

VARIATION IN NEOTROPICAL RIVER OTTER (*Lontra longicaudis*) DIET: EFFECTS
OF AN INVASIVE PREY SPECIES

By

ANTONIO DIEGO ALEJANDRO JUÁREZ-SÁNCHEZ

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2017

© 2017 Antonio Diego Alejandro Juárez-Sánchez

To my parents, Julita y Beto, for being role models to follow and for always encouraging me to follow my dreams wherever they take me

ACKNOWLEDGMENTS

I thank all the institutions that funded and supported me during my graduate program: Fulbright, Department of Wildlife Ecology and Conservation at the University of Florida, Eli.S.A., WCS-Guatemala, BALAM, CONAP-Peten, Propeten, Defensores de la Naturaleza Peten, FUNDAECO, CECON, Escuela de Biología USAC; and all the people who helped me through those institutions by providing me with equipment, supplies, institutional or personal funds: Roan Balas, Byron Castellanos, Yobany Tut, Julio Madrid, Rony Garcia, Rafael Cevallos, Mercedes Barrios, Rosalito Barrios, Manuel Lepe, Werner Paz and Silja Ramirez..

Thanks also to all the people that helped me in the field, especially Andrea Paiz and Francisco Cordova, I couldn't have done my fieldwork without you guys, thanks for being the best companions. Also to Alejandro Chen, Alejandro Mérida, Alfredo Choc, Belarmino García, Carlos Cifuentes, Dastin Ramírez, Elder Godoy, Elmer Monzón, Ervin Flores, Fredy Tot, Jeovany Nolberto Tut Pacheco, René de Jesús Mauricio Te, Ricardo Coc Caal, Samuel Yatz, Juan Rodas and to many others that helped me in the biological station Las Guacamayas, in the military post, park rangers and the community people at Laguna del Tigre National Park, the military post in La Polvora, the park rangers at Sierra Lacandon, El Rosario, Syache, and Sarstun, all the workers at CONAP-Peten wildlife department, to my good friends Leonel Zisse and Marta Pujol, also the employees at the Hermano Pedro Hotel and at La Casa de Don David Hotel, especially Doña Rosita and Yohana Rodas.

To my wonderful wife Yasmín, thanks for always challenging me to be a better person and scientist and for being my lighthouse in this journey. To my parents for being my biggest donors and supporters, for always having good advice, and for

listening to my histories, adventures, and concerns. To my sisters Eli and Cielo for always being there for me when I needed you. And to my nephews Bruno and Matias, you are the reason for me to want to be a good person and a good example.

To my committee members, thanks Christina Romagosa for supporting me in hard moments and helped me to face them. Thanks John Blake and Eric Hellgren for not despairing with my stubbornness. Thanks Bill Pine for always having a positive attitude towards the potential of my work. And to all four of you for giving me the best advice on how to improve my work.

To all the professors, fellows and friends who reviewed my work and gave me comments and suggestions especially Harry Jones, Laura Gelin, Jose Soto, Claudio Moraga, Audrey Wilson, Yasmín Quintana, Flavia Montalvo, Farah Carrasco, Jason Curtis, Ignacio Rodriguez-Jorquera, and Bill Giuliano.

To all those friends who became my family away from home Laura Gelin, Claudio Moraga, Juliana Bedoya, Julia Salvador, Fernando Noriega, Eric Suarez, Gustavo Contreras, Farah Carrasco, Diego Garcia, Audrey Wilson, Macarena Deij, Harry Jones, Carolina Oliveira-Fiorini, Elise Morton, Marta Prat, Daniel Montalvo, Cate de la Torre, Ivelis Ruiz, Wes Anderson, Jan Archer, Emily Olson, Filipe Da Silva, Felipe Hernandez, Marcela Marquez, Evelyn Del Valle, Emilio Moraga, Debra Anderson, Carlos Maestzu, Jon Dain, and so many others thanks for being there for me at any time that I needed you.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGMENTS.....	4
LIST OF TABLES.....	7
LIST OF FIGURES.....	8
LIST OF ABBREVIATIONS.....	9
ABSTRACT.....	10
CHAPTER	
1 INTRODUCTION.....	12
2 METHODS.....	22
Study Area.....	22
Scat Collection.....	23
Scat Sample Preparation and Analysis.....	24
Statistical Analysis.....	26
3 RESULTS AND DISCUSSION.....	34
Results.....	34
Discussion.....	37
APPENDIX: SCALE GUIDE TO IDENTIFY MEDIUM AND LARGE FRESHWATER FISH FROM NORTHERN GUATEMALA.....	52
LIST OF REFERENCES.....	53
BIOGRAPHICAL SKETCH.....	64

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1-1	Species and locations of known Loricariidae invasions.	20
1-2	Food items reported as present in diets of Neotropical river otters across their geographic range.....	21
2-1	Potential prey of Neotropical river otters found in basins sampled during this study.....	29
3-1	Scats of Neotropical river otters collected in northern Guatemala.	43
3-2	Number of records (No), and percentage of the total of prey species (%) found in otter scats	44

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2-1 Study area	33
3-1 Species accumulation curves for Pasion River	46
3-2 Species accumulation curves for San Pedro Rive	47
3-3 Species accumulation curves for Mopan River	48
3-4 Isotopic values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from Neotropical river otter scats collected from the study area.....	49
3-5 Variance from the mean for $\delta^{15}\text{N}$ in fecal samples from Neotropical river otters in Guatemala.. ..	49
3-6 Variance from the mean for $\delta^{13}\text{C}$ in fecal samples from Neotropical river otters in Guatemala.	50
3-7 Boxplots for $\delta^{15}\text{N}$ in fecal samples from Neotropical river otters in Guatemala. .	51

LIST OF ABBREVIATIONS

ACF	Armored catfish, referring to <i>Pterygoplichthys</i> sp. (Loricariidae)
FTL	Fractional trophic level
GSA	Gross scat analysis
NRO	Neotropical river otter
SIA	Stable isotope analysis

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

VARIATION IN NEOTROPICAL RIVER OTTER (*Lontra longicaudis*) DIET: EFFECTS
OF AN INVASIVE PREY SPECIES

By

Antonio Diego Alejandro Juárez-Sánchez

May 2017

Chair: Eric C. Hellgren
Major: Wildlife Ecology and Conservation

As a result of human activities, some species have expanded their distribution into areas that were historically difficult or impossible to reach by natural dispersal. Such species may become invasive if they successfully establish reproductive populations and may represent a threat to native species. Predation on invasive species by native species can affect trophic interactions with other prey species, resulting in a cascading restructuring of the trophic web.

I examine effects of an invasive fish (armored catfish: *Pterygoplichtys* sp.) on the dietary niche breadth and trophic level of a native piscivorous predator (Neotropical river otter: *Lontra longicaudis*) in northern Guatemala. I collected otter scats from three rivers: two where the invasive catfish occurred (San Pedro River, located in Laguna del Tigre National Park, and Pasion River, outside of the protected area) and one without the invasive fish (Mopan River, outside of protected area). Samples were collected 5 and 10 years after the first report of the catfish in each area. Gross scat analysis (GSA) and nitrogen and carbon stable isotopes analyses (SIA) were conducted using those scat samples.

In the rivers where the armored catfish occurred, it was the main prey item for *L. longicaudis*. Occurrence of catfish in scat samples was highest (49%) in samples collected from Pasion River 10 years after the first report of the catfish. I found concordance between the two techniques to estimate niche breadth and trophic level. The niche breadth of otters was narrower 10 years after the invasion in comparison to 5 years after the invasion in both invaded rivers but the intensity of the reduction was less in Pasion River than in San Pedro River, likely because the niche breadth of otters from the Pasion River was already low 5 years after the first report of the invasive armored catfish. The trophic level of otters also showed a reduction in relation to the time of first occurrence of the armored catfish.

Consistently lower values in Pasion River compared to San Pedro River may be related to differences in the resilience of the two rivers due to differences in habitat conservation. Neotropical river otters may act as a buffer to hold armored catfish populations at low levels and minimize their potential negative effects on the system. It is necessary to determine if invasive prey such as the armored catfish can facilitate native predators which, in turn, also may depredate native prey that may be threatened by overexploitation or habitat loss.

CHAPTER 1 INTRODUCTION

Human activities have allowed many species to expand their distribution into areas that were historically difficult or impossible to reach by natural dispersal (Lockwood et al. 2007, Meyerson and Mooney 2007). Many of these species have established reproductive populations in their introduced ranges, becoming invasive species that may threaten native species (LaBastille 1974, Bunkley-Williams et al. 1994, Towns et al. 2006, Jones et al. 2008, Shine 2010, McCleery et al. 2015). For example, in North America, invasive fish are considered the second most important cause of native fish extinction (Burkhead 2012). Interactions between native and exotic species can be direct through competition or predation, and indirect by modifying habitat structure or native predators' foraging behavior (King et al. 2006, Rodriguez 2006, Wanger et al. 2011).

Depending on the interactions between invasive and native species, impacts of invasive species can have top-down effects, affecting the community structure by interacting with lower trophic levels, or bottom-up effects by interacting with higher trophic levels (Keeler et al. 2006, Capps et al. 2014). After an exotic species has established a reproductive population and interactions with local species become more common, the effects on local species can be positive by enhancing populations of endangered predators (King et al. 2006, Cattau et al. 2016) or can be negative by competing with indigenous species for resources (Capps and Flecker 2015) or increasing mortality rates of native species (McCleery et al. 2015).

Predators play important roles in ecosystems both directly by regulating prey species' abundances (Rosenzweig and MacArthur 1963, Estes et al. 1998) and through the indirect effects of perceived predation risk by modifying prey behavior, leading some prey species to avoid certain areas or spend more time being vigilant (Brown et al. 1999, 2001, Laundré et al. 2001). When a predator is presented with a new potential prey species, such as an invasive species, it can adapt its behavior or physiological response by using its existing pool of phenotypes or emerging mutations to prey upon or avoid the invasive species, thereby fixing these new adaptations by natural selection (Phillips et al. 2004, Phillips and Shine 2006, Carlsson et al. 2009, Llewelyn et al. 2010). Through adaptation or phenotypic plasticity, a predator can regulate the population dynamics of an invasive species if the predator prefers to feed upon it (Shinen et al. 2009, Ward-Fear et al. 2010, Wanger et al. 2011, Ritchie et al. 2012, Cabrera-Guzmán et al. 2015). Native predation pressure on invasive species can also affect the overall structure of the community by changing trophic interactions with other natives, resulting in a cascading restructuring of the trophic web (Roemer et al. 2002, Tablado et al. 2010).

Niche is defined as the hyper-volume of environmental and biological variables within which a species can live. It can be divided into the fundamental niche, which is the range of the hyper-volume where all the requirements of a species can be fulfilled; and the realized niche, which is the range of the hyper-volume, that the species actually inhabits. The realized niche may be more limited than the fundamental niche because a species may be excluded from some regions of the hyper-volume as a result of negative interactions with other species or the presence of natural barriers limiting the ability of a

species to access specific resources (Hutchinson 1957). The niche of a species can be subdivided by types of resources for analysis and easier understanding, and its width or breadth can be evaluated using indexes that measure the evenness with which a species uses available resources (Krebs 1999, Peers et al. 2012). The realized dietary niche of a predator can vary throughout its distribution depending on the assembly of prey and competitors present in different locations. When a native predator starts to interact with an invasive prey species, the niche of the predator may change, becoming wider or narrower, depending on the intensity of use of the new resource and changes in the use of alternative native prey.

The type of prey that a predator eats defines its trophic level, which can be evaluated with the fractional trophic level index (FTL). This index describes the trophic distance of a consumer species from producers. For example, plants and detritus are set to a value of one, a value of two defines herbivores and detritivores, and increasing values are assigned to predators. The FTLs of carnivores and omnivores are typically not integer values because they feed on items that come from different FTLs. Therefore, the FTLs of carnivores and omnivores are the weighted averages of all the FTLs of their prey, plus one. Changes in the consumption of prey types by a predator can change its FTL (Pauly and Palomares 2005) which can be estimated using Pauly and Palomares' (2005) formula and data from a gross scat analysis (GSA), where the proportions of consumption of each prey item have been estimated. These findings can be corroborated using nitrogen stable-isotope values (Vander Zanden et al. 1999, Post 2002).

Stable isotope analysis (SIA) measures the proportion of heavy to light stable isotopes in a sample (Petersen and Fry 1987, Fry 2008); its values are expressed in delta notation (δ) or per mil (‰) and estimated with this equation:

$$\delta = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$$

where R = heavy isotope / light isotope obtained with a mass spectrometer. When presenting delta notation to specify the stable isotope in question, the atomic weight of the heavier isotope is placed next to the delta and before the element symbol; for example, $\delta^{13}\text{C}$ indicates isotopic value of carbon 13. Negative δ values indicate a smaller proportion of the heavy isotope in relation to the standard, whereas positive values indicate a larger proportion. In trophic ecology, the most common elements used for isotopic analysis are nitrogen (N) and carbon (C). International standards are atmospheric air for N and Peedee Belemnite (PDB) for C (Kelly 2000, Fry 2008). Normally, $\delta^{13}\text{C}$ values are negative and represent the type of plant that supports the food chain (C_3 , C_4 or aquatic plants). Tissues made from C fixed by C_3 plants have more negative values of $\delta^{13}\text{C}$ in relation to tissues made with C fixed by C_4 plants; and tissues with C fixed by aquatic plants have intermediate $\delta^{13}\text{C}$ values (Kelly 2000).

Isotopic values of a predator are higher than those of its prey due to a process called fractionation, wherein the molecules with the lighter isotopes, given their lighter overall weight, react faster and can be metabolized and excreted faster than the heavier ones. This process results in the predator being enriched with a higher proportion of heavier isotopes than its prey (Post 2002, Fry 2008). The mean value of this fractionation across taxa is 3.4‰ (1 SD = 1‰) for $\delta^{15}\text{N}$ and 0.4‰ (1 SD = 1.3‰) for

$\delta^{13}\text{C}$ (Post 2002). These values are the expected increment of the isotopic value when molecules are assimilated from prey tissue to predator tissue (from lower to higher trophic levels; Kelly 2000).

