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Stable isotopes uncover trophic ecology of the West African crocodile (*Crocodylus suchus*)

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ABSTRACT

Stable isotope analysis is a widespread tool in ecological studies of diet composition and habitat use. In deserts, freshwater environments constitute threatened local hotspots of biodiversity. In these environments, stable isotopes may help to describe trophic ecology of top-predators. We examined stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes from scute keratin samples of 33 *Crocodylus suchus* and muscle samples from 39 potential prey collected in Southern Mauritania. Isotope ratios were compared among crocodiles according to size (non-adult and adult), and habitat (rock pools and floodplains). There was a significant interaction effect of habitat and size on crocodile $\delta^{13}C$ values. Whereas $\delta^{13}C$ was similar for all crocodiles collected in rock pools, adults had lower signatures than non-adults in seasonal floodplains. $\delta^{15}N$ indicated an ontogenetic dietary shift with adult crocodiles foraging on prey from higher trophic level. Standard ellipse areas showed wider isotopic niches for adult than non-adult crocodiles, and within adults, for those from floodplains than those from rock pools. These environments are small, seasonal, overexploited for livestock watering, and polluted. They support very small and isolated crocodile populations. This study is aimed to provide conservation authorities with baseline information to strictly protect water-bodies where these predators subsist in arid environments.

1. Introduction

After the mid-Holocene humid period (around 6.000 years ago), arid conditions developed throughout North Africa and culminated in the formation of the Sahara, the largest warm-climate desert in the world (Schuster et al., 2006). In this arid environment, some species adapted to extreme dryness and developed physiological mechanisms to avoid water-loss. Other species need to be permanently in contact to water bodies (Brito et al., 2014). For aquatic species, water is the most important limiting and temporally variable resource in deserts. Their suitable habitats are naturally patchy and connectivity is important for their populations. Populations of these freshwater species are often irregularly distributed in mountains, where environmental conditions are less harsh and have more available water (Brito et al., 2014). These patches constitute local hotspots of biodiversity and may contain threatened endemic taxa (Vale et al., 2015).

One of the iconic organisms living in the Sahara and completely dependent of water resources is the West African crocodile (*Crocodylus suchus*). In Mauritania, populations persist mostly in two habitat types: mountain rock pools (locally known as *gueltas*) and seasonal floodplains (locally known as *tâmoûrts*) that are surrounded by inhospitable desert areas (Brito et al., 2011). Most water-bodies have extremely small crocodile populations (Campos et al., 2016). Moreover, water-bodies are affected by overexploitation, faecal contamination and eutrophication (Tellería et al., 2008; Velo-Antón et al., 2014; Vale et al., 2015). Mauritanian crocodiles have high levels of genetic structure and limited gene flow among populations (Velo-Antón et al., 2014). Recent surveys suggest that *C. suchus* is declining or extirpated throughout much of its distribution, and currently inhabits the western and central-southern Sahara, Sahel and tropical Guinean gulf, as well as the Congo Basin and parts of Uganda (Brito et al., 2011; Hekkala

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et al., 2011; Shirley et al., 2015). Data on the biology, ecology, and behaviour of *C. suchus* is notably unavailable, which currently hinders extensive conservation planning.

Stable isotope analysis (SIA) is a widespread tool in studies of diet composition, trophic interactions, and habitat use and migration (Caut, 2013). The most commonly used elements in ecological SIA are carbon (C) and nitrogen (N). Since the carbon isotope ratio ($\delta^{13}C$) changes minimally (~1‰) as carbon moves through food webs (Rounick and Winterbourn, 1986), it is commonly used to evaluate the source of carbon at the base of food webs. The nitrogen isotope ratio ($\delta^{15}N$) in consumer tissues is typically considered to be enriched by ~3‰ relative to that in the diet (Minagawa and Wada, 1984); it is thus commonly used to estimate trophic position along food chains (Vanderklift and Ponsard, 2003). Thus, $\delta^{13}C$ can be used to track the original source of a consumer' nutrients, and $\delta^{15}N$ can be used to estimate a consumer relative trophic position, i.e. higher $\delta^{15}N$ indicates higher trophic position (Post, 2002).

We quantified carbon and nitrogen stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$ respectively) to infer the trophic ecology of *C. suchus* in Mauritania with emphasis on ontogenetic (adults and non-adults individuals) and spatial (habitat types) variation. Additionally, we measured stable isotope ratios from potential crocodile prey since identification of baseline isotopic signatures is necessary to infer predator's trophic position and carbon source (Post, 2002). Due to multiple logistic constraints, this technique is an advantageous alternative and a complementary tool to describe crocodile trophic ecology over traditional methods, such as stomach content analysis, scat analysis and feeding observations (Radloff et al., 2012; Wheatley et al., 2012; Caut, 2013). Moreover, stable isotope analysis has been proposed as a surrogate of measuring trophic niche width (Bearhop et al., 2004). This approach provided important advances in food-web ecology in recent years (Layman et al., 2012). We expect that our results could be useful for the management of *C. suchus* populations and the Mauritanian freshwater habitats in which crocodiles persist.

