

BIODIVERSITY CONSERVATION IN SUB-SAHARAN AFRICA: A CASE STUDY
OF THE AFRICAN DWARF CROCODILES (*OSTEOCLAEMUS* SPP.)

A Dissertation

by

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ABSTRACT

Overexploitation of wildlife is a leading threat to biodiversity in tropical Africa. Effective management requires integrating information on the extent of exploitation, distribution, and status of exploited species. I explore how trade filters affected the final destination of bushmeat for different species involved in the trade. I highlight the trade in reptiles, in particular African Dwarf Crocodiles (*Osteolaemus tetraspis*) to investigate why they are rare in markets yet ubiquitously hunted. Hunting locations and methods determined the types of species entering bushmeat markets while selling conditions and prices determined whether species were traded locally or in urban markets.

To prioritize conservation efforts of over-exploited species, it is important to determine the distribution and status of populations. I conducted detailed sampling of *Osteolaemus* populations in Cameroon and around the Cameroon Volcanic Line (CVL), to investigate the distributional limits and number of cryptic *Osteolaemus* species in the country. I found that *O. tetraspis* extends west beyond the CVL, thus, this mountain chain does not represent the distributional limit of this species. I also found *O. osborni* in Cameroon. I provided information on the population ecology of *O. tetraspis* and *O. osborni* in Cameroon to facilitate independent conservation of these two species. Both species are threatened in Cameroon based upon low encounter rates, young population structures and continued threats of habitat loss and hunting pressure.

Crocodylians link nutrients and energy between food webs through their movements across heterogeneous habitats. These connections may differ among habitats and as they

undergo ontogenetic shifts in diet. I compared food web associations of *Osteolaemus* species inhabiting a large river and small tributary using stable isotope analyses of carbon and nitrogen. *Osteolaemus* species inhabiting perennial rivers have aquatic food web associations as opposed to the largely terrestrial food web associations detected when they occupy swamp habitats. These species have large dietary overlap between juveniles, adults and, sexes.

Through my research, I have provided a working knowledge of the distribution, ecology, and hunting pressure of *Osteolaemus* species necessary for assessing their conservation status and developing sound management. These widely distributed species should be regionally managed to conserve their evolutionary diversity.

DEDICATION

The unregulated extraction of natural resources is one of Sub-Saharan Africa's greatest threats to biodiversity and forest peoples. This dissertation is dedicated to the people dependent upon these resources, and park guards, conservation practitioners, and researchers that have devoted their lives toward ensuring biodiversity persists in concert with the advancement local forest peoples.

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CHAPTER I

INTRODUCTION

Biodiversity is essential to ecosystems and the social, political, and economic sectors of many developing nations. There is global concern about declining biodiversity and its ramifications on gross national production levels, fuel energies, and food security (Jenkins *et al.* 1990; Webb *et al.* 2000; Bowen-Jones *et al.* 2003; Milner-Gulland & Bennett 2003; Cardinale *et al.* 2012). In Sub-Saharan Africa, rural populations practice shifting agriculture for subsistence and livelihoods. They are also dependent upon adjacent forests for fuel wood and wildlife that are sold to urban populations (Robinson *et al.* 1999; Malhi *et al.* 2013). The growth rates of rural populations have resulted in unsustainable exploitation of natural resources, leading to habitat loss and declining populations of species. These threats may act synergistically to cause population extirpation or species extinction (Gilpin & Soulé 1986; Frankham 2005; Brook *et al.* 2008). There are few alternative livelihoods for peoples residing in rural areas, thus the loss of this biodiversity has been viewed as a social, economic and ecologic crisis (Bennett & Robinson 2000; Bowen-Jones *et al.* 2003; Fa *et al.* 2003).

Developing sustainable use systems is imperative for rural communities and the biodiversity they depend upon. However, these systems are multifaceted, operating at various spatial scales, and differ by region (Cowlshaw *et al.* 2005; Boucher *et al.* 2011; Rudel 2013). For example the consumption of wildlife, hereafter referred to as bushmeat, is partially dependent upon demand from urban and rural communities and

differs by region (Wilkie & Carpenter 1999; Fa *et al.* 2003; Robinson & Bennett 2004; Fa *et al.* 2006). Consumption of bushmeat is lower in urban areas of South America than urban areas of sub-Saharan Africa due to South America's extensive production and heavy reliance on the livestock (Rushton *et al.* 2005). Within the Congo Basin, consumption and trade of bushmeat is also dependent the extent of road networks, proximity to urban cities and availability of alternative protein sources (Brashares *et al.* 2004; Willcox & Nambu 2007; Brashares *et al.* 2011; Evans 2014). Although biological data needed to evaluate the sustainability of exploitation is often lacking for many species the bushmeat trade is thought to be unsustainable for many exploited species (Robinson & Bennett 2004; Fa *et al.* 2005; Fa *et al.* 2006; Brook *et al.* 2008; Laurance *et al.* 2012; Weinbaum *et al.* 2013).

The inherent complexity of biodiversity and its importance to humans requires an integrative approach to conservation that identifies factors influencing the exploitation of species and the levels of exploitation for species to be self-sustaining despite exploitation and changing landscapes (Lindenmayer *et al.* 2008; Redford *et al.* 2011). Studies that incorporate regional, local, and species specific information on exploitation are needed to develop conservation strategies. In this dissertation, I integrate information on the trade of African Dwarf Crocodiles (*Osteolaemus* spp.), their geographic distribution, and population status, to facilitate ecologically sound management that results in self-sustaining species that can be exploited.

Osteolaemus species are heavily utilized for food throughout their geographic distribution from Senegal to the Democratic Republic of Congo (Eaton 2010). The levels

of their exploitation vary by orders of magnitude from hundreds to thousands of individuals sold annually in bushmeat markets (Behra 1993; Thorbjarnarson & Eaton 2004; Fa *et al.* 2006). They may be rare in urban markets or be one of the most commonly sold species (Thorbjarnarson & Eaton 2004; Fa *et al.* 2006). Reasons for this variation in exploitation are unknown and merit further investigation to determine the factors influencing their trade which is the subject I investigate in my first chapter.

The statuses of species of *Osteolaemus* are unknown due to lack of data on abundances and their recent discovery as cryptic species (Eaton 2009; Eaton 2010; Shirley *et al.* 2014). Currently there are three cryptic species of *Osteolaemus*, *O. sp. nov.* located in the upper Guinean rain forests, *O. tetraspis* in the lower Guinean and Congolian rain forests, and *O. osborni* in the Congolian rain forests (Eaton 2009; Shirley *et al.* 2014). Putative distributional limits are based on phylogeographic barriers observed for cryptic species complexes of other lowland rain forests fauna (Fjeldsaa & Lovett 1997; Grubb 1999; Lawson & Klemmens 2001; Stewart 2001; Blackburn 2010; Nicolas *et al.* 2011). Additional sampling is needed around these hypothesized phylogeographic barriers to improve our understanding of each species' status and to develop management that protects their evolutionary diversity. My second and third chapters entail phylogeographic and population status studies of *Osteolaemus* populations in Cameroon. I expand on previous phylogeographic work by conducting detailed sampling of *Osteolaemus* populations around a hypothesized phylogeographic barrier - the Cameroon Volcanic Line (CVL) (Eaton 2009; Shirley *et al.* 2014). I also provide distribution maps for each species to facilitate their independent conservation.

Little is known about the biology of *Osteolaemus* including their functional roles in their environments. Crocodylians are recognized as important functional connectors of disparate food webs through their movement of nutrients and energy (Fittkau 1973; Subalusky *et al.* 2009; Rosenblatt & Heithaus 2011). *Osteolaemus* occupy a variety of habitats and it is likely that their functional roles as nutrient and energy vectors may differ among habitats (Quevedo *et al.* 2009; Matich *et al.* 2011; Schriever & Williams 2013). Many species undergo ontogenetic shifts in diet that can add complexity to trophic interactions in food webs (Joanen & Mcnease 1987; Magnusson *et al.* 1987; Magnusson & Lima 1991; Tucker *et al.* 1996; Platt *et al.* 2006; Wallace & Leslie 2008; Subalusky *et al.* 2009). In my fourth chapter I examine the spatial and ontogenetic variation in the terrestrial and aquatic food web associations *Osteolaemus tetraspis* and *O. osborni*. This study offers the first spatial comparison of the trophic ecology of these species.

In summary, this dissertation couples ecological and socioeconomic studies of *Osteolaemus*. Understanding what factors influence the exploitation and trade of crocodiles is important in designing sustainable harvest programs and there is currently little information on their trade other than estimated exploitation rates from urban market studies. The distributions of *Osteolaemus* species are poorly understood and very few population surveys of these species making it difficult to determine each species' status and conserve their evolutionary diversity. This dissertation addresses some of these knowledge gaps to work toward developing sustainable use programs.

CHAPTER II
THE ROLE OF TRADE FILTERS IN ASSESSMENTS OF BUSHMEAT
EXPLOITATION IN AFRICA

Introduction

Meat from wild game, known as bushmeat, serves as a primary source of protein and income for forest peoples and is a highly valued economic and cultural resource (Muchaal & Ngandjui 1999; Wilkie & Carpenter 1999; Bowen-Jones *et al.* 2003; Davies & Brown 2007; Foerster *et al.* 2012). Several studies suggest the current scale of bushmeat trade, particularly of large-bodied vertebrates is unsustainable (Noss 1998; Peres 2000; Wilkie & Godoy 2000; Maisels *et al.* 2001; Milner-Gulland & Bennett 2003; Robinson & Bennett 2004; Fa *et al.* 2006). Overexploitation of bushmeat is a leading crisis in sub-Saharan Africa because the resulting extirpation of wildlife threatens food security and livelihoods of forest peoples, national economies, and ecosystem functions (Robinson *et al.* 1999; Bowen-Jones *et al.* 2003; Fa *et al.* 2003; Laurance *et al.* 2012; Effiom *et al.* 2013).

Efforts to manage the crisis are contingent upon characterizing the magnitude of bushmeat trade (Bowen-Jones *et al.* 2003; Fa *et al.* 2004; Cowlshaw *et al.* 2005). The trade is often viewed as a hierarchy with demand from large-scale urban markets controlling the species and numbers of individuals hunted in forests surrounding small villages (Cowlshaw *et al.* 2005; Brashares *et al.* 2011). Consequently the urban market is often the scale at which assessments of exploitation are conducted, and the trade

managed (Fa *et al.* 2000; Fa *et al.* 2004; Cowlshaw *et al.* 2005). However estimates of bushmeat exploitation based on market surveys may severely underestimate the magnitude of wildlife that is hunted and traded (Clayton & Milner-Gulland 2000; Cowlshaw *et al.* 2005; Allebone-Webb *et al.* 2011). Twenty to seventy percent of animals sold by hunters may never make it to urban markets, and instead may be utilized primarily for subsistence, exchanged in the informal economy, lost to scavengers or may decompose in traps (Noss 1998; Muchaal & Ngandjui 1999; Curran & Tshombe 2001; Fa & Yuste 2001; Fitzgerald *et al.* 2004; Ashley & Mbile 2005; Solly 2007; Willcox & Nambu 2007; Hayashi 2008; Foerster *et al.* 2012). Of the bushmeat that does make it to urban markets, 85% may be directly sold to restaurant owners rather than in stalls at markets, and these multiple trade routes complicate assessments of bushmeat exploitation (Cowlshaw *et al.* 2005).

Several factors may act as trade filters influencing the supply of species and numbers of individuals traded in urban markets (Milner-Gulland & Clayton 2002; De Merode & Cowlshaw 2006; Kümpel *et al.* 2008; Allebone-Webb *et al.* 2011). For example, transportation costs, selling price, and condition of the product (e.g. smoked or fresh), result in differing volumes (kg) of ungulates, rodents, and insects traded in Ghana (Cowlshaw *et al.* 2005). The remoteness of villages and the number of traders involved in the exchange of bushmeat between villages and urban markets can determine the types of species traded (Allebone-Webb *et al.* 2011). Additionally, larger species are legally protected from hunting, resulting in reduced and clandestine trade (Ashley & Mbile 2005; De Merode & Cowlshaw 2006). Mammals are the most commonly hunted

and traded species thus few studies focus on or evaluate trade and filters that influence the trade of other vertebrate species (Cowlshaw *et al.* 2005; Davies & Brown 2007). Reptiles have served as an important source of protein, traditional medicine, and income throughout the tropics (Fitzgerald *et al.* 1991; Fitzgerald 1994; Klemens & Moll 1995; Klemens & Thorbjarnarson 1995; Fitzgerald & Painter 2000; Mieres & Fitzgerald 2006). They are ubiquitously hunted throughout Sub-Saharan Africa yet appear rare in some urban markets and common in others (Abercrombie 1978; Butler & Shitu 1985; Akani *et al.* 1998; Lawson 2000; Thorbjarnarson & Eaton 2004; Fa *et al.* 2006; Whiting *et al.* 2011). There is little information on how frequently they are hunted, traded and if their trade is sustainable. I suggest this gap in knowledge and their rarity in urban markets may be due to some of the aforementioned trade filters, that result in underestimates of their exploitation in the bushmeat trade. To address this prediction I focused part of this research on understanding the trade in reptiles, in particular African Dwarf Crocodiles (*Osteolaemus tetraspis*). This study draws attention to the value and level of trade in reptiles, particularly of *Osteolaemus tetraspis*, which may be threatened by this trade (Pooley 1982; Waitkuwait 1989; Kofron 1992; Agnanga *et al.* 1996; Thorbjarnarson & Eaton 2004; Eaton 2010; Gonwouo & Lebreton 2010; Chapter 3). Understanding the levels of trade in reptile species might help explain why they are ubiquitously hunted but rare in markets, and point to conservation strategies that can provide better information on assessing sustainability of hunted reptiles.

I also explored how hunting patterns, the condition of bushmeat products, sale prices, and legal status affected the final destination of bushmeat for different species. I focused

data collection at the lowest level of the bushmeat trade, working with hunters rather than vendors in urban markets or traders. This provided information about localized exploitation and consumption of wildlife that may not enter urban markets, and provided insight on how supply affects higher levels of the bushmeat trade hierarchy.

Materials and methods

Study area

This study took place in Campo Ma'an National Park, located in southwest Cameroon between latitudes N2°09' and N2°53' and longitudes E9°48' and E10°54' (Figure 1). Campo Ma'an has approximately 61,000 inhabitants distributed among 119 villages and a population density between 7.3-10 people per km² (Simo 2004). One third of the population lives and works in rubber and oil plantations or logging camps (Simo 2004). The rest live in small hamlets or villages practicing shifting agriculture, hunting, fishing and collection of non-timber forest products. These villages are surrounded by subsistence or cash crop farmlands that transition to secondary and old growth forests toward the interior of the Campo Ma'an National Park.

There are eight indigenous communities. Six are Bantu including the Bulu, Ntumu, Batanga, Iyassa, Mabea and Mvae. Two are pygmy, the Bagyeli and Bakola. The Bulu and Mvae are the dominant ethnic groups thus most of our subjects were from these communities but some were from the Iyassa and Bagyeli communities (Table S1). The Bulu and Mvae chiefly practice swidden agriculture and secondarily hunting (Simo 2004; Ashley & Mbile 2005). The Iyassa are also fishermen, and the Bagyeli are

primarily hunters and gatherers. Both the Bantu and pygmy communities depend on bushmeat as their primary source of protein and secondarily as a source of income.

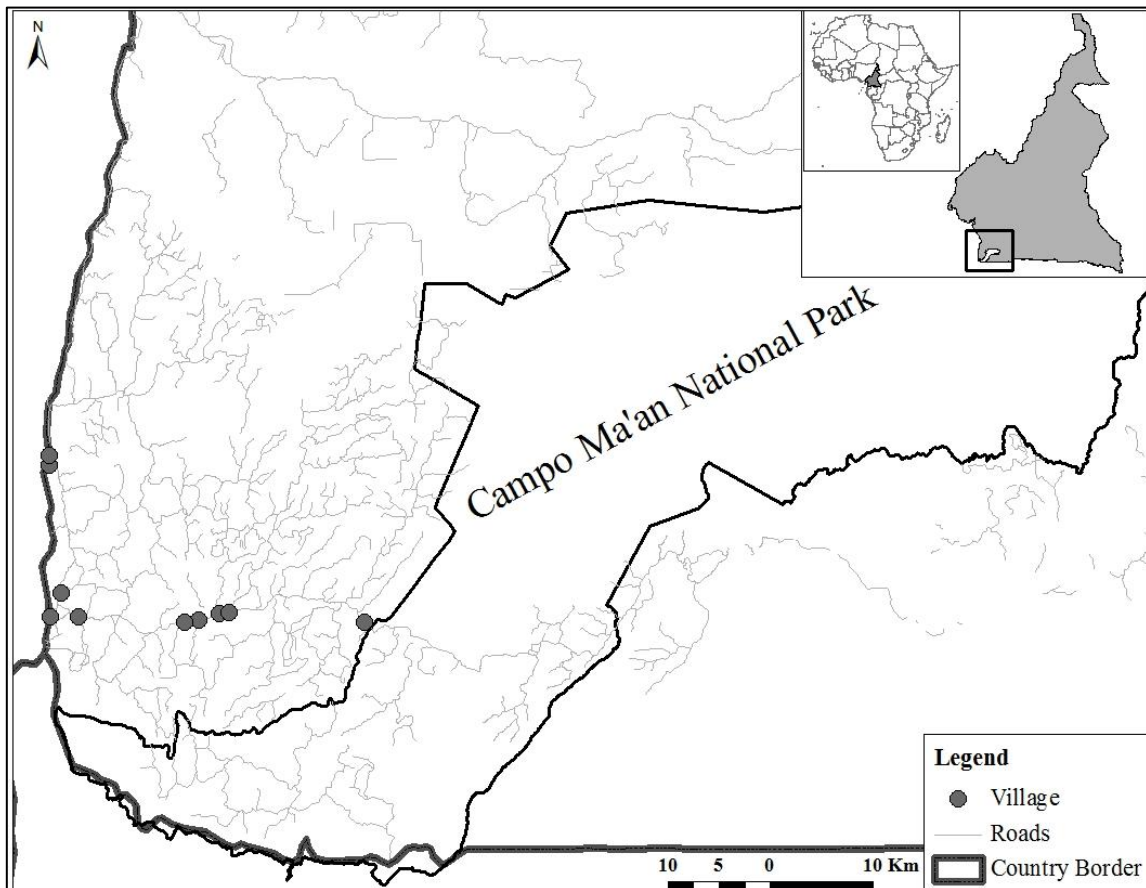


Figure 1. Locations of villages where surveys took place in relation to the Campo Ma'an National Park, Cameroon.

Data collection and statistical analyses

Between January 26 and February 14 2013, I interviewed 26 hunters in 11 villages (Figure 1, Table S1). Hunters were recruited opportunistically and the interviews were voluntary, anonymous, and conducted by a Cameroonian technician who abided by an

institutionally approved protocol (IRB #2013-0487). The interviews were structured and based on a questionnaire designed to investigate the hunters' activities (Appendix A) including hunting effort, travel distance, methods, types of species hunted and their associated economic value. I also included questions on the hunting periods for capturing crocodiles and demographics of captured crocodiles (Appendix A).

