		-	-
Species*Sex						
	100		49		2	
P. onca - male	66	66.0	28	57.1	-	-
P. onca - female	34	34.0	21	42.9	2	100.0
	1.9		1.3		-	
	5		24		-	
P. concolor - male	5	100.0	14	58.3	-	-
P. concolor - female	-	-	10	41.7	-	-
	-		1		-	
Method of hunt	130		101		3	
shotgun	70	53.8	52	51.5	-	-
shotgun and dogs	26	20.0	37	36.6	-	-
harpoon	25	19.2	3	3.0	3	100.0
shotgun trap	4	3.1	5	5.0	-	-
bush knife	3	2.3	2	2.0	-	-
other	2	1.5	2	2.0	-	-
Type of hunt	129		94		3	
opportunistic	78	60.5	49	52.1	3	100.0
intentional	49	38.0	44	46.8	-	-
accidental	2	1.6	1	1.1	-	-

Table 3-2. Continued

	Várzea		Terra Firme		River	
	N	%	N	%	N	%
Motive of hunt	138		104		3	
depredation	60	43.5	55	52.9	-	-
attack on human	7	5.1	6	5.8	-	-
commerce	7	5.1	-	-	-	-
other	3	2.2	-	-	-	-
not identified	61	44.2	43	41.3	3	100.0
Activity of hunter	122		86		2	
hunting large cats	46	37.7	37	43.0	-	-
subsistence hunting	26	21.3	27	31.4	-	-
fishing	33	27.0	8	9.3	2	100.0
other	17	13.9	14	16.3	-	-
Meat consumed	121		95		1	
yes	67	55.4	28	29.5	1	100.0
no	54	44.6	67	70.5	-	-

Table 3-3. Results from Capture analysis for the estimation of total number of jaguars killed. Minimum number of animals killed, total number of captures, number of sampling occasions, best model selected by Capture, detection rates (p-hat), estimated total number of jaguars killed, standard error of estimate (SE), 95% confidence interval (95% CI), and closure test

Period	Animals captured (minimum number of jaguars killed)	Total number of captures	Sampling occasions	Model selected	p-hat	Estimated number of jaguars killed	SE	95% CI	Closure test	
									z-value	p-value
2009	38	63	48	M_h	0.018	73	15.55	54-118	-0.217	0.414
2010	24	48	48	M_o & M_h	0.035	29/33	3.28/5.03	25-38/27-48	-1.875	0.030
2009-2010	62	111	48	M_h	0.021	108	16.85	86-154	-1.144	0.126

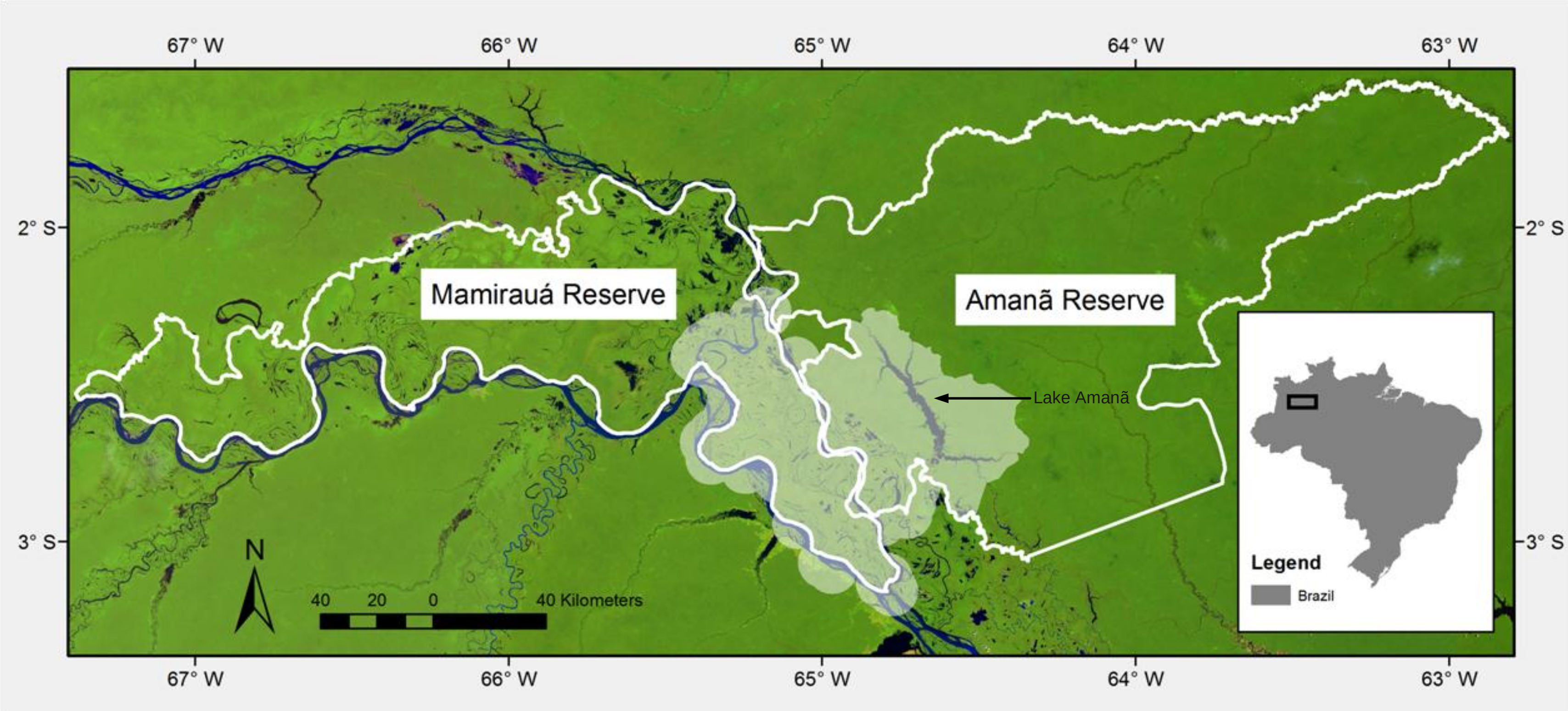

Figure 3-1. Smaller map shows location of the study area within Brazil. Larger map shows the limits of Mamirauá and Amanã Sustainable Development Reserves (white lines) and the area covered during the hunting survey (white shaded area)