2. Material and methods

2.1. Study area

The study area comprises the mountains of Tagant, Assaba and Afollé, in southern Mauritania (Fig. 1). These massifs are the origin of a number of seasonal rivers organized in six seasonal hydrographic sub-basins that occasionally flow from north to south up to the Senegal River. These seasonal rivers generally are composed of rock pools in mountain slopes and seasonal floodplains at the foothills of the mountains (Campos et al., 2012; Vale et al., 2015).

Within the study area, altitude ranges from 9 m a.s.l. on the Senegal River to 625 m a.s.l. in the Tagant. Climate is characterized by three seasons: a cool and dry period from November to February, a hot and dry period from March to June, and a wet season from July to October, with most precipitation in August and September. Annual precipitation has a north-south gradient, and it ranges from 100 mm in the northern desert areas to 900 mm in the extreme southern region of the study area. Variation in average annual temperature is relatively small and tends to follow the altitudinal gradient (Cooper et al., 2006; Brito et al., 2011).

2.2. Water-bodies

In Mauritania, *C. suchus* are mostly found in two freshwater habitats, *gueltas* and *tâmoûrts* (Fig. 1). *Gueltas* are located upstream of narrow valleys at the base of the mountains. Generally, water is only available during the rainy season (July to September), when torrential waterfalls fill up the pools. The small area of rock pools (ranging between 0.001 ha and 1.0 ha) restricts their carrying capacity and crocodile populations usually do not exceed eight individuals, and in some cases there are only one to three crocodiles per pool (Brito et al., 2011; Campos et al., 2016). *Tâmoûrts* are located on the foothills of the mountains which are larger in size than *gueltas* and frequently reach more than 1000 ha; water is usually shallow and floodplains are mostly dry during the dry season (October to June), forcing crocodiles to find shelter in nearby rock outcrops during this period. In this habitat type, crocodiles can number up to 30–40 individuals (Brito et al., 2011).

2.3. Fieldwork and sample collection

We collected scute keratin samples of *C. suchus* ($n = 33$) and muscle of their potential prey ($n = 39$) from fieldwork expeditions conducted from 2003 to 2015. We opportunistically captured crocodiles by hand or using hand nets ($n = 15$), and immediately released them at the point of capture after clipping a 5 mm piece of tail tissue for isotopic analysis. We also collected samples from dead crocodiles found near water-bodies ($n = 15$) or body remains that included scute samples ($n = 3$). We obtained tissue samples following ethical guidelines for use of live reptiles (Brito et al., 2011). All samples were stored in 70% ethanol.

We sampled potential prey (insect, fish, amphibian, and mammal) in and around water bodies. We took whole insects ($n = 3$ aquatic beetles) or vertebrate muscle tissue. Fish samples were collected from the genera *Coptodon/Sarotherodon* ($n = 8$), *Clarias* ($n = 5$), *Barbus* ($n = 2$), *Schilbe* ($n = 1$) and *Allestes* ($n = 1$), and amphibian samples from the genera *Hoplobatrachus* ($n = 7$) and *Amietophrynus* ($n = 2$). We also collected mammal tissues from cow ($n = 4$), goat ($n = 2$), sheep ($n = 1$) and dromedary ($n = 2$) specimens found dead near water-bodies. Although we found feeders around water bodies, this birds' keratinized structure is not assimilated by crocodiles. For this reason, we decided to exclude these samples (bird feeders) from lab analyses, and bird muscle was not available.

All samples were preserved in 70% ethanol for further lab procedures. Some studies have demonstrated that ethanol did not affect isotope signatures (Hobson et al., 1997; Sarakinos et al., 2002). For example, Barrow et al. (2008) observed in tissues of freshwater and sea turtles subject to lipid extraction, there were no differences between samples dried at 60 °C and those preserved in ethanol.

We sampled prey items at the same localities as crocodiles (Fig. 1), although some of the prey types had to be collected in some other water-bodies because of fieldwork logistic constraints. We acknowledge that pooling samples from different sites could increase prey isotope variance if sources vary spatially (Layman et al., 2012), thus losing power to detect some small-scale dietary differences.

2.4. Sample preparation and isotope analyses

We did not extract lipids from crocodile scales as it mainly corresponded to keratin and because this tissue has low fat content. Crocodile scales have a tough outer keratinized epidermis and a rigid dermal core of extremely dense collagen. Keratin is metabolically inert after formation, and stable isotope values reflect the diet at the time of scale formation (Radloff et al., 2012). Scales were cleaned in 0.1 M NaOH solution for 30 s to remove waste. Afterwards, samples were thoroughly washed in distilled water and dried at 60 °C for 24 h.

Prey muscle tissue samples were lipid extracted following the Folch method (1957) by rinsing in a 2:1 chloroform: methanol solvent, as tissue lipid content can influence carbon isotope values.

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