Although hunting of certain kinds of species, including crocodiles, was illegal (Djeukam 2012), there was little enforcement, our interviews were anonymous, and I had no authority to enforce wildlife laws, (Muchaal & Ngandjui 1999; Willcox & Nambu 2007; NLS *pers. obs.*). Thus under-reporting of hunting these species was unlikely. Self-reporting may result in biases in the quantities of each species hunted and species misidentification (Sheil & Wunder 2002; Jones *et al.* 2008). As such, analyses were limited to the frequency of broad species groups hunted, rather than counts of each species hunted. The species groups were rats, porcupines, ungulates, primates, birds, turtles, tortoises, monitor lizards, large-bodied snakes (e.g. *Python sebae*, *Bitis spp.*), crocodiles and frogs. I calculated frequency statistics to describe the characteristics of the hunters, their hunting methods and distance traveled relative to their village locations. I conducted cross tabulations and used Fisher's Exact test with Monte Carlo simulations ($n = 10,000$) and Bonferonni corrected comparisons to test for statistical differences in the frequency of the species groups hunted, and to identify statistically significant relationships between species group and the condition or destination of bushmeat. The strength of associations of species group and condition or destination, were assessed via Cramer's V and Contingency Coefficient statistics. The conditional

states of bushmeat were live, smoked, whole carcass, or parts. To reduce complication or confusion in quantifying bushmeat prices, as different parts of different species are likely to differ in value, I focused on unit prices of whole carcasses. The destinations of bushmeat were: household; village; and urban market. Chi-square analyses were used to assess the association between species group and selling price. I used correlation analyses to assess relationships between mean biomass (kg) for each species group and selling price. Mean biomass was estimated by averaging the mean body mass for each species known to be hunted in the Campo Ma'an for the given species group. Mean body mass was obtained from published literature (Fa & Purvis 1997; Branch 1998; Lawson 1999; Spawls *et al.* 2002; Clements 2007; Smolensky *unpublished data*) and online sources (Animal Diversity Web; Avibase; Encyclopedia of Life). I used a Kruskal-Wallis test to determine if a relationship existed between prices of bushmeat and the type of community (Bantu and Bagyeli). All analyses were conducted in SPSS v. 22. I also described the hunting methods and hunting periods specifically for *O. tetraspis* and the size-classes targeted. Size-class divisions were hatchlings (<24 cm total body length (TL)), juveniles (24-99 cm TL) and adults (>100 cm TL) (Hara & Kikuchi 1978; Sims & Singh 1978; Teichner 1978; Tyron 1980; Waitkuwait 1989; Kofron & Steiner 1994; Eaton 2009).

Results

Characteristics of hunters and their hunting methods

Mean age of hunters was 42 years (SD = 8.99). Most were born in their villages (Table S1), and primarily practiced farming in addition to hunting. Two Bulu hunters from different villages listed hunting as their primary profession. Hunting took place in proximity to the village, with 69.2% of the hunters traveling no more than one day's walk from their villages which is estimated to be <15-20 km (Allebone-webb et al. 2011; Foerster et al. 2012; Kümpel et al. 2009; Muchaal and Ngandjui 1999). Some hunters (23.1%) traveled farther, taking hunting trips that lasted several days. All the hunters used snares and nearly all (25/26 hunters) used machetes to capture wildlife. Animals were also taken with shotguns, by hand, or with hunting dogs (Table S1). Hunting occurred in both dry and rainy seasons, but more often in the dry season (Table S1).

Composition, condition, selling price, and destination, of hunted species

I observed a significant difference in the frequency of the types of animals hunted ($F = 171.91$ p -value <0.01 , Cramer's $V = 0.71$, Contingency Coefficient = 0.58) (Figure 2). Mammals, (rats, porcupines, and ungulates), were the most commonly hunted group both in terms of the numbers of hunters that captured them and the frequency of capture by each hunter. Reptiles were the second most commonly hunted group, followed by birds, and none hunted frogs (Figure 2). Crocodiles, monitor Lizards, and tortoises were caught by more hunters than primates; however, hunters that targeted primates ($n = 13$), more often than reptiles.

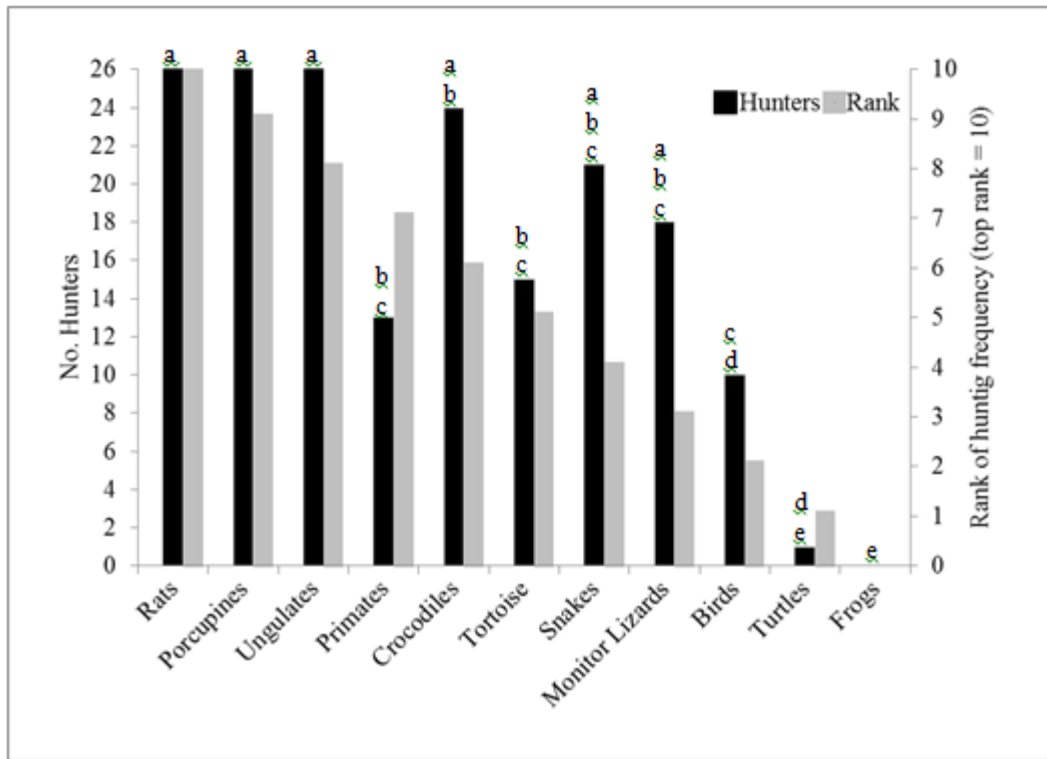


Figure 2. Frequency of each species group hunted (n = 26 hunters), and the ranks of species hunted from most (10) to least hunted (1) reported by hunters of the Campo Ma'a region of Cameroon. Letters denote statistically significant ($\alpha = 0.05$) difference in the number of hunters that hunt each group.

I also observed significant associations between the type of taxon that was hunted and its condition ($F = 172.93$, p – value <0.01 , Cramer's $V = 0.51$, Contingency Coefficient = 0.78), selling price ($X^2 = 109.34$, p -value <0.01), and destination ($F = 146.38$, p – value <0.01 Cramer's $V = 0.62$, Contingency Coefficient = 0.73). Mammals were mainly sold in the smoked state, either as whole carcasses or in parts, whereas reptiles were sold live with few exceptions (snakes and monitor lizards) (Table 1). These latter taxa were also sold smoked, as whole carcasses, or in parts. Hunters did not provide information on the condition of bird meat sold. With the exception of snakes ($\bar{x} =$

2,937.50 CFA, SD = 1,116.04), larger bodied taxa were more valuable ($R = 0.247$ p-value <0.01 , Table 1, Figure 3). Rats, tortoises and birds were the lowest priced taxa valued under 1,000 CFA (\$2.05) per carcass, while ungulates and crocodiles were the most valuable ($\bar{x} = 6,770.83$ CFA, SD = 3,250.35 and $\bar{x} = 20,238.10$ CFA, SD = 8,251.70 respectively, Table 1). All of the bushmeat was either consumed within the household or sold locally within the village, with just one exception in which one hunter sold porcupines to vendors in the urban market (Table 1). Birds, tortoises and snakes were primarily consumed in household whereas crocodiles were sold in the village. The other taxa were consumed in the household and sold within the village (Table 1). Price varied by destination for porcupines and ungulates (Table 1). These taxa were consumed in the household and sold in the village, but when these taxa were destined for the village, they had higher sale prices. I also found differences in the price of some bushmeat among the Bantu and Bagyeli communities. The Bantu communities had significantly higher mean sale prices per carcass for porcupines ($H = 4.58$, p-value <0.02) and crocodiles ($H = 5.54$, p-value <0.02).

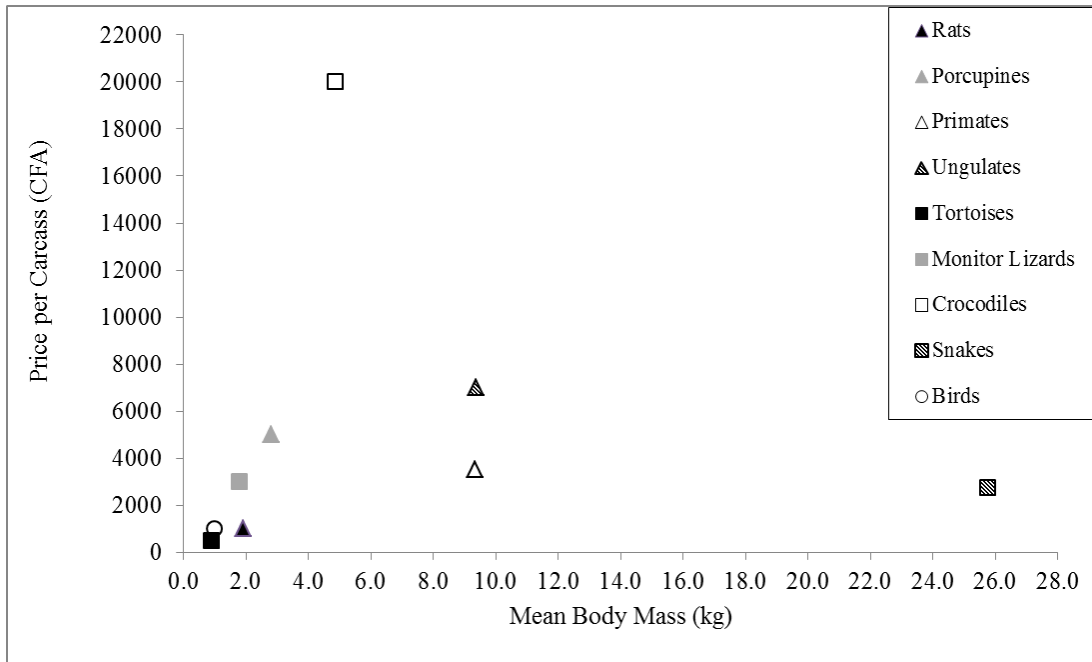


Figure 3. Relationship between the mean selling price (per carcass) and mean body mass (kg) for each species group hunted in the Campo Ma’an region of Cameroon. Triangles are mammals, and square symbols are reptiles.

When examining the relationship between these trade filters across all taxa, I found sale price varied with condition ($F = 140.99$, $p - \text{value} < 0.01$, Cramer’s $V = 0.53$, Contingency Coefficient = 0.77) and destination ($F = 81.88$, $p - \text{value} < 0.01$, Cramer’s $V = 0.48$, Contingency Coefficient = 0.64), and condition varied with destination ($F = 48.19$, $p - \text{value} < 0.01$, Cramer’s $V = 0.34$, Contingency Coefficient = 0.51). At the lowest sale prices (500-2,000 CFA per carcass), most of the bushmeat was sold in the smoked state as whole carcasses (Table S2). At mid level sale prices (2,500 – 7,000 CFA) the bushmeat was still sold in the smoked state and whole, but also sold as smoked meat in parts, or alive (Table S2). At the highest sale prices (7,500 – 30,000 CFA) higher proportions of the bushmeat were sold live (Table S2). The sale price also changed with

the destination of the meat in that more expensive meat was destined for sale in the village rather than consumed in the household (Table S2). Between 70-80% of the bushmeat sold in the smoked condition was destined for the household or village, whereas animals sold alive were predominantly destined for the village (58.8%) and secondarily for the household (14.7%) (Table S3).

Osteolaemus tetraspis was the main crocodile species hunted, as only 2 hunters from Mintom and Nko'olong, also targeted *Crocodylus niloticus*. Crocodiles were captured by all but three hunters (23/26) (Figure 2). Methods to specifically capture *O. tetraspis* included snares in front of burrows, machetes, and shotguns (Table S1). Other less common methods included baited hooks, applying poison, smoke, or barricades to burrows, or grabbing them by hand. There was no bias in the size of *O. tetraspis* hunted ($X^2 = 4.46$, p-value <0.14). Eight hunters captured all three size classes, half of the hunters captured adults or juveniles, and three hunters exclusively captured adults. One hunter occasionally collected the eggs of *O. tetraspis*. While *O. tetraspis* can be hunted during both the rainy and dry season (n = 8 hunters), *O. tetraspis* were hunted significantly more during the dry season (n = 13 hunters) than the rainy season (n = 1 hunter) ($X^2 = 11.37$, p-value <0.01). I observed large variation in the price per carcass of *O. tetraspis* ($\bar{x} = 20,238.10$ SD = 8,251.70 CFA). The Bagyeli sold *O. tetraspis* at significantly lower prices ($\bar{x} = 12,000$ CFA) than the Iyassa-Bantu ($\bar{x} = 27,500$ CFA) community (F = 3.35, p-value <0.04).

Table 1. Destination, condition and mean price per carcass of bushmeat by species group based on frequencies of hunter participants (n = 26). Letters denote statistically significant ($\alpha = 0.05$) differences among species groups within a category (i.e. columns). Destination abbreviations: H – Household, V- Village, U – Urban Market. Condition abbreviations: W – Whole, A – Alive, P – Parts, S – Smoked. Hunters did not provide information on the condition of bird meat.

	Destination					Condition								Price
	H	V	H/V	H/V/U	Total	W	A	W/P	W/S	W/P/S	W/P/A/S	W/S/A	Total	CFA (SD)
Rats	1 _a	2 _a	23 _a	0 _a	26	2 _a	0 _a	1 _a	20 _a	0 _a	1 _a	0 _a	24	804.35 (291.51)
Porcupines	0 _a	9 _{a, b}	13 _{a, b}	1 _a	23	0 _a	0 _a	2 _a	9 _{a, b, c, d}	11 _{b, c}	0 _a	0 _a	22	4160.00 (1187.79)
Ungulates	0 _a	9 _{a, b}	14 _{a, b}	0 _a	23	0 _a	0 _a	3 _a	3 _{d, e}	15 _c	0 _a	0 _a	21	6770.83 (3250.35)
Primates	0 _a	0 _a	10 _a	0 _a	10	0 _a	0 _a	0 _a	8 _{a, c}	2 _{a, b, c}	0 _a	0 _a	10	4090.91 (1997.73)
Birds	8 _b	0 _a	0 _b	0 _a	8	-	-	-	-	-	-	-	-	875.00 (250.00)
Tortoises	9 _b	0 _a	1 _b	0 _a	10	0 _a	6 _{b, c}	0 _a	0 _{b, c, d, e}	0 _{a, b, c}	0 _a	0 _a	6	700.00 (273.86)
Monitor Lizards	1 _a	4 _{a, b}	8 _{a, b}	0 _a	13	0 _a	9 _{b, c}	0 _a	0 _{b, d, e}	0 _{a, b}	3 _a	1 _a	13	2791.07 (982.21)
Snakes	14 _b	0 _a	3 _b	0 _a	17	1 _a	1 _{a, c}	1 _a	1 _{b, c, d, e}	2 _{a, b, c}	0 _a	0 _a	6	2937.50 (116.04)
Crocodiles	0 _a	17 _b	3 _b	0 _a	20	0 _a	20 _b	0 _a	0 _e	0 _a	1 _a	0 _a	21	20238.10 (8251.70)
Total	33	41	75	1	150	3	36	7	41	30	5	1	123	

Discussion

This study exemplifies how trade filters that affect the supply of bushmeat at local scales can affect the trade in urban markets. The types of species hunted and sold were related to trade filters such as hunting methods, sale price and the condition that the meat was sold (fresh, smoked, dried). I documented minimal variation in results among villages, indicating these trade filters were common features determining aspects of bushmeat trade throughout the region. Understanding of the role of trade filters provides an explanation of how reptiles can be ubiquitously hunted but rare in urban markets. Below I discuss how each trade filter influenced the types and numbers of species entering the bushmeat trade.

Hunting locations and methods determined the types of species entering bushmeat markets and thus served as one of the most basic filters affecting the trade. I found that hunting primarily occurred in the farm-bush matrix surrounding their villages with snares as the most common method to capture species. Most of the subjects indicated farming was their primary profession and consequently did not travel far from the villages; a finding consistent with similar studies conducted in other regions of Cameroon and sub-Saharan Africa (Wilkie & Curran 1991; Wilkie & Carpenter 1999; Pailler *et al.* 2009). The farm and the secondary forest surrounding it attract certain ungulate, rodent, primate and reptile species thus influencing the kinds of species hunted (Lawson 2000; Naughton-Treves *et al.* 2003). Snares were more amenable to catching rodents, porcupines, and ungulates than arboreal fauna such as some primates and birds (Wilkie & Carpenter 1999; Fa & Yuste 2001; Hayashi 2008; Kümpel *et al.* 2009). There

was likely an interaction between the use of snares, and hunting locations that was reflected in the rank of rodents, porcupines and ungulates being most frequently hunted, a finding consistent with other studies in the Congo basin (Wilkie & Carpenter 1999; Fa & Yuste 2001; Naughton-Treves *et al.* 2003; Fa *et al.* 2006; Rist *et al.* 2008). Hunting patterns among villages of various sizes and ethnic majorities in southwest Cameroon were consistent with patterns observed in studies conducted elsewhere in sub-Saharan Africa (Noss 1998; Kümpel *et al.* 2009). Thus this trade filter is likely to be a common element influencing the kinds of species involved in the bushmeat trade generally, and provides a focal point to direct conservation efforts.

Clear differences existed in the selling condition of bushmeat among taxa, particularly between mammals and reptiles, which influenced their transport to urban markets. While several market studies indicate that relatively few reptiles are traded (Noss 1998; Fa & Yuste 2001; Fa *et al.* 2006; Foerster *et al.* 2012), there may not always be a correlation between the numbers of individuals hunted and their sale in urban markets (Fa & Yuste 2001). The rarity of reptiles in urban bushmeat markets may be a result from how they are sold at lower levels of the trade. I showed that a majority of hunters captured crocodiles, snakes and monitor lizards. They were sold alive and generally consumed within the household with the exception of crocodiles. Conversely, mammals were sold in the smoked condition and sold in villages in addition to being consumed in the household.

Bushmeat destined for the village may be purchased by local consumers and outside traders that subsequently transported the meat to urban markets (Cowlshaw *et al.* 2005;

Kümpel *et al.* 2007; Solly 2007; Willcox & Nambu 2007). Most vehicles transporting bushmeat lack refrigeration or space, thus smoked meat or meat parts can be transported more easily than fresh meat or live animals (Hart 2000; Thorbjarnarson & Eaton 2004; Cowlshaw *et al.* 2005; East *et al.* 2005; Kümpel *et al.* 2007; Willcox & Nambu 2007; Macdonald *et al.* 2011). Consequently, the condition the meat is sold as may affect whether it is more likely to be consumed locally or traded in markets. This trend has also been documented in other studies in Cameroon and Gabon (Willcox & Nambu 2007; Foerster *et al.* 2012). I demonstrated that some reptiles species are commonly hunted, thus the rarity of reptiles in the bushmeat trade may be due to the condition in which they are sold. Crocodiles were mostly sold in the village albeit clandestinely. It is illegal to trade crocodile meat, and their rarity in urban markets may be due to the condition they are sold and their protected status. While few reptile species may be a part of the bushmeat trade, assessments of their exploitation are likely to be underestimated in urban market studies due these trade filters of selling condition and legal status.