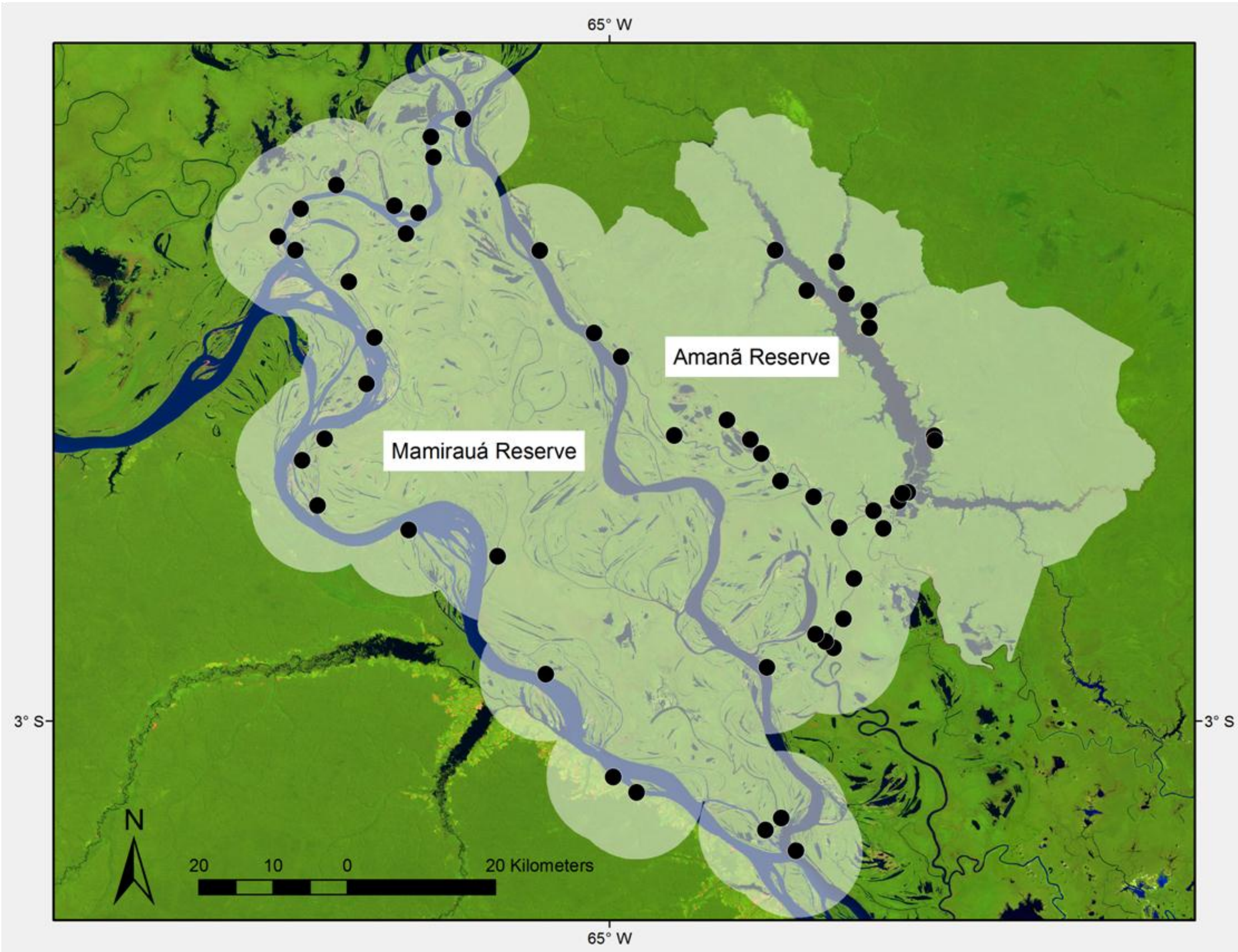

Figure 3-2. Area surveyed in Mamirauá and Amanã Reserves (white shaded area) and villages visited during survey (black circles)

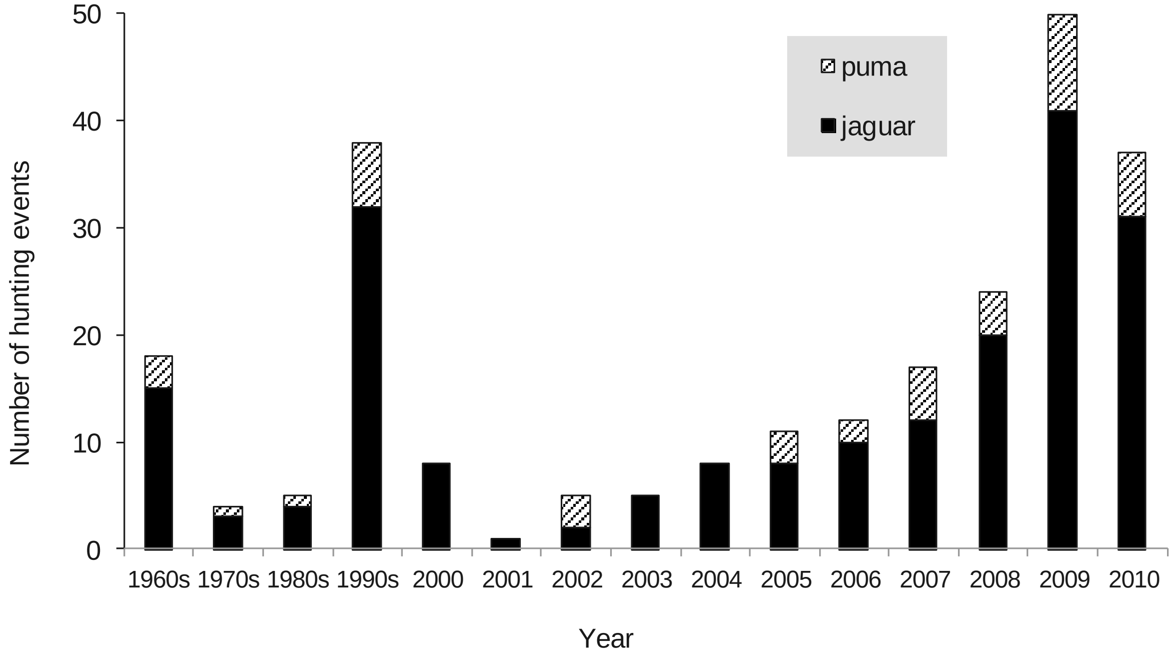

Figure 3-3. Number of large cat hunting events reported per decade until the 1990s, and per year between 2000 and 2010 (n=179)

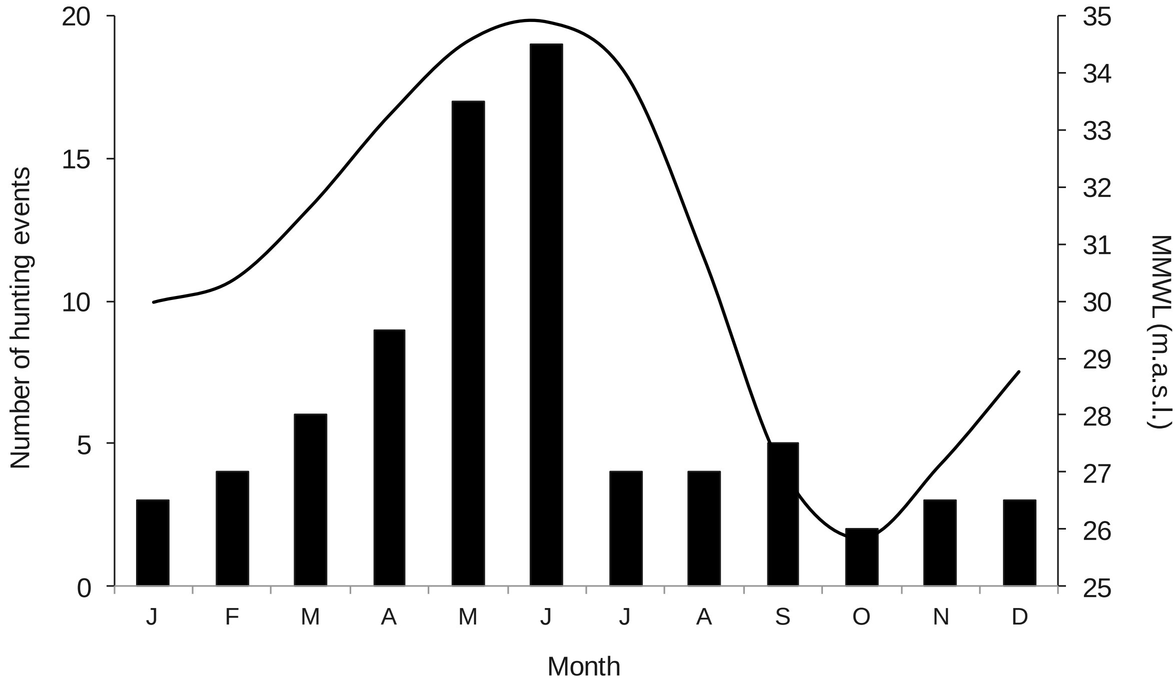

Figure 3-4. Number of jaguar hunting events reported per month (n=79) (designated by bars), and mean monthly water level (MMWL, designated by line) in the study area from 1990-2008 (data from Ramalho et al. 2009)