Isotopic values of different sources of tissue such as bone, blood, hair or muscle, have been used to evaluate the diet of a wide range of species (Schoeninger et al. 1983, Angerbjorn et al. 1994, Blundell et al. 2002, Darimont and Reimchen 2002, Newsome et al. 2004, Aurióles-Gamboa et al. 2009, Wengeler et al. 2010, Fortin et al. 2013). Normally, tissue samples are obtained from dead or captured specimens but these invasive techniques are sometimes difficult or impossible to use, especially for secretive, rare or endangered species. However, controlled experiments have shown that the SIA in feces is sensitive to changes in the diet over periods of 3 hours for insectivorous bats (Salvarina et al. 2013) and thus represent the isotopic values of the latest meals of the individual that produced the scat (Crowley et al. 2013). In carnivores and omnivores, SIA in scats can be used to estimate the main type of prey and nutrient flow, using $\delta^{15}\text{N}$ to infer the range of trophic positions or FTL at which a predator eats, and $\delta^{13}\text{C}$ to determine the type of producers that supported the specific trophic chain (Post 2002, Codron et al. 2005, Crait and Ben-David 2007, Hatch et al. 2011). It has been suggested that the variance of isotopic values of a population can represent the niche width (or breadth) of a consumer (Bearhop et al. 2004).

Important invasive species in freshwater communities are the armored catfishes of the South American family Loricariidae, a diverse group of fishes with 928 valid species and eight subfamilies, including the genus *Pterygoplichthys*, commonly known

as the suckermouth armored catfish (hereafter ACF; Eschmeyer and Fong 2016). These catfish are very popular in the aquarium trade, easily domesticated, exhibit parental care (Nico et al. 2009a), possess physiological tolerance to adverse conditions (de Oliveira et al. 2001, Stevens et al. 2006, Capps et al. 2011, da Cruz et al. 2013, Corcuera Zabarrburú 2015), have wide distribution ranges (Froese and Pauly 2016), and possess high reproductive and growth rates (Gibbs et al. 2008, 2013). They feed on detritus, an abundant resource, especially in human-modified areas, and therefore have a low FTL (2, according to FishBase database; Froese and Pauly 2016). These traits contribute to their invasiveness, as they fulfill the six life-history variables associated with species that successfully establish invasive populations (Marchetti et al. 2004). The presence of ACF as an invasive species has been documented for at least 12 countries around the globe (Table 1-1). In 2005, an established population of *Pterygoplichthys pardalis* was found in Laguna Frontera at the mouth of the Usumacinta River, Tabasco, Mexico (Wakida-Kusunoki et al. 2007). The same year, *P. pardalis* was reported in Guatemala in the headwaters of the San Pedro River, a tributary of the Usumacinta River (J. F. Moreira, Wildlife Conservation Society-Guatemala, personal communication) but the species identification has not been confirmed because *P. pardalis* can be misidentified and confused with other species of *Pterygoplichthys* given that identification is based on ventral color patterns (Hubbs et al. 2008, Wakida-Kusunoki and Amador-Del-Angel 2008). Specimens captured in Guatemala have a high variability in the ventral color patterns. In 2009, an estimated 30% of fish captures in San Pedro River were *Pterygoplichthys* sp., composing 24% of the total biomass captured (D. Juarez-Sanchez, unpublished data).

The ACF has been reported to have positive effects by generating nutrient hotspots, making nutrients available for producers in nutrient-depleted areas (Capps and Flecker 2013). However, the same researchers have found that the amount of nutrients released by the ACF does not compensate for the grazing pressure (Capps and Flecker 2015). Other negative impacts of ACF have been documented in places where they have established invasive populations. These impacts include asphyxiating native predators in Puerto Rico (Bunkley-Williams et al. 1994); preying on native fish eggs and first-feeding fry in Thailand (Chaichana et al. 2013); competing for forage with native species, reducing biofilm from the substrate, and changing the proportions of dissolved nutrients in the Philippines and Mexico (Hubilla et al. 2007, Capps et al. 2014, Capps and Flecker 2015); harassing manatees (Nico et al. 2009b, Gibbs et al. 2010, Nico 2010); and possibly promoting erosion with their nesting burrows in Florida (Nico et al. 2009a). These impacts could occur anywhere ACF establish an invasive population. Invasive ACF are preyed upon by native piscivorous predators such as common snook (*Centropomus undecimalis*) and the Neotropical cormorant (*Phalacrocorax brasilianus*; Toro-Ramírez et al. 2014, Ríos-Muñoz 2015), although their effects on these and other native predators have not been evaluated.

Otters (Lutrinae) are mid-sized carnivores that are top predators in freshwater wetlands and riverine systems because of their high energetic demand and trophic position (Kruuk et al. 1994, Pfeiffer and Culik 1998). The Neotropical river otter (*Lontra longicaudis*; hereafter NRO) is a semi-aquatic mustelid that preys primarily on benthic slow-moving fish (Rheingantz et al. 2012), but also feeds on crustaceans, mollusks, reptiles, and mammals (Table 1-2). This species is distributed from northern Mexico to

northern Argentina, coexisting with different community assemblages of prey species, and adapting its foraging behavior according to the local community (Chemes et al. 2010). Where ACF are native, they coexist with the NRO and constitute one of the most important prey items in its diet (Kasper et al. 2008, Chemes et al. 2010, Mayor-Victoria and Botero-Botero 2010, Silva et al. 2012). However, the role of ACF as a prey item for NRO in areas where ACF has been introduced is unknown and may be reshaping the foraging ecology of the NRO in those areas.

The main objective of this study was to determine if invasive armored catfish affected the diet of Neotropical river otters. Given that NRO feed on ACF in areas where native populations overlap (Pardini 1998, Kasper et al. 2004a, 2008), I hypothesized that NRO will change their diet to include ACF in rivers where invasive populations of ACF occur. I predicted that where ACF are present, they will become the main prey of NRO and that, as a consequence, the niche breadth of the NRO will be lower where ACF are present because NRO will focus on ACF as prey. If ACF become the main prey of the NRO, I also predicted a lower fractional trophic level for the NRO in areas where ACF are present due to the low trophic level of the ACF.

Table 1-1. Species and locations of known Loricariidae invasions.

Place	Species	Citation
Tabasco, Mexico	<i>Pterygoplichthys pardalis</i>	(Wakida-Kusunoki et al. 2007)
Campeche, Mexico	<i>Pterygoplichthys disjunctivus</i> and <i>Pterygoplichthys pardalis</i>	(Wakida-Kusunoki and Amador-Del-Angel 2008)
Texas, USA	<i>Pterygoplichthys disjunctivus</i> , <i>Pterygoplichthys multiradiatus</i> , <i>Pterygoplichthys anisitsi</i> and <i>Hypostomus plecostomus</i> .	(Nico and Martin 2001, Hubbs et al. 2008, Pound et al. 2011)
Puerto Rico	<i>Pterygoplichthys multiradiatus</i>	(Bunkley-Williams et al. 1994)
Florida, USA	<i>Hypostomus</i> sp./ <i>plecostomus</i> and <i>Pterygoplichthys</i> sp	(Rivas 1965, Schofield and Loftus 2014)
Philippines	<i>Pterygoplichthys disjunctivus</i> and <i>Pterygoplichthys pardalis</i>	(Chavez et al. 2006)
Singapore	<i>Pterygoplichthys pardalis</i> and <i>Pterygoplichthys disjunctivus</i>	(Page and Robins 2006)
Malasia	<i>Pterygoplichthys pardalis</i>	(Page and Robins 2006)
Java	<i>Pterygoplichthys pardalis</i> and <i>Pterygoplichthys disjunctivus</i>	(Page and Robins 2006)
Sumatra Taiwan	<i>Pterygoplichthys pardalis</i> <i>Pterygoplichthys multiradiatus</i> and <i>Pterygoplichthys disjunctivus</i>	(Page and Robins 2006) (Liang et al. 2005, Page and Robins 2006)
India	<i>Pterygoplichthys</i> sp	(Bijukumar et al. 2015)
*Serbia	<i>Pterygoplichthys pardalis</i>	(Simonovic et al. 2010)
*Vietnam	<i>Pterygoplichthys pardalis</i>	(Levin et al. 2008)

* One specimen captured reproductive populations present elsewhere

Table 1-2. Food items reported as present in diets of Neotropical river otters across their geographic range. Percent values are frequency of occurrence and do not add to 100%.

Citation	Primary item	Other items	Locality
Casariego-Madorell et al. 2008	crustaceans (53.0%)	fish (33.1%), insects (9.8%) and amphibians (4.0%)	Oaxaca, México.
Kasper et al. 2008	fish (Loricariidae 41.1%, Cichlidae 21%, Pimelodidae 12.6%, Characidae 6.5%)	other fish (12.5%), Megaloptera (3.6%), mammals (1.2%), insects (0.4%), Decapoda (0.1%), birds (0.3%), snakes (0.3%) and plant matter (0.4%)	Rio Grande do Sul, Brazil.
Marques Quintela et al. 2008	fish (82.6%)	crustaceans (20.6%), birds (4.5%), mammals and snakes (3.7%), Coleoptera (1.2%), amphibians (0.8%) and mollusks (0.4%)	Rio Grande do Sul, Brazil.
Monroy-Vilchis and Mundo 2009	fish (92.4%)	invertebrates (3.5%), amphibians (2.9%) and plant matter (1.8%)	México state, México.
Chemes et al. 2010	fish (53%)	insects (24%), crustaceans (16%), amphibians (7%), and reptiles, mammals and mollusks (<0.1%)	Salta, Argentina.
Mayor-Victoria and Botero-Botero 2010	fish (76.7%)	insects (12.7%), reptiles (0.7%), and others (9.9%)	Alto Cauca, Colombia.
Rheingantz et al. 2011	fish (86%)	crustaceans (71%), amphibians (10%), mammals (3%), birds (0.6%), reptiles (0.2%) and others (0.7%)	Rio de Janeiro, Brazil.
Sousa et al. 2013	fish	mammals, amphibians, birds, snakes, insects, crustaceans mollusks and eggs.	Rio Grande do Sul, Brazil

CHAPTER 2 METHODS

Study Area

The study area is located in northern Guatemala in the districts of Petén and Izabal (between 15.50° and 17.50° N and -88.50° and -91.25° W), and includes the Usumacinta and Mopan rivers (Figure 2-1). Precipitation ranges from 1,200 to 4,000 mm/year on a gradient decreasing northwards (INSIVUMEH, 2016). Major habitat types in the study area consist of subtropical moist forest in the north, subtropical very moist forest in the south, and tropical very moist forest in the southeast (Holdridge et al. 1971). The entire study area consists of lowland forest, with elevations ranging from 0 to 1000 masl.

In northern Guatemala, rivers flow into the Gulf of Mexico or into the Caribbean Sea (Figure 2-1). Thus, bodies of fresh water are isolated by large expanses of land in the headwaters, and large distances between river mouths along the coast. The Mopan River flows northwards from southern Petén and then east in central Belize into the Caribbean Sea. The Usumacinta River runs northwest into the Gulf of Mexico. Samples were collected from the Mopan River and two tributaries of the Usumacinta River: the San Pedro River and the Pasion River. In Guatemala, the San Pedro River flows along the southern border of Laguna del Tigre National Park whereas the Pasion and the Mopan rivers mainly run through private lands that are under different land uses.

The Usumacinta basin has at least 61 fish species distributed in 25 families. The two main families in Usumacinta basin are Cichlidae with 18 species and Poeciliidae with 10 species (Willink et al. 2000, Granados-Dieseldorff et al. 2012, Eschmeyer and

Fong 2016, Froese and Pauly 2016). To my knowledge, no peer-reviewed document has been published that describes fishes of the Mopan River within the borders of Guatemala. Thus, information about the fish assemblage in this river is based on information from the estuarine area in Belize. As a consequence, the number of fish species that I am considering as present in the river headwaters within Guatemalan territory may be inflated. In Mopan River, there are at least 103 fish species distributed in 32 families, including the invasive tilapia (*Oreochromis aureus*). The main families are Cichilidae with 14 species and Poeciliidae with 16 species (Greenfield and Thomerson 1997, Eschmeyer and Fong 2016, Froese and Pauly 2016). Exotic tilapia is widespread across all Guatemala as a consequence of multiple introductions, both accidental and deliberate from aquaculture or governmental fisheries restocking. The Asian grass carp (*Ctenopharyngodon idella*) and the ACF have been found in the Usumacinta basin, but the origins of these invasions are not clear.

Scat Collection

I collected scat samples for gross scat analysis (GSA) to characterize the dietary breadth of the NRO across the study sites. Samples were collected during three periods: May 2009–April 2010, May–July 2015, and June 2016. The search for otter scats was conducted from a small boat moving at slow speeds (< 5 km/h) close to the shoreline, with scats and latrines typically found on protruding structures (e.g. rocks or fallen trees). This search was conducted along both shorelines of the river in opposite directions. All scats were collected, placed in paper and/or plastic bags with silica gel, and stored in a dry environment. Otter scats were identified by their appearance, as no other species present in the study area have similar scats (located on protruding sites

along the river shore, low fecal matter and high content of fish or crab remains; Aranda-Sánchez 2012). If a scat was found but its identification was doubtful, it was collected and included in the analysis only if otter hair from grooming was found on it. Each scat was assigned a unique code and the geographic coordinates of its location were recorded using a handheld GPS unit (GARMIN © Astro 320, Garmin Ltd. Kansas City, USA).

During 2009-2010, I sampled the Usumacinta basin using continuous searches along the rivers, including 38.5 km of the San Pedro River (starting from Paso Caballos village and moving west) and 89.1 km of the Pasion River (starting from Sayaxche town and heading west). In 2015, I sampled the Usumacinta and Mopan basins, by organizing the search for scats into segments of 10 km, with segments separated by at least 10 km. In the Usumacinta basin, I sampled along 40, 50, and 30 km of the San Pedro, La Pasion, and Usumacinta rivers, respectively. Surveys began in Paso Caballos for the San Pedro, in Sayaxche for the Pasion, and in Betel town for the Usumacinta River. The Mopan River was sampled along 10 km in 2015 in the vicinity of La Polvora military base. In June 2016, the Mopan River was sampled using an *ad libitum* sampling methodology near the La Polvora military base (Figure 2-1).