The sale price of species has been hypothesized as a trade filter affecting what is sold in urban markets and my study partially supported this (Albrechtsen *et al.* 2007; Kümpel *et al.* 2010; Allebone-Webb *et al.* 2011; Macdonald *et al.* 2011). Taxa with higher body mass such as ungulates and crocodiles were more valuable than smaller taxa and the more valuable taxa were often sold in the village. However some large bodied reptiles like crocodiles and snakes had sale prices higher and lower, respectively, than what would be predicted from mass alone. Price also did not predict which species were most exploited. Smaller bodied taxa like rodents and porcupines with lower economic value

were the most exploited. Sale price, body mass, selling condition, and hunting methods results in complex interactions between these trade filters and their relationships with the types of species hunted that ultimately influence bushmeat trade in urban markets.

Osteolaemus tetraspis provides an interesting case on how trade filters affect species' prevalence in urban markets and how trade filters confound our ability to determine sustainability of the bushmeat trade. This study and another study in the Republic of Congo found that the sale price for *Osteolaemus* was higher than what would be predicted by mass alone, suggesting either demand, capture costs, or rarity of *Osteolaemus* species make them valuable (Thorbjarnarson & Eaton 2004). This should result in high exploitation and trade, yet in this study they were hunted and traded within the village in lower numbers relative to the mammalian taxa. Other studies in Cameroon also suggest that *Osteolaemus* are relatively rare in urban markets with estimated annual trade of hundreds of individuals (Fa *et al.* 2005). Conversely in the Republic of Congo *Osteolaemus* are one of the most commonly traded species in urban markets with estimated annual trade of thousands of individuals (Behra 1990; Thorbjarnarson & Eaton 2004; Eaton 2010). The combination of the aforementioned trade filters may explain this observation. In Campo Ma'an, Cameroon, the hunters' methods and locations may have resulted in fewer captures of *O. tetraspis* because it is an aquatic species and hunting mostly occurred in the farm-bush matrix. In the Republic of Congo hunters are also fisherman increasing their encounters with *Osteolaemus* species. In both the Republic of Congo and Cameroon *Osteolaemus* are sold alive but in the Republic of Congo, large numbers of *Osteolaemus* are traded via boat whereas in Cameroon they are traded via

roads (Thorbjarnarson & Eaton 2004; Willcox & Nambu 2007). Conversely, in Gabon, *Osteolaemus* are killed before or during trade but Gabon vendors and traders have access to ice chests. Fewer *Osteolaemus* are traded in Gabon either due to lower human population densities and thus lower exploitation, and/or their body size limits the number of individuals that can be stored in ice chests (Thorbjarnarson & Eaton 2004). and but (Thorbjarnarson & Eaton 2004). Thus the state that *Osteolaemus* may be sold as and the mode of transportation may affect the amount and spatial scale of trade. Nonetheless, the magnitude of exploitation in urban market studies is likely to be underestimated for these reasons and additionally due to the illegality of sale that results in clandestine trade of these species (Thorbjarnarson & Eaton 2004; Fa *et al.* 2005; Willcox & Nambu 2007).

The clandestine sale of this species makes it difficult to obtain broad scale assessment of the sustainability of the trade of *O. tetraspis*. However the younger demographic structure and low encounter rates of populations of *O. tetraspis* in Campo Ma'an can be problematic for the persistence of these populations (Smolensky 2014). The dynamics and growth of populations is most sensitive to the number of adults (Nichols 1987; Webb *et al.* 2000; Tucker 2001). Thus even though *O. tetraspis* is the fifth most commonly hunted species and rare in urban markets, hunting can still have a negative impact on the populations. These trade filters may confound earlier conclusions of their roles in the bushmeat trade and estimates of their exploitation.

In summary, the bushmeat trade is subject to many filters including hunting patterns, selling conditions, sale prices, and legality of sale, that affect the kinds of species and numbers of individuals that enter urban markets. I examined these filters at the base of

the trade with hunters in rural communities and found hunting locations and methods influence the kinds of species captured while species specific selling conditions and prices influence the destination of hunted species. This study illustrated that a wide variety of species are part of the bushmeat trade and merit further study on the magnitudes of their exploitations. While urban markets reflect the general composition of broad species groups involved in the bushmeat trade, trade filters will result in underestimates of the magnitude of bushmeat exploitation for many non-mammalian species. As mammals become extirpated due to overexploitation other vertebrates may become more prevalent in the trade (Alvard 1993; Brashares *et al.* 2004), warranting focus on the trade of other vertebrates in villages.

CHAPTER III

DNA BARCODING OF CAMEROON SAMPLES ENHANCES OUR KNOWLEDGE ON THE DISTRIBUTIONAL LIMITS OF PUTATIVE SPECIES OF AFRICAN DWARF CROCODILES (*OSTEOLAEMUS* SPP.)

Introduction

""Cryptic diversity can hinder recognition of conservation units and their distributions (Bickford *et al.* 2007), which is essential for managing and preserving biodiversity. This is especially problematic in groups of conservation concern where cryptic diversity is common, such as African crocodiles. Recent molecular work revealed that the Nile crocodile, previously considered a single genetically homogeneous species (*Crocodylus niloticus*), is comprised of two divergent lineages: *Crocodylus niloticus* and the resurrected cryptic species *C. suchus* (Schmitz *et al.* 2003; Hekkala *et al.* 2011). The latter species is declining or extirpated throughout much of its distribution (Hekkala *et al.* 2011). Therefore, management policies, which currently include harvesting quotas and translocation, must be revised to take into account the vulnerable *C. suchus* lineage (Hekkala *et al.* 2011). Similarly, multi-locus analyses of the monotypic slender-snouted crocodile (*Mecistops cataphractus*) revealed the presence of two highly divergent lineages that likely represent two species (Shirley *et al.* 2014). One of these cryptic species is on the verge of extinction, making its recognition critical to current

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management plans (Shirley *et al.* 2014). Recent molecular work has also revealed that the African dwarf crocodile *Osteolaemus tetraspis*, listed as ‘Vulnerable’ by the IUCN Red List (IUCN 2012b), is comprised of three highly divergent lineages that may represent distinct species and merit independent management: *O. sp. nov.* in the Upper Guinean rainforest; *O. tetraspis* in the Lower Guinean rainforest; and *O. osborni* in the Congolian rainforest (Eaton *et al.* 2009; Franke *et al.* 2013). Limited sampling across geographic regions, however, precludes identification of the geographic boundaries of these lineages, which is needed for their effective conservation and management (Eaton *et al.* 2009).

The Cameroon Volcanic Line (CVL; Figure 4a) is a hypothesized phylogeographic barrier for several vertebrate taxa (Stewart 2001; Nicolas *et al.* 2011; Linder *et al.* 2012), and is proposed to represent the geographic limit between *O. sp. nov.* and *O. tetraspis* (Eaton 2010; Shirley *et al.* 2014). The CVL, however, may not constitute an effective barrier for crocodylians, because rivers could have allowed dispersal across this putative barrier as has been shown for crocodylians in other regions (Ryberg *et al.* 2002).

Osteolaemus osborni is hypothesized to be restricted to the central part of the Congo River Basin (Eaton 2010). Although upper portions of this basin reach Cameroon, it is unclear whether *O. osborni* occurs in this country. Current management programs operate under the assumption that *O. tetraspis* is the only species present in Cameroon (Eaton 2010; Djeukam 2012). In this study, I expanded previous phylogeographic work on *Osteolaemus* by conducting detailed sampling in Cameroon, including the southern range of the CVL (Figure 4a). These results shed light on the distributions of the three

main *Osteolaemus* lineages, which has important implications for their conservation and management.

Materials and methods

Between August 2009 - February 2010 and December 2011 - March 2012, I collected tissue samples from 65 wild caught *O. tetraspis* throughout Cameroon, including both sides of the CVL. I also collected tissues from individuals in a captive population housed in the Mvog-Betsi Zoo, in Yaoundé, Cameroon (Figure 4b). Tissue samples were stored in 95% ethanol at room temperature.

I extracted total genomic DNA using Qiagen DNeasy tissue kits, and PCR-amplified fragments of a subset of the genes used by Eaton et al. (2009) to facilitate comparison between studies. My dataset included two mitochondrial gene fragments, CO1 (413 bp) and 12S rDNA (372 bp), and one nuclear gene fragment, LDH-A (658 bp). Primers and PCR conditions are listed in Table S3. I sequenced gene fragments in forward and reverse directions. Sequences and chromatographs were examined, edited, and assembled using Sequencher 4.6 (Gene Codes Corp., Ann Arbor, MI). None of the protein-coding sequences had premature stop codons or frame shifts, suggesting that they are not pseudogenes.

I conducted phylogenetic analyses to determine the membership of the new Cameroon samples in relation to the three divergent *Osteolaemus* lineages reported in Eaton et al. (2009). I included sequences reported in GenBank from that and other studies, and used *Mecistops cataphractus* and *Crocodylus niloticus* as outgroups

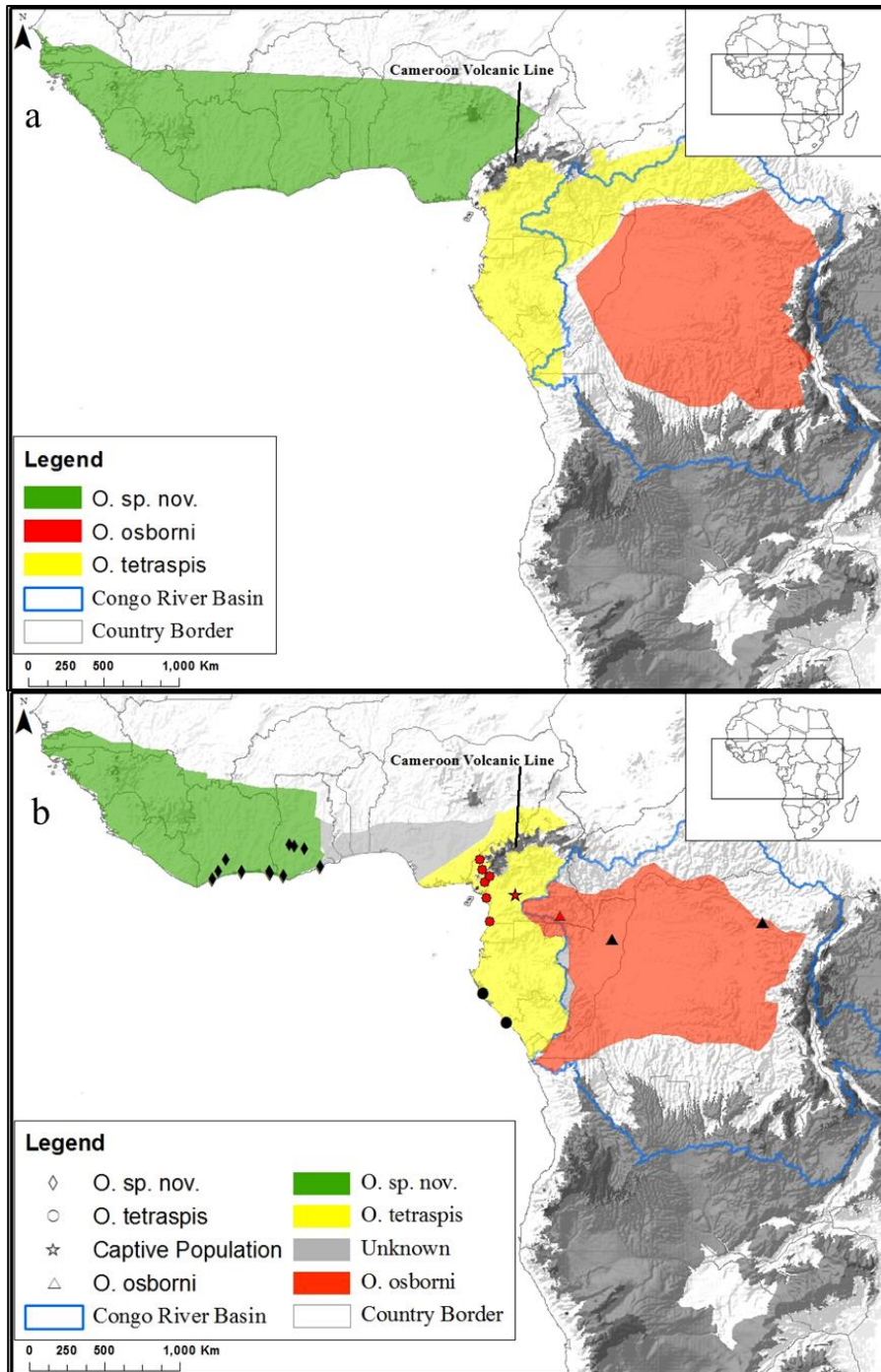


Figure 4.(a) Map of the current hypothesized distributions of *Osteolaemus* lineages (b) Revised map based on this studies' findings with sampling localities from this study (red) and from Eaton et al. (2009) (black). Diamonds, circles and triangles correspond to tissue samples of *O. sp. nov.*, *O. tetraspis*, and *O. osborni* respectively. The star represents a captive population containing *O. tetraspis* and *O. osborni* at the Mvog-Betsi Zoo in Yaoundé, Cameroon.

(Table S4). I analyzed each gene individually, as concatenation of the three genes resulted in excessive taxa with missing genes. Additionally, different portions of the genes were amplified across studies; thus, I trimmed sequences to include only the overlapping portions. There were 97 sequences obtained for CO1, 70 sequences for 12S rDNA and 57 sequences for LDH-A.

I aligned sequences using the program MCOFFEE (Moretti *et al.* 2007), and visually inspected the alignments in MacClade v. 4.08 (Maddison & Maddison 2005). I used MEGA 5.1 (Tamura *et al.* 2011) to infer the best substitution model for each dataset. Maximum Likelihood (ML) and Bayesian analyses were implemented in raxmlGUI v. 1.3 (Silvestro & Michalak 2012) and Mr.Bayes v. 3.2.1 (Ronquist *et al.* 2012), respectively. For ML analysis, I used an ML search and a thorough bootstrap analysis with the number of bootstrap replicates determined by a stopping criterion based on the majority rule consensus method (Silvestro & Michalak 2012). For the Bayesian analysis, I implemented two runs each with 4 chains for more than 1,000,000 generations. The chains were sampled every 250 generations. The analysis was terminated once the standard deviation of split frequencies and Potential Scale Reduction Factor values approached 0 and 1 respectively, and when the posterior probability distribution reached apparent stationarity (Ronquist *et al.* 2012). I also calculated statistical parsimony networks for each gene in TCS v. 2.1 (Clement *et al.* 2000), with connection limits set to 100 steps, and treated gaps as missing data. The geographic distribution of the lineages and haplotypes were compared to the locations of the CVL in a Geographic Information System (GIS) using ArcMap v. 10.0 (ESRI, Redlands CA).

Results

The best-fit models of nucleotide substitution and descriptive statistics for each gene are listed in Table S5. Sequences representing distinct haplotypes were deposited in GenBank. The new samples from Cameroon clustered with *O. tetraspis* (western localities) or *O. osborni* (eastern locality) in the phylogenetic reconstructions and statistical parsimony analyses for CO1 and 12SrDNA (Figure 5a-b and 6a-b). Samples from Cameroon originating west of the CVL fell within the *O. tetraspis* lineage and samples from the Ivory Coast and Ghana, clustered with *O. sp. nov.*. The captive population in the Mvog-Betsi Zoo contains a mixed stock of adult male and female *O. tetraspis* and *O. osborni*. For the mitochondrial gene markers, only one novel CO1 haplotype for *O. tetraspis* was found in the new samples, which differed at one or two positions from the previously reported haplotypes in this lineage. No new 12S rDNA haplotypes were found. LDH-A was highly conserved among lineages, with only five haplotypes for the three lineages separated by one or two positions (Figures 5c and 6c). Two of them represent new LDH-A haplotypes for *O. tetraspis*. The LDH-A and RAG1 markers used by Eaton et al. (2009) are highly conserved within *Osteolaemus*, providing low resolution in phylogenetic reconstructions, and their concatenated phylogenetic analyses were dominated by mtDNA markers.

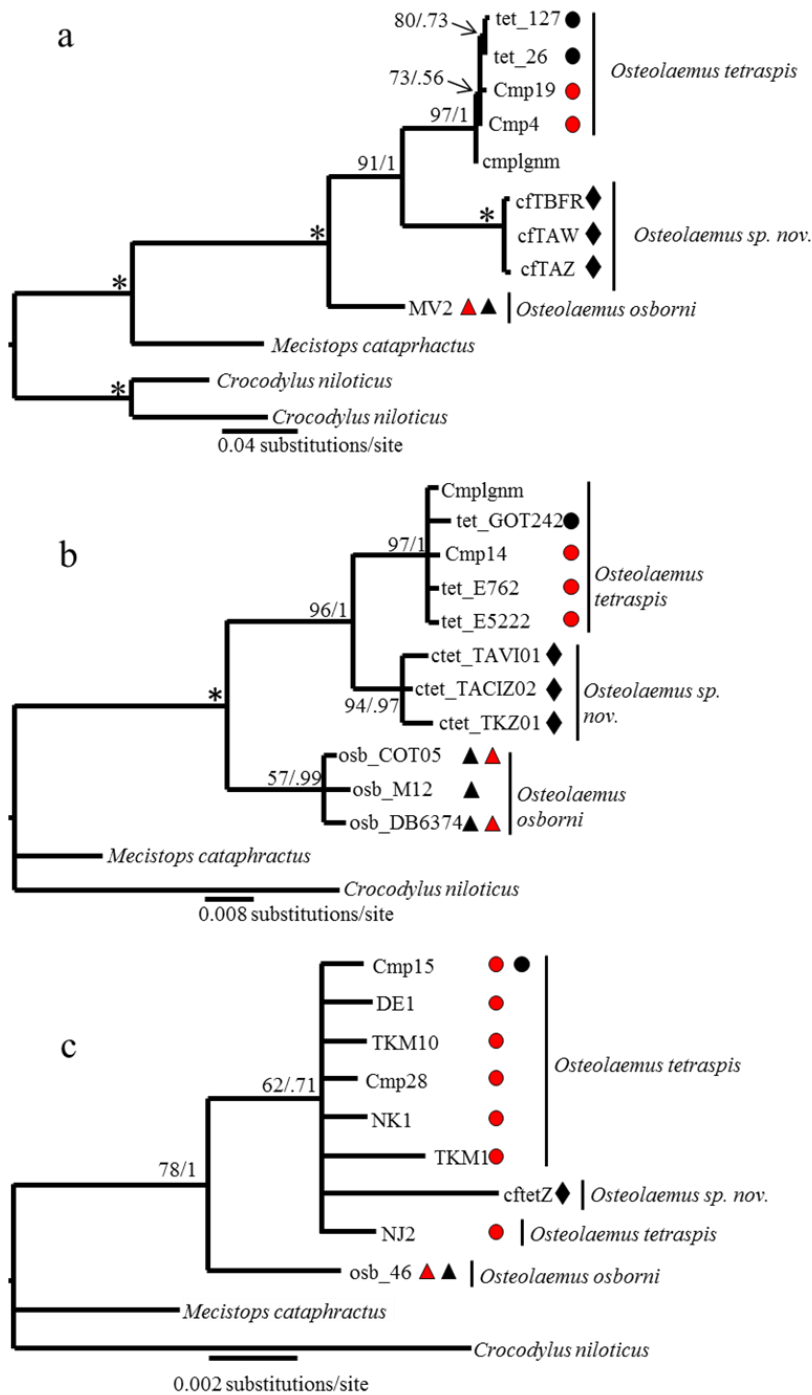


Figure 5. Phylogenetic relationships among *Osteolaemus* lineages for the CO1 (a), 12S rDNA (b) and LDH-A (c) gene fragments. Statistical support for nodes are bootstrap and posterior probabilities. Asterisks denote nodes with 100% for both methods. Symbols correspond to localities in Figure 4. Sequences without symbols had no locality information. Duplicate sequences for each haplotype are not displayed.