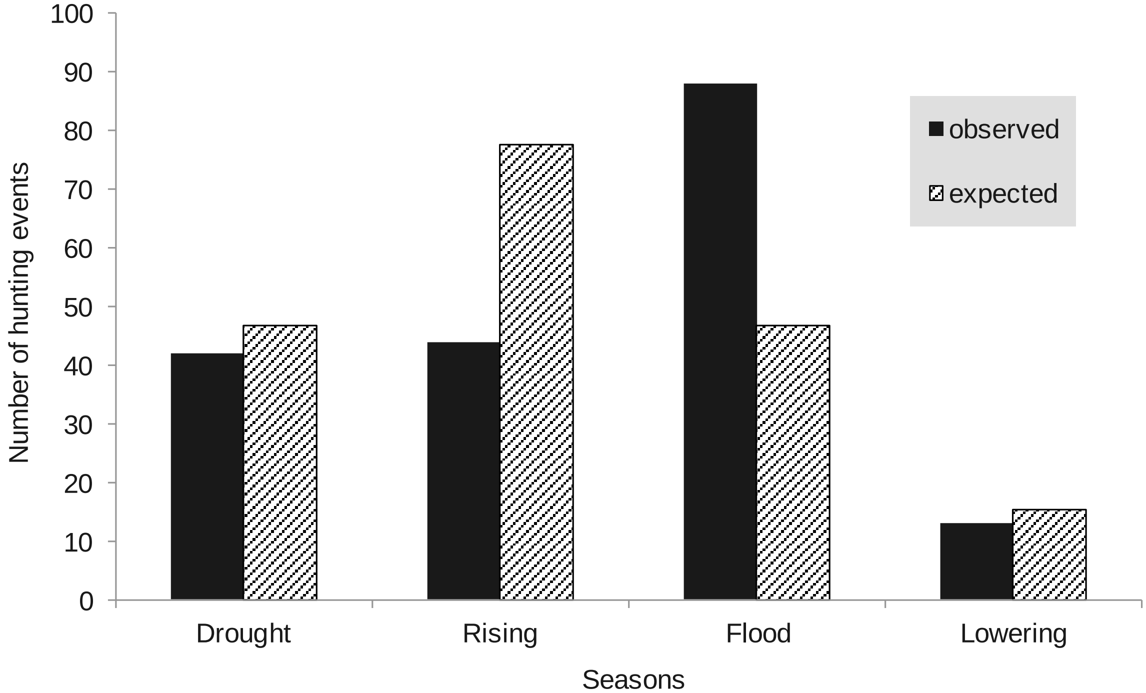

Figure 3-5. Number of jaguar hunting events observed and expected per season (n=187)

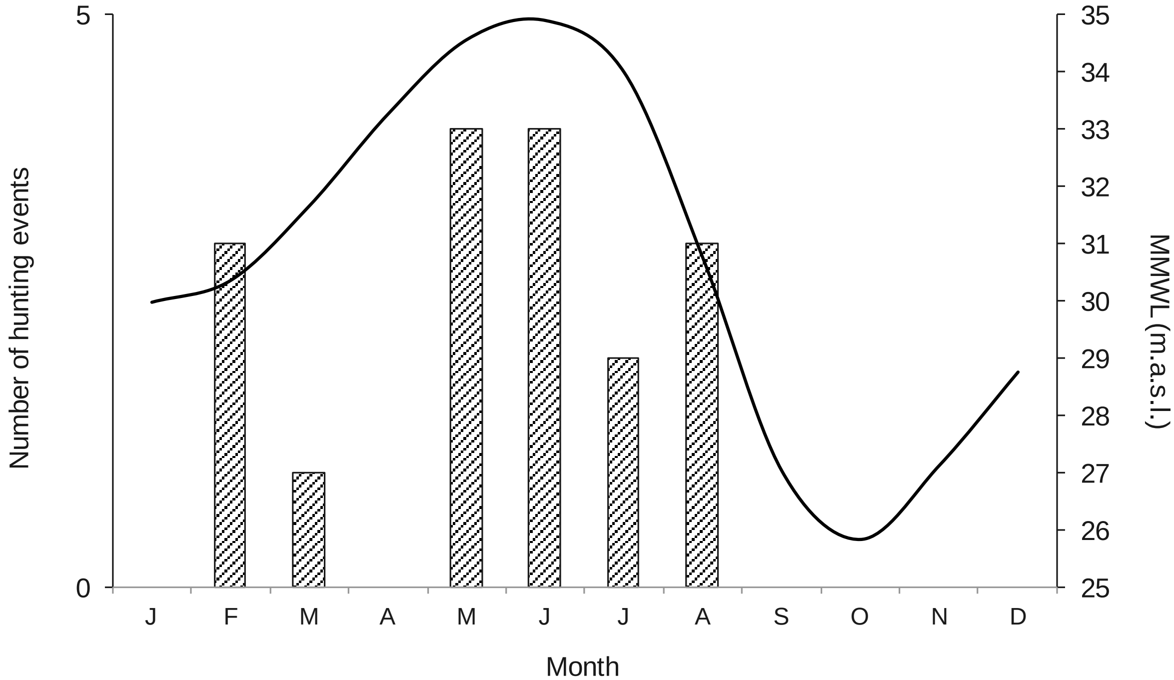

Figure 3-6. Number of puma hunting events reported per month (n=17) (designated by bars), and mean monthly water level (MMWL, designated by line) in the study area from 1990-2008 (data from Ramalho et al. 2009)

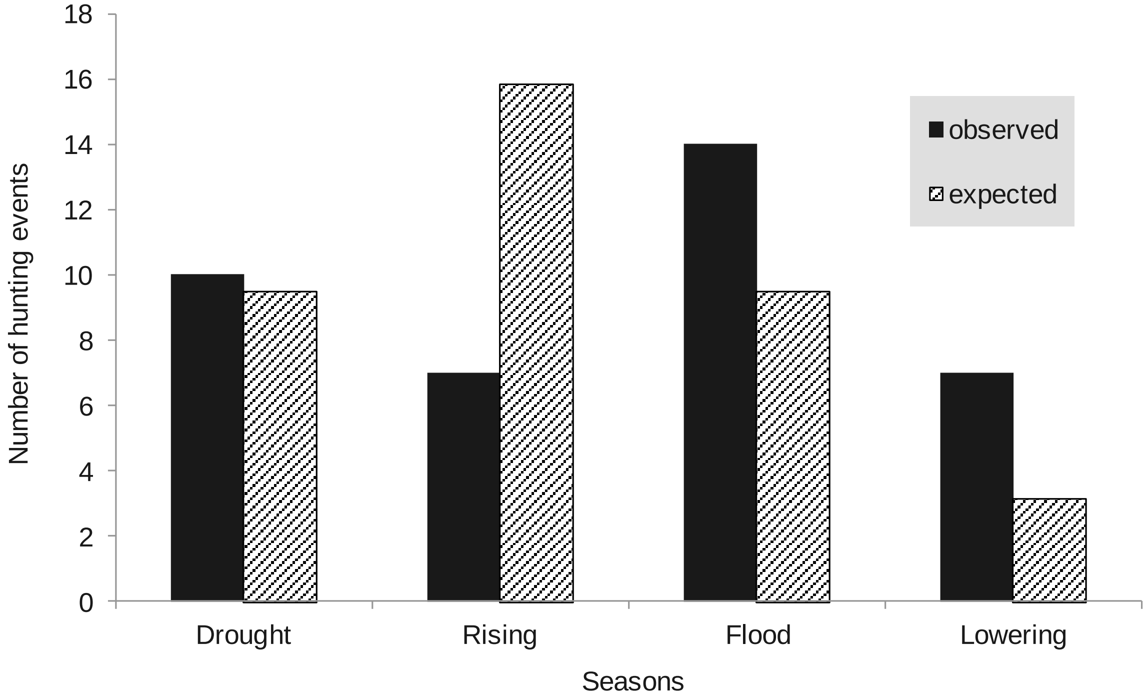

Figure 3-7. Number of puma hunting events observed and expected per season (n=38)