Scat Sample Preparation and Analysis

Samples of fecal matter were collected from each scat, homogenized using a porcelain mortar and pestle, stored in glass vials and sent to the Light Stable Isotope Mass Spectrometry Laboratory in the Department of Geological Sciences at the University of Florida for stable isotope analysis (SIA) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Hard remains (i.e., scales,

skeleton pieces) were separated and identified to the lowest possible taxonomic level. A list of potential prey species for otters was made, consisting of all the fish species reported in the study area that have a reported maximum total length ≥ 100 mm (Table 2-1). Size selection was based on the assumption that otters prefer to feed on fish within the 100-150 mm size range (Kasper et al. 2004b). Prey remains that could be identified were fish scales, otoliths or vertebra; crustacean shells; and mammal hairs. Because I was using museum reference material I could only obtain non-destructive samples. I prepared a guide of scales from the list of fish species to identify fish (Appendix). Scales were obtained from museum specimens at the Florida Museum of Natural History (FLMNH) and El Colegio de la Frontera Sur in México (ECOSUR). Scales from these fish species were cleaned with water and alcohol, placed on glass slides with nail polish, and sealed with a coverslip to make semi-permanent slides. A scale guide was constructed for 68 of the 80 scaled fish species that are found in the sampled river basins and that were considered potential prey of the NRO. For 10 catfish species that do not have scales, the identification was based on fin spines, using reference material from the zooarchaeological collection at FLMNH. Hairs found in the scats were identified using a hair-identification guide (Juárez-Sánchez et al. 2010) and reference material from the mammal collection of the Museo de Historia Natural (MUSNAT) at the Universidad de San Carlos de Guatemala (USAC). Otter hair (product of grooming) was saved, and pressed between glass slides and coverslips for future analysis.

Statistical Analysis

For data analyses, the sampling units were the rivers (San Pedro, La Pasion, Mopan) with year as factor (2009-2010 and 2015-2016). The year effect represents 5 and 10 years after the advent of the ACF invasion. Comparisons were made over time (i.e., same river, different year) only using data from Pasion and San Pedro rivers where the ACF are present; I additionally looked at differences across river basins in the same sampling years (i.e., different river, same year), combining 2015-2016 records as one year and including the Mopan River where ACF do not occur.

Gross scat analysis (GSA) of predators can be biased by abundant and conspicuous hard remains that are identifiable for some species, even if those species are consumed in low numbers, due to differential digestibility of prey items. This overestimation of some species can then lead to an underestimate of overall diet diversity. On the other hand, when using SIA of predators, one can measure diet diversity breadth and comparative trophic levels but with no taxonomic information about the prey. For this reason, I used both techniques, expecting to find concordance between them.

The importance of different food items, including the ACF, in the NRO diet was assessed through GSA, using the percentage of occurrence. Percentage of occurrence was estimated for a particular prey item by dividing the number of scats with item i by the total number of reported items. To compare the niche breadth between basins with allopatric NRO populations and different prey communities, Levins' index was used:

$$B = 1 / \sum p_j^2$$

where p is the proportion of food items from category j (Levins, 1968). The Levins' niche-breadth index can be standardized using:

$$B_a = B-1 / n-1$$

where B_a is the standardized Levins' niche-breadth index, B is Levins' niche-breadth index, and n is the number of recorded species. Levins' index ranges from 1 to n and from 0 to 1 in its standardized version. In both cases, its minimum value is reached when all reported prey belong to only one species (specialist predator) and is at its maximum when all the species are consumed in the same proportion (generalist predator). It has been suggested that values of $B_a > 0.6$ represent a generalist and values of $B_a < 0.4$ a specialist (Krebs 1999, Novakowski et al. 2008).

Accumulation curves were constructed using program EstimateS (© Colwell 2013, Connecticut, USA) where the expected number of prey species found in a given number of scats is obtained by

$$\tau(h) = S_{obs} - \sum \alpha_{jh} S_j$$

$$\alpha_{jh} = (H-h)!(H-j)! / (H-h-j)! H!$$

where $\tau(h)$ is the estimated number of species for h number of scats; S_{obs} is the number of species actually observed; S_j is the number of prey species found in j scats; α_{jh} is a combinatorial coefficient; H is the total number of scats; h is the number of possible combination of scats that add up to j scats; and j is the number of scats per moment or segment of the curve (Colwell et al. 2004).

Taking $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from individual scats as samples from each river, I evaluated the data for normality using histograms, qq-plots and a Shapiro-Wilk normality test; all values followed a normal distribution. To evaluate differences between variances in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, a Levene's homoscedasticity test was used.

The NRO's fractional trophic level in each basin was estimated using Pauly and Palomares's (2005) formula:

$$\text{FTL}_i = 1 + \sum_j (\text{FTL}_j \text{DC}_{ij})$$

where FTL_i is the fractional trophic level of the consumer, +1 is a constant increment for the FTL of a consumer, FTL_j is the fractional trophic level of the prey j , and DC_{ij} is the proportion of contribution of prey j to the diet of consumer i . Prey FTL_j values were obtained from FishBase database (Froese and Pauly 2016). The DC_{ij} was based on proportion of occurrence values by river-year combination. I tested for differences in mean $\delta^{15}\text{N}$ values between rivers and years using a two-factor ANOVA after a log transformation of the data to correct for lack of homoscedasticity; a post-hoc paired t -test with Bonferroni adjusted p -values was used to evaluate where the differences occurred.

Table 2-1. Potential prey of Neotropical river otters found in basins sampled during this study: Usumacinta (U) and Mopan (M). The Usumacinta basin includes Pasion and San Pedro rivers. Fish species that have a maximum reported total length ≥ 10 cm were considered as potential prey. The maximum total length (MTL) of each species as well as its fractional trophic level index (FTL) and standard errors (SE) are from Froese and Pauly (2016). Scientific names follow Eschmeyer and Fong (2016).

Species	Basin	MTL	FTL	SE
Anguillidae				
<i>Anguilla rostrata</i> (Lesueur 1817)	U	153	3.8	0.2
Ariidae				
<i>Bagre marinus</i> (Mitchill 1815)	M	69	3.5	0.5
<i>Cathorops aguadulce</i> (Meek 1904)	UM	22.7	4.4	0.8
<i>Potamarius nelsoni</i> (Evermann & Goldsborough 1902)	U	39	3.6	0.5
<i>Sciades assimilis</i> (Günther 1864)	M	35	3.6	0.5
Batrachoididae				
<i>Batrachoides gilberti</i> Meek & Hildebrand 1928	M	23	3.7	0.6
<i>Batrachoides goldmani</i> Evermann & Goldsborough 1902	U	21.6	3.5	0.6
Belonidae				
<i>Strongylura hubbsi</i> Collette 1974	U	49.8	4.1	0.7
<i>Strongylura marina</i> (Walbaum 1792)	M	111	3	0
<i>Strongylura notata</i> (Poey 1860)	M	61	4.4	0.7
Bryconidae				
<i>Brycon guatemalensis</i> Regan 1908	UM	59	2.3	0.3
Carangidae				
<i>Caranx latus</i> Agassiz 1831	M	101	4.2	0.4
<i>Oligoplites saurus</i> (Bloch & Schneider 1801)	M	35	4.3	0.5
Centropomidae				
<i>Centropomus ensiferus</i> Poey 1860	M	36.2	4.2	0.6
<i>Centropomus parallelus</i> Poey 1860	M	72	4.2	0.7
<i>Centropomus pectinatus</i> Poey 1860	M	56	4	0.7
<i>Centropomus undecimalis</i> (Bloch 1792)	UM	140	4.2	0.6
Characidae				
<i>Astyanax fasciatus</i> (Cuvier 1819)	M	16.8	3	0.3
Cichlidae				
<i>Chuco godmanni</i> (Günther 1862)	M	30	2.7	0.3
<i>Chuco intermedium</i> (Günther 1862)	UM	20	2.7	0.3
<i>Cincolichthys pearsei</i> (Hubbs 1936)	U	20	2	0
<i>Cribroheros robertsoni</i> (Regan 1905)	UM	19	3.4	0.4

Table 2-1. Continued

Species	Basin	MTL	FTL	SE
<i>Cryptoheros cutteri</i> (Fowler 1932)	M	11.2		
<i>Cryptoheros spilurus</i> (Günther 1862)	M	12	2	0
<i>Kihnichthys ufermanni</i> (Allgayer 2002)	U	25	3.6	0.5
<i>Maskaheros argenteus</i> (Allgayer 1991)	U	27		
<i>Mayaheros alborus</i> (Hubbs 1936)	U	39.4	3.9	0.6
<i>Mayaheros urophthalmus</i> (Günther 1862)	M	39.4	3.9	0.6
<i>Oreochromis aureus</i> (Steindachner 1864)	U	45.7	2.1	0
<i>Oscura heterospila</i> (Hubbs 1936)	U	24	2.7	0.3
<i>Parachromis friedrichsthalii</i> (Heckel 1840)	UM	28	4.2	0.7
<i>Parachromis managuensis</i> (Günther 1867)	M	55	4	0.6
<i>Petenia splendida</i> Günther 1862	UM	50	4.5	0.8
<i>Rheoheros lentiginosus</i> (Steindachner 1864)	U	25	2.8	0.3
<i>Rocio octofasciata</i> (Regan 1903)	UM	25	3.5	0.5
<i>Thorichthys affinis</i> (Günther 1862)	?	14	3.2	0.5
<i>Thorichthys aureus</i> (Günther 1862)	M	15	3.2	0.5
<i>Thorichthys helleri</i> (Steindachner 1864)	U	14.5	3.2	0.5
<i>Thorichthys meeki</i> Brind 1918	UM	17	2	0
<i>Thorichthys pasionis</i> (Rivas 1962)	U	17	3.2	0.5
				0.5
<i>Trichromis salvini</i> (Günther 1862)	UM	22	3.7	2
<i>Vieja bifasciata</i> (Steindachner 1864)	U	30	2	0
<i>Vieja melanura</i> (Günther 1862)	UM	19	2.6	0.3
Clupeidae				
<i>Dorosoma anale</i> Meek 1904	UM	20	3.4	0.4
<i>Dorosoma petenense</i> (Günther 1867)	UM	33	2.8	0.1
<i>Harengula jaguana</i> Poey 1865	M	21.2	3.4	0
<i>Opisthonema oglinum</i> (Lesueur 1818)	M	38	4.5	0
Cyprinidae				
<i>Ctenopharyngodon idella</i> (Valenciennes 1844)	U	150	2	0
Cyprinodontidae				
<i>Floridichthys polyommus</i> Hubbs 1936	M	11	2.9	0.4
Eleotridae				
<i>Dormitator maculatus</i> (Bloch 1792)	M	70	2.5	1
<i>Erotelis smaragdus</i> (Valenciennes 1837)	M	20	3.4	0.1
<i>Gobiomorus dormitor</i> Lacepède 1800	UM	90	3.6	0.1
Gerreidae				
<i>Diapterus rhombeus</i> (Cuvier 1829)	M	40	3	0.2
<i>Eucinostomus gula</i> (Quoy & Gaimard 1824)	M	23	2.7	0.1

Table 2-1. Continued

Species	Basin	MTL	FTL	SE
<i>Eucinostomus melanopterus</i> (Bleeker 1863)	M	30	3.4	0.5
<i>Eugerres brasilianus</i> (Cuvier 1830)	M	50	3.4	0.4
<i>Eugerres mexicanus</i> (Steindachner 1863)	U	21.6	3.4	0.5
<i>Eugerres plumieri</i> (Cuvier 1830)	M	40	2.2	0
<i>Gerres cinereus</i> (Walbaum 1792)	M	20	3.5	0.2
Gobiidae				
<i>Evorthodus lyricus</i> (Girard 1858)	M	15	3.4	0.4
<i>Gobioides broussonnetii</i> Lacepède 1800	M	55.3	3.7	0.5
Hemiramphidae				
<i>Hyporhamphus mexicanus</i> Álvarez 1959	U	16.1	3	0.4
<i>Hyporhamphus roberti</i> (Valenciennes 1847)	M	32	3	0.4
<i>Hyporhamphus unifasciatus</i> (Ranzani 1841)	M	30	2	0
Heptapteridae				
<i>Rhamdia guatemalensis</i> (Günther 1864)	UM	47.4	3.9	0.3
<i>Rhamdia laticauda</i> (Kner 1858)	UM	22.5	3.6	0.4
<i>Rhamdia quelen</i> (Quoy & Gaimard 1824)	UM	47.4	9.9	0.3
Ictaluridae				
<i>Ictalurus furcatus</i> (Valenciennes 1840)	U	165	3.4	0.4
<i>Ictalurus meridionalis</i> (Günther 1864)	U	73	3.7	0.4
Lacantuniidae				
<i>Lacantunia enigmatica</i> Rodiles-Hernández, Hendrickson & Lundberg 2005	U	42.7	3.3	0.5
Lepisosteidae				
<i>Atractosteus tropicus</i> Gill 1863	U	125	4.2	0.7
Lobotidae				
<i>Lobotes surinamensis</i> (Bloch 1790)	M	110	4	0.5
Loricariidae				
<i>Pterygoplichthys disjunctivus</i> (Weber 1991)	U	70		
<i>Pterygoplichthys pardalis</i> (Castelnau 1855)	U	42.3	2	0
Lutjanidae				
<i>Lutjanus griseus</i> (Linnaeus 1758)	M	89	4.2	0.3
<i>Lutjanus jocu</i> (Bloch & Schneider 1801)	M	128	4.4	0.3
Megalopidae				
<i>Megalops atlanticus</i> Valenciennes 1847	UM	250	4.5	0
Mugilidae				
<i>Mugil cephalus</i> Linnaeus 1758	U	100	2.5	0.2
<i>Mugil curema</i> Valenciennes 1836	UM	90	2	0
<i>Mugil liza</i> Valenciennes 1836	M	80	2	0