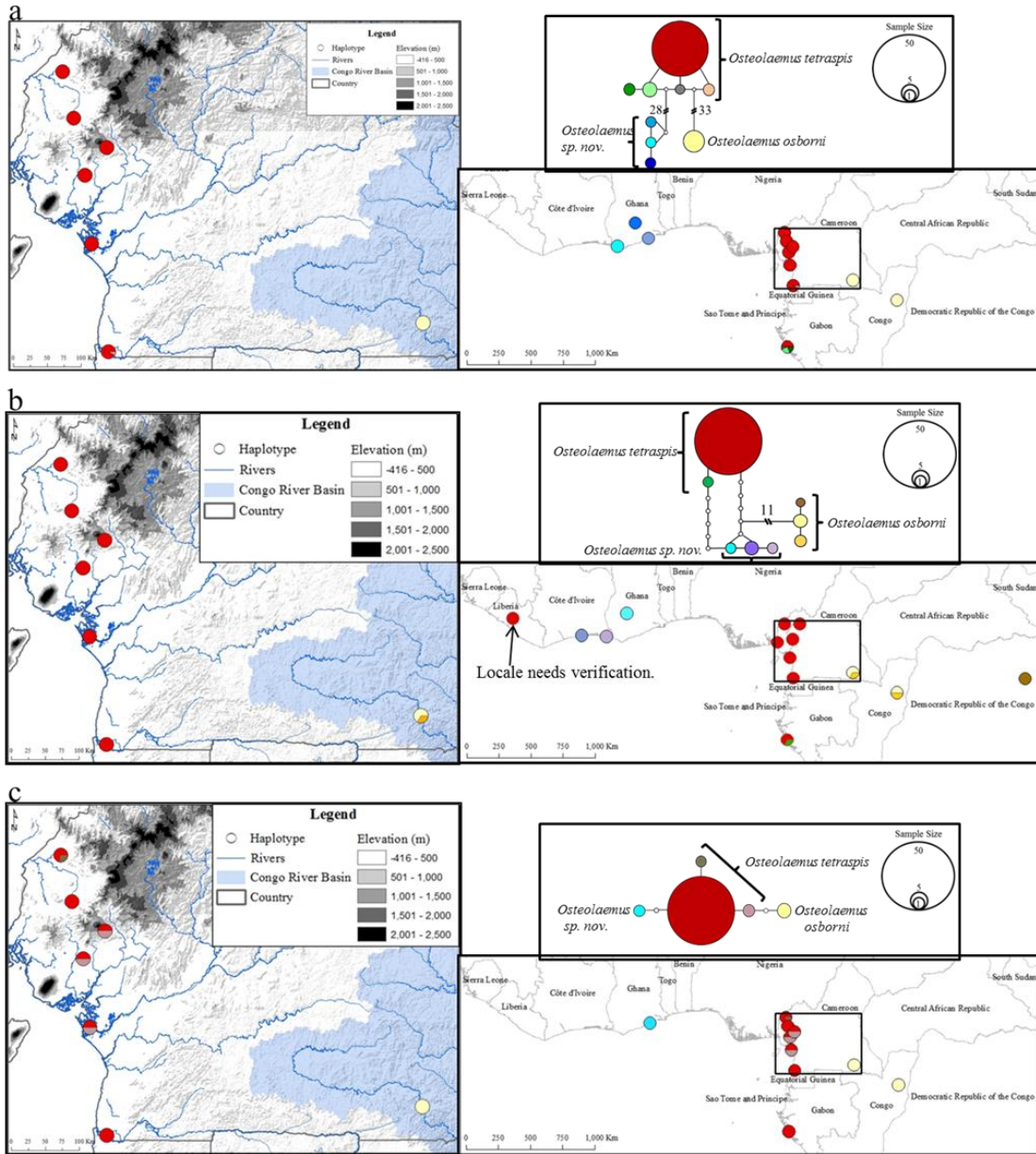


Figure 6. Haplotype network and distribution of haplotypes of the CO1 (a), 12S rDNA (b) and LDH-A (c) gene fragments from *Osteolaemus* lineages. Open circles represent putative haplotypes. The inset map of Cameroon features the distribution of haplotypes relative to the Cameroon Volcanic Line (grey) and the Congo River Basin (blue).

Discussion

The presence of *O. tetraspis* on the western side of the CVL implies that this putative biogeographic barrier does not represent the limit between this lineage and *O. sp. nov.*, as previously suggested (Eaton 2010). It is possible that small rivers present in a 30-40 km gap between Mt. Cameroon and the rest of the mountain chain (Figure 6) facilitated dispersal of *O. tetraspis* across the CVL. The ubiquitous bushmeat trade of *Osteolaemus* offers an alternative explanation for the presence of *O. tetraspis* across the CVL.

Equivocal evidence suggests that the *O. tetraspis* distribution may extend as far west as Liberia. A 12S rDNA sequence from Liberia reported by Schmitz et al. (2003) corresponds to an *O. tetraspis* haplotype (Figure 6b), but this sample lacks specific locality information and the listed origin may be incorrect (Franke et al. 2013).

Our results also show that *O. osborni* occurs in Cameroon, demonstrating the presence of this lineage in the far reaches of the Congo River basin (Figure 4b and 6). Therefore, it is important that management plans in Cameroon take into account this lineage. Detection of both *O. osborni* and *O. tetraspis* in the Mvog-Betsi Zoo illustrates the potential for unintended hybridization between these two lineages, which has been already documented in captivity (Franke et al. 2013). *Osteolaemus* can be traded alive for the bushmeat market and individuals rescued from the trade are sometimes released back into the wild, but not necessarily at the point of origin. Release of individuals away from their source population creates potential for hybridization in the wild.

I endorse previous studies that consider each of the three main *Osteolaemus* lineages as a distinct species (Eaton et al. 2009; Franke et al. 2013; Shirley et al. 2014). As such I

recommend management that best conserves their evolutionary history including conservation status assessments of each species (Smolensky 2014), and detailed genetic surveys for *Osteolaemus* west of the CVL, from Nigeria to Benin, to determine the distributional limits between *O. tetraspis* and *O. sp. nov.* Genetic characterization of additional populations in Cameroon is also needed to obtain better resolution of the distributions of *O. tetraspis* and *O. osborni* (Figure 4b).

CHAPTER IV
CO-OCCURRING CRYPTIC SPECIES POSE CHALLENGES FOR
CONSERVATION: A CASE STUDY OF THE AFRICAN DWARF CROCODILE
(*OSTEOLAEMUS* SPP.) POPULATIONS IN CAMEROON

Introduction

The conservation status of species is determined by its distribution, population sizes, demographic structures and associated threats (Iucn 2012a). This information also provides the scaffolding for management and conservation strategies (Meffe & Carroll 1997; Mills 2007). However these data are lacking for 24% of species listed in the Red List of the IUCN (IUCN 2012b). New molecular evidence indicates that several listed species may actually be comprised of a complex of cryptic species (Pfenninger & Schwenk 2007; Murray *et al.* 2008). This taxonomic challenge can have significant ramifications on our understanding of species' distributions, population statuses, management, and legislative protection (Bell *et al.* 1998; Mace 2004; Sattler *et al.* 2007). For example two endangered species, *Brachyteles arachnoides* and *B. hypoxanthus* were formerly thought to be one species. Captive breeding programs designed to augment *B. arachnoides* populations were comprised of hybrids between the two. Introductions of those hybrids into the small population of *B. hypoxanthus* could have resulted in its genetic extinction (Brito 2004). The status and management of threatened taxa must be

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repeatedly assessed as taxonomies are refined.

The African dwarf crocodiles (*Osteolaemus spp.*) provide an exemplary case on the heuristic approach needed to effectively manage and conserve biodiversity as species' taxonomies change. *Osteolaemus* was formerly a monotypic genus containing two subspecies *O. tetraspis tetraspis* and *O. t. osborni*, widely distributed in equatorial lowland rain forests of West and Central Africa. They were managed as a single species listed under CITES Appendix I with a conservation status of 'Vulnerable' (IUCN) due to threats of habitat loss and hunting pressure (Eaton 2010). Recent studies show the genus is comprised of three species, *O. sp. nov.*, *O. tetraspis* and *O. osborni* (Eaton *et al.* 2009; Franke *et al.* 2013; Shirley *et al.* 2014; Smolensky *et al.* 2014). Consequently this study and other current efforts are underway to characterize the distribution, population status, and captive breeding programs for all three species (Eaton *et al.* 2009; Eaton 2010; Franke *et al.* 2013; Smolensky *et al.* 2014).

Osteolaemus sp. nov. occurs in the upper Guinean rain forests (Figure 7). It has been extirpated from the extreme western part of its range. The southern coasts of Ghana and Cote d'Ivoire may be the remaining strongholds for this species (Waitkuwait 1989; Kofron 1992; Shirley *et al.* 2009; Eaton 2010). *Osteolaemus tetraspis* and *O. osborni* occur in the lower Guinean and Congo rain forests respectively (Figure 7). Population assessments of *O. tetraspis* and *O. osborni* are few, mostly outdated, and indicate low densities where they are exploited (Riley & Huchzermeyer 1999; Wild 2000; Eaton 2006, 2010). In light of these taxonomic revisions and their current threats, population assessments are needed to update the conservation status of *Osteolaemus* species.

Management must reflect our current knowledge of *Osteolaemus* taxonomy to conserve their evolutionary diversity.

An additional factor that complicates the conservation status assessments of species is the co-occurrence of cryptic taxa within countries. Smolensky et al. (2014) recently demonstrated the co-occurrence of *O. tetraspis* and *O. osborni* in Cameroon.

Osteolaemus tetraspis is widely distributed in Cameroon, but is vulnerable based on threats of hunting pressure and deforestation (Wild 2000; Gonwouo & Lebreton 2010). Assessments of *O. tetraspis* were conducted between ten and fifteen years ago and were mostly presence/absence surveys with the exception of one site in which population density surveys were conducted (Wild 2000). No population density assessments of *O. osborni* have been conducted.

The aim of this chapter is to provide information on the population ecology of *O. tetraspis* and *O. osborni* in Cameroon to facilitate independent conservation of these two species. I provide distribution maps of the two species, the first population assessments of *O. osborni* and *O. tetraspis*, and a second assessment of western populations of *O. tetraspis*.

Materials and methods

Study area

Between 18 August and 21 November 2010, and between 17 December 2011 and 16 February 2012 I conducted population surveys in three study regions designated ‘West’, ‘Southwest’, and ‘Southeast’ located in lowland Congo-Guinean rainforest of Cameroon (Figure 7). In the ‘West’ region surveys were conducted within the Mone River Reserve

(MRR), on the southern border of the Takamanda National Park (TNP), and between MRR and TNP, near the villages of Okpambe and Ebinsi (Figure 7). The ‘Southwest’ region served as an additional site for a spatial comparison of *O. tetraspis* populations to assess the status of the species at a broad scale. It was located in the Campo Ma’an National Park. Surveys were conducted in 2010 and 2012 in the southwest portion of the park specifically in the sections called Ile Dipikar and Corridor. The Southeast region is the only region known to harbor *O. osborni* and was chosen to provide the first assessment for this species in the country (Smolensky *et al.* 2014). This region was located in the Dja River at the periphery of the Nki national park.

Sites within regions were selected due to road access, proximity to a protected area and anecdotal evidence of *Osteolaemus* presence. All sites were at low elevations (<500 m) with dense canopy cover and gallery forest vegetation. Streams in the ‘West’ and ‘Southwest’ regions had clear water and slow flow. Depth ranged from less than 0.25 m to 1 m, but was typically less than 0.5 m. The width of the streams ranged from 1 m to 10 m. The Dja river is a major tributary of the Congo river basin with widths up to 120 m, mean annual discharge between 450 – 500 m³/s, and turbid waters (Seyler *et al.* 1993). I surveyed the edges of the river where flow was greatly reduced and canopy cover was dense.

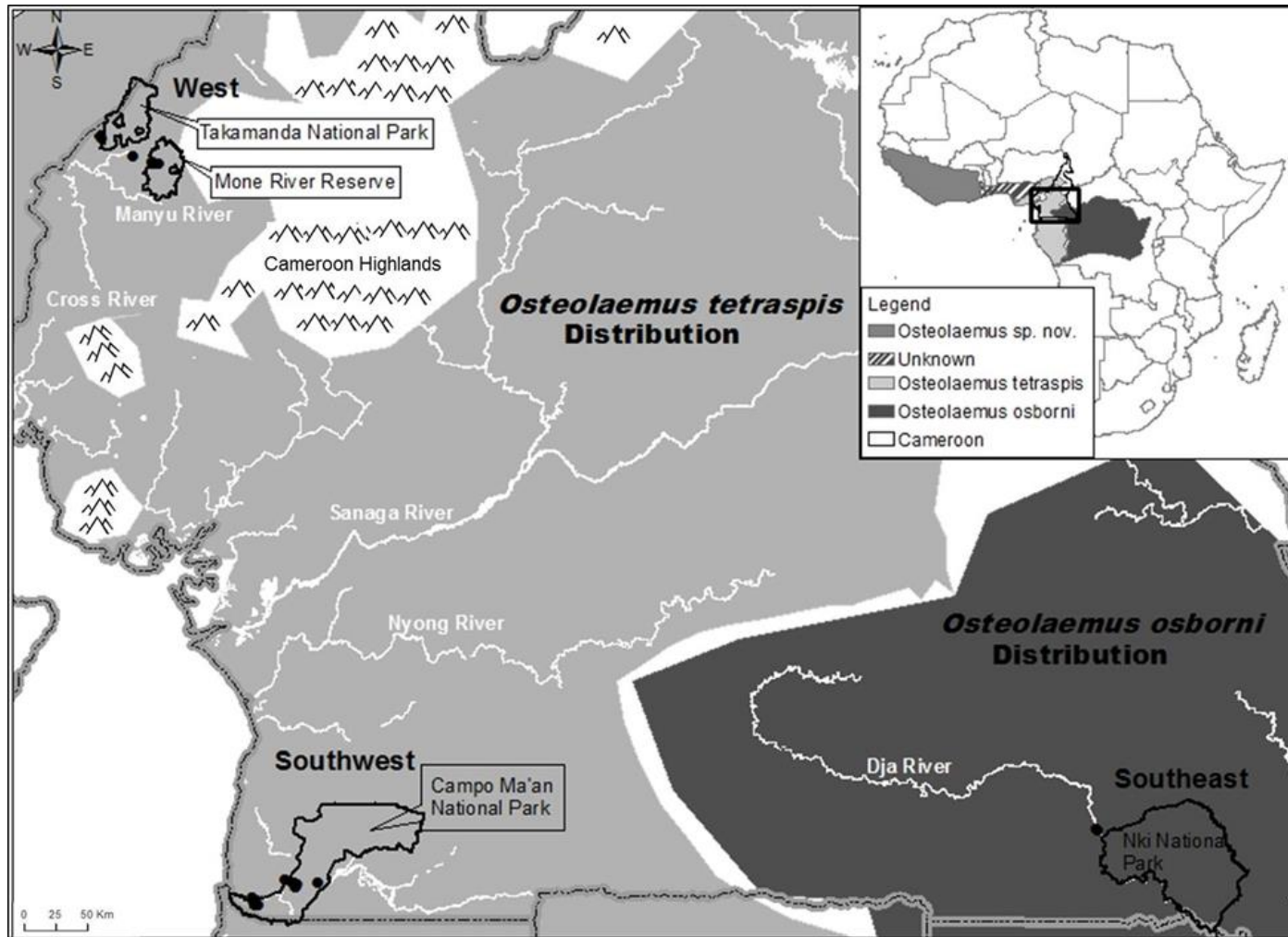


Figure 7. Map of study regions in Cameroon with the shaded distributions of *O. tetraspis* and *O. osborni*. National parks outlined in black, specific sites in black circles, and major rivers in white. Inset map shows the distributions of all three *Osteolaemus* species.

Survey methods

Nocturnal spotlight surveys were conducted to census crocodile populations (Chabreck 1966). When initial surveys resulted in low crocodile encounters, the number of surveys was reduced at that particular site within the region. Surveys entailed wading and walking along bank-sides and by canoe in the Dja River. Each survey began two hours after dusk, and ended two to four hours before dawn. Each stream was searched from one to three nights covering non-overlapping sections of the stream. Beginning and end locations were recorded using a GPS unit to map the location and length of each survey. An LED headlamp (white LED light, 200 lumens) was used to detect and count crocodiles. Crocodiles were typically solitary and the waters were clear and shallow, and I was able to detect submerged crocodiles. I attempted to capture all crocodiles to obtain morphometric measurements and tissue samples for species identification via genetic analyses. Capture techniques included hand-grabbing for smaller animals and a snare-pole for larger animals (Hutton *et al.* 1987). For each crocodile I recorded its location, snout-vent length (SVL), total length (TL), and sex. Crocodiles were given unique identifying marks by caudal scute removal (Webb & Messel 1977) and released at the site of capture.

Sex was reliably determined for individuals with TL >40 cm. Crocodiles were assigned to one of three life-stage classes based upon studies of captive and wild *Osteolaemus* populations (Beck 1978; Teichner 1978; Tyron 1980; Eaton 2009). These classes were hatchlings (<24 cm), juveniles (24-99 cm) and adults (>100 cm). Crocodiles that evaded capture were not assigned to a stage-class.

Statistical analyses

The population statuses of *O. tetraspis* and *O. osborni* were assessed via encounter rates and population structure. Encounter rates were the number of crocodiles detected per km of river habitat and served as relative population density indices. Population structure was the relative proportions of crocodiles in each size class. Analyses of population structure were limited to crocodiles that were captured and measured. Encounter rates and population structures were compared among regions using Kruskal-Wallis and Fisher's Exact tests respectively. At the Southwest site for which I had two years of surveys, I used a Wilcoxon Signed-Rank test to compare encounter rates and population structure between years.

Results

I conducted 43 nocturnal spotlight surveys, covering 105.4 km of stream or river habitat. Sixty-five *O. tetraspis* and 13 *O. osborni* were encountered among the three regions. Crocodiles were detected in all regions and at 75% of the sites ($n = 8$) (Table 2). However the encounter rates were generally low across sites (Table 2). The mean encounter rates for *O. tetraspis* and *O. osborni* were 1.02 crocodiles/km ($SD = 1.34$, $n = 39$) and 0.61 crocodiles/km ($SD = 0.38$, $n = 4$) respectively. Encounter rates did not differ among regions ($H = 0.06$, $p\text{-value} < 0.81$) nor among sites ($H = 6.25$, $p\text{-value} < 0.52$). In the Southwest, the mean encounter rate decreased from 1.31 crocodiles/km ($SD = 1.13$, $n = 11$) in 2010 to 0.44 crocodiles/km ($SD = 0.46$, $n = 16$) in 2012, but this decrease was not significant ($W = -1.94$ $p\text{-value} < 0.05$). No individuals marked in 2010 were re-captured in 2012.

