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INSIGHTS ON THE TRANSLOCATION OF A CRITICALLY ENDANGERED
CROCODYLIAN: DIET AND BODY CONDITION OF HEADSTART AND WILD
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JOSEPH BROWN

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INSIGHTS ON THE TRANSLOCATION OF A CRITICALLY ENDANGERED
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By

Dr. Cameron D. Siler, Chair

Dr. Jeffrey Kelly

Dr. Caryn Vaughn

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Abstract

Studies of diet are fundamental to understanding a species' ecology, and in relation to conservation translocations, dietary studies of headstart populations are particularly rare and valuable. These studies can yield insights into effects of headstarting on a population's ability to adjust and become established in the wild. With less than 150 mature individuals remaining in the wild, the critically endangered Philippine crocodile (*Crocodylus mindorensis*) is one of the most severely threatened species on the planet. We conduct the first analysis of stomach contents and characterize the diet of Philippine crocodiles from Isabela Province on the island of northern Luzon, Philippines. Additionally, we address concerns regarding captive-release programs by analyzing stomach contents of headstart crocodiles released into the wild over the last decade. Our study of diet from a resident wild population (N = 20) acts as a baseline comparison for evaluating the dietary habits of headstart crocodiles (N = 10), from which we found no evidence for dietary differences in percent occurrence, percent composition, and prey diversity. Overall, we demonstrate the use of 17 different prey species across eight prey categories (snails, fish, birds, reptiles, amphibians, mammals, crabs, and insects). 70% of Philippine crocodiles contained snails as the prominent prey type, where 50.0% of all *C. mindorensis* consumed *Pomacea canaliculata* (the golden apple snail), an invasive species and one of the leading agricultural pests in the Philippines. Additionally, fish were consumed by 36.7% of *C. mindorensis*, birds 33.3%, and reptiles 33.3%. Finally, we calculate the first body condition index (Relative condition factor K_n) for *C. mindorensis* and examine variation in body condition between headstart and wild crocodiles and find that wild crocodiles have significantly higher condition scores than headstart individuals. Overall, headstart crocodiles adjust well post-release and exhibit similar dietary habits compared to their wild counterparts, even within an

agriculturally dominated landscape where they are likely exploiting an invasive species in high abundance. Our focused monitoring methods reveal broader relevance for conservation, highlighting the importance for a long-term commitment to both ecological monitoring and enhancing the capacity of in-country local communities.

1. Introduction

Wildlife population declines are evident at a global scale (Barnosky et al., 2011; Dirzo et al., 2014). As a result, management strategies involving conservation translocations are becoming increasingly vital for species recovery plans (Armstrong and Seddon, 2008). Following the official guidelines recently defined by the International Union for Conservation of Nature (IUCN), conservation translocations (hereafter, translocations) consist of introductions, reintroductions, and reinforcements (i.e., re-stocking)—all of which involve the deliberate movement and release of organisms, guided by an underlying conservation objective (IUCN/SSC, 2013). However, reviews of translocation projects worldwide have found generally low to average success rates (Griffith et al. 1989; Dodd and Siegel, 1991; Wolf et al., 1996; Fischer and Lindenmayer, 2000; Germano and Bishop, 2008), compounded by difficulties inherent in the evaluation of success for certain long-lived species (Ewen and Armstrong, 2007; Canessa et al., 2016). Given the increasing use of translocations, increased effort on monitoring is essential for evaluation of project outcomes, and to measure progress and post-release performance of released individuals (IUCN/SSC, 2013). To improve the probability of success for both ongoing and future translocation efforts, research has advocated for rigorous, long-term monitoring protocols, more broadly applicable monitoring techniques, and regular reporting of progress throughout the course of a translocation project (Dodd and Siegel, 1991; Seddon, 1999; Fischer and Lindenmayer, 2000; Armstrong and Seddon, 2008; Germano and Bishop, 2008; IUCN/SSC, 2013).

