CONSERVATION AND SUSTAINABLE MANAGEMENT OF THE DWARF CROCODILE (*OSTEOLAEMUS TETRASPIS*) IN CENTRAL AFRICAN FORESTS

A Final Report to the
Rufford Foundation & Small Grants Program

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March 2008

ABSTRACT

The rainforests of the Central African Basin support a biologically rich flora and fauna, as well as some of the highest human population growth rates in the world (UNEP 2002). While exploitation of natural resources is key to both national economic development and local livelihoods, wildlife harvest has become the single most widespread form of resource extraction in tropical forests (Peres and Terborgh 1995) and poses a serious threat to the long-term viability of animal populations in this region. The African dwarf crocodile (*Osteolaemus tetraspis*) is among the least studied of the world's 23 crocodilian species and has been subject to high levels of hunting for food by many of the 33 million inhabitants of Central Africa dependent on wildlife for their livelihood. Currently, insufficient data on the ecology and taxonomy of the dwarf crocodile has impeded the development of appropriate conservation and management guidelines. This project gathered basic ecological data on the dwarf crocodile on the central coast of the Republic of Gabon, focusing on habitat requirements, population demographics, and genetic structure. Comparative habitat and abundance data were also collected for the two other crocodilians found in the Central African forests – the Nile crocodile (*Crocodylus niloticus*) and slender-snouted crocodile (*Mecistops cataphractus*). The second major theme of this project is long-term harvest monitoring of crocodiles, fish and other wildlife in a community reserve of the Republic of Congo. These data are providing information to reserve managers and the community on seasonal resource partitioning, habitat-specific wildlife use and harvest levels that will be use to evaluate current and future sustainability of harvest practices.

To date, more than 600 km of nocturnal surveys have been conducted in Gabonese National Parks, offering a robust approximation of population size-structure as well as the habitat requirements and division among the three crocodile species. Four seasons of capture-mark-recapture have provided the first data on wild dwarf crocodile growth rates, movement and are being analyzed for population survival and other demographic parameters. Genetic sequence data have revealed a deep evolutionary split between populations in Gabon and the Congo Basin, suggesting they are two distinct species requiring independent management consideration. The first year of harvest monitoring in the Lac Tele Community Reserve has shown that resource-use varies significantly across seasons and habitats, offering insights to managers for directing conservation activities, such as alternative protein sources & education, most effectively.

INTRODUCTION

The crocodiles of Central and West Africa are among the least known of the world's 23 species, and include the only two species for which information on population status was listed as "extremely poor" by the IUCN Crocodile Specialist Group – the dwarf and the slender-snouted crocodiles (Thorbjarnarson 1992, Ross 1998). The third species, the Nile crocodile (*Crocodylus niloticus*), has been well-studied in East and southern Africa, but is almost unknown from Central and West Africa (see Behra 1987, Kofron 1992). Recent molecular studies have revealed greater levels of subdivision among populations of the Nile crocodile and within the *Crocodylus* genus, resulting in revisions of the taxonomic status of the Nile (Schmitz *et al.* 2003) and slender-snouted (McAliley *et al.* 2006) crocodiles. Such newly discovered genetic variation suggests a more complicated evolutionary history of crocodiles in Africa, and the need to carefully delimit operational taxonomic units (OTUs) for conservation and management. Since the end of the unregulated harvest of crocodiles for the skin trade, current threats to African crocodiles include some illegal skin hunting, the bushmeat trade, and habitat loss (mainly due to commercial logging).

The hunting of crocodiles to supply the international leather market decimated certain populations of Nile and slender-snouted crocodiles in Central Africa during the 20th Century (Thorbjarnarson and Eaton 2003). Although the illegal skin trade largely ended with the implementation of CITES regulations, all three African crocodiles are hunted for food in Central and West Africa. The African dwarf crocodile (*Osteolaemus tetraspis*, Cope 1861) is the most heavily targeted species and is an important food and economic resource in forested Africa. While subsistence hunting of crocodiles has likely been sustainable in most regions, modern widespread commercial hunting now constitutes the most significant threat to Central African crocodiles. Along with high rates of human growth and urbanization, expanding transportation infrastructure has led to a proliferation of commercial bushmeat hunting and