Osteolaemus tetraspis populations were mostly comprised of juveniles and secondarily by adults (Figure 8). In the Southwest juveniles made up 75.0% (n = 24) of the population structure and adults made up 25.0% (n = 8). No hatchlings were detected though 22.0% of the juveniles had recently entered this size class and were between 30-35 cm TL (Figure 8). The population structure remained the same between 2010 and 2012. In the West juveniles made up 83.3% (n = 10) of the population structure and adults the remaining 16.7% (n = 2). Two of the juveniles were between 30-35 cm TL. Two adult *O. osborni* and one juvenile were captured at the Southeast region. Individuals detected but not captured fell within those two size classes. There was no significant difference in the population structure of *O. tetraspis* between regions (F = 2.89, p-value <0.20). The sex ratio was male-biased 1.75:1 (n = 22) for the Southwest region and female biased for the West 0.67:1 (n = 5) and Southeast 1:2 (n = 3) regions.

Table 2. Mean encounter rates (crocodiles/km) for *Osteolaemus tetraspis* in the Southwest and West regions, and *O. osborni* in the Southeast region in Cameroon.

Study Region	Site	No. Surveys	Survey Distance (km)	No. Detected	No. Captured	Mean Encounter Rates (SD)
Southwest	Ile Dipikar	16	40.54	35	25	1.01 (0.98)
	Corridor	11	26.20	10	7	0.48 (0.58)
	Total	27	66.70	45	32	0.79 (0.88)
West	Mone River	5	3.38	9	6	2.16 (2.75)
	Okpambe	2	3.70	2	1	0.56 (0.11)
	Ebinsi	1	1.30	0	0	0.00
	Kekukesem	3	3.91	9	5	2.17 (0.84)
	Takamanda	1	1.70	0	0	0.00
	Total	12	13.99	20	12	1.54 (2.04)
	Collated for both regions		39	80.69	65	44
Southeast	Nki	4	24.71	13	3	0.61 (0.38)

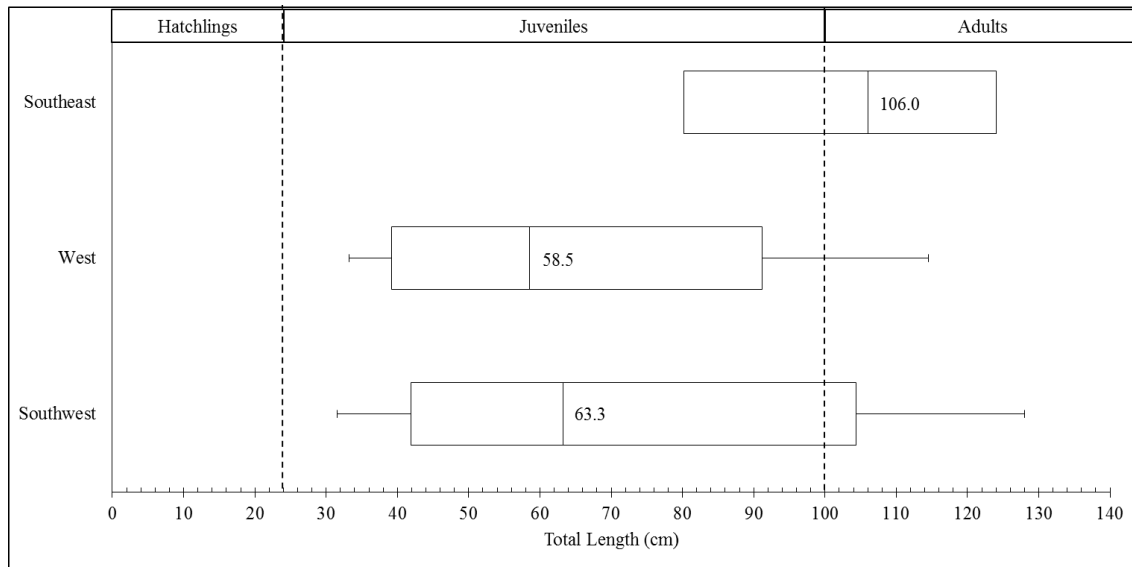


Figure 8. Size distribution of *Osteolaemus tetraspis* in the West (n = 12) and Southwest (n = 32) regions, and of *O. osborni* in the Southeast (n = 3) region. Vertical Bars represent population structure divisions between hatchlings (<24 cm total length), juveniles (<100 cm total length), and adults based upon the literature. Mean encounter rate values are included to the right of the median and error bars represent minimum and maximum sizes of captured crocodiles.

Discussion

These results provide the most updated information on the population status of *O. tetraspis* throughout its distribution and the first estimate of *O. osborni* population densities in Cameroon. Encounter rates of both species were low. They were comparable to exploited populations occurring in similar habitats in the Republic of Congo, and 4.5 times lower than encounter rates of unexploited *O. tetraspis* populations in Gabon (Eaton, 2009). Although populations of *O. tetraspis* occur throughout Cameroon the species is still vulnerable to unregulated exploitation (Wild 2000). The low encounter rates of both species, and juvenile biased size class structure of *O. tetraspis* may be indicative of unsustainable exploitation of *Osteolaemus* populations (Webb *et al.* 2000). Additional factors not associated with hunting that may have influence observed encounter rates are discussed below.

Encounter rates of *O. tetraspis* were similar across its broad distribution. Many of the surveys in the Southwest and West contained 1 or no individuals in 2.5 km of river habitat, but encounter rates of 2 crocodiles/km or greater were more common in the West. The habitats were similar in their physical and vegetative characteristics, but differed in levels of anthropogenic disturbance. The sites adjacent to or in protected areas of the West were remote with lower human population densities, fewer logging concessions and roads in the surrounding area relative to the sites in the Southwest (World Bank 2014). The interiors of protected areas of the west like Takamanda National Park, harbor higher densities (3 crocodiles/km) (Wild 2000) than peripheries (this study). Sites far from protected areas (e.g. Ebinsi), had even lower encounter rates

which were attributed to degraded habitats, low enforcement of illegal hunting, and fishing methods involving the use of poisonous organo-chloride insecticides (Gonwouo & Lebreton 2010). Cameroon's population densities, infrastructure development and agriculture sector have doubled over the last ten years (De Wasseige *et al.* 2012; World World 2014). These results suggest that protected areas serve as important havens for populations of *O. tetraspis* as development ensues, and that they should be large with limited access toward their interiors.

In the Southwest, encounter rates also decreased between 2010 and 2012 although not significantly. While it may take several years to detect changes in population structures of crocodiles (Webb *et al.* 2000), the observed differences may reflect a change in activity rates. In 2010 surveys were conducted at the end of the rainy and beginning of the dry season which likely coincides with the end of their mating and beginning of their nesting periods (Waitkuwait 1989; Kofron & Steiner 1994; Eaton 2009). Whereas in 2012 surveys were conducted at the end of the dry season, when aquatic prey availability is low, thus more individuals may be inactive residing in burrows until the onset of rainy season (Brummett & Teugels 2004). Additional studies on reproductive phenology and seasonal activity patterns will facilitate our understanding of the spatial and temporal variability of *O. tetraspis* populations which should be considered when assessing the status and trend of populations.

The *O. osborni* population had the lowest encounter rates which may be attributed to the combined threats of drowning in gillnets and hunting pressure. The turbid waters of the Dja River was very different from the clear water streams surveyed for *O. tetraspis*

resulting in lower detection rates that may have also contributed to lower encounter rates (Bayliss 1987; Hutton & Woolhouse 1989). It is unlikely that low encounter rates were a result of poor habitat for *Osteolaemus* species since they use a variety of aquatic habitats including rivers (Eaton 2009).

The structure of the population may be influenced by the type of aquatic habitat. Although few *O. osborni* were caught they were adults and large juveniles, whereas small and large crocodiles were detected in tributaries of the West and Southwest. These findings are likely a result of ontogenetic shifts in habitat use in which small crocodiles are less common in large rivers due to higher predation risks compared to small tributaries (Subalusky *et al.* 2009). Within the Southwest and West the population structure was skewed toward juveniles which is often attributed to size-selective hunting pressure (Montague 1983; Webb *et al.* 2000). However these population structures were similar to those of Gabon not subject to hunting pressure (Eaton 2009). Thus proportionally higher numbers of juveniles in the population may be typical of *O. tetraspis* populations surveyed during the dry season. Females are nesting during this period which may be located several meters away from water and may account for the male biased sex ratio observed in the Southwest population (Waitkuwait 1989). Additional monitoring over several years at these same sites will elucidate whether the observed juvenile biased population structures are typical of *Osteolaemus* populations or indicators of over-exploitation.

The low encounter rates of both species, the young population structure of *O. tetraspis*, and the increasing threats of habitat loss and hunting pressure, indicate that

both species have vulnerable statuses in Cameroon and merit independent conservation. The conservation status of *O. osborni* may worsen if it is not recognized as a unique species. The similar morphologies of *O. tetraspis* and *O. osborni* pose a hybridization risk for both in situ and *ex situ* management programs. In Cameroon, management authorities and conservation organizations confiscate live crocodiles from the bush meat trade and release them back into the wild but not necessarily into their original populations creating the potential for hybridization. The distribution maps provided in this study and elsewhere (Smolensky *et al.* 2014) should mitigate some of these hybridization risks and I recommend that confiscated crocodiles be released back to their original populations. Hybridization has been detected in captive breeding programs in European zoos and efforts are underway to mitigate this and curtail translocations or reintroductions of hybrids into wild populations (Franke *et al.* 2013). Crocodile ranching and farming are common conservation strategies for heavily exploited crocodile species (Crocodile Specialist Group 2014) however preliminary assessments indicate that this would not be an economically viable strategy for *Osteolaemus* species in Cameroon (Behra 1993). A multi-faceted approach that includes large protected areas with enforcement and sustainable livelihoods for local communities, are needed to conserve *Osteolaemus* species and other wildlife in Cameroon.

Cameroon provides an important case study for *Osteolaemus* species and cryptic taxa in general, as it is one of two countries known to harbor two *Osteolaemus* species, the other being the Republic of Congo (Eaton 2010; Smolensky *et al.* 2014). Thus separate population assessments were conducted and distribution maps provided to promote

awareness of the two cryptic species in Cameroon. This exemplifies the approach needed to conserve this evolutionary biodiversity and provides a much needed baseline to determine the stability of the observed populations densities and structures of *O. tetraspis* and *O. osborni* in Cameroon.

CHAPTER V
TROPHIC ECOLOGY OF AFRICAN CROCODILES (*OSTEOLAEMUS* SPP.) IN
PERENNIAL AND EPHEMERAL AQUATIC HABITATS

Introduction

Mobile amphibious predators, such as crocodylians link the flow of nutrients and energy between food webs of heterogeneous aquatic habitats (Fittkau 1973; Subalusky *et al.* 2009; Rosenblatt & Heithaus 2011). They inhabit a variety of wetland and fluvial ecosystems, and therefore their roles in transporting nutrients and energy among food webs may differ according to habitat type and region (Quevedo *et al.* 2009; Matich *et al.* 2011; Schriever & Williams 2013). For example, species inhabiting perennial rivers are generally associated with river food webs whereas species inhabiting small ephemeral streams and pools may be associated with terrestrial, riparian and aquatic food webs (Jackson *et al.* 1974; Magnusson *et al.* 1987; Magnusson & Lima 1991; Wallace & Leslie 2008).

Changes in diet and habitat with ontogeny add complexity to food web structure and function (Polis 1984; Polis *et al.* 1989; Post 2003; Baxter *et al.* 2005). Many crocodylians have concomitant ontogenetic shifts in habitat and diet (Joanen & Mcnease 1987; Magnusson *et al.* 1987; Fitzgerald 1988; Tucker *et al.* 1996; Platt *et al.* 2006; Wallace & Leslie 2008; Subalusky *et al.* 2009). As they increase in size, they transition from aquatic to terrestrial back to aquatic habitats, and their diets are initially composed of arthropods, and subsequently shift toward including larger prey such as crustaceans and

vertebrate species (Cott 1961; Fitzgerald 1988; Tucker *et al.* 1996; Wallace & Leslie 2008). While ontogenetic shifts are thought to occur in all crocodylians, it has yet to be evaluated in all species, particularly in dwarfed species such as the African dwarf crocodiles (*Osteolaemus* spp.) that only undergoes increases in body size by two orders of magnitude as compared to other crocodylians that may increase by four to five orders of magnitude.

Many dietary studies based on analyses of stomach contents can be biased by different digestion rates of prey and short-term abundance of prey types. For example, invertebrate prey with chitinous exoskeletons are digested more slowly than soft-bodied vertebrates, and stomach contents largely reflect diet only of the past two weeks (Jackson *et al.* 1974; Garnett 1985). Individuals often have empty stomachs, necessitating large sample sizes to capture the range and variation of diet in the population (Fitzgerald 1989; Wallace & Leslie 2008). Thus short-term dietary studies involving analyses of stomach contents alone may not reveal the entire picture of trophic ecology and its role in nutrient and energy transfer between food webs. Stable isotopes of carbon and nitrogen offer insight into general dietary patterns and food web associations because they reflect assimilated diet and provide insight into temporal variation depending on the turnover rates of the tissues analyzed (DeNiro & Epstein 1978, 1981; Tieszen *et al.* 1983; Hobson & Clark 1992a).

Here I report findings from an investigation of spatial and ontogenetic variation in the terrestrial and aquatic food web associations of *Osteolaemus tetraspis* and *O. osborni*. These species occur in a variety of aquatic habitat types in the rain forests of west and

central Africa (Waitkuwait 1989; Kofron 1992; Thorbjarnarson & Eaton 2004; Shirley *et al.* 2009; Eaton 2010; Smolensky 2014). Early dietary studies based on stomach contents of wild and harvested *Osteolaemus* species indicate a generalized diet of terrestrial, amphibious and aquatic vertebrate and invertebrate fauna (Schmidt 1923; Luiselli *et al.* 1999; Riley & Huchzermeyer 2000; Pauwels *et al.* 2007). Insecta, Diplopoda and Crustacea were the predominant prey, but their proportional contributions to the diet varied by location. Stable isotope analyses are well suited to compliment stomach content analyses but have been rarely, and only recently used to investigate the trophic ecology of crocodylians (Rosenblatt & Heithaus 2011; Wheatley *et al.* 2011; Radloff *et al.* 2012; Caut 2013). This is the first study to use stable isotope signatures to investigate the trophic ecology of *Osteolaemus* species.

I compared the food web associations of *Osteolaemus* species inhabiting a large river and small tributary using stable isotope analyses of carbon and nitrogen. I hypothesized that *Osteolaemus* species inhabiting perennial rivers predominantly forage in aquatic habitats throughout the year. When these species inhabit small streams, they will shift toward more terrestrial food sources during the dry season as small streams dry out. I also hypothesized that these species undergo ontogenetic shifts in food web association and trophic positions. I predicted that all size classes will have trophic connections to both aquatic and terrestrial food webs, but that the relative contributions of prey from these two food webs will differ among size classes, and trophic position will increase size.

Materials and methods

Study region

Sampling was conducted at two sites located in lowland Congo-Guinean rainforest of Cameroon (Figure 9). The first site was in the Dja River at the periphery of the Nki national park between latitudes N2°05' – N2°50' and longitudes E14°05' – E14°50'. The Dja River is a right bank tributary of the Congo River. The hydrologic regime is pluvial and bimodal, with peak discharges in October and July (451 -487 m³/s) (Seyler *et al.* 1993). The river is slightly acidic (pH 6.39 – 6.89), has low conductivity (48 µS/cm), low suspended sediment levels (26.0 mg/L) but high particulate (2.3 mg/L) and dissolved (6.0 mg/L) organic carbon levels. The ionic composition values are intermediate between whitewater and blackwater rivers (Seyler *et al.* 1993; Coynel *et al.* 2005). The second site was in a first order stream associated with the Ntem River inside the Campo Ma'an National Park between latitudes N2°10' – N2°52' and longitudes E9°50' – E10°54'. The Ntem river is a blackwater river with lower levels of bimodal discharge (290 m³/s), acidity (5-6 pH), and conductivity (20-30 µS/cm) compared to the Dja River. The Ntem streams and rivers are clear, with low dissolved nutrient concentrations, dense canopy cover, and high amounts of allochthonous inputs (Toham & Teugels 1997; Toham & Teugels 1998; Brummett & Teugels 2004). The substrate consists of a thick layer of leaf litter, woody debris, and fine organic particulate matter over sand and gravel. Both sites are low elevation, in humid evergreen forest. Climate is similar at the two sites; mean annual precipitation is 1700 mm/yr and mean annual temperatures are 25° C. In both regions, there are two dry seasons from late November

to late February and from late June to early August. Sampling occurred during the dry season of 2011-2012, at the Dja River site in December 2011 and at the Campo Ma'an site in February 2012.

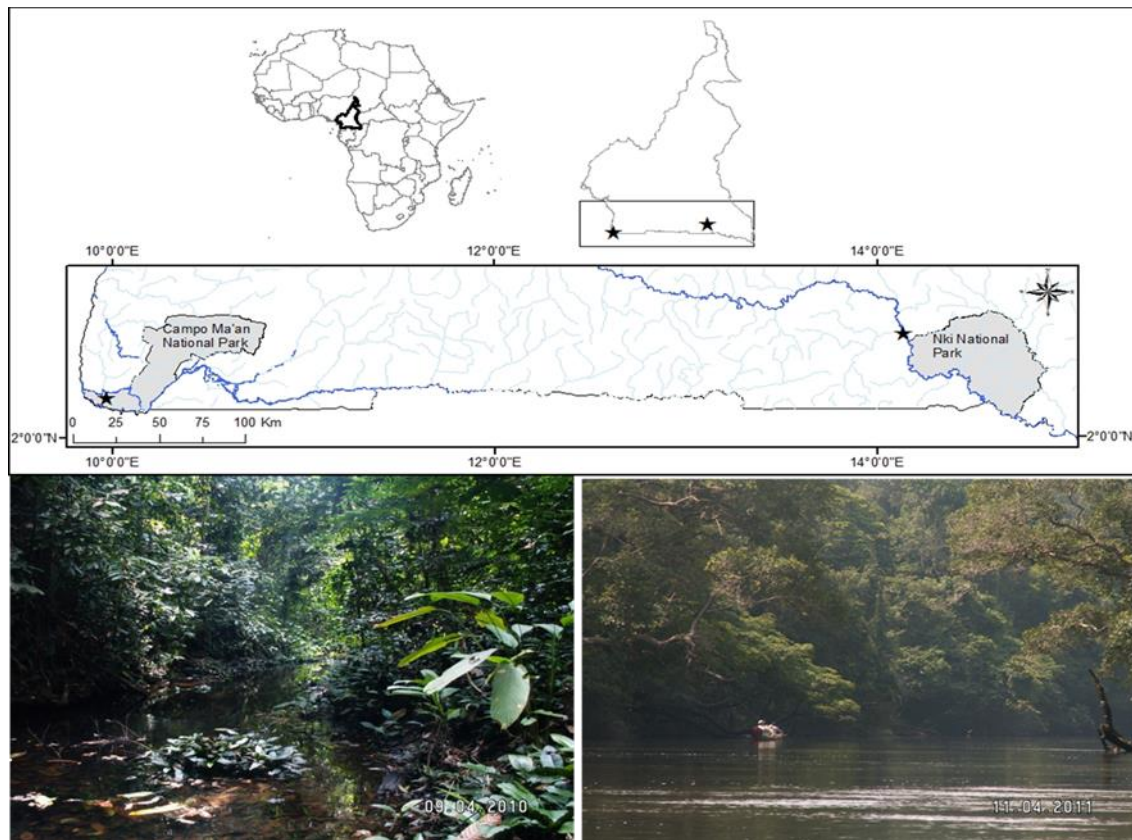


Figure 9. Location and images of the aquatic habitats of the Campo Ma'an and Dja River sites in the southwest and southeast regions of Cameroon.