Table 2-1. Continued

Species	Basin	MTL	FTL	SE
<i>Mugil trichodon</i> Poey 1875	M	46	2	0
Poeciliidae				
<i>Belonesox belizanus</i> Kner 1860	UM	20	2.9	0.4
<i>Poecilia latipinna</i> (Lesueur 1821)	M	15	2	0
<i>Poecilia mexicana</i> Steindachner 1863	UM	11	2	0
<i>Xiphophorus hellerii</i> Heckel 1848	UM	14	3.2	0.4
Sciaenidae				
<i>Aplodinotus grunniens</i> Rafinesque 1819	U	95	3.4	0.4
Sparidae				
<i>Archosargus aries</i> (Valenciennes 1830)	M	91	3.5	0.5
Synbranchidae				
<i>Ophisternon aenigmaticum</i> Rosen & Greenwood 1976	UM	80	3.3	3
<i>Synbranchus marmoratus</i> Bloch 1795	M	150	2.8	0.5

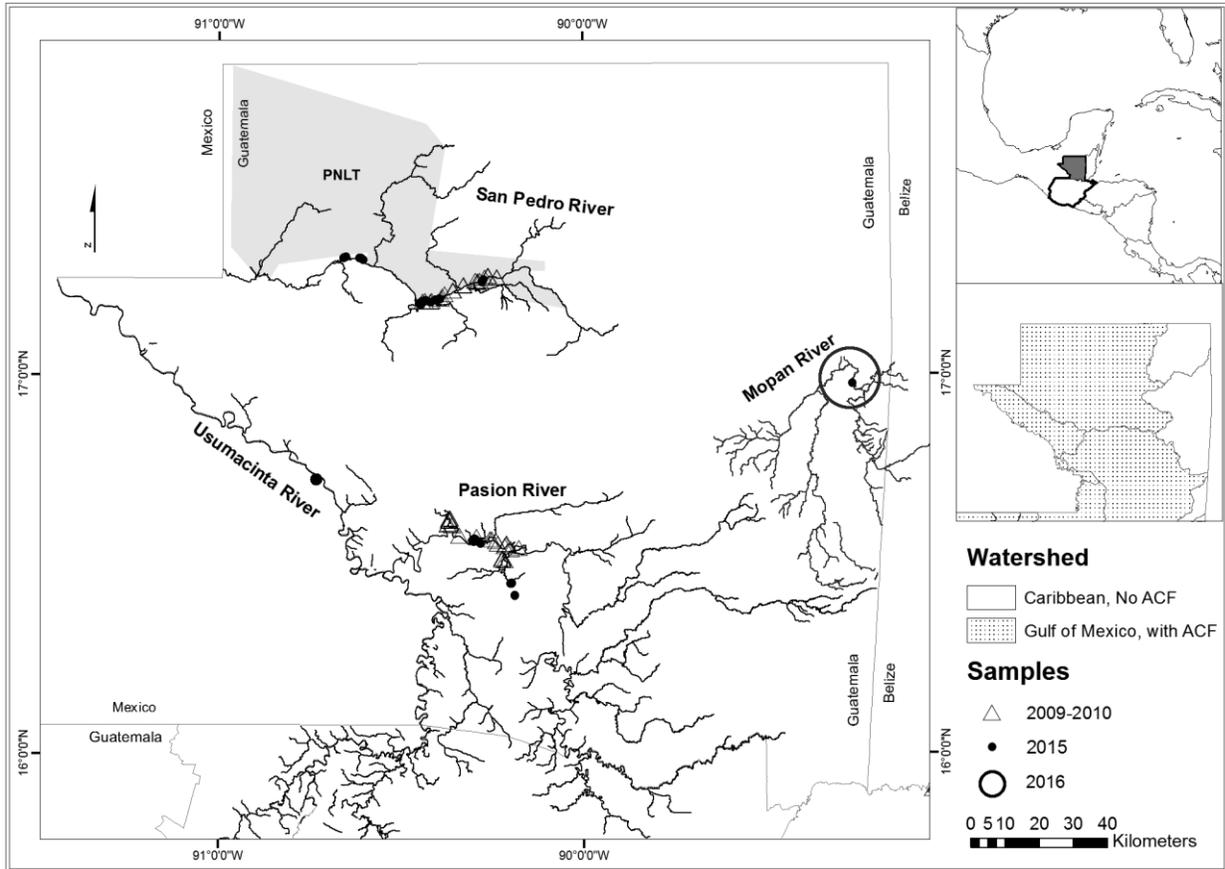


Figure 2-1. Study area for collection of Neotropical river otter scats in northern Guatemala. Triangles represent samples collected in 2009-2010; dots represent samples collected in 2015; circle represents the area where samples were collected in 2016. Dashed area represents the Usumacinta basin divided in sub-basins, where the armored catfish has been reported (ACF). The un-dashed area represents the Caribbean runoff where no ACF has been reported. PNLT = Laguna del Tigre National Park (for its initials in Spanish).

CHAPTER 3 RESULTS AND DISCUSSION

Results

Field collection of scats yielded 286 samples identified as coming from the NRO. After eliminating scats that had some type of contamination (e.g., wood, mud, or termite nest) in the fecal matter, 177 samples were sent for isotopic analysis (Table 3-1). I identified 35 scaled fish species, including three nonnative fish species (*Oreochromis aureus*, *Ctenopharyngodon idella* and *Pterygoplichtys* sp.), and one morphospecies of native catfish from otter scats. In addition, remains of unidentified insects, one reptile, one unidentified mammal, and unidentified crabs and crayfish were recovered from the scats (Table 3-2).

Pterygoplichtys sp. was the main identifiable prey item in all samples from the Usumacinta basin. Occurrence of ACF in scat samples was highest (49%) in samples collected from Pasion River 10 years after the first report of the catfish, an increase from 9.9% in 2010. ACF occurrence also increased in the San Pedro River, but less than in the Pasion River (from 16% in 2009 to 26% in 2015). *O. aureus* was an important item (percentage of occurrence > 5%) for otters in the Pasion and San Pedro rivers in 2015 and the Mopan River in 2016 (Table 3-2).

Based on species accumulation curves and comparing species numbers expected with equal number of scats, the expected number of prey species was relatively lower in 2015 than in 2010 in Pasion River samples (Figure 3-1); no difference was seen for San Pedro River samples (Figure 3-2). When all three rivers were compared based on data from 2015, otters from the San Pedro River were expected to

have more prey species, those from the Pasion River fewer species, and those from the Mopan River were expected to have a middle number of prey species. Confidence intervals around expected numbers were wide and overlapped, especially between curves from the Mopan River and the other two rivers (Figure 3-3). Further, the assumption that all samples used to construct the accumulation curves were independent may have been violated because some of the scats were collected from the same latrine.

Niche breadth (Levins' index, B_a) of the Neotropical river otter was lower 10 years after the ACF invasion in Pasion River when compared to 5 years after the invasion ($B_a = 0.48$ in 2010 vs 0.18 in 2015). A similar situation was found in the San Pedro River ($B_a = 0.53$ in 2009 vs 0.29 in 2015). NRO niche breadth varied among the three rivers in 2015, with similar values in San Pedro River and Mopan River and lower values in Pasion River ($B_a = 0.29, 0.28$ and 0.18 respectively).

Isotope values did not depart from a normal distribution so no transformations were needed (Figure 3-4). Variance of $\delta^{15}\text{N}$ signatures from fecal samples differed among groups (Levene's test for homoscedasticity; $W = 2.54, p = 0.042$; Figure 3-5). Based on pairwise comparisons, variance of $\delta^{15}\text{N}$ signatures from the Pasion River did not differ between years ($\sigma^2 = 2.45$ in 2010 and $\sigma^2 = 1.80$ in 2015; $W = 0.78, p = 0.37$; Figure 3-5). In contrast, variance of $\delta^{15}\text{N}$ differed significantly between years in samples from San Pedro River ($\sigma^2 = 4.83$ in 2009 and $\sigma^2 = 1.73$ in 2015; $W = 6.68, p < 0.01$; Figure 3-5). The $\delta^{13}\text{C}$ variances also differed ($W = 3.23, p < 0.01$; Figure 3-6), with pairwise contrasts indicating that $\delta^{13}\text{C}$ variances did not differ across years for Pasion

River ($\sigma^2 = 3.65$ in 2010 and $\sigma^2 = 6.49$ in 2015; $W = 3.83$, $p = 0.05$; Figure 3-6) but did differ in San Pedro River ($\sigma^2 = 2.04$ in 2009 and $\sigma^2 = 7.09$ in 2015; $W = 6.75$, $p = 0.01$; Figure 3-6).

Calculations of FTL values excluded information from *Maskaheros argenteus* (found in one sample from the Pasion River), insects, reptiles and unknown species because no data on the FTL of those prey items were available. Similarly, crabs and crayfish were excluded because they consume items from different trophic levels and their specific diets are not known for the study area (crabs were important prey items in Mopan 2016 and Pasion 2010 and this can hinder the FTL analysis using GSA). The highest FTL values for NRO came from the Mopan River in 2016, Pasion River in 2010, and San Pedro River in 2009 (3.79, 3.78 and 3.68, respectively). Lowest values came from the Pasion and San Pedro rivers in 2015 (3.48 and 3.47, respectively).

Values of $\delta^{15}\text{N}$ from NRO samples were highest in the Mopan River in 2015-16 (based on only one specimen), followed by mean values from the Pasion River in 2010 and the San Pedro River in 2009 (Figure 3-7). Lowest values came from the Pasion and San Pedro rivers in 2015 (Figure 3-7). Values of $\delta^{15}\text{N}$ from sites in the Usumacinta basin differed across years (ANOVA, $F_{1,141} = 67.98$; $p < 0.001$) and across rivers (ANOVA, $F_{1,141} = 15.53$; $p < 0.001$) with no interactions between the two factors (ANOVA, $F_{1,141} = 2.76$; $p = 0.10$). Higher values were found from scats collected during the early sampling years in the Pasion and San Pedro rivers, five years after the first report of the ACF (post-hoc pairwise t -test with Bonferroni adjusted p -values: Pasion 2010 vs. 2015 $t = 5.37$, $df = 68$, $p < 0.001$; San Pedro 2009 vs. 2015, $t = 5.31$, $df =$

24.122, $p < 0.001$). Mean values of NRO $\delta^{15}\text{N}$ did not differ between the Pasion and San Pedro rivers from equivalent sample years (Pasion vs. San Pedro 2010-2009 $t = -0.40$, $df = 54$, $p = 1.0$; Pasion vs. San Pedro 20015, $t = 2.42$, $df = 87$ $p = 0.23$).

Discussion

Concordance between the GSA and SIA values strongly supports the idea that an increase in consumption of the ACF reduced the dietary NRO niche breadth and trophic level at which the NRO feeds in northern Guatemala. As predicted, ACF became the main prey species for the NRO in invaded rivers and, as a consequence, NRO $\delta^{15}\text{N}$ variances and mean values decreased over time in both invaded rivers (with a weaker decline in Pasion River). The same pattern was observed in the standardized niche breadth index (B_a). Further, the wider niche breadth (B_a values) in the San Pedro River may be related to its higher environmental integrity (located adjacent to a national park) that could help sustain the richness of native NRO prey or reduce the invasiveness of the ACF. This conclusion is supported by the species accumulation curves. Invasive species are predicted to have better chances of establishment in native assemblages that are depleted or disrupted and more likely to have long-term success in systems highly altered by human activity (Moyle and Light 1996). The increase in $\delta^{13}\text{C}$ variation over time suggests that the NRO diet included a prey that consumes a wider range of producer types, likely as a consequence of the ability of ACF to exploit a wider range of plant resources. Furthermore, the decrease in FTL across rivers (Mopan River showing similar values to San Pedro River and higher than Pasion River) combined with lower mean values of $\delta^{15}\text{N}$ provide evidence of a reduction in the NRO trophic level associated with ACF presence.

The range of prey types exploited by NRO changed after the invasion of ACF, with the lowest dietary niche breadth found in Pasion River 10 years after the invasion. The dietary NRO niche breadth changed from that of a mild generalist to that of a specialist ($0.6 > B_a > 0.4$ to $B_a < 0.4$, Levins' standardized index) in Pasion and San Pedro rivers, despite the fact that the number of prey species consumed by NRO was highest in the San Pedro River in 2015. This result is concordant with the idea that a specialist can use a wide range of resources but still concentrate on a subset of those resources (Peers et al. 2012). It also supports the statement that NRO prey mostly on slow-moving and territorial prey species (Rheingantz et al. 2012) that constitute the main prey species for NRO in this study with ranges of importance for Loricariidae from 9.9 to 49.3%, Cichlidae from 34.1 to 46.5%, large Poeciliidae from 1.1 to 25.2%, and crabs from 0 to 35.2%.

The results based on GSA and $\delta^{15}\text{N}$ variances were similar for both indexes, with narrower niche breadth 10 years after initiation of the ACF invasion compared to 5-6 years after the invasion. The narrow dietary niche breath found in the Pasion River in all situations and with both indexes in relation to the San Pedro River support the idea that the Pasion River prey community was already depleted before the introduction of the ACF, and that the Laguna del Tigre National Park provided some type of protection to the San Pedro River. A similar result was seen in a Bahamas mangrove system for grey snapper (*Lutjanus griseus*) with a reduced niche breadth (based on SIA) found in disturbed areas (Layman et al. 2007). Therefore, I suggest that the higher values of the NRO niche breadth in San Pedro River in relation to Pasion River, are related to differences in the resilience of the two rivers due to differences in habitat conservation.

Disturbances may facilitate the ACF or depress populations of native fish. For example, in the Guadalquivir marshes of southwestern Spain, the Eurasian otter (*Lutra lutra*) included high levels of an invasive species (75%; North American red swamp crayfish, *Procambarus clarkii*) in its diet within 10 years of the invasion. In the same area, various water birds similarly consumed this invasive species at higher rates in disturbed locations than in natural marshes (Tablado et al. 2010).