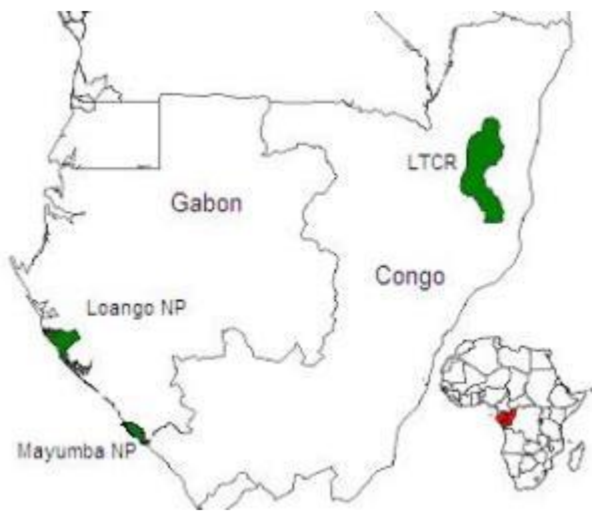

Figure 1. Study sites for the Central African Crocodile Conservation Project.

increasing pressure on natural resources (Wilkie *et al.* 1992). The dwarf crocodile is particularly well-suited for the commercial trade - its small size and slow metabolism allow it to be captured and transported live over long distances without the need for refrigeration. Vendors often store live crocodiles and sell them only when other game becomes temporarily scarce, elevating the crocodile to the biological equivalent of a savings account. Preliminary survey and hunter-interview data suggest that high harvest levels may lead to considerable reductions in crocodile abundance (Eaton, unpub. data). The objectives of this study are to increase our understanding of the current threats, habitat needs, population demography, taxonomy, and population genetic structure to improve the ability to manage and conserve crocodiles in Central Africa. My research will also focus on quantifying the extent and impact of crocodile hunting to evaluate its importance in local economies and develop effective management programs for sustainable use. With appropriate management, other crocodile species have been able to withstand relatively high levels of commercial exploitation (Jenkins 1987).

STUDY SITES

Loango National Park (LNP), on Gabon's central coast, has been an ideal site to study crocodile population demographics and gene flow patterns (Figure 1). LNP and surrounding landscapes support diverse crocodile habitat, including swamp forests, seasonally inundated river forests, and a vast network of coastal lagoons and riverways. Crocodile populations in LNP are assumed to be healthy, as human population density in the region is low, and there is little evidence of poaching within Park borders. The Lac Tele Community Reserve (LTCR) in northeastern Republic of Congo contains important wetland habitat and was declared the country's only Ramsar site in 1998 (Figure 2). The LTCR is managed by the

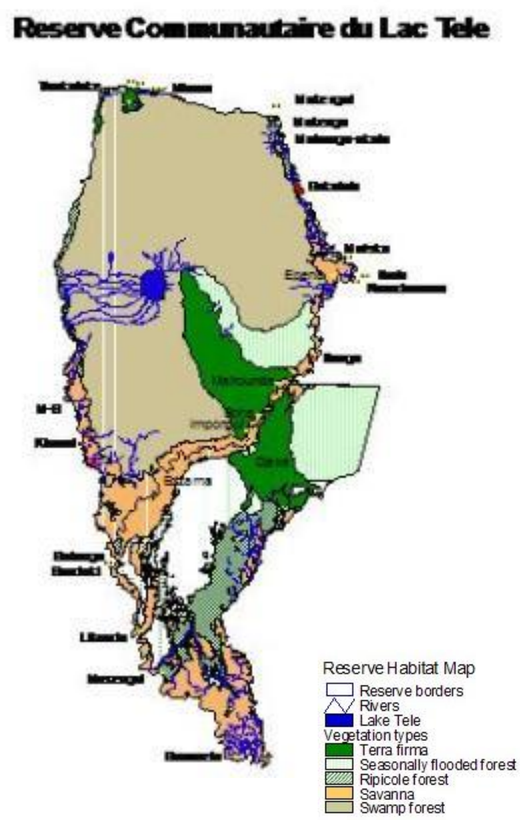

Figure 2. Lac Tele Community Reserve, northern Republic of Congo, with habitat types and villages.

Wildlife Conservation Society (WCS) and the Congo's Ministry of Forest Economy, and supports nearly 16,000 human inhabitants largely dependent on natural resources for their livelihood. The Reserve was recently linked to the regional capitol by paved road and, consequently, to the nation's capitol through river and air traffic. Burgeoning human populations and rapid urbanization have resulted in a concomitant increase in the extraction of bushmeat for commercial sale outside the Reserve. A major objective of this study was to work with Reserve managers to initiate a program for monitoring the harvest of fish, crocodiles, and other bushmeat in LTCR villages in the three major habitat types (terra firma, swamp forest, seasonally flooded forest).