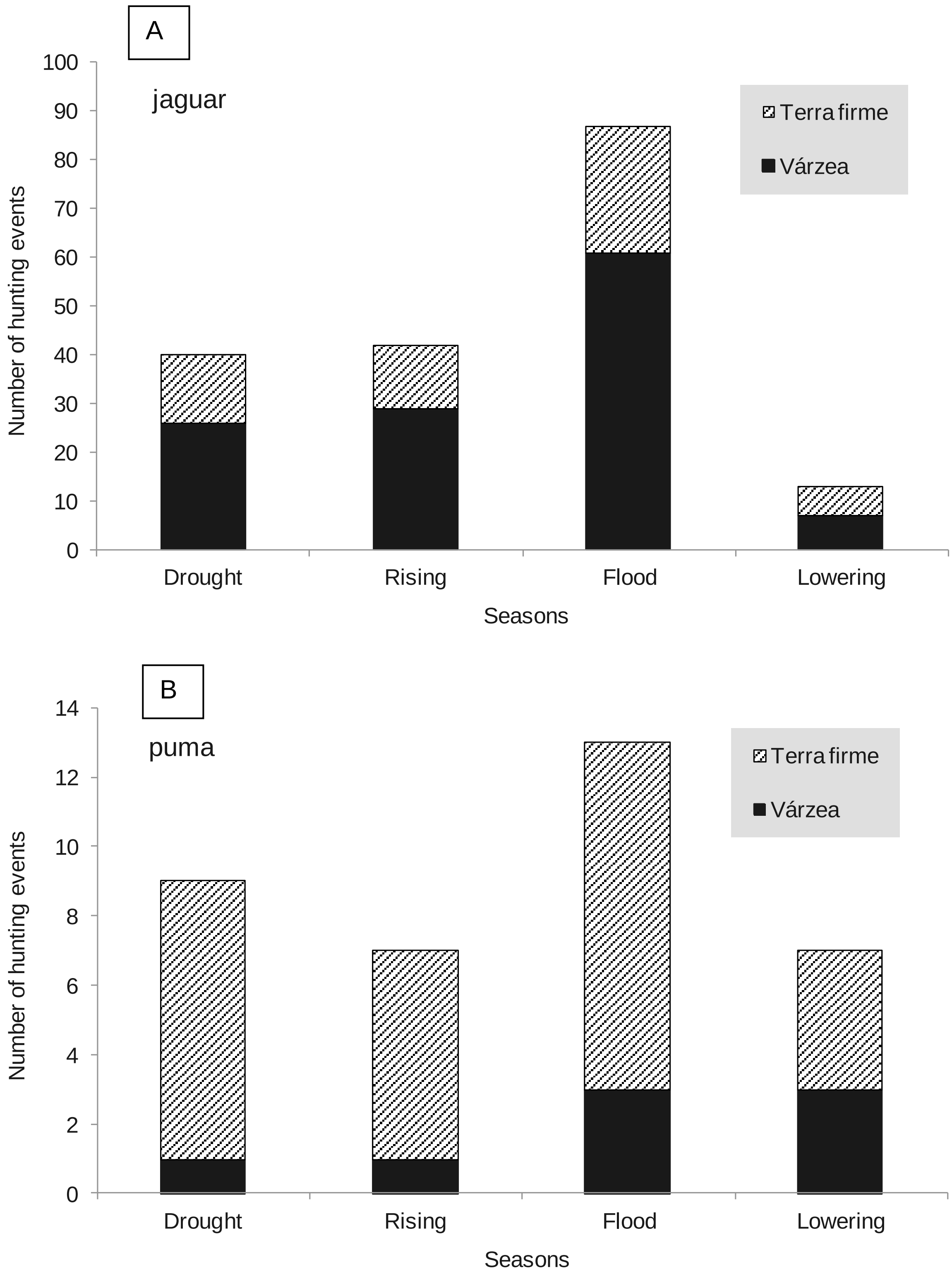

Figure 3-8. Number of hunting events recorded per season of the year and environment type for jaguars (A) and puma (B) (n=182 and 37, respectively)

CHAPTER 4
THE IMPORTANCE OF CAIMANS AND ARBOREAL MAMMALS IN THE DIET OF THE JAGUAR (*PANTHERA ONCA*) IN THE VÁRZEA FLOODPLAIN FORESTS OF AMAZONIA.

Felids are exclusively carnivorous animals, and, as such, their survival, and a large portion of their ecology and behavior, depends on the prey species they consume. In turn, felid population size and density, population structure, and social behavior are largely determined by prey abundance and biomass (Pierce et al., 2000; Carbone & Gittleman 2002; Karanth et al. 2004). Therefore, information about diet is fundamental to understanding the ecology and behavior of felids in a specific habitat and should form the basis for the development of sound conservation actions.

Jaguar (Panthera onca) feeding habits have been investigated in various regions throughout the jaguar's distribution. In Brazil, jaguar feeding habits were described in the Atlantic Forest (Crawshaw 1995; Facure & Giaretta 1996; Leite 2000; Garla et al. 2001; Crawshaw et al. 2003), in the Cerrado (Silveira 2004), in the Pantanal (Schaller & Vasconcelos 1978; Dalponte 2002), and in the Caatinga (Olmos 1993). Feeding habits of the jaguar were also described in sub-humid forests (Aranda & Sánchez-Cordero 1996; Aranda 1993, 1994) and in dry deciduous forests (Nuñez et al. 2000) in Mexico, in the Peruvian Amazon (Emmons 1987), in the Llanos of Venezuela (Polisar et al. 2003; Scognamillo 2003), in Paraguayan Chacos (Taber et al. 1997), in humid subtropical forests in Belize (Rabinowitz & Nottingham 1986) and Costa Rica (Chinchilla 1997), and in low tropical forests in Guatemala (Novack et al. 2005). These studies have shown that the jaguar is an opportunistic predator, consuming prey in the proportion of their availability (Rabinowitz & Nottingham 1986; Emmons 1987). They have also shown that the jaguar has great ecological adaptability (Rabinowitz &

Nottingham 1986), consuming over 85 different species of prey (Seymour, 1989). Despite this large number of prey reported as being consumed by jaguars, studies conducted to date show that terrestrial mammals of large and medium size are the most frequently consumed prey species in most environments (Oliveira 2002), although other mammals, reptiles and birds may also be important items of the jaguar diet (Emmons 1987; Ramalho 2006; Da Silveira et al. 2010). Despite the large number of diet studies that have been conducted, there is a lack of information regarding diets of jaguars in Amazonia, where jaguar feeding habits are largely unknown (Fig. 4-1).

The Várzea Floodplain Forests (hereafter, Várzea) of Amazonia are an area of high density of jaguars (Ramalho 2012 – Chapter 2), which suggests abundant prey populations. The Várzea, however, is a seasonally flooded environment, where only animals that are arboreal and/or have good swimming capacity are able to survive (Ayres 1993). The flooding dynamics makes Mamirauá Reserve, which is a protected Várzea Floodplain Forest site in Amazonia, an unlikely home to terrestrial mammals. In two years of transect surveys conducted in the Reserve, terrestrial mammals were observed only once (Santos 1996), and in five years of camera trap surveys, with the notable exception of jaguars, terrestrial mammals were never observed (E. Ramalho, unpublished data). Consequently, the most commonly reported prey species of the jaguar are not available in Mamirauá Reserve and the objective of this study was to describe the jaguar's feeding habits in Mamirauá Reserve.

Methods

Study Area

Mamirauá Sustainable Development Reserve (hereafter, Mamirauá Reserve), is located in the western portion of Brazilian Amazonia, approximately 30 km northwest from the city of Tefé, in Amazonas state (1°49’-3°09’S, 64°45’-67°23’W)(Figure 4-2). The Reserve is delimited by the Japurá and Amazon Rivers, and the Auati-paranã channel, and encompasses an area of 11,240 km² of Várzea forests (6.25% of the total area of the Várzea ecosystem in Amazonia). It is the largest protected area exclusively dedicated to protecting this type of environment. The climate in the region is tropical humid with average annual precipitation of 2,373 mm (Ayres 1993). This study was conducted in a 566 km² area in the Southern part of the Reserve, around Lake Mamirauá (Figure 4-2). For a more detailed description of the study area see Ramalho (2012 – Chapter 2).

Collection and Analysis of Scats

Scats and carcasses of prey were collected opportunistically along the margins of lakes and trails during the low water season which occurs between September-December (Ramalho et al. 2009). Jaguar scats were identified by size and width and tracks found near the place where the sample was collected. Scats of adult jaguars are generally larger than 19 mm in width (Farrel et al. 2000). I was confident that these scats were from jaguars and not from pumas (*Puma concolor*) because during this period I recorded jaguars ~100 times using camera traps and food snares (Ramalho 2012 – Chapter 2), but never recorded pumas. Carcasses of prey found were identified to species in the field or brought back to Mamirauá Institute for identification when necessary. Identification of remains was conducted using the same procedure described below for scats. For caiman (i.e., *Melanosuchus niger* or *Caiman crocodilus*), total length of animal was measure when possible or estimated from the size of the head.