Translocations remain an effective conservation tool (Fischer and Lindenmayer, 2000; IUCN/SSC, 2013; Yang et al., 2018), and one such strategy—headstarting—has become a more common management activity to augment wild populations threatened by extinction (Perez-

Buitrago et al., 2008; Redford et al., 2011; McGowan et al., 2017). Headstarting aims to improve the survival rate of young (collected from the wild or captive-bred) by rearing them in captivity during early and more vulnerable life stages, and then releasing them into the wild at a more advantageous size (Ferguson et al., 1982; Alberts, 2007). Theoretically, this strategy is expected to increase wild population numbers by counteracting high mortality in the wild when nests and young are exposed to natural threats (e.g., predation, starvation; Alberts, 2007) and anthropogenic pressures (e.g., habitat alteration, invasive species; Alberts and Philips, 2004; Wilson et al., 2004). Since its initial conservation application in the 1970's for marine turtles (Pritchard, 1979; Bowen et al., 1994), headstart (i.e., captive-release) programs have continued to play an integral role in wildlife recovery plans over the last half-century (Cayot et al., 1994; Seijas, 1995; Haskell et al., 1996; Heppell et al., 1996; Pedrono and Sarovy, 2000; Hudson and Alberts, 2004; van de Ven et al., 2009; Yang et al., 2018).

Despite the potential success of headstarting, concerns have been expressed questioning the efficacy of this conservation tool (Dodd and Siegel, 1991; Reinert, 1991; Alberts, 2007). For example, there are concerns that captivity may decrease survival rates post-release due to either captive conditions (Matthews et al., 2005) or stress during the release process (Hartup et al., 2005), or a combination of the two, resulting in poor health of captive-reared individuals (Kleimann et al., 1994; Snyder et al., 1996). In addition, individuals reared in captivity must possess behavioral competencies similar to their wild counterparts to survive and reproduce after release (Alberts, 2007). The potential inability to forage efficiently on natural food resources can have a detrimental impact on behavioral and physiological processes post-release, which is a major concern for captive-release programs (Brambell, 1977; Campbell, 1980; Bowen et al., 1994; Alberts, 2007). Nevertheless, it may be possible to enhance the competency of headstart individuals when well-designed headstart programs and captive-rearing protocols are based on a

thorough understanding of the basic ecology and natural history of the target species (Burghardt and Layne, 1995; Burghardt and Milostan, 1995; Wallace, 2000; Dietz, 2004; Martins, 2004; Alberts, 2007).

Since the aim of headstart programs is to ensure a viable, self-sustaining population in the wild, post-release monitoring efforts focus often on vital rates (i.e., survival and recruitment rates; Armstrong and Seddon, 2008). Yet, monitoring these parameters for some long-lived species with delayed sexual maturity may take years, if not decades to evaluate successfully (Germano and Bishop, 2008). However, monitoring parameters specifically focused on animal behaviors, such as those involved with foraging and diet habits, as well as animal health, can yield insights into the organism's adjustment to release sites and can act as valuable early indicators for translocation success (Pinter-Wollman et al., 2009). Even though the value of these parameters is dependent on baseline comparative data from a natural (i.e., resident) wild population (IUCN/SSC, 2013), they can address any life stage between release and breeding age, proving especially useful for some long-lived species whose reproductive success may take years to assess, and when management decisions must be reached rapidly (Pinter-Wollman et al., 2009; IUCN/SSC, 2013; Muths et al., 2014).

Crocodylians, a group that includes the world's crocodiles, alligators, caiman, and gharial (Grigg and Kirschner, 2015), are long-lived reptiles characterized by delayed sexual maturity (5–15 years depending on species; Ross, 1998), high fecundity, and an iteroparous life cycle met with high egg and hatchling mortality rates (Kushlan and Mazzotti, 1989; Briggs-Gonzalez et al., 2017). These large amphibious predators are distributed throughout tropical and subtropical aquatic habitats in over 90 countries (Ferioli, 1998; Ross, 1998). Following an extensive global analysis on the conservation status and distribution patterns of reptiles, those occurring in freshwater environments and tropical regions were found to have the highest extinction risk,

where above all, crocodylians were highlighted amongst the most severely threatened taxa and identified as a key priority for conservation (Böhm et al., 2013). As keystone species that help maintain aquatic ecosystem structure and function, the loss of any crocodylian species would represent a critical loss of biodiversity and ecosystem stability (King, 1988; Craighead, 1968; Ross, 1998).