In contrast to results from $\delta^{15}\text{N}$, variances of $\delta^{13}\text{C}$ in fecal samples were greater 10 years after the ACF invasion compared to 5 years after. Values of $\delta^{13}\text{C}$ represent the plant source of a food chain and a wider variance may indicate that primary consumers exploit a greater range of producers. Loricariidae (family of the ACF) may exploit a diverse variety of basal sources, which may help explain the increase in the variance of $\delta^{13}\text{C}$ in NRO scats, given the increased presence of ACF in the NRO diet (Burress et al. 2013).

Native predators may act to reduce invasive species numbers (Ward-Fear et al. 2010, Wanger et al. 2011), an idea supported by an analysis of streams in California suggesting that predation could be one of the main biological drivers by which streams can resist the invasion of exotic species (Baltz and Moyle 1993). Further, predators from different taxa often adapt to and benefit from the consumption of invasive species (King et al. 2006, Skewes et al. 2012, Cattau et al. 2016). In this context, NRO may act as a buffer to hold ACF populations at low levels and minimize their potential negative effects on the system. The question that arises from this situation, as in other systems where an invasive species becomes the main prey of a native predator (Tablado et al. 2010),

is whether the consumption of ACF by NRO and other native predators can facilitate the predators. Denser predator populations, may depredate native prey that are threatened by overexploitation or habitat loss (Roemer et al. 2002). This effect is a valid concern in our study area, where cichlids were exploited as a group without much change when the consumption of ACF increased (Table 3-2).

Both GSA and $\delta^{15}\text{N}$ values indicated a reduction in the trophic level at which otters feed in rivers where ACF are present in northern Guatemala. Based on GSA, there were reductions in the FTL of NRO of approximately 0.33 FTL in the Pasion River and 0.2 FTL in the San Pedro River. These reductions may not represent much ecological difference. GSA may, however, under-estimate the consumption of some species and over-estimate the consumption of others either as a consequence of differences in digestibility of prey or because I measured presence of prey remains rather than consumed biomass, regardless of the amount of remains (not all remains were identifiable; e.g., spines). In contrast to GSA, SIA may give a more accurate result. Differences in mean $\delta^{15}\text{N}$ were as great as 1.88‰ for Pasion River and 2.78‰ for San Pedro River. If we use the widely accepted 3.4‰ enrichment ($\Delta^{15}\text{N}$) per FTL, these differences in mean $\delta^{15}\text{N}$ may represent changes of 0.5 to 0.8 FTLs in the Pasion and San Pedro rivers, respectively. The 3.4‰ $\Delta^{15}\text{N}$ value has, however, been criticized. Models and empirical data have shown that this enrichment factor can underestimate FTL of marine predators (Hussey et al. 2014). In any case, the observed mean $\delta^{15}\text{N}$ values for NRO in both the Pasion and San Pedro rivers may represent a change from one FTL to a lower one.

The reduction in the trophic level at which the otters fed can have diverse effects on the riverine ecosystem. These effects may be difficult to anticipate and can compete with or interact with each other. It could mean predator release for other prey species that would benefit from reduced predation pressure (Grosholz et al. 2000, Rodriguez 2006). On the other hand, consumption of the invasive species may benefit the predator, eventually leading to higher predator densities that could increase pressure on other native species. A model evaluating this situation suggests that predation on native prey by a native predator whose numbers have been enhanced by consumption of an invasive species can be more harmful than direct competition between native and invasive species (Noonburg and Byers 2005). Empirical data using SIA for golden eagles (*Aquila chrysaetos*) suggests that these eagles were able to colonize the California Channel Islands after the introduction of feral pigs (*Sus scrofa*; Roemer et al. 2002). Nonetheless, eagles still preferred to prey on endemic meso-carnivores, including a fox (*Urocyo littoralis*) and skunk (*Spilogale gracilis amphiala*), pushing the fox towards extinction (Roemer et al. 2002).

Another potential effect that needs to be evaluated is the reduction of trophic levels in the system by moving energy directly from primary consumers to top predators and by eliminating food-web links in the mid-trophic levels through competition or predation facilitated by higher densities of predators in response to the high abundance of the invasive (Tablado et al. 2010). A similar situation was found in the United Kingdom, where researchers compared the complete community of fishes in a pond with a low-trophic-level invasive cyprinid (*Pseudorasbora parva*) composing > 99% of fish present with that in another pond without the cyprinid. They reported a reduction in

the $\delta^{15}\text{N}$ values of piscivorous fish and a mean reduction in the $\delta^{15}\text{N}$ of the complete fish community (Britton et al. 2010). Further studies are needed to investigate the effect of different types of land management, as well as factors that indicate the ecological integrity of communities, on the ability of communities to resist or facilitate the invasion of exotic species and their interactions with native predators.

Table 3-1. Scats of Neotropical river otters collected in northern Guatemala. Scats without contamination were used for fecal matter isotope analyses

River	No. of scats collected (year)	No. of scats without contamination (year)
Usumacinta	1 (2015)	0
	1 Total	0 Total
San Pedro	36 (2009)	20 (2009)
	117 (2015)	55 (2015)
	153 Total	75 Total
La Pasion	52 (2010)	36 (2010)
	40 (2015)	34 (2015)
	92 Total	70 Total
Mopan	1 (2015)	1 (2015)
	39 (2016)	31 (2016)
	40 Total	32 Total

Table 3-2. Number of records (No), and percentage of the total of prey species (%) found in otter scats collected from the Mopan, Pasion and San Pedro (San Pe.) rivers, northern Guatemala, during 2009-2010 (09-10) and during 2015-2016 (15-16). Fish family and species names follow Eschmeyer and Fong (2016).

	Mopan		Pasion		Pasion		San Pe.		San Pe.	
	15-16		09-10		15-16		09-10		15-16	
	No	%	No	%	No	%	No	%	No	%
Belonidae										
<i>Strongylura hubbsi</i>	0	0	0	0	0	0	3	2.2	0	0
<i>Strongylura marina</i>	1	1.1	0	0	0	0	0	0	0	0
Carangidae										
<i>Caranx latus</i>	1	1.1	0	0	0	0	0	0	0	0
Centropomidae										
<i>Centropomus ensiferus</i>	1	1.1	0	0	0	0	0	0	0	0
Characidae										
<i>Astianax fasciatus</i>	0	0	0	0	0	0	9	6.5	1	0.3
Cichlidae										
<i>Chuco intermedius</i>	6	6.6	0	0	0	0	0	0	1	0.3
<i>Cincelichthys bocourti</i>	1	1.1	0	0	1	1.4	0	0	1	0.3
<i>Cincelichthys pearsei</i>	0	0	0	0	0	0	0	0	1	0.3
							15.			
<i>Cribroheros robertsoni</i>	1	1.1	13	9.1	4	5.5	22	8	12	4.1
<i>Kihmchithys ufermammi</i>	0	0	0	0	0	0	3	2.2	1	0.3
<i>Maskaheros argenteus</i>	0	0	1	0.7	0	0	0	0	0	0
<i>Mayaheros urophtalmus</i>	2	2.2	5	3.5	5	6.8	5	3.6	17	5.9
<i>Oreochromis aureus</i>	8	8.8	5	3.5	6	8.2	4	2.9	21	7.3
<i>Parachromis</i>										
<i>friedrichsthalii</i>	2	2.2	9	6.3	5	6.8	1	0.7	4	1.4
<i>Petenia splendida</i>	0	0	1	0.7	0	0	0	0	3	1
<i>Rheoheros lentiginosus</i>	0	0	1	0.7	1	1.4	0	0	0	0
<i>Rocio octofasciata</i>	0	0	2	1.4	1	1.4	0	0	3	1
<i>Thorichthys affinis</i>	0	0	2	1.4	0	0	0	0	1	0.3
<i>Thorichthys aureus</i>	6	6.6	0	0	0	0	0	0	0	0
<i>Thorichthys meeki</i>	5	5.5	11	7.7	2	2.7	10	7.2	25	8.6
<i>Thorichthys pasionis</i>	0	0	10	7.0	1	1.4	10	7.2	8	2.8
<i>Trichromis salvini</i>	0	0	0		0	0	0	0	2	0.7
<i>Vieja bifasciata</i>	0	0	3	2.1	6	8.2	1	0.7	21	7.3
<i>Vieja melanurus</i>	0	0	3	2.1	1	1.4	0	0	8	2.8
Cyprinidae										
<i>Ctenopharyngodon idella</i>	0	0	7	4.9	0	0	0	0	5	1.7
Eleotridae										
<i>Dormitator maculatus</i>	1	1.1	0	0	0	0	0	0	0	0

Table 3-2. Continued

	Mopan 15-16		Pasion 09-10		Pasion 15-16		San Pe. 09-10		San Pe. 15-16	
Gerreidae										
<i>Eugerres mexicanus</i>	0	0	0	0	0	0	0	0	4	1.4
Hemiramphidae										
<i>Hyporhamphus mexicanus</i>	0	0	0	0	0	0	9	6.5	2	0.7
Lepisosteidae										
<i>Aractosteus tropicus</i>	0	0	0	0	0	0	1	0.7	0	0
Loricariidae										
<i>Pterygoplichthys</i> sp	0	0	14	9.9	36	49. 3	23	16. 5	75	25. 9
Megalopidae										
<i>Megalops atlanticus</i>	0	0	0	0	0	0	0	0	1	0.3
Mugilidae										
<i>Mugil cephalus</i>	0	0	1	0.7	0	0	0	0	0	0
Poeciliidae										
<i>Belonesox belizanus</i>	0	0	5	3.5	0	0	1	0.7 12.	12	4.1
<i>Poecilia mexicana</i>	1	1.1	3	2.1	1	1.4	17	2 12.	24	8.3
<i>Poecilia petenensis</i>	0	0	11	7.7	1	1.4	17	2	26	9
Ariidae, Heptapteridae, Ictaluridae										
Catfish	8	8.8	3	2.1	1	1.4	3	2.2	4	1.4
Crab		35.		21.						
Crayfish	32	2	30	1	0	0	0	0	3	1
Insect	0	0	0	0	0	0	0	0	1	0.3
Reptile	3	3.3	0	0	0	1.3 7	0	0	0	0
Unknown	8	8.8	2	1.4	0	0	0	0	2	0.7
Unknown mammal	1	1.1	0	0	0	0	0	0	0	0
Totals	44	100	109	100	72	100	13 8	100	283	100

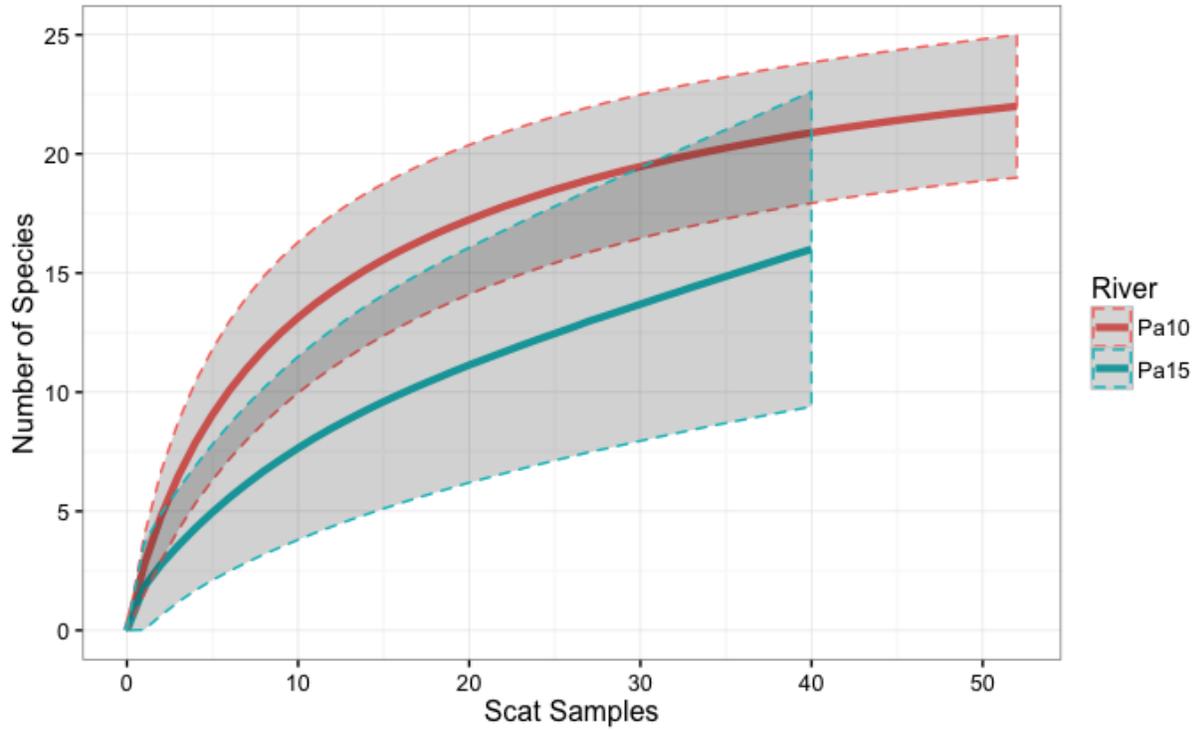


Figure 3-1. Species accumulation curves for prey species found in scats of Neotropical river otter in the Pasion River, Guatemala 2010 (Pa10) and 2015 (Pa15)