Sample collection

I obtained two to five replicate samples from basal sources including grasses, leaves, mosses, aquatic macrophytes, Course Particulate Matter, detritus; and from consumers

(macro invertebrates, amphibians, fishes) that were considered putative prey sources based on the literature (Schmidt 1923; Luiselli *et al.* 1999; Riley & Huchzermeyer 2000; Pauwels *et al.* 2007; Eaton 2010) (Table 3). Samples from putative prey sources were collected via seine, dip net, by hand, or by noose pole in the case of *Osteolaemus* species. Macroinvertebrates and small fish species were preserved whole. Dorsal muscle tissue was extracted from medium to large species of euthanized fish. Caudal scutes were removed from live *Osteolaemus* species and morphometric measurements were taken. All samples except the *Osteolaemus* tissues were preserved in salt and stored in plastic bags for subsequent processing. *Osteolaemus* tissue samples were preserved in ethanol for use in a concurrent genetic study (Smolensky *et al.* 2014). Neither preservation technique has significant effects on isotope signatures (Hobson *et al.* 1997; Arrington & Winemiller 2002).

In the laboratory, samples were rinsed and soaked with deionized water for 24 hours to remove salts and subsequently dried at 60° C for 48 hours. The caudal scutes of *Osteolaemus* are comprised of an outer keratinous epidermis and collagen dermal core that may result in different isotope signatures (Tieszen *et al.* 1983; Hobson & Clark 1992a, b). Tissues were first soaked in a 0.1 M NaOH solution for 12 hours, rinsed with deionized water, and then manually separated into keratin and collagen prior to drying (Radloff *et al.* 2012). The collagen samples were placed in glass vials, while the keratin samples and the rest of the collected samples were ground to a homogenous fine powder using a ball-mill grinder. Subsamples were placed in Ultra-Pure tin capsules (Costech Analytical Technologies, Valencia CA USA) and weighed to the nearest 0.01 mg. All

Table 3. Sample collection.

Site	Taxa	Abbrv	N
Dja River	Detritus	Dtrt	2
Dja River	Broad Leaf Tree Sp. A	BrdA	3
Dja River	Broad Leaf Tree Sp. B	BrdB	3
Dja River	Broad Leaf Tree Sp. C	BrdC	3
Dja River/Campo Ma'an	Moss	Mss	3
Dja River	Grass	Grs	1
Dja River	Lepidoptera	Lpd	1
Dja River	Orthoptera	Ort	1
Dja River	Naucoridae	Ncd	5
Dja River	Nepidae	Npd	4
Dja River	Odonata	Odt	1
Dja River	Formicidae	An	3
Dja River	<i>O. osborni</i> _Keratin	OstK	3
Dja River	<i>O. osborni</i> _Collagen	OstC	3
Dja River/Campo Ma'an	Gastropod (Aquatic)	AqGstp	5/1
Dja River	<i>Hylarana</i> sp.	Am	1
Dja River	<i>Conraura crassipes</i>	F	1
Dja River	Atyidae	F	2
Dja River	<i>Hemichromis elongatus</i>	F	4
Dja River/Campo Ma'an	<i>Hepsetus odoe</i>	F	1/1
Dja River	<i>Tilapia</i> sp.	F	3
Dja River/Campo Ma'an	<i>Clarias</i> sp.	F	3/1
Dja River	<i>Ctenopoma</i> sp.	F	2
Dja River	<i>Micralestes</i> sp.	F	7
Campo Ma'an	<i>Emergent Macrophyte</i>	Fac	1
Campo Ma'an	<i>Course Particulate Organic Matter</i>	CPOM	1
Campo Ma'an	<i>Achatina</i> sp.	Ach	1
Campo Ma'an	<i>Macrobrachium vollenhovenii</i>	Mvo	2
Campo Ma'an	<i>Potamonemus</i> sp.	Pot	1
Campo Ma'an	<i>Grayia ornate</i>	Gry	1
Campo Ma'an	<i>Scotobleps gabonicus</i>	Sct	1
Campo Ma'an	<i>Labeo</i> sp.	Lab	2
Campo Ma'an	<i>Epiplatys sexfasciatus</i>	Esp	1
Campo Ma'an	<i>Brycinus</i> sp.	Bry	2
Campo Ma'an	<i>O. tetraspis</i> _Keratin	OstK	27
Campo Ma'an	<i>O. tetraspis</i> _Collagen	OstC	29

samples were sent to the Analytical Chemistry Laboratory University of Georgia for stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

Statistical analyses

Bi-plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated certain species (e.g. fish, amphibians) had similar isotopic ratios (Figure 10a). These were combined for analysis. Dual isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) mixing models implemented in IsoSource (Phillips & Gregg 2003) were used to determine proportional contributions of prey sources supporting *Osteolaemus* species. I ran separate mixing model analyses for each site. For the Dja River and Campo Ma'an sites, eight and seven putative sources were included, respectively. Isotope values were corrected for trophic fraction using values $\Delta\delta\text{C} = 0.61\text{‰}$ and $\Delta\delta\text{N} = 1.22\text{‰}$, obtained from an experimental study on discrimination and turnover rates in alligators (*Alligator mississippiensis*) (Rosenblatt & Heithaus 2013). Mass balance tolerance levels were set to $\pm 0.1\text{‰}$ and $\pm 0.4\text{‰}$ for the Dja River and Campo Ma'an sites respectively. Larger tolerances were used for Campo Ma'an to minimize exclusion of potential sources and to accommodate the greater source variability at this site (Figure 10b) (Phillips & Gregg 2003). IsoSource model solutions representing feasible solutions were generated by iteratively adjusting the source proportions by 1% increments (Phillips & Gregg 2003). I used these solutions to create histograms and determine minimum and maximum percentile contributions of each putative prey source (Figure 11).

Ontogenetic shifts were examined for *Osteolaemus* species at the Campo Ma'an site where samples sizes were large enough for analyses. I used Kruskal-Wallis tests to determine if there were differences in isotope signatures of both tissue types between

males, females and juveniles. I used multivariate adaptive regression analyses (MARS) (Friedman 1991) to investigate ontogenetic diet shifts based on isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and Snout-Vent-Length (SVL) for each tissue type. One outlier for the nitrogen isotopic ratio of collagen clustered with keratin samples, and was therefore excluded from this analysis. I estimated trophic positions for crocodiles at each site using the following equation (Post 2002):

$$\text{TP} = \lambda + (\delta^{15}\text{N}_{\text{secondary consumer}} - \delta^{15}\text{N}_{\text{base}}) / \text{TEF},$$

where TP is the trophic position, λ and $\delta^{15}\text{N}_{\text{base}}$ are the trophic position and $\delta^{15}\text{N}$ isotope signature of the organism used as the baseline. Orthoptera and *Scotobelps gabonicus* from the Dja and Campo Ma'an sites respectively were used as the baseline organisms (Figure 10). $\delta^{15}\text{N}_{\text{secondary consumer}}$ is the isotope signature from *Osteolaemus*, and TEF is the trophic enrichment factor (1.22) for crocodylians (Rosenblatt & Heithaus 2013). Mann-Whitney U test was used to determine if trophic positions differed between juveniles and adults at Campo Ma'an.

Results

Food web structure

""Aquatic food web structures at both sites appear to be strongly supported by terrestrial plant material, mostly in the form of detritus (Figure 10). *Osteolaemus* species at both sites had carbon isotope signatures indicating assimilation of prey from the terrestrial and aquatic food webs (Figure 10). However the proportional contributions of aquatic and terrestrial prey species differed among sites (see below, Figure 11). At the Dja site, there were two trophic pathways leading to *Osteolaemus*: an aquatic pathway containing

the fishes supported by broadleaf tree species and detritus, and a terrestrial pathway containing the terrestrial insects supported by basal sources intermediate between the detritus and C4 grasses in the riparian zone (Fig. 5.2A).

Species at the Campo Ma'an site had relatively enriched nitrogen isotopic ratios as compared to species at the Dja site. For example *Macrobium vollehni* and *Labeo batesii* are algivores in the Campo Ma'an site (Toham & Teugels 1998; Jimoh *et al.* 2011) but had higher nitrogen isotope signatures than predatory Nacurid and Nepidae species that prey upon algivorous invertebrates at the Dja River (Table 3, Figure 10). *Hepsetus odoe* occurred at both sites and had similar carbon isotope signatures, but was 1.89‰ enriched in nitrogen at the Campo Ma'an site relative to the Dja River.

Osteolaemus species occupied similar isotopic space in both habitats for both tissue types. They were not apex predators in these environments, containing nitrogen isotope signatures less enriched than samples from predatory fishes and snakes (Figure 10). Mean trophic positions were higher at Dja (keratin = 5.51, SD = 0.09, collagen = 6.73, SD = 0.28 n = 3) than at Campo Ma'an (keratin = 3.86, SD = 0.34, collagen = 5.11, SD = 0.47 n = 24). *Osteolaemus* samples obtained from the Dja site were all adults and samples obtained from the Campo Ma'an site included adults and juveniles.

Proportional contributions of alternative prey to crocodile biomass

At both sites the two tissue types resulted in different relative contributions of prey to the diet of *Osteolaemus* evidenced by their locations within the mixing polygon (Figure 11). Most of the model solutions predicted that the putative prey contributed less than 10 % to the assimilated diet of *Osteolaemus* species at the Dja River (Figure 11). Aquatic

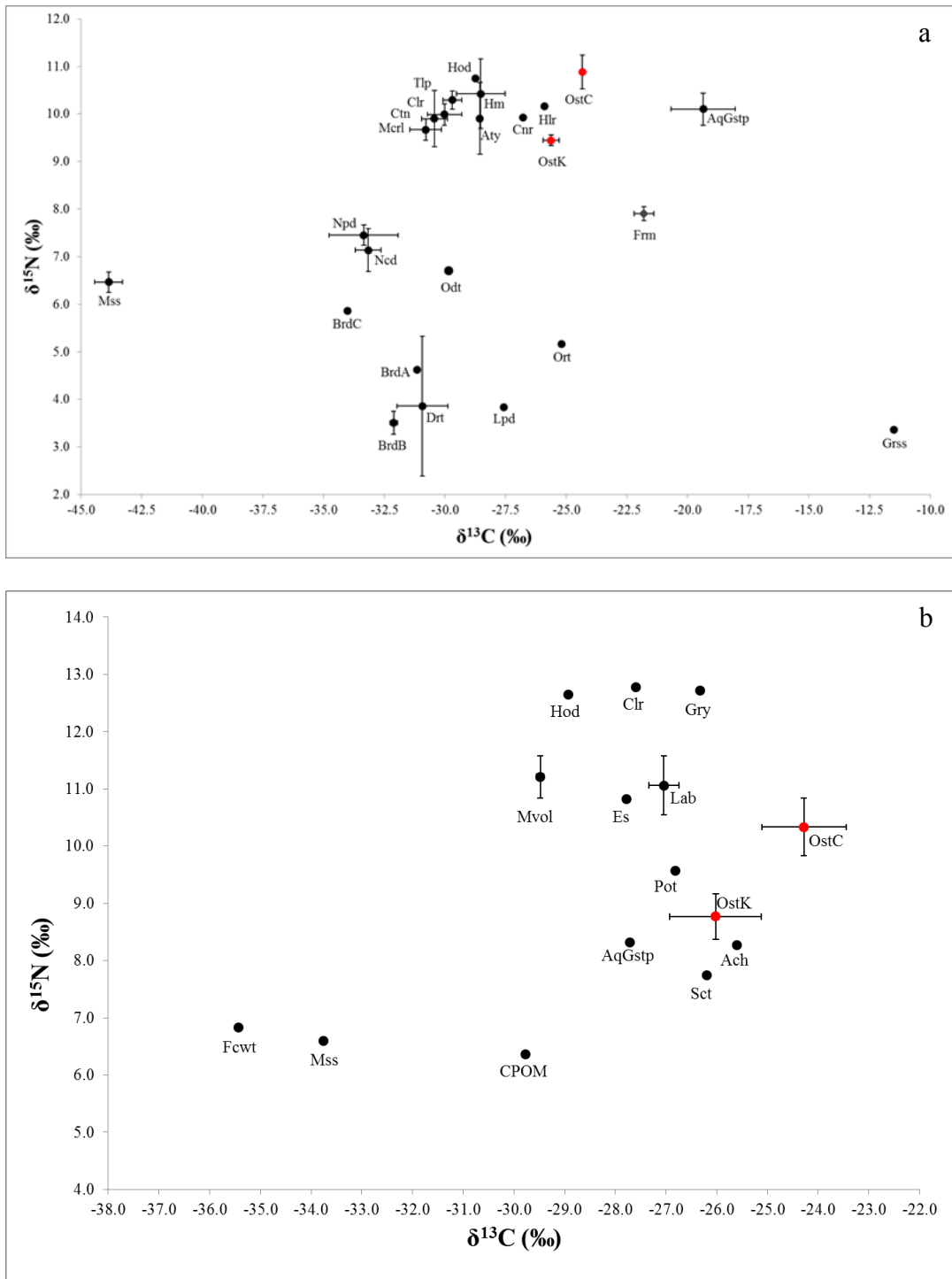


Figure 10. Isotope signatures of basal sources, potential prey sources and *Osteolaemus* species (red) at the Dja River (a) and Campo Ma'an (b). Abbreviations of samples are explained in Table 3. Samples have not been adjusted for trophic fractionation. Points are means and error bars are standard deviations.

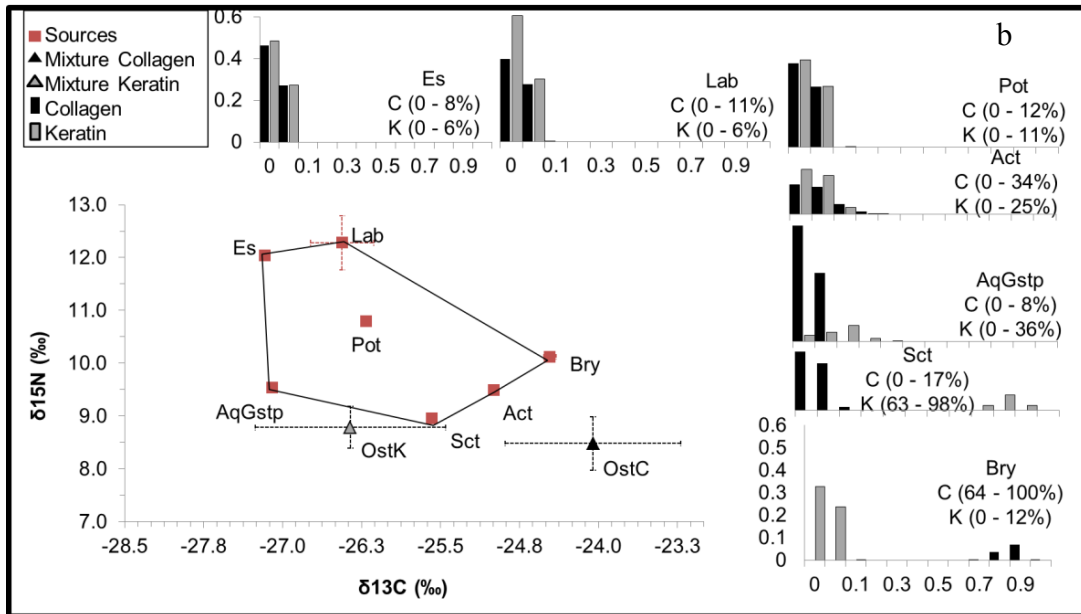
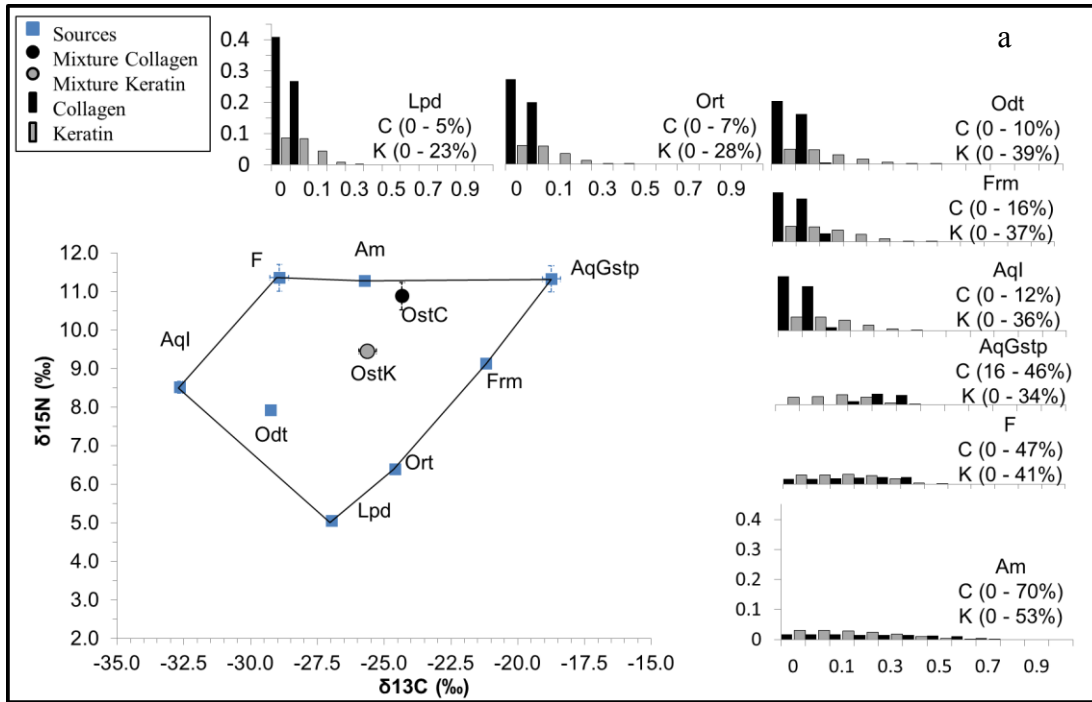


Figure 11. Mixing polygons and histograms of feasible proportional contributions of sources to *Osteolaemus* species (mixture) isotope signatures of collagen and keratin at Dja (a) and Campo (b). The convex hull area connecting putative prey sources delineates the mixing space. Percentages are the 1-99th percentile ranges of feasible proportional contributions.

gastropods, fish and amphibians had higher maximum feasible contributions to the biomass of *Osteolaemus* than the terrestrial invertebrates, particularly when estimates were based on collagen tissue (Figure 11). However the wide distribution of estimated proportional contributions (e.g. range for fish = 0-47%) reduced resolution for estimates of prey contributions to *Osteolaemus* biomass. At Campo Ma'an, *Osteolaemus* isotopic ratios plotted outside the mixing model indicating consumption of one or more sources that were not collected. Taking into account the broad confidence intervals for model estimates, amphibians (Sct = 67-94%) and fish (Bry = 71-95%) were inferred to be the major contributors to *Osteolaemus* biomass at the Campo Ma'an site.