All scats were dried in the sun, stored in hermetical containers and frozen until analysis. For the analysis of content, scats were sifted in running water and then dried. Fur, bones, nails, scales, feathers and other undigested remains were separated and analyzed macroscopically, with magnifying lenses and a microscope when necessary. Identification was done through comparison with a reference fauna collection from Mamirauá Reserve. Caiman and other reptile scales were identified to species by a group of herpetologists from the Federal University of Amazonas with extensive experience in Amazonian reptiles, or when identification was not possible, categorized as unidentified caiman species.

To determine the importance of each prey species in the diet of the jaguar, I calculated several parameters. The frequency (F) that each prey species was identified in scats was calculated by dividing the number of scats a prey species was identified by the total number of scats collected. To facilitate comparison with other studies, I also calculated percent occurrence (Po) for each prey species by dividing the number of individuals of each prey species observed in the sample of scats (n) by the total number of individuals of all species found in the sample (T), multiplied by 100 ($Po = n/T \times 100$) (Ackerman et al., 1984). To estimate the biomass contributed to jaguar diet be each prey species indentified in scats, I obtained average weights of all prey species and used a correction factor developed by Ackerman et al. (1984), represented by the linear relation $Y = 1.98 + 0.035X$ (where Y = biomass of the prey species consumed, and X = biomass of the prey in kilograms). I did not use this correction factor for prey species with average body weights of <2 kg because I assumed that the occurrence of these small species in a scat represented a whole individual (Ackermann et al. 1984). The relative biomass of each prey species consumed was then calculated using equation 4.1, where i = prey species 1, 2, 3,…i.

$$\text{Relative Biomass of species X} = \frac{P_o \text{ of prey species X} \times \text{Bio of prey species X consumed per scat}}{\sum\left(P_{oi} \times \text{Bio}_i\right)} \quad \text{(Equation 4-1)}$$

Results

A total of 78 jaguar scats were collected in Mamirauá Reserve between 2004 and 2010. From these scats a total of 142 individual prey, belonging to 10 species and several combined species categories from classes Mammalia, Reptilia, and Aves (Table 4-1). Evidence of plant and invertebrate (*Pomacea* spp.) were also documented. An average of 1.68 prey species was observed per scat. Mammals were the most frequently consumed prey class representing 55% of all prey items observed, and also contributed the most to the total biomass consumed, 52.1% (Table 4-1). All identified species of mammals consumed were arboreal, with the exception of one instance of domestic cattle (*Bos taurus*). Reptiles were also important representing 42.1% of all prey items observed and 47.2% of the biomass. These two classes alone represented ~97% of all prey items and >99% of the total biomass.

The two species of prey most frequently consumed were the brown-throated three-toed sloth (*Bradypus variegatus*), present in 53% of samples, and the spectacled caiman (*Caiman crocodilus*), present in 41% (Table 4-1). These two species represented 30% and 24% of all items and 33% and 31.7% of the total biomass, respectively. It is important to note, however, that 13 caiman samples could not be identified to species, but given the ratio of spectacled caiman consumed by jaguars in comparison to black caiman (32:1), it is likely that these unidentified caiman were spectacled caiman. If this was the case, spectacled caiman would be the most frequently consumed prey (34%) and also represent the largest part of the biomass (44.6%) consumed by jaguars in Mamirauá Reserve. The lesser tamandua (*Tamandua tetradactyla*) and the red howler monkey were also found relatively frequently, and represented 8% and 7% of all prey items respectively.

Birds were present in only four samples and were insignificant diet components. Remains of freshwater snails from the genus Pomacea were found in four samples and vegetable matter in two. We believe that the presence of snails in scats is associated with the consumption of caiman and other reptiles which may eat snails. Consumption of vegetable matter, often grass, is a common behavior in felids and is thought to help the digestive system and elimination of feces. Vegetable matter could also have been ingested by prey and appear in the sample because of that, rather than the jaguar intentionally eating it.

Carcasses were also used in identifying prey of jaguars. All carcasses found were from the same species identified in scats and included 5 spectacled caiman, 5 black caiman, and 2 brown-throated three-toed sloths. Caiman carcasses were easily identified because the hard armor and head of caiman were not consumed. All carcasses of spectacled caimans were adult individuals with an average total length of 1.4 m. Carcasses of black caimans included one juvenile and one adult individual, with total lengths of 1.5 and 3 m, respectively. Both black caiman carcasses were found on the same day and were 5 m apart. Both black caiman carcasses were fresh when discovered, and the signs of struggle in the flooded grass a few meters from where the carcasses were found suggests these prey were killed and not eaten as carrion.

Carcasses of the lesser tamandua and of red howler monkeys were not found, probably because jaguars consume the whole animal. In the case of sloths, the carcass can be identified from their claws, which are not consumed.

Discussion

The diet of the jaguar in Mamirauá Reserve is almost entirely composed of reptiles and arboreal mammals, which represented >95% of all prey items consumed. The diet of the jaguar in Mamirauá is largely dependent on four species of prey: the brown-throated three-toed sloth, the spectacled caiman, the lesser tamandua, and the red howler monkey. Although all of these species have been reported in jaguar diets in other environments, they usually represent a small percentage of prey consumed. Arboreal mammals and reptiles together have never been reported to represent more than 32.5% of prey items, and, although reptiles are usually more important in jaguar diets in flooded environments, rarely in other environments do reptiles contribute to more than 10% of the jaguar's diet (Da Silveira et al. 2010). Consequently, jaguar diets in the Amazonian Várzea differ radically from diets of jaguars reported from any other environment.

These results can be explained by the abundance of aquatic and arboreal prey and the absence of terrestrial prey at Mamirauá Reserve. Whereas terrestrial mammals are rare, caimans are abundant. Total caiman density in Lake Mamirauá, the center of the study area, is estimated at 23.7 individuals/ km^2, or 230 caimans/km of lake margin (Da Silveira 2002). This equates to a total population estimate of 13,340 caimans in Lake Mamirauá, and the surrounding lakes and other waterways in the immediate study area. The most abundant species of caiman in this area is the black caiman, which represents 81% of the total caiman population. Spectacled caimans are less abundant and have been estimated to occur at densities of 4.4 individuals/km², or 43 individuals/km in that same area and compose the other 19% of the caiman population (Da Silveira, 2002). Based purely on abundance, it would be expected that black caimans might occur more frequently in the diet of jaguars, but evidence of predation on this species was only found once. Spectacled caiman are found on land much more frequently and for longer periods of time than black caimans, making this species more available and vulnerable to jaguar predation. Spectacled caiman are also much smaller than black caimans (Rebello & Magnusson 2003), which should make them easier and safer for jaguars to capture. Jaguars are also known to eat the eggs of both species of caimans. A survey of caiman nests in the same area of this study reported that between 12-27% of all caiman nests surveyed were predated by jaguars (Ramalho 2006; Da Silveira et al. 2010). However, jaguars do not typically eat the egg whole and the presence of eggs in the diet of jaguars is undetectable in scats and cannot be compared to other diet items.

Arboreal mammals usually do not represent a large portion of the jaguar's diet. The greatest representation of arboreal mammals reported in the diet of jaguars was 14% in the Atlantic Forest in Brazil (Garla 2001). Even in areas where the abundance of arboreal mammals is greater than reported for Mamirauá Reserve, arboreal mammals represent a small percentage of jaguar diets than found in this study. In the Llanos of Venezuela, for example, the density of red howler monkeys can reach >100 individuals/km² but no evidence of this prey species was reported in the diet of jaguars from this area (Scognamillo et al. 2003). Instead, terrestrial mammals represented 83% of the identified prey. Presumably, the concentration of terrestrial mammals in jaguar diets represents a higher encounter rate and less difficulty in capture, which results in a better cost/benefit ratio in energetic terms.