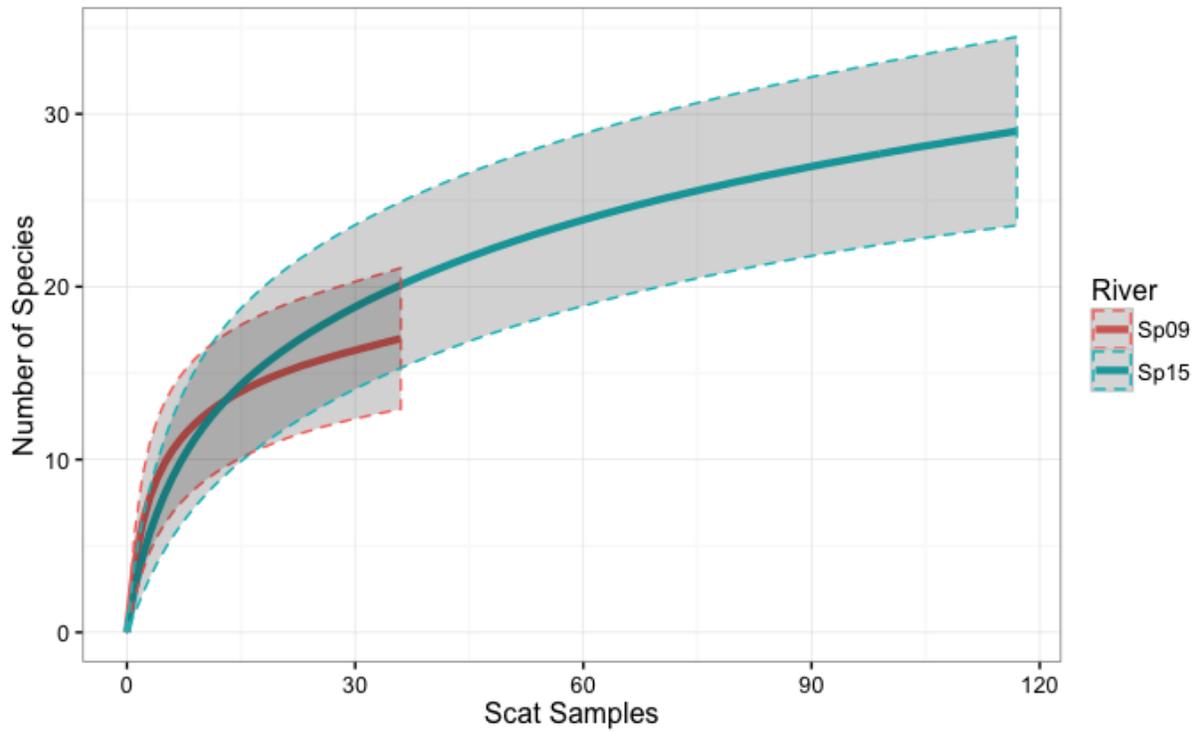


Figure 3-2. Species accumulation curves for prey species found in scats of Neotropical river otter in the San Pedro River, Guatemala, in 2009 (Sp09) and 2015 (Sp15)

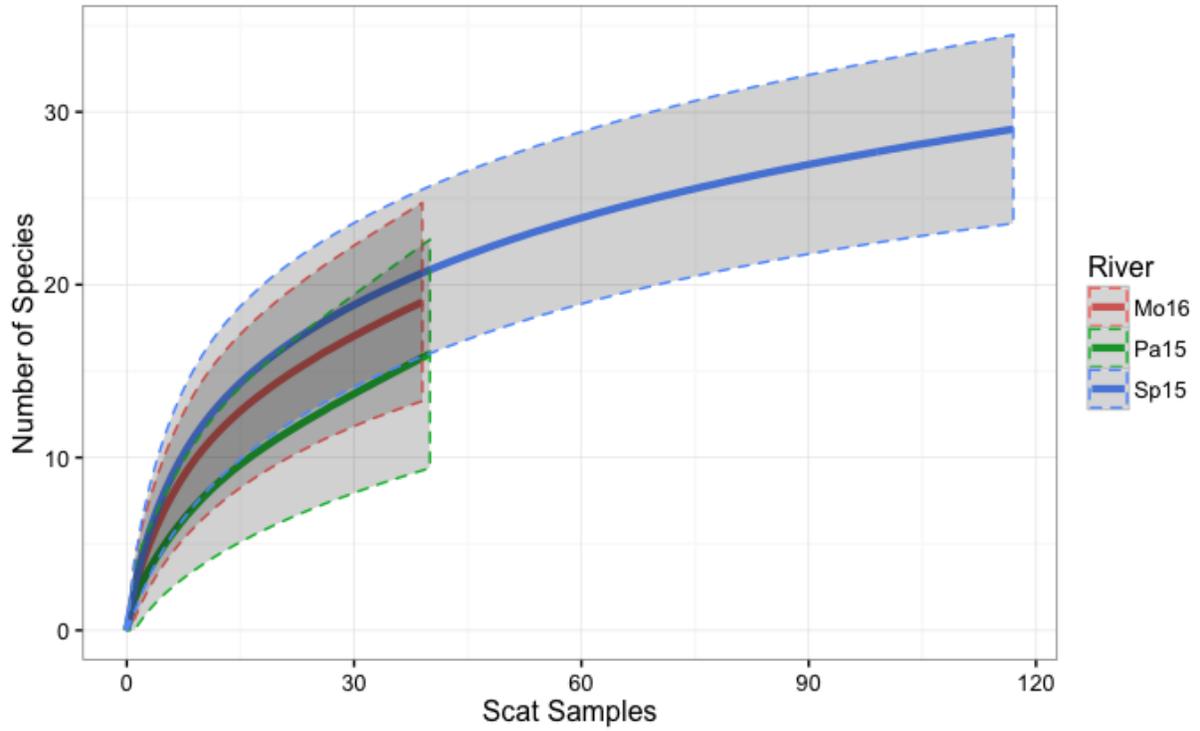


Figure 3-3. Species accumulation curves for prey species found in scats of Neotropical river otter in Mopan River 2016 (Mo16), Pasion River 2015 (Pa15) and San Pedro River 2015 (Sp15).

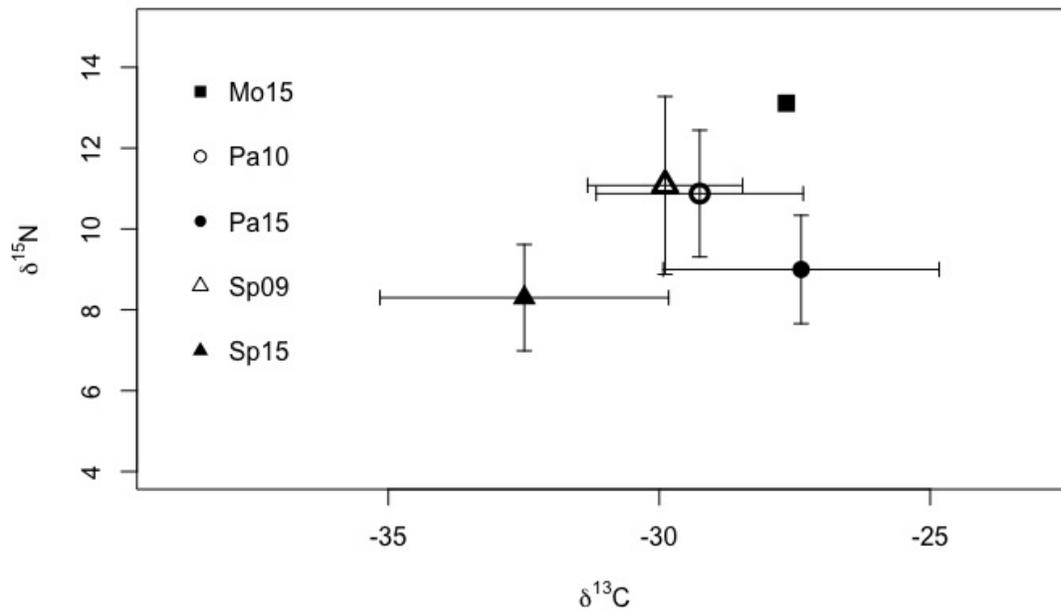


Figure 3-4. Isotopic values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from Neotropical river otter scats collected from the study area. Error bars are one sd. Mo15= samples from Mopan River 2015 (n=1); Pa10, Pa15 = samples from Pasion River 2010 and 2015 (n = 36 in 2010 and 34 in 2015); Sp09, Sp15 = samples from San Pedro River 2009 and 2015 (n = 20 in 2010 and 55 in 2015).

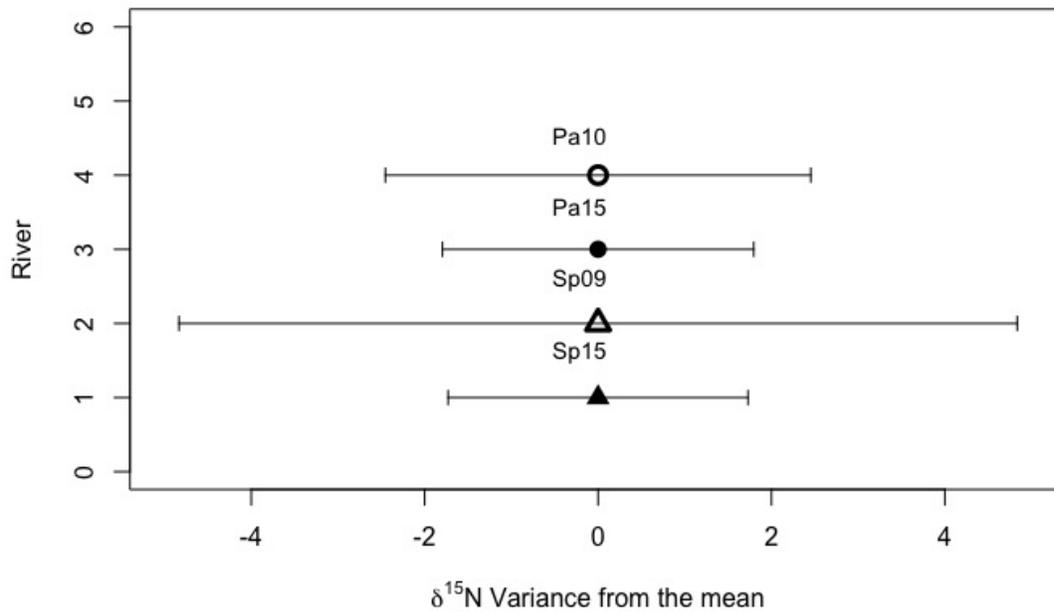


Figure 3-5. Variance from the mean for $\delta^{15}\text{N}$ in fecal samples from Neotropical river otters in Guatemala. The mean is set to 0 to help visualize the magnitude of the variances. Pa10, Pa15 = samples from Pasion River 2010 and 2015 (n = 36 in 2010 and 34 in 2015); Sp09, Sp15 = samples from San Pedro River 2009 and 2015 (n = 20 in 2010 and 55 in 2015).

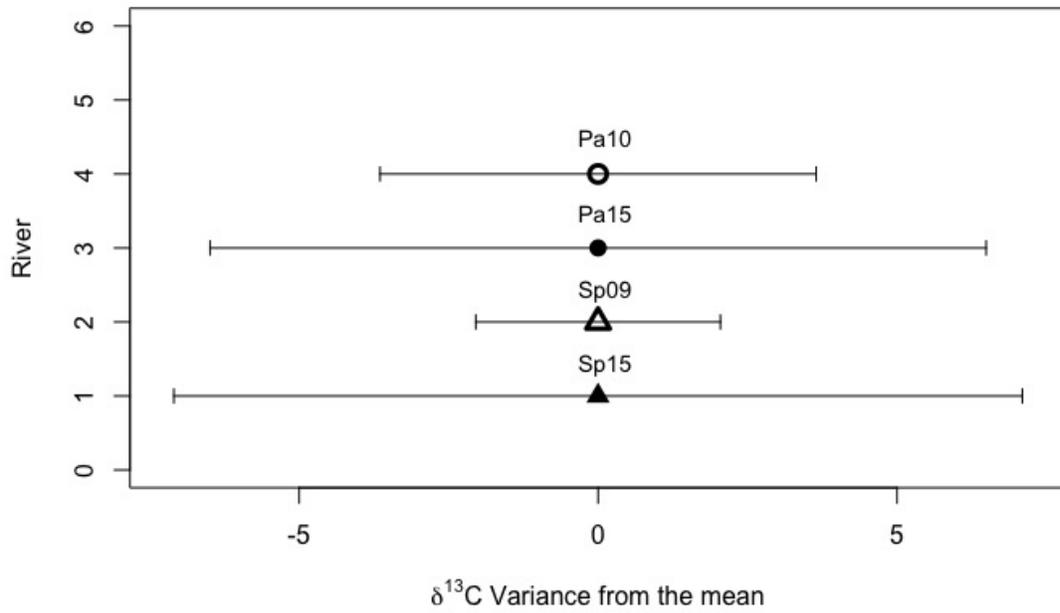


Figure 3-6. Variance from the mean for $\delta^{13}\text{C}$ in fecal samples from Neotropical river otters in Guatemala. The mean is set to 0 to help visualize the magnitude of the variances. Pa10, Pa15 = samples from Pasion River 2010 and 2015 (n = 36 in 2010 and 34 in 2015); Sp09, Sp15 = samples from San Pedro River 2009 and 2015 (n = 20 in 2010 and 55 in 2015).