METHODS

Demographics and Ecology

In LNP, I have conducted a multi-year ecological and demographic study on the dwarf crocodile, with supplemental data collected on the other two sympatric crocodile species. Using a combination of nighttime spotlight surveys, mark-recapture, and radio telemetry, I am deriving estimates of relative and absolute abundance, population demographic structure and growth, habitat use, movement rates, and reproduction (standardized methods outlined by Webb and Smith 1987). Since 2003, I have performed nighttime capture surveys along numerous waterways inside LNP. Three to five survey nights per water body cover non-overlapping sections of river or forest, during which attempts are made to observe or capture all crocodiles encountered. Crocodiles not captured are size-estimated and their location recorded. Captured animals marked during a previous year are recorded and new marks added to first-time captures. Individuals are permanently and individually marked by clipping a unique combination of caudal scutes. After the initial capture event, populations are left to re-mix for several days or weeks; a series of re-sighting surveys then follows. The combination of within- and between-season recapture surveys allows the construction of a robust mark-recapture model (Pollock 1982, Kendall 2001) to estimate population abundance and sighting probability under closed population assumptions (White *et al.* 1982), and survival estimates with a less restrictive open-population model (Cormack-Jolly-Seber model, Lebreton *et al.* 1992). I am using multi-stage mark-recapture (MSMR) methods to estimate transition probabilities between life stages (Nichols *et al.* 1992, Fujiwara and Caswell 2002). Estimates of population demographic parameters and abundance will be calculated using the software program MARK (White and Burnham 1999).

Systematics and Population Genetics

I have amassed the largest collection of genetic material for *Osteolaemus* to date, and this is the only study to obtain a comparative set of samples from both putative sub-species of dwarf crocodile. Samples come from multiple geographic scales within and across study sites, and are being analyzed hierarchically to test: 1) the taxonomic status of the genus *Osteolaemus* between the Congo Basin, Ogooué Basin and West Africa, 2) the phylogeographic relationship of *Osteolaemus* across its range to determine patterns of evolution, movement, and isolation, and 3) population genetic structure and contemporary patterns of gene flow to estimate dispersal rates and quantify the size of conservation units. Additional *Osteolaemus* samples have been provided by collaborators working in Ivory Coast and Ghana. Museum collections have expanded our phylogeographic analyses to include individuals from Cameroon and the Democratic Republic of Congo. Of special note, samples obtained from the American Museum of Natural History (AMNH) reptile collection include the holotype and paratypes of *O. t. osborni*, collected in the Ituri Forest during the Lang and Chapman expedition (1909-1915, Schmidt 1919). Tissue samples collected in this study from Nile and slender-snouted crocodiles are contributing to other ongoing phylogenetic investigations.

In most cases, I have collected ≥25 dwarf crocodile samples from putative populations, most of which are wild-caught, separated by distances of 3, 15, 40, 250, 500, and 1,000 kilometers. Samples collected from bushmeat markets are assumed to be harvested within a limited distance of the market and will only be tested at the largest spatial scales (250-1,000 kilometers).

I use both nuclear and cytoplasmic genetic markers to evaluate the systematics and population structuring of the dwarf crocodile. Using the laboratory facilities of the American Museum of Natural History, I sequenced five gene-regions, including three mitochondrial genes (*cyt-b*/control region, COI, 12S) and two nuclear genes [LDH-A (intron), RAG1 (exon)] totaling more than 4,000 nucleotide basepairs. I have also collaborated with researchers in Australia to screen samples of *Osteolaemus* with markers designed for the saltwater crocodile (*C. porosus*). These efforts have resulted in a suite of 12-16 highly informative microsatellite markers with which I will continue population genetic analysis.

I evaluate the taxonomy and phylogenetic relationships of *Osteolaemus* populations within and among West Africa and the Congo and Ogooué Basins using tree-based and discrete character-based methods. Reconstructing phylogenetic trees under maximum parsimony provided evidence of the evolutionary relationships among dwarf crocodile populations, historic patterns of dispersal and vicariance, and extent of conservation units meriting separate management consideration. Population aggregation analysis (PAA, Davis and Nixon 1992), a discrete character-based method, uses alternate fixed characters to define phylogenetic species (Cracraft 1983). I used PAA to construct a phylogenetic analysis of fixed character differences between populations in the Congo Basin, Gabon, and West Africa, and so test the hypothesis of discrete terminal taxa first proposed by Schmidt (1919).