The brown-throated three-toed sloth occurs at high densities in Mamirauá Reserve and its population is estimated to be over 100,000 animals (Queiroz, 1995), which is ~43% of the total individuals of all other species (Table 4-2). This high density may explain why three-toed sloths appear so frequently in the diet of jaguars in Mamirauá Reserve. Two-toed sloths were also documented in jaguar scats but in only two samples. This may be because of their lower abundance and nocturnal habits, which may make them less vulnerable to jaguar predation. The only other jaguar diet study that describes the consumption of sloths was conducted in an Atlantic Forest site in southeast Brazil by Garla et al. (2001), who reported three-toed sloths in 3% of the scats analyzed (n=101), or 2,1% of the prey identified (n=142). The solitary, silent and arboreal behavior of three-toed sloths, their camouflaged pelt and small biomass, together with the availability of terrestrial mammals, are probably important factors that explain why this species is not consumed more frequently in other regions. In Mamirauá Reserve, however, jaguars may actively hunt sloths. Jaguars in this area are active mostly during the day (Ramalho 2012 – Chapter 2), which is also when three-toed sloths are most active (Sunquist & Montgomery 1973). Once detected, sloths are probably easy prey for jaguars because of their limited mobility and lack of defenses.

The only other species that constituted more than 5% occurrence or biomass were the lesser tamandua and the red howler monkey. The lesser tamandua is a nocturnal species and generally occurs in low densities. Red howler monkeys are consumed at approximately the same frequency as the tamandua, but are reported to occur at higher densities and live in social groups of 4-10 animals (Boubli et al. 2008). Red howler monkeys are much more agile than either the lesser tamandua or the sloth, which would make it more difficult to catch and may explain why this species wasn't found more often in scats.

The abundance of prey, especially the concentration of spectacled caiman during low-water periods, may be responsible for the high densities of jaguars reported in this area (Ramalho 2012 – Chapter 2). An adult jaguar has to consume a minimum of 34 g of meat per kg of cat biomass per day to survive (Altman & Dittmer 1973). The average weight of jaguars in Mamirauá Reserve is ~50 kg (based on weights of 4 adult males and 5 females, E. Ramalho, unpublished data), which means that each jaguar needs to eat roughly 1.7 kg of meat per day or 620.5 kg per year. Based on reported jaguar densities of ~17 jaguars/km^2 in Mamirauá during the low- water season (Ramalho 2012 – Chapter 2), jaguars are estimated to consume ~12,848 kg of prey (Table 4-2). Based on estimates of prey biomass in the region (Table 4-2), this represents only 0.9 % of the available prey population and only 1.3 of standing biomass of prey, which indicates jaguars are not being limited by food resources in Mamirauá during the low-water months of September-November.

The results of this study give further support to the importance of reptiles, especially caiman, in the diet of the jaguar in seasonally flooded environments. It also raises attention to the key role that arboreal mammals, the three-toed sloth in particular, may have in the maintenance of jaguar populations in the Várzea Floodplain Forests of Amazonia. These findings are, in part, encouraging because these prey species are generally not highly sought or consumed by local people, and, in turn this should facilitate their conservation in the densely human populated Várzea.

Table 4-1. List of jaguar prey identified from scats, average prey body weight, estimated density of prey, abundance, biomass of prey species population available (Biomass available=average weight of prey species x abundance), number of times each prey was identified (n), percent of scats which contained that species of prey, percent occurrence (Po), biomass represented in scats (Contributed biomass), percent of total biomass represented by contributed biomass (% Biomass=relative biomass*100)

Prey		Weight (kg)	Density (ind/km²)	Abundance	Biomass available	n	% scats	P_o	Contributed Biomass (kg)	% Biomass
Reptiles										
Spectacled caiman	*Caiman crocodilus* [a,f]	16.8	4.4	2,494	24,940	32	0.41	0.24	82.2	31.7
Black caiman	*Melanosuchus niger* [a,f]	16.8	19.2	10,846	108,460	1	0.01	0.01	2.6	1.0
Crocodile tegu	*Crocodilurus amazonicus* [c]	1	-	-	-	1	0.01	0.01	2.0	0.8
Northern caiman lizard	*Dracaena guianensis* [c]	2	-	-	-	1	0.01	0.01	2.0	0.8
Unidentified caiman	Caiman sp. [a]	16.8	-	-	-	13	0.17	0.10	33.4	12.9
Unidentified chelonian	Chelonia sp.	-	-	-	-	1	0.01	0.01	-	-
Unidentified lizards and snakes	Squamata spp.	-	-	-	-	4	0.05	0.03	-	-
Unidentified reptile		-	-	-	-	4	0.05	0.03	-	-
Total				13,340	133,400	57		0.42	122.1	47.2
Mammals										
Brown-throated three-toed sloth	*Bradypus variegatus* [b]	2.98	212	119,992	357,576	41	0.53	0.30	85.5	33.0
Lesser tamandua	*Tamandua tetradactyla* [c]	4.5	3	1,698	7,641	11	0.14	0.08	23.5	9.1
Red howler monkey	*Alouatta seniculus* [b]	5.31	38	21,508	114,207	9	0.12	0.07	19.5	7.5
Two-toed sloth	*Choloepus didactylus* [b]	6	88	49,808	298,848	2	0.03	0.01	4.4	1.7
Unidentified squirrel monkey	*Saimiri* sp. [c]	0.95	72	40,752	38,714	1	0.01	0.01	2.0	0.8
Cattle	*Bos taurus*	30	-	-	-	1	0.01	0.01	3.0	1.2
Unidentified mammals		-	-	-	-	10	0.13	0.07	-	-
Total				233,758	816,987	75		0.55	134.9	52.1
Birds										
Black-bellied Whistling Duck	*Dendrocignia autumnalis* [e]	0.7	-	-	-	1	0.01	0.01	2.0	0.8

Table 4-1. Continued

Prey		Weight (kg)	Density (ind/km²)	Abundance	Biomass available	n	% scats	P_o	Contributed Biomass (kg)	% Biomass
Unidentified birds		-	-	-	-	3	0.04	0.02	-	-
Total				-	-	4		0.03	2.0	0.8
Others										
Unidentified snail	Pomacea sp.	-	-	-	-	4	0.05	-	-	-
Vegetable matter		-	-	-	-	2	0.03	-	-	-
Total						6		-	-	-
Grand Total				247,098	950,387	136			259.0	

a - Mean weight of caiman consumed by jaguars during the study, based on total length of the carcasses found; b - Queiroz 1995; c - Valsecchi 2005; d – R. Cintra (INPA), unpublished data; f - Da Silveira 2002

Table 4-2. Weight, density, and abundance of the most important prey species in study area and the estimated consumption of each species by jaguars during the three months of low water level (September-November). Estimates are calculated assuming a jaguar population density of 17 jaguars/100 km² (Ramalho 2012 – Chapter 2), which would represent a jaguar population size of 96 adult jaguars within the study area

Prey	Weight (kg)	Density (ind./km²)	Population Size	Biomass	Biomass consumed	% of biomass consumed	Number of individual prey	% of prey population consumed
Caiman crocodilus	10.0	43.0	2,494	24,940	4,667	18.7	278	11.1
Bradypus variegatus	4.2	212.0	119,992	503,966	4,858	1.0	1,157	1.0
Tamandua tetradactyla	4.6	3.0	1,698	7,811	1,340	17.2	291	17.2
Alouatta seniculus	5.5	35.0	19,810	108,955	1,104	1.0	201	1.0
Choloepus didactlyus	6.0	88.0	49,808	298,848	250	0.1	42	0.1
Melanosuchus niger	10.0	19.2	1,111	11,114	147	1.3	9	0.8
Saimiri sp.	1.0	72.0	40,752	38,714	118	0.3	124	0.3
Total		472.2	235,665	994,349	12,484	1.3	2,101	0.9