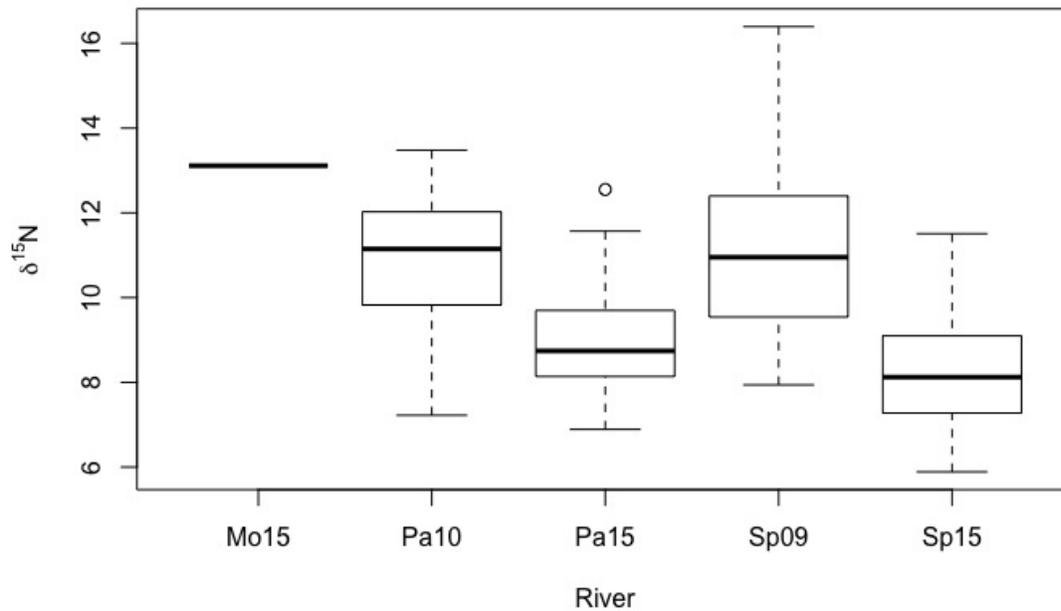


Figure 3-7. Boxplots for $\delta^{15}\text{N}$ in fecal samples from Neotropical river otters in Guatemala. Mo16 = samples from Mopan River 2016 ($n = 1$); Pa10, Pa15 = samples from Pasion River 2010 and 2015 ($n = 36$ in 2010 and $n = 34$ in 2015); Sp09, Sp15 = samples from San Pedro River 2009 and 2015 ($n = 20$ in 2009 and $n = 55$ in 2015).

APPENDIX
SCALE GUIDE TO IDENTIFY MEDIUM AND LARGE FRESHWATER FISH FROM
NORTHERN GUATEMALA

To access to the guide with fish scales images follow this [link](#)

LIST OF REFERENCES

- Angerbjorn, A., P. Hersteinsson, K. Liden, and E. Nelson. 1994. Dietary variation in arctic foxes (*Alopex lagopus*): An analysis of stable carbon isotopes. *Oecologia* 99:226–232.
- Aranda-Sánchez, J. M. 2012. Manual para el rastreo de mamíferos silvestres de México. H. K. Suárez Huesca, L. Hernández Vázquez, and F. de J. Escobar Ramírez, editors. Primera ed. Ciba Diseño y Arte Editorial, México D.F.
- Aurioles-Gamboa, D., S. D. Newsome, S. Salazar-Pico, and P. L. Koch. 2009. Stable isotope differences between sea lions (*Zalophus*) from the Gulf of California and Galapagos Islands. *Journal of Mammalogy* 90:1410–1420.
- Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* 3:246–255.
- Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology* 73:1007–1012.
- Bijukumar, A., R. Smrithy, U. Sureshkumar, and S. George. 2015. Invasion of South American suckermouth armoured catfishes *Pterygoplichthys* spp. (Loricariidae) in Kerala, India - a case study. *Journal of Threatened Taxa* 7:6987–6995.
- Blundell, G., M. Ben-David, and R. Bowyer. 2002. Sociality in river otters: Cooperative foraging or reproductive strategies? *Behavioral Ecology* 13:134–141.
- Britton, J. R., G. D. Davies, and C. Harrod. 2010. Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: A field investigation in the UK. *Biological Invasions* 12:1533–1542.
- Brown, J. S., B. P. Kotler, and A. Bouskila. 2001. Ecology of fear: Foraging games between predators and prey with pulsed resources. *Annales Zoologici Fennici* 38:71–87.
- Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385–399.
- Bunkley-Williams, L., E. H. Williams Jr., C. G. Lilystrom, I. Corujo-Flores, A. J. Zerbi, C. Aliaume, and T. N. Churchill. 1994. The South American sailfin armored catfish, *Liposarcus multiradiatus* (Hancock), a new exotic established in Puerto Rican fresh waters. *Caribbean Journal of Science* 30:90–94.
- Burkhead, N. M. 2012. Extinction rates in North American freshwater fishes, 1900–2010. *BioScience* 62:798–808.

- Burress, E. D., A. Duarte, M. M. Gangloff, and L. Siefferman. 2013. Isotopic trophic guild structure of a diverse subtropical South American fish community. *Ecology of Freshwater Fish* 22:66–72.
- Cabrera-Guzmán, E., M. R. Crossland, and R. Shine. 2015. Invasive cane toads as prey for native arthropod predators in tropical Australia. *Herpetological Monographs* 29:28–39.
- Capps, K. A., and A. S. Flecker. 2013. Invasive fishes generate biogeochemical hotspots in a nutrient-limited system. *PLoS ONE* 8:e54093.
- Capps, K. A., and A. S. Flecker. 2015. High impact of low-trophic-position invaders: Nonnative grazers alter the quality and quantity of basal food resources. *Freshwater Science* 34:784–796.
- Capps, K. a., L. G. Nico, M. Mendoza-Carranza, W. Arévalo-Frías, A. J. Ropicki, S. a. Heilpern, and R. Rodiles-Hernández. 2011. Salinity tolerance of non-native suckermouth armoured catfish (Loricariidae: *Pterygoplichthys*) in south-eastern Mexico: Implications for invasion and dispersal. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21:528–540.
- Capps, K. A., A. Ulseth, and A. S. Flecker. 2014. Quantifying the top-down and bottom-up effects of a non-native grazer in freshwaters. *Biological Invasions* 17:1253–1266.
- Carlsson, N. O., O. Sarnelle, and D. L. Strayer. 2009. Native predators and exotic prey: An acquired taste? *Frontiers in Ecology and the Environment* 7:525–532.
- Casariego-Madorell, A., R. List, and G. Ceballos. 2008. Tamaño poblacional y alimentación de la nutria de río (*Lontra longicaudis annectens*) en la costa de Oaxaca, México. *Acta Zoológica Mexicana* 24:179–200.
- Cattau, C. E., R. J. Fletcher Jr., B. E. Reichert, and W. M. Kitchens. 2016. Counteracting effects of a non-native prey on the demography of a native predator culminate in positive population growth. *Ecological Applications* 26:1952–1968.
- Chaichana, R., S. Pouangcharean, and R. Yoonphand. 2013. Foraging effects of the invasive alien fish *Pterygoplichthys* on eggs and first-feeding fry of the native *Clarias macrocephalus* in Thailand. *Kasetsart Journal* 47:581–588.
- Chavez, J. M., R. M. De La Paz, S. K. Manohar, R. C. Pagulayan, and J. R. Carandang. 2006. New Philippine record of South American sailfin catfishes (Pisces: Loricariidae). *Zootaxa* 68:57–68.

- Chemes, S. B., A. R. Giraudo, and G. Gil. 2010. Dieta de *Lontra Longicaudis* (Carnivora, Mustelidae) en el Parque Nacional El Rey (Salta, Argentina) y su comparación con otras poblaciones de la cuenca. *Mastozoología Neotropical* 17:19–29.
- Codron, D., J. Codron, J. A. Lee-Thorp, M. Sponheimer, and D. de Ruiter. 2005. Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research* 35:43–52.
- Colwell, R. K., X. M. Chang, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85:2717–2727.
- Colwell, R. K. 2013. EstimateS 9.1.0: Statistical estimation of species richness and shared species from samples. (Software and User's Guide) Department of Ecology & Evolutionary Biology, University of Connecticut, USA. <http://viceroy.eeb.uconn.edu/estimates> version (6/2013)
- Corcuera Zababurú, C. A. 2015. Evaluación de la temperatura letal máxima para *Hypostomus hemicochiodon* y *Pterygoplichthys pardalis* en el centro de investigaciones Carlos Miguel Castañeda Ruiz. Universidad nacional Toribio Rodríguez de Mendoza de Amazonas.
- Crait, J. R., and M. Ben-David. 2007. Effects of river otter activity on terrestrial plants in trophically altered Yellowstone Lake. *Ecology* 88:1040–1052.
- Crowley, S., C. J. Johnson, and D. P. Hodder. 2013. Spatio-temporal variation in river otter (*Lontra canadensis*) diet and latrine site activity. *Écoscience* 20:28–39.
- da Cruz, A. L., H. R. da Silva, L. M. Lundstedt, A. R. Schwantes, G. Moraes, W. Klein, and M. N. Fernandes. 2013. Air-breathing behavior and physiological responses to hypoxia and air exposure in the air-breathing loricariid fish, *Pterygoplichthys anisitsi*. *Fish Physiology and Biochemistry* 39:243–256.
- Darimont, C. T., and T. E. Reimchen. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Canadian Journal of Zoology* 80:1638–1642.
- Eschmeyer, W. N., and J. D. Fong. 2016. Catalog of Fishes. <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>, version (08/2016).
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.

- Fortin, J. K., C. C. Schwartz, K. A. Gunther, J. E. Teisberg, M. A. Haroldson, M. A. Evans, and C. T. Robbins. 2013. Dietary adjustability of grizzly bears and American black bears in Yellowstone National Park. *The Journal of Wildlife Management* 77:270–281.
- Froese, R. and D. Pauly. Editors. 2016. FishBase. <http://www.fishbase.us/>, version (06/2016).
- Fry, B. 2008. *Stable isotope ecology*. 3rd edition. Springer Science+Business Media, LLC, United States of America.
- Gibbs, M. a., B. N. Kurth, and C. D. Bridges. 2013. Age and growth of the loricariid catfish *Pterygoplichthys disjunctivus* in Volusia Blue Spring, Florida. *Aquatic Invasions* 8:207–218.
- Gibbs, M. A., J. H. Shields, D. W. Lock, K. M. Talmadge, and T. M. Farrell. 2008. Reproduction in an invasive exotic catfish *Pterygoplichthys disjunctivus* in Volusia Blue Spring, Florida, U.S.A. *Journal of Fish Biology* 73G:1562–1572.
- Gibbs, M., T. Futral, M. Mallinger, D. Martin, and M. Ross. 2010. Disturbance of the Florida manatee by an invasive catfish. *Southeastern Naturalist* 9:635–648.
- Greenfield, D. W., and J.E. Thomerson. 1997. *Fishes of the continental waters of Belize*. University Press of Florida.
- Granados-Dieseldorff, P., M. F. Christensen, and P. H. Kihn-Pineda. 2012. Fishes from Lachuá lake, upper Usumacinta basin, Guatemala. *Check List* 8:95–101.
- Grosholz, E. D., G. M. Ruiz, C. a Dean, K. a Shirley, L. John, P. G. Connors, S. Ecology, and N. May. 2000. The impacts of a nonindigenous marine predator in a California Bay. *Ecology* 81:1206–1224.
- Hatch, K. A., B. L. Roeder, R. S. Buckman, B. H. Gale, S. T. Bunnell, D. L. Eggett, J. Auger, L. A. Felicetti, and G. V. Hilderbrand. 2011. Isotopic and gross fecal analysis of American black bear scats. *Ursus* 22:133–140.
- Holdridge, L. R., Genke, W. C., Hatheway, W. H., Liang T. and Tosi, J. A. 1971. *Forest environment in tropical life zones: a pilot study*. Oxford: Pergamon Press.
- Hubbs, C., R. J. Edwards, and G. P. Garrett. 2008. *An annotated checklist of the freshwater fishes of Texas, with keys to identification of species*. Second Edi. Texas Academy of Science, Austin.
- Hubilla, M., F. Kis, and J. Primavera. 2007. Janitor fish *Pterygoplichthys disjunctivus* in the Agusan Marsh: A threat to freshwater biodiversity. *Journal of Environmental Science and Management* 10:10–23.

- Hussey, N. E., M. A. Macneil, B. C. Mcmeans, J. A. Olin, S. F. J. Dudley, G. Cliff, S. P. Wintner, S. T. Fennessy, and A. T. Fisk. 2014. Rescaling the trophic structure of marine food webs. *Ecology Letters* 17:239–250.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- INSIVUMEH. 2016. Atlas Climatológico de Guatemala. <http://www.insivumeh.gob.gt> (09/2016)
- Juárez-Sánchez, A. D., C. G. Estrada, M. Bustamante, Y. Quintana, and J. E. López. 2007. Guía ilustrada de pelos para la identificación de mamíferos medianos y mayores de Guatemala. Dirección General de Investigación, Universidad de San Carlos de Guatemala.
- Jones, H. P., B. R. Tershy, E. S. Zavaleta, D. A. Croll, B. S. Keitt, M. E. Finkelstein, and G. R. Howald. 2008. Severity of the effects of invasive rats on seabirds: A global review. *Conservation Biology* 22:16–26.
- Kasper, C. B., V. A. G. Bastazini, J. Salvi, and H. C. Z. Grillo. 2008. Trophic ecology and the use of shelters and latrines by the Neotropical otter (*Lontra longicaudis*) in the Taquari Valley, Southern Brazil. *Iheringia Série Zoologia* 98:469–474.
- Kasper, C. B., M. J. Feldens, J. Salvi, H. César, and Z. Grillo. 2004a. Estudo preliminar sobre a ecologia de *Lontra longicaudis* (Olfers) (Carnivora, Mustelidae) no Vale do Taquari, Sul do Brasil. *Revista Brasileira de Zoologia* 21:65–72.
- Kasper, C. B., J. Salvi, and H. C. Zanardi Grillo. 2004b. Estimativa do tamanho de duas espécies de ciclídeos (Osteichthyes, Perciformes) predados por *Lontra longicaudis* (Olfers) (Carnivora, Mustelidae), através de análise das escamas. *Revista Brasileira de Zoologia* 21:499–503.
- Keeler, M. S., F. S. Chew, B. C. Goodale, and J. M. Reed. 2006. Modelling the impacts of two exotic invasive species on a native butterfly: Top-down vs. bottom-up effects. *Journal of Animal Ecology* 75:777–788.
- Kelly, J. F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78:1–27.
- King, R. B., J. M. Ray, and K. M. Stanford. 2006. Gorging on gobies: Beneficial effects of alien prey on a threatened vertebrate. *Canadian Journal of Zoology* 84:108–115.
- Krebs, C. J. 1999. *Ecological Methodology*. Second Edition. Addison-Wesley Educational Publishers, Inc., New York.