Harvest Impact Monitoring

In collaboration with Congo's Ministry of Forest Economy (MEF) and the Wildlife Conservation Society, I designed and field-tested a bushmeat monitoring program in 2005 to track natural resource use by villagers in the LTCR. We selected and trained a total of 12 local assistants in five reserve villages to collect data on the harvest of fish, crocodiles, and other vertebrate fauna over a 14-month period. The monitoring program was fully implemented in late 2006, and is currently on-going. Due to constraints in project resources and the logistical difficulties of monitoring villages distributed over a large area, we opted for a research design allocating four days of consecutive monitoring to be performed each one or two months, rather than a selection of random monitoring days. Such an approach runs the risk of temporal autocorrelation of data, but is the most practical method given the conditions in the Reserve. Monitoring is conducted from 7:30 am until 5:00 pm each survey day. Each data collector covers a pre-defined area of the village and visits each household at least twice daily. Each survey day, all fish and vertebrate wildlife in the village are recorded. The major sampling unit is the daily household volume of fish and bushmeat. Data collected for bushmeat include: species, sex, age class, weight, area, and method used for hunting, intended destination and use (i.e., sale, consummation, export), and price, if bought or sold. Additionally, crocodiles are measured (head length and total length) and a tissue sample collected, if permitted, by the head of the household. The large volume and diversity of fish species harvested by villagers permits only an approximation of the biomass per household per day, estimated by standardizing the biomass of fish weighed in containers commonly used by fishers for storage or transport.

Long-term harvest data will allow us to quantify seasonal and habitat-specific patterns in exploitation of fish and wildlife resources. To assess the importance of crocodiles to LTCR inhabitants, we are measuring differences in crocodile harvest rates between major habitat types within the Reserve, and estimating seasonal shifts in crocodile/fish ratios based on habitat type and water levels. Comparing the size-class distribution of harvested animals to wild-caught populations will provide insights into hunter behavior and size selection bias. Harvested size class are also being compared between animals selected for local consumption versus those destined for export to regional or national commercial markets. Discrepancies between the two distributions may help better understand the demographic impacts on this species from expected increases in commercial hunting. While not a regular feature of the research protocol, monitoring sales price and crocodile size distributions in regional commercial markets may also prove a valuable index measure of changes in the relative abundance and demography of crocodiles in the wild. Data collected during this initial study phase will serve as a baseline for future monitoring in the LTCR.

RESULTS TO DATE

Demographics and Ecology

With the help of local research assistants, I conducted nearly 130 nighttime surveys, covering more than 600 kilometers of lagoon shoreline, and streams of varying size, in and around Gabon's LNP and northern Congo. A substantial range in relative crocodile abundance has been revealed (0 – 30 crocodiles/km; mean = 4.4/km), largely dependent on habitat variables (i.e., water body size, forest type, water temperature), but some can be attributed to hunting pressure, especially in heavily hunted areas of Congo (mean crocodile abundance = 0.17/km) and heavily fished areas around Mayumba NP in southern Gabon (mean = 0.8/km). Averaged over all regions, dwarf

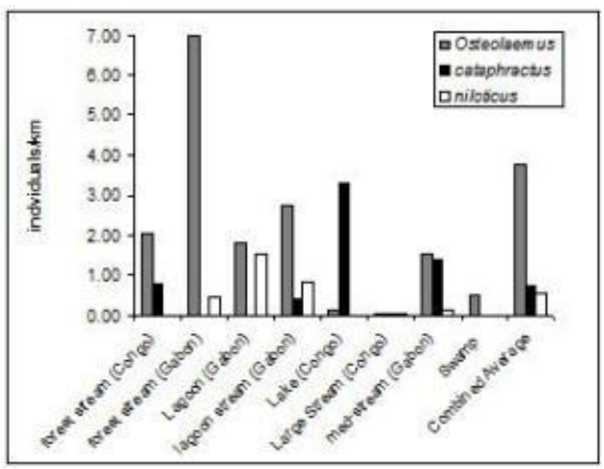

Figure 3. Relative abundance of crocodiles by habitat.

crocodiles were at least five times more abundant than slender-snouted crocodiles, and nearly seven times more abundant than the Nile crocodile (Figure 3).