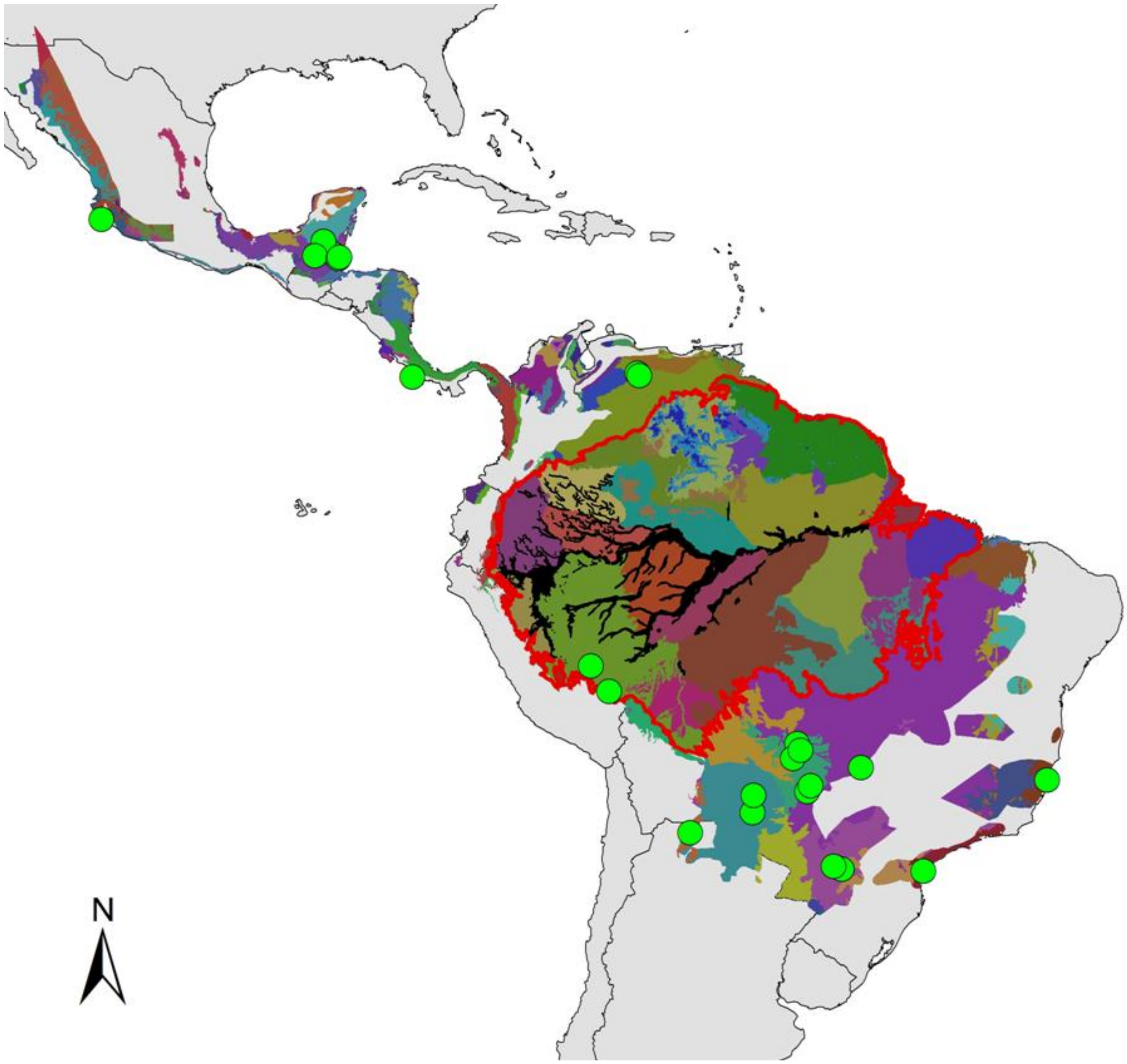

Figure 4-1. Location of all diet studies conducted to date (green circles), Ecoregions within the jaguar present distribution (other colors), and extent of Amazonia (red line)

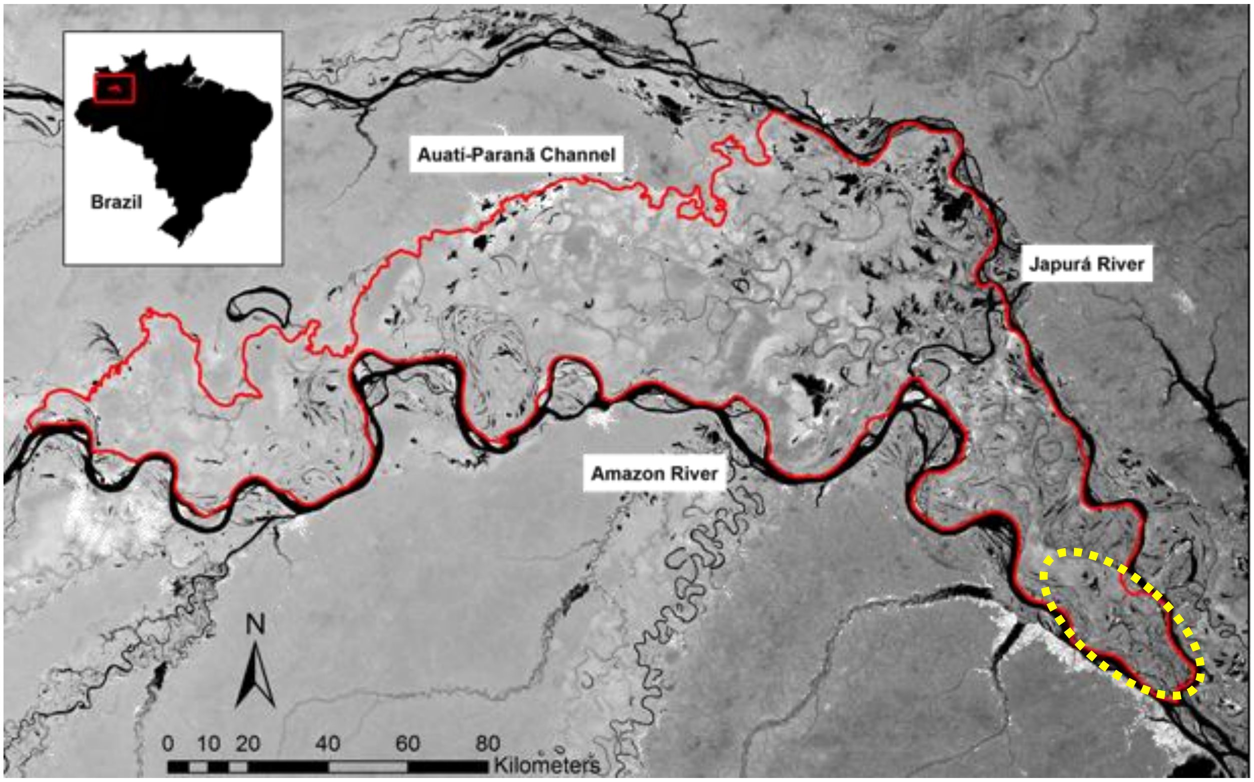

Figure 4-2. Smaller frame shows location of Mamirauá Sustainable Development Reserve within Brazil. In larger frame red line represents the limits of the Reserve. Dashed yellow ellipse represents location where samples were collected

APPENDIX
BIBLIOGRAPHY REVIEW METHODS

To assess the current knowledge base on jaguars I used the major biomes of Brazil (Amazonia, Caatinga, Cerrado, Atlantic Forest, Pantanal, and Pampas) as the management regions and their populations as the units. To evaluate knowledge within these biomes I used five web based search engines: Thomson Reuters (formerly ISI) Web of knowledge (via University of Florida - www.isiwebofknowledge.com), Periódicos CAPES (www.periodicos.capes.gov.br), Scielo (www.scielo.org), Google Scholar (scholar.google.com) and IUCN's Cat Library (www.catsg.org/catsglib/index.php). I merged these results with the compilation of Inskip and Zimmerman (2009; available from: www.jaguarnetwork.org/Jaguar%20Bibliography%20Updated.pdf). I also used the cited references of the publications found to search for other publications not encountered in the first search.