Ontogenetic niche shifts

Collagen was enriched in ^{15}N and ^{13}C relative to keratin, but the ranges for both tissue types were narrow across crocodile size classes (keratin: 1.33‰, min = 8.81, max = 9.51; 2.23‰, min = -27.23, max = -25.00) (Figure 12). There was a significant relationship between SVL and isotopic ratios for both elements and both tissue types. Nitrogen and carbon isotope signatures initially declined with body size in smaller juveniles and subsequently increased in larger juveniles and adults (Figure 12). This shift occurred between 46.50 and 51 cm SVL, near the transition between juvenile and adult stage classes (Table 4). Smaller shifts at 38 cm and 58.5 cm SVL were detected prior to and after this main break point for specific isotope and tissue types (Table 4). There were no differences in carbon and nitrogen isotope signatures for keratin and collagen between sexes ($\delta^{13}\text{C}_{\text{keratin}}$: $H = 4.96$, $p\text{-value} < 0.19$; $\delta^{13}\text{C}_{\text{collagen}}$ $H = 6.50$, $p\text{-value} < 0.10$; $\delta^{15}\text{N}_{\text{keratin}}$ $H = 5.54$, $p\text{-value} < 0.15$; $\delta^{15}\text{N}_{\text{collagen}}$ $H = 0.79$, $p\text{-value} < 0.86$). Estimated

trophic positions of juveniles and adults did not differ significantly ($U_{\text{keratin}} = 84.5$, p-value <0.22 ; $U_{\text{collagen}} = 33.5$, p-value <0.27).

Discussion

Depending upon sediment loads, canopy cover and hydrology, aquatic food webs of tropical rivers are supported by varying proportions of autochthonous and allochthonous primary production sources (Jepsen & Winemiller 2007; Lau *et al.* 2009). In my study, streams were characterized by low nutrient concentrations, low suspended sediment loads, dense canopy cover, abundant particulate organic matter (Seyler *et al.* 1993; Toham & Teugels 1998; Brummett & Teugels 2004; Coynel *et al.* 2005). The small streams at Campo Ma'an also had ephemeral low flows. My results indicated that allochthonous inputs provided important sources of carbon to support food webs. Although I was not able to collect periphyton or algae samples to ascertain the role of autochthonous carbon sources supporting food webs, the lack of visible growth of periphyton and the aforementioned literature indicate that aquatic primary production was very low in both the Dja and Campo Ma'an study systems.

In large rivers like the Dja, *Osteolaemus* consume species from multiple trophic pathways supported by allochthonous sources. Aquatic gastropods provided only moderate contributions to *Osteolaemus* species' biomass but these species and terrestrial invertebrates integrated different sources of carbon from the aquatic food web. Aquatic gastropods were enriched in carbon and nitrogen isotopes, indicating that the aquatic gastropods may also have assimilated terrestrial plant materials.

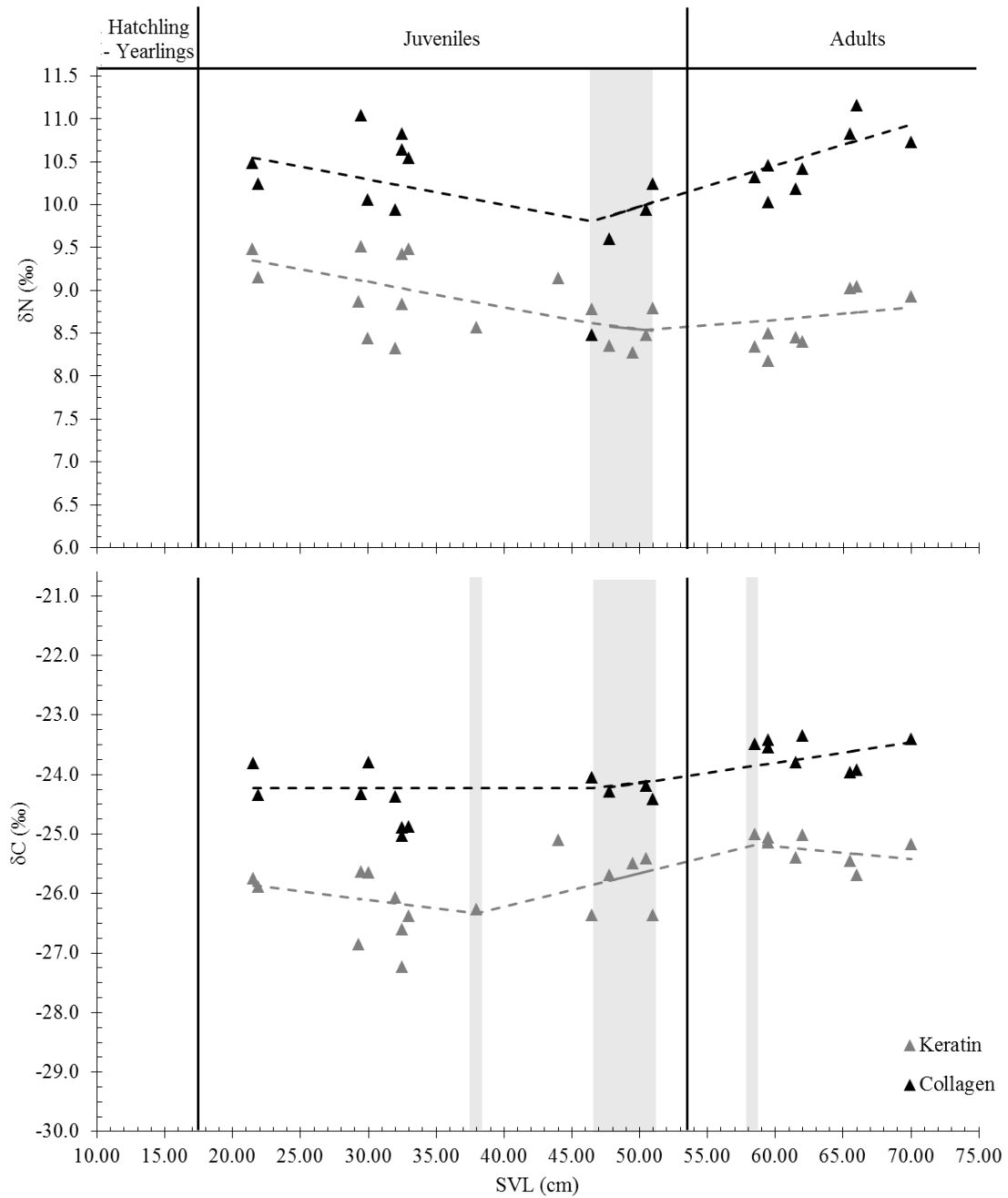


Figure 12. Relationship between body size and isotopes of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from keratin and collagen tissues of *Osteolaemus tetraspis* at Campo Ma'an National Park. Broken lines are multivariate adaptive regression splines (MARS). Grey bars indicate break points in the data from MARS based on both tissue types.

Table 4. Results from multivariate adaptive regression splines of the relationship between isotopes and snout vent length (SVL cm) from caudal scutes of 24 crocodiles. Analyses were separated by keratin and collagen tissues derived from the scutes.

Isotope and Tissue type	Model	Basis Function (BF)	Knot	R ²	F-statistic	P-value
$\delta^{15}\text{N}$ Keratin	$Y = 8.74 + 0.04 * \text{BF2} - 0.35 * \text{BF3} + 0.38 * \text{BF5}$	BF2 = max(0, 51.00 - SVL) BF3 = max(0, SVL - 46.50) BF5 = max(0, SVL - 47.62)	51.00 46.50 47.62	0.44	3.72	0.04
$\delta^{15}\text{N}$ Collagen	$Y = 8.66 + 0.06 * \text{BF1} + 0.01 * \text{BF2} - 0.06 * \text{BF3} + 0.01 * \text{BF5}$	BF1 = max(0, SVL - 50.50) BF2 = max(0, 50.50 - SVL) BF3 = max(0, SVL - 46.55)	50.50 50.50 46.55	0.48	3.34	0.06
$\delta^{13}\text{C}$ Keratin	$Y = -25.86 - 0.03 * \text{BF1} + 0.09 * \text{BF2} - 0.08 * \text{BF4}$	BF1 = max(0, SVL - 21.50) BF2 = max(0, SVL - 38.00) BF4 = max(0, SVL - 58.50)	21.50 38.00 58.50	0.48	5.31	0.01
$\delta^{13}\text{C}$ Collagen	$Y = -24.31 + 0.01 * \text{BF2} - 0.03 * \text{BF3} + 0.06 * \text{BF5}$	BF2 = max(0, 46.05 - SVL) BF3 = max(0, SVL - 51.00) BF5 = max(0, SVL - 47.45)	46.50 51.00 47.45	0.44	3.52	0.05

For *Osteolaemus* species inhabiting small ephemeral streams the assimilation of terrestrial and aquatic prey was less clear. At Campo Ma'an, *Osteolaemus* samples lay outside the mixing polygon implying missing prey sources (Phillips & Gregg 2003). Inclusion of terrestrial insects may lead to a mixing polygon enveloping *Osteolaemus* mixtures. The wide ranges of feasible contributions of all of the putative prey produced by the IsoSource models indicate two alternative hypotheses on the trophic ecology of *Osteolaemus* species. *Osteolaemus* species may have a broad diet, or additional sources such as terrestrial Diplopoda, may be missing that may contribute significantly to *Osteolaemus* species biomass. Both hypotheses are feasible, based upon previous literature (Luiselli *et al.* 1999; Riley & Huchzermeyer 2000; Pauwels *et al.* 2007). Diplopoda and Insecta are the dominant prey types of *Osteolaemus* species in swamp habitats of Gabon, and Congo while Malacostraca and Gastropoda dominate stomach contents of *Osteolaemus* species inhabiting creeks (Luiselli *et al.* 1999; Riley & Huchzermeyer 2000; Pauwels *et al.* 2007). Thus previous studies and the results from the perennial river of my study suggest that *Osteolaemus* species inhabiting perennial rivers will have aquatic food web associations as opposed to the largely terrestrial food web associations detected when they occupy swamp habitats. In both study systems, *Osteolaemus* species were characterized at a trophic level below apex predatory species and above invertebrates suggesting a largely invertivorous diet across size classes.

Many crocodylian species exhibit ontogenetic niche shifts in diet and habitat (Cott 1961; Fitzgerald 1988; Webb *et al.* 1991; Tucker *et al.* 1996; Platt *et al.* 2006; Wallace & Leslie 2008; Subalusky *et al.* 2009), and my results were consistent with this general

pattern of niche shifts. I detected an initial decline in isotope signatures with body size in smaller juveniles and subsequent increases in larger juveniles and adults. However the narrow range and similar signatures between juveniles and adults suggest dietary overlap between stage classes. Similar patterns of dietary overlap and shifts in isotope ratios with size have been seen in other crocodylians (Cott 1961; Webb *et al.* 1991; Radloff *et al.* 2012). The initial decline and subsequent increase in isotopic ratios with body size observed here and among other crocodylian species could be associated with dietary differences as well as physiological changes associated with growth that affect isotopic incorporation and routing (Reich *et al.* 2008; Rio *et al.* 2009; Rio & Carleton 2012).

For isotope analyses involving crocodylians, caudal scutes are commonly used because they can be sampled non-invasively and additionally used for population and genetic studies (Rosenblatt & Heithaus 2011; Wheatley *et al.* 2011; Radloff *et al.* 2012; Caut 2013; Smolensky *et al.* 2014). However, it is uncommon to separate the caudal scute into keratin and collagen tissues for isotope analyses. Consequently estimates of relative fractionation rates and of these tissues are limited compared to other tissue types for crocodylians (Rosenblatt & Heithaus 2013). This is the first study to report isotope signatures from both collagen and keratin and I demonstrated that collagen tissues are enriched in ^{15}N and ^{13}C isotopes relative to keratin tissues. Differences in enrichment could be due to differing fractionation rates or turn-over rates (Tieszen *et al.* 1983; Kelly 2000; Dalerum & Angerbjörn 2005). Previous studies indicated that keratin from crocodylian scutes has a faster turn-over rate than collagen and should reflect assimilated diet within the last few months whereas collagen may reflect diets of approximately a

year prior (Spearman 1966; Radloff *et al.* 2012; Rosenblatt & Heithaus 2013). If these differences were mainly due to turnover rates then they provide important insight into temporal variation in diet.

One difficulty in determining relative contributions of prey for generalist species is to collect representative samples of prey that adequately reflect the variety in the diet. Limited samples of potential prey probably biased my IsoSource models resulting in broadly overlapping distributions of estimated prey contributions. Stomach content analyses provide insight into relative proportions of ingested prey that can guide future sample collection of prey species that were missing in this current study.

Osteolaemus species occupy a variety of habitats, and little is known about the spatial and temporal variation in their trophic ecology. This study offers one of the first spatial comparisons of *Osteolaemus* trophic ecology and demonstrates a high degree of trophic niche conservatism between aquatic habitats. I also found very low dietary variation associated with ontogeny. Additional research is needed to determine whether or not these are general patterns that hold within other *Osteolaemus* populations. Future work should include greater replication of sampling in space, time and among species. Analysis of stomach contents should be conducted for comparisons with results from stable isotope analyses of collagen, keratin and other tissues. In linear mixing model analyses, the number of sources that can be partitioned to estimate their contributions to biomass of species is constrained by the number of elements used in analyses (Ben-David *et al.* 1997; Phillips & Gregg 2001). For species with broad diets, additional elements such as Hydrogen or Sulfur can be included to obtain solutions including more prey sources.

Future studies should also explore how hydrologic regimes affect relative contributions of terrestrial and aquatic prey to the biomass of *Osteolaemus* species.

CHAPTER VI

SUMMARY AND CONCLUSION

Sustainable use systems seek to achieve a balance between production and harvest of natural resources such that the biomass of natural resources can persist through time (Wilkie & Carpenter 1999; Lindenmayer *et al.* 2008; Redford *et al.* 2011; Weinbaum *et al.* 2013). This requires information on the exploitation, density and distribution of exploited species, which is lacking for many for species involved in the bushmeat trade. The aims of this dissertation were to address some of these knowledge gaps for *Osteolaemus* species. Without a working knowledge of the distribution, population ecology, or hunting pressure of species, the most basic inferences on their conservation status are speculative. Through these four chapters I highlight the need for localized conservation efforts of *Osteolaemus* populations based upon threatened populations of cryptic species, spatially variable trophic ecologies, and bushmeat trade patterns that may bias regional assessments of their exploitation.

My research provides some of the first population assessments of *O. osborni* and *O. tetraspis* in Cameroon. Although *O. tetraspis* is widespread in Cameroon (Chapter 2), encounter rates of this species and *O. osborni* were low (Chapter 3). The low encounter rates, young population structures, and continued threats of habitat loss and hunting pressure indicate a threatened status for these species and merits continued monitoring of their populations. Reproductive ecology is an important yet missing component in our understanding of the population statuses of *O. osborni* and *O. tetraspis* in Cameroon.

Future studies will include the movement patterns of females and nesting phenology to develop estimates and models of production and recruitment into populations.

Ecological or functional diversity of populations has recently been viewed as a criterion for conserving populations (Dieckmann & Doebeli 1999; Crandall *et al.* 2000). *Osteolaemus* species occupy a variety of habitats, and little is known about the spatial and temporal variation in the trophic ecology of these species. Stable isotopes analyses suggest that *Osteolaemus* species inhabiting perennial rivers will have aquatic food web associations as opposed to the largely terrestrial food web associations detected when they occupy swamp habitats (Luiselli *et al.* 1999; Riley & Huchzermeyer 2000; Chapter 5; Pauwels *et al.* 2007) Among aquatic habitats they demonstrate some niche conservatism in trophic positions, largely being invertivores. While their spatial variation in trophic ecology needs further investigation, my results suggest that populations inhabiting different types of aquatic habitats merit conservation as their roles as nutrient vectors between disparate food webs may differ.

Prioritizing conservation efforts has largely been based upon the distinctiveness of populations and their contributions to the evolutionary diversity of the species (Ryder 1986; Waples 1991; Moritz 1994). The status of all three species is unknown as they were only recently described as cryptic species and little data are available on their distributions and population statuses (Eaton *et al.* 2009; Eaton 2010; Shirley *et al.* 2014; Smolensky 2014; Smolensky *et al.* 2014). My research provides refined distribution maps for *Osteolaemus* species through investigation of landscape features used to delineate their distributions (Chapter 3). The Cameroon Volcanic Line was a hypothesized

phylogeographic barrier between *O. sp. nov.* to the west and *O. tetraspis* to the east. I found that *O. t. tetraspis* extends west beyond the CVL and thus this mountain chain does not represent the distributional limit of this lineage. A second important finding was the presence of *O. osborni* in Cameroon. Both species are currently managed as a single species and housed together in zoo facilities. The potential for unintended hybridization exists. Future studies include exploration of a potential hybrid zone between *O. tetraspis* and *O. osborni* in Cameroon.

Osteolaemus species are not hunted by specialized crocodile hunters, but rather by the general hunter population (Chapter 2). Thus wherever hunters and *Osteolaemus* co-occur, *Osteolaemus* species will be exploited. Rates of exploitation of *Osteolaemus* are likely to vary according to a variety of factors including some detected in this study such as economic value, their live sale, and legality of hunting. Thus assessments of exploitation and sustainability of hunting should be conducted at the village scale. For cryptic species like *Osteolaemus* it is especially important to determine the distribution of each species to manage and conserve their evolutionary diversity. Cameroon contains two *Osteolaemus* species (Chapters 3) reiterating the need for village based assessments of trade as opposed to urban market assessments where both species may be traded confounding assessments of species specific exploitation rates. Future studies include coupling hunter follows with household and trader interviews to obtain more refined quantitative data on the trade filters that affect the kinds and numbers of species entering the bushmeat trade. The aim would be to elucidate the decisions made by hunters and traders to facilitate the design of sustainable harvest programs for species important to hunters and traders.

All crocodylian species were threatened or endangered due to habitat loss and hunting pressure but through regulations of harvest and trade more than half of these species have recovered (Thorbjarnarson 1992, 1999). The economic value of these crocodylian species is what led to their overexploitation and their conservation through market-based conservation strategies. Although there is no global market for *Osteolaemus*, the regular hunting, trade, and high economic value of these species suggest the possibility of a sustainable use program as a strategy for their conservation. Sustainable use programs for crocodylians involve a combination of regulated wild harvest, sale of captive bred and ranched animals, and re-stocking of wild populations (Thorbjarnarson 1999; Webb *et al.* 2004). In Cameroon, infrastructure and investment are lacking for captive breeding and ranching programs thus local community based enforcement of regulated trade is the most plausible strategy for conservation. For this strategy to occur hunting of *Osteolaemus* must be legalized so it can be regulated (Fitzgerald 1994; Djeukam 2012). However additional measures must be incorporated to offset the costs of reduced hunting and regulated trade (Bodmer & Lozano 2001). As most of these hunters are also farmers, one possible offset measure may be to reduce costs associated with farming (e.g. transportation of farm products, products to increase crop yield, etc.). Communities must also have the land tenure rights and authority to manage their forests if they are expected to regulate their trade. The process of decentralizing wildlife management toward community based forest management is occurring, gradually, in Cameroon (Egbe 2001). These requirements are needed for many unsustainably exploited species involved in the bushmeat trade.