Assessing relative population abundance by habitat type reveals both niche specialization and overlap among the three crocodile species (Figure 3). The dwarf crocodile appears to be the most generalist of the African crocodiles, occupying all habitat types. It was found at highest densities in small, cool water streams where hunting is absent, but also in relatively high numbers in brackish lagoon waters. Nile crocodiles, preferring coastal lagoons and associated streams, overlap considerably with the dwarf crocodile, with individuals of both species occasionally found in close association. Nile crocodile numbers are generally low, but appear to be recovering following intensive skin hunting up to the 1980s, especially in protected coastal lagoons of LNP (Thorbjarnarson and Eaton 2003). Slender-snouted crocodiles are restricted to freshwater lakes and streams, never having been observed in brackish lagoons or streams. While found to tolerate a range of water temperatures (from 23°C in forest streams to more than 35°C in Lac Tele, Congo), the slender-snouted crocodile appears to be sensitive to particular aspects of its habitat, as it was found in high densities in a very limited number of localized areas.

A total of 535 dwarf, 53 Nile, and 12 slender-snouted crocodiles were captured and marked in LNP. Sixty-four dwarf crocodiles were recaptured a total of 151 times over the course of four field seasons, resulting in relatively low recapture probabilities for robust demographic modeling of population size and survival rates. Initial demographic model selection tests of the mark-recapture data suggest better support for grouping all size classes in estimating survival (0.90, SE=0.4) and recapture probabilities (0.14, SE=0.09). By successively increasing and decreasing individual model parameters by ten percent, holding all others constant, the model produced asymptotic population growth rates for the dwarf crocodile ranging from λ=0.96 to 1.12. While magnitudes varied between trials, the greatest relative impact on growth was survivorship in stages 3-5, which is expected for long-lived animals (Lebreton and Clobert 1991), followed by growth in stage 3 which was most influential on population dynamics when mortality is highest among reproductive classes, a likely scenario since hunting may be biased toward larger animals. The reduced sensitivity to vital rate changes in younger classes suggests the life history strategy of dwarf crocodiles may be dependent on high adult survival and, unlike other crocodilians, on early maturation to offset low annual fecundity (avg. clutch size=14.3, Eaton, unpubl. data).

Movement Data

will be compared with longer term, indirect genetic methods to estimate the temporal and spatial scale over which dwarf crocodile populations operate. The radio telemetry study was undertaken in a

Population Genetics and Taxonomy

I have collected tissue samples from 469 dwarf crocodiles, 43 Nile crocodiles, and 19 slender-snouted crocodiles in Congo and Gabon. Of the dwarf crocodiles, 9.4 percent come from the LTCR, 3.4 percent from Mayumba NP in southern Gabon, and the remainder from approximately 11 localities in Loango NP. I have acquired from museum collections and other researchers an additional 20 dwarf crocodile samples from across West and Central Africa to better resolve *Osteolaemus* phylogenetic and systematic questions.

Table 1. Gene regions sequenced in this study for the dwarf crocodile and the level of fixed character divergence between currently recognized subspecies *O. t. tetraspis* and *O. t. osborni.*

	Gene Region	**Size (bp)**	***N***	**Diagnostic sites (%)**	**Source[1]**
mtDNA	12S	405	76	19 (4.7%)	Schmitz et al. 2003
	COI	565	82	45 (8.0%)	C. Borgwardt, pers. comm.
	cytb/CR	776	47	95 (12.2%)	This study, Quinn et al.1996
nuDNA	LDH-A (intron)	705	55	3 (0.004%)	Gatesy et al. 2004
	RAG1 (exon)	1783	52	7 (0.004%)	Gatesy et al. 2003

[1]references for primer pairs used for sequencing

From a subset of samples representing nearly all of the surveyed dwarf crocodile populations, I successfully sequenced more than 4,200 base pairs (bp) from five mitochondrial and nuclear genes (Table 1). Grouping individuals *a priori* by region (far West Africa, near West Africa, and Congo Basin), a population aggregation analysis (Davis and Nixon 1992) finds ample evidence of fixed character site differences between the regions, and rejects a null hypothesis of gene flow between these