- Kruuk, H., E. Balharry, and P. T. Taylor. 1994. Oxygen consumption of the Eurasian Otter *Lutra lutra* in relation to water temperature. *Physiological Zoology* 67:1174–1185.
- LaBastille, A. 1974. Ecology and management of the Atitlan Grebe, Lake Atitlan, Guatemala. *Wildlife Monograph* 37:3–66.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: Reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.
- Layman, C. A., J. P. Quattrochi, C. M. Peyer, and J. E. Allgeier. 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters* 10:937–944.
- Levins, R. 1968. Evolution in changing environments: Some theoretical explorations. *Monographs in Population Biology* (No. 2). Princeton University Press, Princeton, NJ.
- Levin, B. A., P. H. Phuong, and D. S. Pavlov. 2008. Discovery of the Amazon sailfin catfish *Pterygoplichthys pardalis* (Castelnau, 1855) (Teleostei: Loricariidae) in Vietnam. *Journal of Applied Ichthyology* 24:715–717.
- Liang, S.-H., H.-P. Wu, and B.-S. Shieh. 2005. Size structure, reproductive phenology, and sex ratio of an exotic armored catfish (*Liposarcus multiradiatus*) in the Kaoping River of Southern Taiwan. *Zoological Studies* 44:252–259.
- Llewelyn, J., L. Schwarzkopf, R. Alford, and R. Shine. 2010. Something different for dinner? Responses of a native Australian predator (the keelback snake) to an invasive prey species (the cane toad). *Biological Invasions* 12:1045–1051.
- Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2007. *Invasion Ecology*. Blackwell Publishing. Singapore.
- Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Alien fishes in California watersheds: Characteristics of successful and failed invaders. *Ecological Applications* 14:587–596.
- Marques Quintela, F., R. Almeida Porciuncula, and E. Pinto Colares. 2008. Dieta de *Lontra longicaudis* (Olfer) (Carnivora, Mustelidae) em um arroio costeiro da região sul do Estado do Rio Grande do Sul, Brasil. *Neotropical Biology and Conservation* 3:119–125.
- Mayor-Victoria, R., and Á. Botero-Botero. 2010. Dieta de la nutria neotropical *Lontra longicaudis* (Carnivora, mustelidae) en el Río Roble, Alto Cauca, Colombia. *Acta Biológica Colombiana* 15:237–244.

- McCleery, R. A., A. Sovie, R. N. Reed, M. W. Cunningham, M. E. Hunter, and K. M. Hart. 2015. Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. *Proceedings of the Royal Society B, Biological Sciences* 282:20150120.
- Meyerson, L. A., and H. A. Mooney. 2007. Invasive alien species in an era of globalization. *Ecological Society of America* 5:199–208.
- Monroy-Vilchis, O., and V. Mundo. 2009. Nicho trófico de la nutria neotropical (*Lontra longicaudis*) en un ambiente modificado, Temascaltepec, México. *Revista Mexicana de Biodiversidad* 80:801–806.
- Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: Empirical rules and assembly theory. *Biological Conservation* 78:149–161.
- Newsome, S. D., D. L. Phillips, B. J. Culleton, T. P. Guilderson, and P. L. Koch. 2004. Dietary reconstruction of an early to middle Holocene human population from the central California coast: Insights from advanced stable isotope mixing models. *Journal of Archaeological Science* 31:1101–1115.
- Nico, L. G. 2010. Nocturnal and diurnal activity of armored suckermouth catfish (Loricariidae: *Pterygoplichthys*) associated with wintering Florida manatees (*Trichechus manatus latirostris*). *Neotropical Ichthyology* 8:893–898.
- Nico, L. G., H. L. Jelks, and T. Tuten. 2009a. Non-native suckermouth armored catfishes in Florida: Description of nest burrows and burrow colonies with assessment of shoreline conditions. *Aquatic Nuisance Species Research Bulletin* 9:1–30.
- Nico, L. G., W. F. Loftus, and J. P. Reid. 2009b. Interactions between non-native armored suckermouth catfish (Loricariidae: *Pterygoplichthys*) and native Florida manatee (*Trichechus manatus latirostris*) in artesian springs. *Aquatic Invasions* 4:511–519.
- Nico, L. G., and R. T. Martin. 2001. The South American suckermouth armored catfish, *Pterygoplichthys anisitsi* (Pisces: Loricariidae), in Texas, with comments on foreign fish introductions in the American Southwest. *The Southwestern Naturalist* 46:98–104.
- Noonburg, E. G., and J. E. Byers. 2005. More harm than good: When invader vulnerability to predators enhances impact on native species. *Ecology* 86:2555–2560.
- Novakowski, G. C., N. S. Hahn, and R. Fugi. 2008. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotropical Ichthyology* 6:567–576.

- de Oliveira, C., S. R. Taboga, A. L. Smarra, and G. O. Bonilla-Rodriguez. 2001. Microscopical aspects of accessory air breathing through a modified stomach in the armoured catfish *Liposarcus anisitsi* (Siluriformes, Loricariidae). *Cytobios* 105:153–162.
- Page, L. M., and R. H. Robins. 2006. Identification of sailfin catfishes (Teleostei: Loricariidae) in southeastern Asia. *Raffles Bulletin of Zoology* 54:455–457.
- Pardini, R. 1998. Feeding ecology of the neotropical river otter *Lontra longicaudis* in an Atlantic Forest stream, south-eastern Brazil. *Journal of Zoology* 245:385–391.
- Pauly, D., and M. Palomares. 2005. Fishing down marine food web: It is far more pervasive than we thought. *Bulletin of Marine Science* 76:197–211.
- Peers, M. J. L., D. H. Thornton, and D. L. Murray. 2012. Reconsidering the specialist-generalist paradigm in niche breadth dynamics: Resource gradient selection by Canada lynx and bobcat. *PLoS ONE* 7:e51488.
- Petersen, B. J., and B. Fry. 1987. Stable Isotopes in Ecosystem Studies. *Annual Review Ecology and Systematics* 18:293–320.
- Pfeiffer, P., and B. M. Culik. 1998. Energy metabolism of underwater swimming in river-otters (*Lutra lutra* L.). *Journal of Comparative Physiology - B Biochemical, Systemic, and Environmental Physiology* 168:143–148.
- Phillips, B. L., and R. Shine. 2006. An invasive species induces rapid adaptive change in a native predator: Cane toads and black snakes in Australia. *Proceedings of the Royal Society B: Biological Sciences* 273:1545–1550.
- Phillips, B. L., R. Shine, and D. B. Wake. 2004. Adapting to an invasive species: Toxic cane toads induce morphological change in Australian snakes. *Proceedings of the National Academy of Sciences of the United States of America* 101:17150–17155.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83:703–718.
- Pound, K. L., W. H. Nowlin, D. G. Huffman, and T. H. Bonner. 2011. Trophic ecology of a nonnative population of suckermouth catfish (*Hypostomus plecostomus*) in a central Texas spring-fed stream. *Environmental Biology of Fishes* 90:277–285.
- Rheingantz, M. L., L. G. Oliveira-santos, H. F. Waldemarin, and E. P. Caramaschi. 2012. Are otters generalists or do they prefer larger, slower prey? Feeding flexibility of the neotropical otter *Lontra longicaudis* in the Atlantic forest. *IUCN Otter Specialist Group Bulletin* 29:80–94.

- Rheingantz, M. L., H. F. Waldemarin, L. Rodrigues, and T. P. Moulton. 2011. Seasonal and spatial differences in feeding habits of the Neotropical otter *Lontra longicaudis* (Carnivora: Mustelidae) in a coastal catchment of southeastern Brazil. *Zoologia* 28:37–44.
- Ríos-Muñoz, C. A. 2015. Depredación de pez diablo (Loricariidae: *Pterygoplichthys*) por el cormorán oliváceo (*Phalacrocorax brasilianus*) en Villahermosa, Tabasco, México. *Huitzil* 16:62–65.
- Ritchie, E. G., B. Elmhagen, A. S. Glen, M. Letnic, G. Ludwig, and R. A. McDonald. 2012. Ecosystem restoration with teeth: What role for predators? *Trends in Ecology & Evolution* 27:265–71.
- Rivas, L. R. 1965. Florida fresh water fishes and Conservation. *Quarterly Journal of the Florida Academy of Sciences* 28:255–258.
- Rodriguez, L. F. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions* 8:927–939.
- Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences of the United States of America* 99:791–796.
- Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *The American Naturalist* 97:209–223.
- Salvarina, I., E. Yohannes, B. M. Siemers, and K. Koselj. 2013. Advantages of using fecal samples for stable isotope analysis in bats: Evidence from a triple isotopic experiment. *Rapid Communications in Mass Spectrometry* 27:1945–1953.
- Schoeninger, M. J., M. J. DeNiro, and H. Tauber. 1983. Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet. *Science* 220:1381–1383.
- Schofield, P. J., and W. F. Loftus. 2014. Non-native fishes in Florida freshwaters: A literature review and synthesis. *Reviews in Fish Biology and Fisheries* 25:117–145.
- Shine, R. 2010. The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology* 85:253–291.
- Shinen, J., S. Morgan, and A. Chan. 2009. Invasion resistance on rocky shores: Direct and indirect effects of three native predators on an exotic and a native prey species. *Marine Ecology Progress Series* 378:47–54.

- Silva, F. A. Da, E. D. M. Nascimento, and F. M. Quintela. 2012. Diet of *Lontra longicaudis* (Carnivora: Mustelidae) in a pool system in Atlantic forest of Minas Gerais State, southeastern Brazil. *Acta Scientiarum. Biological Sciences* 34:407–412.
- Simonovic, P., V. Nikolic, and S. Grujic. 2010. Amazon sailfin catfish *Pterygoplichthys pardalis* (Castellnnau, 1855) (Loricariidae, Siluriformes), a new fish species recorded in the Serbian section of the Danube River. *Biotechnology & Biotechnological Equipment* 24:655–660.
- Skewes, O., C. A. Moraga, P. Arriagada, and J. R. Rau. 2012. El jabalí europeo (*Sus scrofa*): Un invasor biológico como presa reciente del puma (*Puma concolor*) en el sur de Chile. *Revista Chilena de Historia Natural* 85:227–232.
- Sousa, K. S., D. D. Saraiva, and E. P. Colares. 2013. Intra-annual dietary variation in the neotropical otter from southern Brazil. *Mammal Study* 38:155–162.
- Stevens, P. W., D. A. Blewett, and J. P. Casey. 2006. Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of hurricane Charley. *Estuaries and Coasts* 29:997–1003.
- Tablado, Z., J. L. Tella, J. A. Sánchez-Zapata, and F. Hiraldo. 2010. The paradox of the long-term positive effects of a North American crayfish on a European community of predators. *Conservation Biology* 24:1230–1238.
- Toro-Ramírez, A., A. T. Wakida-Kusunoki, L. E. Amador-del Ángel, and J. L. Cruz-Sánchez. 2014. Common snook [*Centropomus undecimalis* (Bloch, 1792)] preys on the invasive Amazon sailfin catfish [*Pterygoplichthys pardalis* (Castelnau, 1855)] in the Palizada River, Campeche, southeastern Mexico. *Journal of Applied Ichthyology* 30:532–534.
- Towns, D. R., I. A. E. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions* 8:863–891.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464–467.
- Wakida-Kusunoki, A. T., and L. E. Amador-Del-Angel. 2008. Nuevos registros de los pecos *Pterygoplichthys pardalis* (Castelnau 1855) y *P. disjunctivus* (Weber 1991) (Siluriformes: Loricariidae) en el Sureste de México. *Hidrobiologica* 18:251–255.
- Wakida-Kusunoki, A. T., R. Ruiz-Carus, and E. Amador-del-Angel. 2007. Amazon sailfin catfish, *Pterygoplichthys pardalis* (Castelnau, 1855) (Loricariidae), another exotic species established in Southeastern México. *The Southwestern Naturalist* 52:141–144.

- Wanger, T. C., A. C. Wielgoss, I. Motzke, Y. Clough, B. W. Brook, N. S. Sodhi, and T. Tschardt. 2011. Endemic predators, invasive prey and native diversity. *Proceedings of the Royal Society B: Biological Sciences* 278:690–694.
- Ward-Fear, G., G. P. Brown, and R. Shine. 2010. Using a native predator (the meat ant, *Iridomyrmex reburrus*) to reduce the abundance of an invasive species (the cane toad, *Bufo marinus*) in tropical Australia. *Journal of Applied Ecology* 47:273–280.
- Wengeler, W. R., D. a. Kelt, and M. L. Johnson. 2010. Ecological consequences of invasive lake trout on river otters in Yellowstone National Park. *Biological Conservation* 143:1144–1153.
- Willink, P. W., C. Barrientos, H. A. Kihn, and B. Chernoff. 2000. An ichthyological survey of Laguna del Tigre National Park, Peten, Guatemala. Pages 41–48 in B. T. Bestelmeyer and L. E. Alonso, editors. A biological assessment of Laguna del Tigre National Park, Petén, Guatemala. RAP bulleting of biological assessment 16. Conservation International, Washintong, DC.

BIOGRAPHICAL SKETCH

Antonio Diego Alejandro Juárez-Sánchez was born in Guatemala City and grew up in a small town in San Juan Sacatepequez on his parent's farm. He obtained his biology bachelor's degree from the University of San Carlos de Guatemala (USAC). He has worked as a wildlife researcher for Wildlife Conservation Society-Guatemala, the General Directorate of Research (DIGI) in USAC, and the National Organization for Conservation and the Environment (ONCA for its initials in Spanish). He has also won grants from the Guatemalan National Council on Science and Technology (CONCYT, for its initials in Spanish), and the Guatemalan National Fund for Nature Conservancy (FONACON, for its initials in Spanish). He is a founding member of the Guatemalan Mastozoological Association where he has held the position of treasurer. He has been a member of the environmental commission of CONCYT, where he served as president in 2012. In 2014 he was the director of the biological department of Tikal National Park. In 2014, he also received a Fulbright scholarship to study for his master's degree in wildlife ecology and conservation at the University of Florida (UF). As a student in UF he was elected president of the Latin Hispanic Graduate Student Association (LOGRAS) to serve during the academic year of 2015-2016