Overexploitation of bushmeat is a multi-faceted problem requiring an interdisciplinary approach that addresses the political, economic, social and ecological components of the trade. Managing the trade is imperative because the resulting extirpation of wildlife threatens food security and livelihoods of forest peoples, national economies, and ecosystem functions. This dissertation provides an example of how interdisciplinary studies can guide conservation and demonstrates that successful conservation strategies require synergy of social, political, economic and ecologic systems.

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APPENDIX A
SUPPLEMENTAL TABLES

Table S1 List of villages, number of hunters interviewed, their associated background and hunting patterns.

Village Name	No. Inhabitants	Ethnic Majority	No. Hunters Interviewed	Hunter Age	Residency ^a	Profession ^b	Hunting Method	Travel Distance ^c	Hunting Season
Afan Essokye	129	Mvae	2	30-35	N, N	HF, HF	Snare, Shotgun, Machete	< 1	Dry and Rainy
Akak	68	Mvae	3	45-70	N, N, N	HF, HF, HF	Snare, Shotgun, Machete	< 1	Dry
Bouendjo	57	Mvae	1	42	N	HF	Snare, Shotgun, Dogs, Machete	< 1	Rainy
Campement Ma'an	4	Bagyeli	3	40-53	N, N, N, N	H, H, HF	Snare, Machete, By-hand	< 1	Dry and Rainy
Campo	1627	Iyassa	3	35-60	I, I, I	HF, HF HF	Snare, Shotgun, Dogs, Machete	> 2	Daily, Dry
Doumb I	37	Mvae	1	46	N	HF	Snare, Machete	< 1	Dry
Etonde Fang/Ecole	181	Bulu	3	35-52	N, N, N	H, HF HF	Snare, Shotgun, Dogs, Machete, By-Hand	< 1, > 2	Dry and Rainy
Mintom	199	Mvae	2	37-43	N, N	HF, HF	Snare, Shotgun, Machete	< 1, 2	Dry
Mvini	9	Mvae	4	35-45	N, N, N, I	HF, HF HF, HF	Snare, Shotgun, Machete	< 1, > 2	Dry and Rainy
Nkoadjap	77	Mvae	3	37-48	N, N, N	HF, HF HF	Snare, Machete	< 1	-
Nko'olong	384	Bulu	3	35-39	N, N, N	H, HF HF	Snare, Shotgun, Machete	< 1, > 2	Dry and Rainy

a. Native or Immigrant

b. Hunter or Hunter & Farmer

c. Number of Travelling Days From Village. One day = 15-20 km, two days or more > 35 km

Table S2. Cross tabulation of prices, destinations, and conditions of bushmeat sold in Campo Ma'an, Cameroon.

		Price (x1000's CFA)																	Total
Destination		0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	5.0	7.0	7.5	8.0	10.0	15.0	20.0	25.0	30.0	
Household	Count	2 _a	1 _a	0 _a	1 _a	2 _a	1 _a	0 _a	1 _a	1 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	9
	% in Price	18.2	8.3	0	25	28.6	12.5	0	14.3	5	0	0	0	0	0	0	0	0	8.7
	% of Total	1.9	1	0	1	1.9	1	0	1	1	0	0	0	0	0	0	0	0	8.7
Village	Count	0 _a	1 _{a, b}	0 _{a, b, c}	2 _{a, b, c}	1 _{a, b, c}	4 _{a, b, c}	0 _{a, b, c}	2 _{a, b, c}	5 _{a, b, c}	6 _c	0 _{a, b, c}	1 _{a, b, c}	1 _{a, b, c}	4 _{a, b, c}	1 _{a, b, c}	3 _{b, c}	5 _c	36
	% in Price	0	8.3	0	50	14.3	50	0	28.6	25	100	0	25	33.3	80	50	100	100	35
	% of Total	0	1	0	1.9	1	3.9	0	1.9	4.9	5.8	0	1	1	3.9	1	2.9	4.9	35
Household and Village	Count	9 _a	10 _a	3 _a	1 _a	3 _a	3 _a	2 _a	4 _a	14 _a	0 _a	1 _a	3 _a	2 _a	1 _a	1 _a	0 _a	0 _a	57
	% in Price	81.8	83.3	100	25	42.9	37.5	100	57.1	70	0	100	75	66.7	20	50	0	0	55.3
	% of Total	8.7	9.7	2.9	1	2.9	2.9	1.9	3.9	13.6	0	1	2.9	1.9	1	1	0	0	55.3
Household Village Urban Market	Count	0 _a	0 _a	0 _a	0 _a	1 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	1
	% in Price	0	0	0	0	14.3	0	0	0	0	0	0	0	0	0	0	0	0	1
	% of Total	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Total	Count	11	12	3	4	7	8	2	7	20	6	1	4	3	5	2	3	5	103
	% in Price	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	% of Total	10.7	11.7	2.9	3.9	6.8	7.8	1.9	6.8	19.4	5.8	1	3.9	2.9	4.9	1.9	2.9	4.9	100
Condition																			
Alive	Count	1 _{a, b}	1 _{a, b}	0 _{a, b}	0 _{a, b}	2 _{a, b}	2 _{a, b}	1 _{a, b}	2 _{a, b}	2 _b	1 _{a, b}	0 _{a, b}	1 _{a, b}	1 _{a, b}	4 _a	2 _{a, b}	3 _{a, b}	4 _{a, b}	27
	% in Price	11.1	8.3	0	0	33.3	28.6	50	33.3	11.1	16.7	0	25	50	100	100	100	80	29
	% of Total	1.1	1.1	0	0	2.2	2.2	1.1	2.2	2.2	1.1	0	1.1	1.1	4.3	2.2	3.2	4.3	29
Whole and Parts	Count	0 _a	0 _a	0 _a	1 _a	1 _a	0 _a	0 _a	1 _a	0 _a	2 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	5
	% in Price	0	0	0	33.3	16.7	0	0	16.7	0	33.3	0	0	0	0	0	0	0	5.4
	% of Total	0	0	0	1.1	1.1	0	0	1.1	0	2.2	0	0	0	0	0	0	0	5.4
Whole and Smoked	Count	8 _{a, b}	11 _b	2 _{a, b}	2 _{a, b}	0 _a	3 _{a, b}	1 _{a, b}	1 _{a, b}	5 _{a, b}	0 _a	1 _{a, b}	1 _{a, b}	0 _{a, b}	0 _{a, b}	0 _{a, b}	0 _{a, b}	0 _a	35
	% in Price	88.9	91.7	66.7	66.7	0	42.9	50	16.7	27.8	0	100	25	0	0	0	0	0	37.6
	% of Total	8.6	11.8	2.2	2.2	0	3.2	1.1	1.1	5.4	0	1.1	1.1	0	0	0	0	0	37.6
Whole Parts Smoked	Count	0 _a	0 _a	1 _a	0 _a	2 _a	2 _a	0 _a	2 _a	11 _a	3 _a	0 _a	2 _a	1 _a	0 _a	0 _a	0 _a	0 _a	24
	% in Price	0	0	33.3	0	33.3	28.6	0	33.3	61.1	50	0	50	50	0	0	0	0	25.8
	% of Total	0	0	1.1	0	2.2	2.2	0	2.2	11.8	3.2	0	2.2	1.1	0	0	0	0	25.8
Whole Parts Alive Smoked	Count	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	1 _a	1
	% in Price	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	1.1
	% of Total	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.1	1.1
Whole Smoked Alive	Count	0 _a	0 _a	0 _a	0 _a	1 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	1
	% in Price	0	0	0	0	16.7	0	0	0	0	0	0	0	0	0	0	0	0	1.1
	% of Total	0	0	0	0	1.1	0	0	0	0	0	0	0	0	0	0	0	0	1.1
Total	Count	9	12	3	3	6	7	2	6	18	6	1	4	2	4	2	3	5	93
	% in Price	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
	% of Total	9.7	12.9	3.2	3.2	6.5	7.5	2.2	6.5	19.4	6.5	1.1	4.3	2.2	4.3	2.2	3.2	5.4	100

Each subscript letter denotes a subset of price categories whose column proportions do not differ significantly from each other at the .05 level.

Table S3. Genes, primers and thermocycling conditions used in this study.

Gene Region	Fragment Length (bp)	Primer	Sequence (5' - 3')	Source	Conditions
CO1	413	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994	1 Cycle: 3min 95°C; 40 Cycles: 1min 95°C, 1min 46°C, 1min 72°C; 1 Cycle: 10min 72°C;
		HCO2198	TAAACTTCAGGGTGACCAAAAAATCA		
12S rDNA	372	12SA-L	AAACTGGGATTAGATACCCACTAT	Schmitz et al. 2003	1 Cycle: 2min 95°C; 35 Cycles: 45s 95°C, 45s 50.5°C, 45s 72°C; 1 Cycle: 5min 72°C;
		12SB-H	GAGGGTGACGGGCGGTGTGT		
LDH-A (intron)	658	LA17-F	TGGCTGAAACTGTTATGAAGAACC	Gatesy et al. 2004	1 Cycle: 2min 95°C; 35 Cycles: 1min 94°C, 1min 53°C, 1min 72°C; 1 Cycle: 5min 72°C;
		LA17-R	TGGATTCCCCAAAGTGTATCTG		

Table S4. List of sequences included in this study with their associated geographic origins, source information, accession numbers, and gene availability. Locality abbreviations: Cameroon (CM), Gabon (GB), Republic of Congo (RoC), Democratic Republic of Congo (DRC), Ghana (GH) and Ivory Coast (IC).

Locality	Latitude/Longitude	Source	Accession	Sequence	CO1	12S rDNA	LDH-A
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp1	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp2	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp3	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp4	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp5	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp6	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp7	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp8	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp9	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp10	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp11	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp12	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp13	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp14	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp15	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp18	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp19	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp20	X	X	
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp21	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp22	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp23	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp24	X	X	
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp25	X	X	X

Table S4 Continued

Locality	Latitude/Longitude	Source	Accession	Sequence	CO1	12S rDNA	LDH-A
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp26	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp27	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp28	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp29	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp30	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp31	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp32	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp33	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		Cmp34	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		CmpA	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		CmpB	X	X	X
Campo Ma'an, CM	2.240811/9.959357	This Study		CmpC	X	X	X
Douala-Edea, CM	3.67091/9.73609	This Study		DE1	X	X	X
Douala-Edea, CM	3.67091/9.73609	This Study		DE2	X	X	X
Banyang-Mbo, CM	5.34268/9.49716	This Study		BM1	X	X	X
Mvog-Betsi Zoo, CM	3.86434/11.4863	This Study		MV1	X		
Mvog-Betsi Zoo, CM	3.86434/11.4863	This Study		MV2	X		
Mvog-Betsi Zoo, CM	3.86434/11.4863	This Study		MV27	X		
Mvog-Betsi Zoo, CM	3.86434/11.4863	This Study		MV3	X		
Mvog-Betsi Zoo, CM	3.86434/11.4863	This Study		MV4	X		

Table S4 Continued

Locality	Latitude/Longitude	Source	Accession	Sequence	CO1	12S rDNA	LDH-A
Mvog-Betsi Zoo, CM	3.86434/11.4863	This Study		MV5	X		
Mvog-Betsi Zoo, CM	3.86434/11.4863	This Study		MV6	X		
Njombe, CM	4.582243/9.647655	This Study		NJ1	X	X	X
Njombe, CM	4.582243/9.647655	This Study		NJ2	X	X	X
Nkongsamba, CM	4.95366/9.9357	This Study		NK1	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM1	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM2	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM3	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM4	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM5	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM6	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM7	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM8	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM9	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM10	X	X	X

Table S4 Continued

Locality	Latitude/Longitude	Source	Accession	Sequence	CO1	12S rDNA	LDH-A
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM11	X	X	X
Takamanda-Mone, CM	5.95901/9.34825	This Study		TKM12	X	X	X
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2009	FJ390082	tet 10			X
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144614	tet 102	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144613	tet 127	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144617	tet 139	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144620	tet 146	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144618	tet 187	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144623	tet 201	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144622	tet 220	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2009	FJ390087	tet 26	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144616	tet 551	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144626	tet 554	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144625	tet 556	X		

Table S4 Continued

Locality	Latitude/Longitude	Source	Accession	Sequence	CO1	12S rDNA	LDH-A
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2010	GQ144624	tet 557	X		
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2009	FJ390088, FJ390071	tet 61	X	X	
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2009	FJ390089	tet 76	X		
Unknown, CM		Eaton et al. 2010	GQ144621	tet M11	X		
Unknown, GB		Borgwardt et al. 2007	EU159866	tet32O	X		
Unknown, Liberia		Schmitz et al. 2003	AY195959	tet E5222		X	
Unknown, CM		Schmitz et al. 2003	AY195958	tet E762		X	
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2009	FJ390072	tet GOT237		X	
Loango Nat'l Park, GB	-1.93064/9.32803	Eaton et al. 2009	FJ390070	tet GOT242		X	
Nki, CM	2.62304/14.1366	This Study		Nki1	X	X	X
Nki, CM	2.62304/14.1366	This Study		Nki2	X	X	
Nki, CM	2.62304/14.1366	This Study		Nki3		X	
RoC	1.64838/17.359	Eaton et al. 2009	FJ390085	osb 105	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144607	osb 108	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144609	osb 109	X		

Table S4 Continued

Locality	Latitude/Longitude	Source	Accession	Sequence	CO1	12S rDNA	LDH-A
RoC	1.64838/17.359	Eaton et al. 2010	GQ144608	osb 115	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144606	osb 117	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144605	osb 120	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144603	osb 46	X		X
RoC	1.64838/17.359	Eaton et al. 2010	GQ144604	osb 92	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144612	osb 93	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144611	osb 94	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144610	osb 95	X		
RoC	1.64838/17.359	Eaton et al. 2009	FJ390066	osb COT05		X	
RoC	1.64838/17.359	Eaton et al. 2009	FJ390067	osb DB6374		X	
DRC	1.647722/27.08519	Eaton et al. 2009	FJ390068	osb M12		X	
GH	5.01295/2.58291	Eaton et al. 2009	FJ390091	cftTAW	X		
GH	5.643319/-0.195465	Eaton et al. 2009	FJ390092, FJ390084	cftTAZ	X		X
GH	6.950125/-1.164509	Eaton et al. 2009	FJ390090	cftTBFR	X		

Table S4 Continued

Locality	Latitude/Longitude	Source	Accession	Sequence	CO1	12S rDNA	LDH-A
IC	5.217877/-4.871727	Eaton et al. 2009	FJ390079	ctet TACIZ01		X	
IC	5.217877/-4.871727	Eaton et al. 2009	FJ390074	ctet TACIZ02		X	
IC	5.14404/-3.1346	Eaton et al. 2009	FJ390075	ctet TAVI01		X	
GH	6.74665/-1.70307	Eaton et al. 2009	FJ390076	ctet TKZ01		X	
Unknown		Roos et al. 2007	NC_009728	Cmplgnm	X	X	
GB	-1.93064/9.32803	Eaton et al. 2010	GQ144581	MctGC14	X		
Unknown		Schmitz et al. 2003	AY195941	McatE512 6		X	
Unknown		Oaks 2011	JF315479	Mcat			X
GB	-1.93064/9.32803	Eaton et al. 2010	GQ144587	Cnl13	X		
Gabon	-1.93064/9.32803	Eaton et al. 2010	GQ144586	Cnl17	X		
RoC	1.64838/17.359	Eaton et al. 2010	GQ144582	CnlC0	X		
South Africa	Natal, no coordinates available	Schmitz et al. 2003	AY195951	Cnil E5133		X	
Unknown		Oaks 2011	JF315522	Cnil			X

Table S5. Descriptive statistics for each gene fragment and best-fit model used in phylogenetic analyses.

Gene	Taxa	Characters	Constant Sites	Variable Sites	Parsimony Informative Sites	Selected Model	Γ	I	BIC
CO1	97	413	302	111	96	HKY	0.229		4674.77
12S rDNA	70	372	323	49	26	K2+G	0.180		3054.5
LDH-A	57	658	643	15	5	K2	N/A		3246.5

APPENDIX B

Settlement Name:

Date:

Settlement Size:

Hunter Information

Age:

Native Immigrant (not born in village)

Profession

Hunter Hunter and Farmer

Method

Snare Shotgun Dogs Machete Trap

Distance traveled from village

Less than or equal to 15 km (a day's walk)

20-30 km (two day's walk)

35-50 km (more than two day's walk)

Number of hours away from village

Less than one day

All day

Several days

Types/Rank (Most commonly hunted = 1, Least Hunted =11)

Rats Porcupine Ungulates Primates Birds

Turtles Tortoises Snakes Monitor Lizards Crocodile

Frogs

Price for each animal group Rats, Porcupine, Ungulates, Primates, Birds, Turtles, Tortoises, Snakes, Monitor Lizards, Crocodiles, Frogs; use group initial).

R	Per Kg:	Per Animal	T	Per Kg:	Per Animal:
P	Per Kg:	Per Animal:	To	Per Kg:	Per Animal:
U	Per Kg:	Per Animal:	S	Per Kg:	Per Animal:
Pr	Per Kg:	Per Animal:	ML	Per Kg:	Per Animal:
B	Per Kg:	Per Animal:	C	Per Kg:	Per Animal:
F	Per Kg:	Per Animal:			

Subsistence or Commercial (Rats, Porcupine, Ungulates, Primates, Birds, Turtles, Tortoises, Snakes, Monitor Lizards, Crocodiles, Frogs; use group initial)

R	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
P	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
U	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
Pr	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
B	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
T	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
To	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
S	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
ML	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
C	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market
F	<input type="checkbox"/> Consumed by Household	<input type="checkbox"/> Sold within the village	<input type="checkbox"/> Sold to City Market

Form Sold (for each animal group Rats, Porcupine, Ungulates, Primates, Birds, Turtles, Tortoises, Snakes, Monitor Lizards, Crocodiles, Frogs; use group initial)

R	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
P	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
U	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
Pr	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
B	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
T	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
To	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
S	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
ML	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
C	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)
F	<input type="checkbox"/> Live	<input type="checkbox"/> Smoked	<input type="checkbox"/> Whole Animal	<input type="checkbox"/> Parts (e.g. head, tail, eggs)

Crocodile Information

Types of Crocodiles Hunted

Dwarf Crocodile Slender-snouted Crocodile Nile Crocodile

Frequency Hunted for Each Crocodile Species

DC Daily Weekly Monthly Dry Season Rainy Season

SC Daily Weekly Monthly Dry Season Rainy Season

NC Daily Weekly Monthly Dry Season Rainy Season

Method of Hunt for Crocodiles (Rank Method from Most used To Least Used (1=

Most 5= Least)

DC Snare Shotgun Dogs Machete Trap

SC Snare Shotgun Dogs Machete Trap

NC Snare Shotgun Dogs Machete Trap

Size Class of Crocodiles Hunted From Snout to End of Tail. Rank Most Commonly

Caught Size-Class

DC Less than 50 cm Between 50 - 100 cm Between 100 - 200 cm
 Greater than 2 meters

SC Less than 50 cm Between 50 - 100 cm Between 100 - 200 cm
 Greater than 2 meters

NC Less than 50 cm Between 50 - 100 cm Between 100 - 200 cm
 Greater than 2 meters