Table A-1. Jaguar peer reviewed publications and book chapters produced in Brazil

Research Category	Research Sub-category	Count	Freq. w/ category	Overall Freq.	Amazonia	Atlantic forest	Caatinga	Cerrado	Pantanal
Ecology and behavior	Diet	18	51.4	16.4	3	6	2	3	7
	Movement, home-range size, and habitat use	10	28.6	9.1	3	3	1	1	6
	Population parameters and structure	10	28.6	9.1	1	5	2	1	4
	Reproduction	2	5.7	1.8	0	0	0	1	2
	NI	1	2.9	0.9	0	1	0	0	0
Sub-total		35		31.8	5	10	3	4	16
Conservation	Proposed measures and threats	15	75.0	13.6	4	7	1	2	4
	Population viability analysis	1	5.0	0.9	0	1	0	0	0
	Habitat loss and fragmentation	1	5.0	0.9	1	0	0	0	0
	Habitat suitability model	1	5.0	0.9	0	2	0	0	0
	Management experiment	0	0.0	0.0	0	0	0	0	0
	NI	3	15.0	2.7	2	2	0	0	0
Sub-total		20		18.2	4	10	1	2	4
Conflict	Depredation	12	54.5	10.9	1	4	0	1	4
	Hunting	8	36.4	7.3	5	2	0	0	0
	Local perception	3	13.6	2.7	1	2	1	1	2
	Attack	1	4.5	0.9	0	0	0	0	1
	NI	0	0.0	0.0	0	0	0	0	0
Sub-total		22		20.0	6	8	1	2	7
Veterinary and pathology		35		31.8	1	2	0	1	0
Status and distribution		11		10.0	1	7	1	0	1

Table A-1. Continued

Research Category	Research Sub-category	Count	Freq. w/ category	Overall Freq.	Amazonia	Atlantic forest	Caatinga	Cerrado	Pantanal
Method		11		10.0	0	2	0	0	1
Biology and morphology		9		8.2	0	0	0	1	2
Genetics		8		7.3	0	2	0	1	0
Total		110			12	24	4	6	21
Overall frequency					19.0	38.1	6.3	9.5	33.3

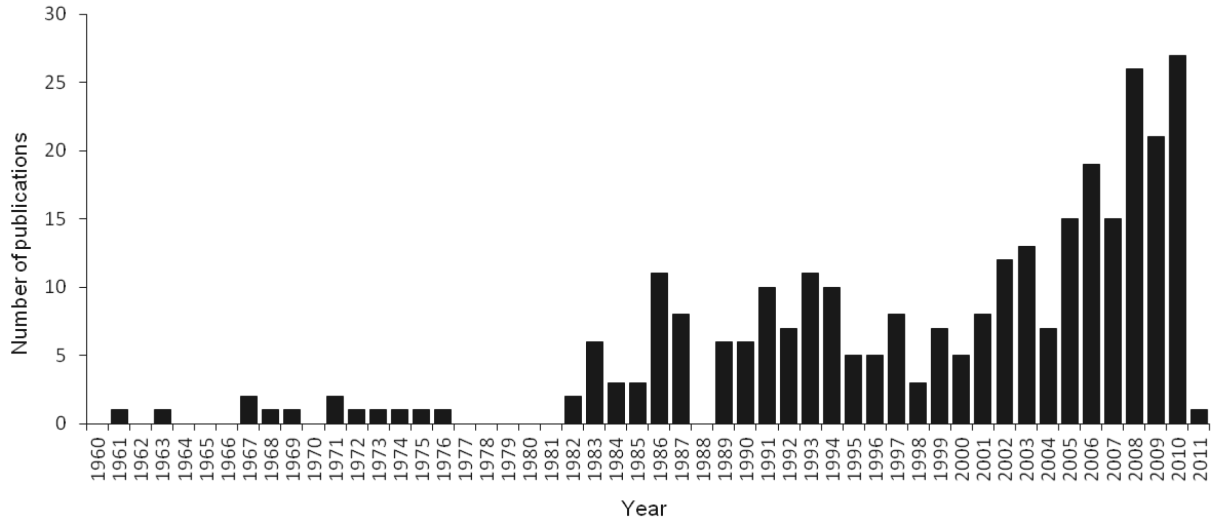

Figure A-1. Number of peer reviewed publications related to the jaguar per year.

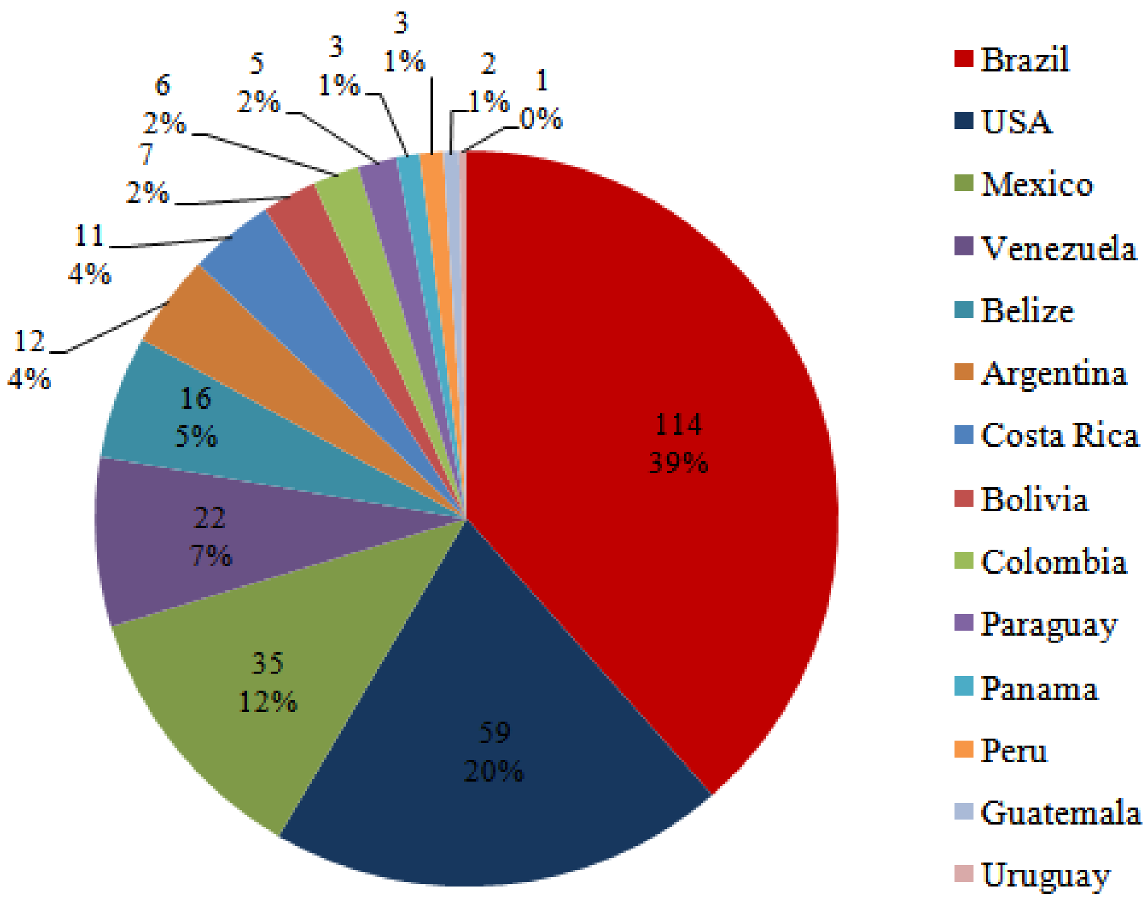

Figure A-2. Number of jaguar related peer reviewed publications per country

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BIOGRAPHICAL SKETCH

I was born in 1978 in Rio de Janeiro, Brazil, where I lived until the age of 23. I completed my undergraduate degree in Biological Sciences, majoring in Ecology, in the Federal University of Rio de Janeiro (UFRJ) in 2003. I concluded my Masters in the National Institute of Research of Amazonia (INPA) in 2006. In 2007 I was awarded a CAPES/Fulbright scholarship to pursue my PhD in the United States, where I studied in the University of Florida, in the Department of Wildlife Ecology and Conservation. I have been involved in jaguar research and conservation since 2003, and have been studying he jaguar in Amazonia since 2004. I am currently coordinating jaguar research in Mamirauá and Amanã Sustainable Development Reserves, and I am also part of a non-governmental organization called Pró-Carnívoros.