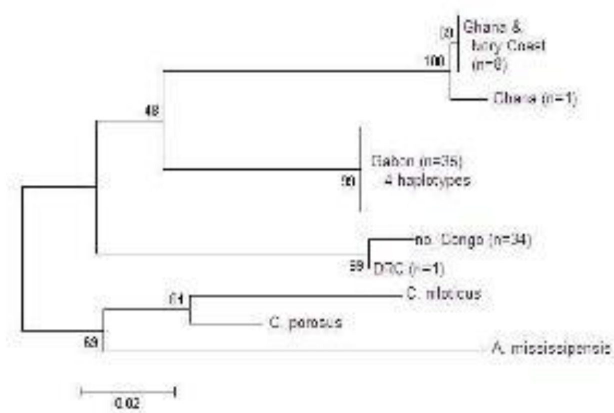

Figure 4. A minimum evolution tree of the African dwarf crocodile based on COI mtDNA sequence haplotypes. Numbers at nodes refer to bootstrap values of 500 replications. Outgroup includes the Nile and saltwater crocodiles and the American alligator.

populations. The number of diagnosable characters found between populations in the putative range of *Osteolaemus tetraspis tetraspis* and *O. t. osborni* range from 95 (12.2%) in the highly variable cytochrome-b and control region to only three (0.004%) in LDH-A, a highly conserved nuclear gene. Regardless of the range of variation among genes, the important point is that all individuals sampled in a given population contain this character state. Interestingly, LDH-A showed a similar percentage of fixed differences as the RAG-1 exon, even though introns are subjected to less selective pressure and would be expected to show greater divergence. Cytochrome *c* oxidase 1 (COI) has been selected by the Consortium for the Barcode of Life (http://www.barcoding.si.edu) as a sufficiently conserved gene to serve as a standard for identifying individual organisms at the species level (Hajibabaei *et al.* 2007, Ratnasingham and Hebert 2007). A survey by Hebert and colleagues (2003) found that 98 percent of congeneric species showed less than two percent sequence divergence in the CO1 barcoding region, and that species-pairs within chordata showed a mean divergence of 9.6 percent (s.d. 3.8). Given that previous phylogenetic work has found the majority of intra-species mitochondrial divergence values below two percent (Avise 2000), our genetic data provide strong inference that the two recognized sub-species of dwarf crocodile are phylogenetically distinct and should be reinstated to full species status. I found a similar level of diagnosable CO1 characters separating populations in far West Africa from Gabon (41 fixed character sites, 7.3%) and from Congo (56 sites, 9.9%), suggesting a much more complicated evolutionary history of the African dwarf crocodile. Phylogenetic assessment of the relationship among populations from the three regions concurs with the PAA (Figure 4). Similar to recent phylogeographic understanding of the South American *Caiman crocodilus*, the dwarf crocodile may represent an entire species complex of old world crocodiles.

Market Monitoring

Village monitoring has been conducted in the LTCR for approximately seven months. Based on anecdotal information from village residents, we hypothesized a temporal segregation of fish and non-fish resource use following water levels in the Reserve. High water levels allow

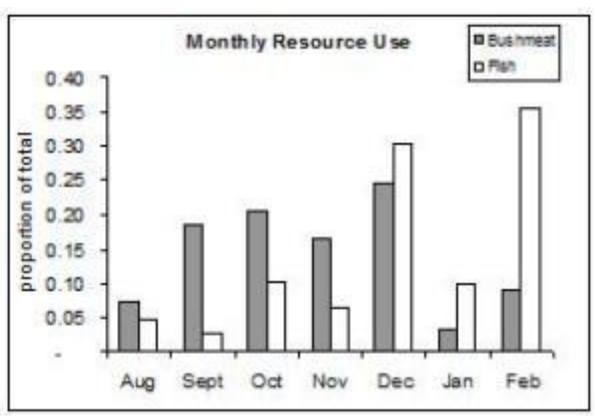

Figure 5. Monthly fish and bushmeat harvest recorded in villages of the Lac Tele Community Reserve.

fish to disperse into the flooded forests, rendering fishing less efficient. Such high water levels, however, permit hunters to travel by pirogue further into these same forests to hunt crocodiles, primates, and other non-fish wildlife. Although monitoring activities do not yet span a full year, preliminary data indeed suggest temporal division of resource use in the LTCR. The highest average hunting activity was recorded in October (Figure 5), corresponding to the period of highest precipitation in northern Congo. The peak fish harvest recorded during village monitoring was between December and February (Figure 5), during the Reserve's major dry season. The relatively high fish and bushmeat harvest during the month of December may reflect increased resource use for village holiday celebrations. An estimated total of nearly 22,000 kilograms of fish biomass has been recorded thus far in village monitoring. When daily village harvests are extrapolated, an estimated 375,000 kilograms of fish biomass are removed by these five villages per year. Approximately 7,800 kilograms of bushmeat were recorded during village surveys, corresponding to nearly 146,000 kg/year of non-fish biomass harvested by these villages. Based on a 2001 census (Poulsen and Clark 2002), the five study villages comprise 39.2 percent of the Reserve's population, suggesting a very approximate estimate of 956,600 kilograms of fish and 372,450 kilograms of bushmeat harvested in the Reserve each year.

Forty-three non-fish vertebrate species have been recorded during LTCR village monitoring. Dwarf crocodiles constitute the largest proportion harvested (22% of all animals taken), followed by the spot-nosed guenon (*Cercopithecus nictitans*, 14%). In Mokengui, a village surrounded by seasonally flooded forest and reputed to be the principal LTCR crocodile hunting locale, the proportion of crocodiles in their bushmeat harvest (22.7%) did not differ from the Reserve average. The highest proportion of crocodiles harvested was at Dzeke (30%), a village situated between a zone of flooded forest and terra firma where hunters may have greater access to crocodile populations. The primary use of crocodiles in the Reserve is subsistence consumption

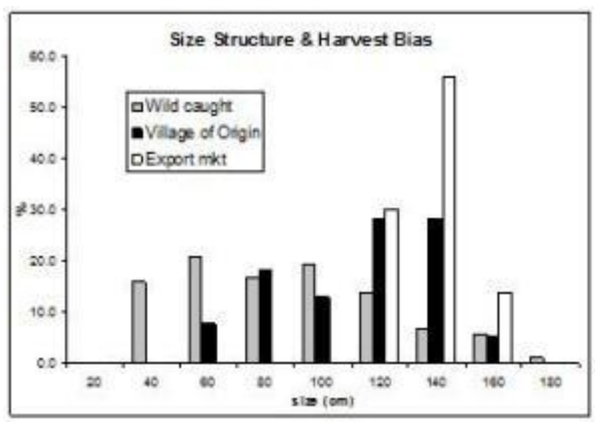

Figure 6. Size structure of dwarf crocodiles in Gabon (wild-caught) and from Congo harvest monitoring. Village of origin includes animals kept for local consumption or sale; export market refers to crocodiles shipped for commercial sale.

(avg=65.8%), but the highest rates of commercial crocodile export was recorded from Mokengui (8.2%) and Epena (6.2%) villages. Mokengui is located upstream from Epena which, in turn, is situated at the end of the solitary road connecting the LTCR to the regional capitol Impfondo. Epena is the Reserve's principal export village.

We have recorded a total of 237 harvested dwarf crocodiles from local villages and from principal export markets; more detailed measurements (length, weight, sex) were taken from 92 of these animals. Comparing the population structure of wild-caught animals in Gabon to harvested animals in the LTCR, I note a significant bias in the size of animals selected for export, with animals no smaller than 120 centimeters sold in commercial markets (Figure 6). A lesser degree of size-class bias was noted in the harvest itself, but suggests that harvest mortality must be modeled as size-dependent. Independently evaluating the size classes of crocodiles harvested at the local village level from those exported to larger market cities also reveals potential sampling errors in monitoring markets that import a large fraction of their bushmeat, indicating the need to evaluate the design of market monitoring studies.

Training

For the LNP Project, I trained a total of eight Gabonese research assistants in crocodile survey and measurement techniques, radio-tracking, and basic computer skills. These and other assistants were also trained in general crocodile biology, ecology, and behavior to lead educational tours for LNP visitors. Research assistants at Congo's LTCR project were trained in crocodile survey and measure techniques, methods for monitoring the subsistence and commercial harvest of crocodiles and other wildlife in the Community Reserve, and database design. A total of 17 LTCR villagers were hired and trained to work as monitoring research assistants. In collaboration with the AMNH and the National Science Foundation's Research Experience for Undergraduates, I trained and supervised two undergraduate students in molecular research on small crocodile-related projects, one of which we intend to publish in a peer-reviewed journal.


Three generations of dwarf crocodile captured in Loango National Park, Gabon.

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