To date, nearly half of the world's 27 extant crocodylian species are threatened with extinction on the IUCN Red List (IUCN, 2019), and headstart strategies have been increasingly applied globally, notably for the world's six most severely threatened species, including: (1) *Crocodylus mindorensis* in the Philippines (van Weerd and van der Ploeg, 2008); (2) *Crocodylus siamensis* in Vietnam, Thailand, and Cambodia (Polet, et al., 2002; Temsiripong et al., 2004; Daltry and Starr, 2010); (3) *Alligator sinensis* in China (Wang et al., 2011); (4) *Gavialis gangeticus* in India and Nepal (Whitaker and Basu, 1983; Maskey et al., 2006); (5) *Crocodylus intermedius* in Venezuela (Munoz and Thorbjarnarson, 2000); and, (6) *Crocodylus rhombifer* in Cuba (Targarona et al., 2010). However, early concern was expressed that captive-released crocodylians may not thrive in the wild, possibly as a result of inadequate foraging and hunting competencies necessary for post-release adjustments (Blake and Loveridge, 1975).

Unfortunately, despite extensive research on the diet of wild crocodylians (Chalbreck, 1972; Delany and Abercrombie, 1986; Magnusson et al., 1987; Wolfe et al., 1987; Platt et al., 1990; Webb et al., 1991; Thorbjarnarson, 1993; Barr, 1994; Pauwels et al., 2003; Rice, 2004; Wallace and Leslie, 2008; Platt et al., 2013; Balaguera-Reina et al., 2018), and the increase in captive-release programs as a conservation tool, few studies have evaluated the dietary habits and foraging competencies of captive-raised crocodylians returned to the wild (Elsley, 1992).

Studies of diet are fundamental to understanding functional roles of key predators in an ecosystem, yielding insights on basic predator-prey relationships and prey utilization (Rice,

2004; Saalfeld et al., 2011). Among crocodylians, diet has been demonstrated to affect growth, behavior, reproduction, and body condition (Balaguera-Reina et al., 2018; Delany et al., 1999; Lang, 1987; Platt et al., 2013), all of which are critical life history characteristics that impact management strategies (Saalfeld et al., 2011). In particular, studies of crocodylian body condition often calculate a condition index (e.g., Fulton's condition factor [K], relative condition factor [K_n]; LeCren, 1951), which acts as a quantitative indicator of animal health and well-being (Taylor, 1979; Brandt, 1991; Elsey et al., 1991; Mazzotti et al., 2012). If used properly, condition indices provide researchers with both an effective and efficient means to track and communicate trends in crocodylian populations for improved management decisions (Fujisaki et al., 2009; Mazzotti et al., 2009).

Of particular conservation concern is the Philippine crocodile (*Crocodylus mindorensis*), a relatively small (maximum length 3.02 m), elusive freshwater crocodylian endemic to the Philippine archipelago in Southeast Asia (Hall, 1989). Both male and female *C. mindorensis* exhibit delayed sexual maturity, taking 10–15 years on average to become reproductively active, often at a body length of 1.5–2.1 m (Ross and Alcala, 1983; van Weerd and van der Ploeg, 2012). The Philippine crocodile is classified as Critically Endangered on the IUCN Red List (van Weerd et al., 2016), Appendix I of CITES, and is protected by Philippine law under the Wildlife Resources Conservation and Protection Act (Republic Act 9147; van Weerd, 2010). Even though initial population decline was associated with commercial hunting, current threats are due primarily to a soaring human population, resulting in extensive habitat loss and persecution by local people (Ross, 1998; van Weerd et al., 2016). Less than 150 adult *C. mindorensis* remain in the wild, and despite translocation efforts, population trends show a continued decline (van Weerd et al., 2016). As such, the Philippine crocodile is likely the most severely threatened

crocodilian species and one of the rarest vertebrates on the planet (van Weerd and van der Ploeg, 2008).

Historically, with over 7,100 islands and a land mass of 300,000 km², the Philippines was >85% forested (Catibog-Sinha and Heaney, 2006) and *C. mindorensis* was distributed widely throughout the archipelago (Ross and Alcala, 1983). The country is recognized as both a Megadiverse nation and Biodiversity Hot Spot—a designation shared only with Madagascar (Mittermeier et al., 1999). As such, the Philippines is one of the planet’s highest conservation priorities (Brown et al., 2013), with the Philippine crocodile ranked as the highest priority species for conservation in the Action Plan by the IUCN/SSC Crocodile Specialist Group (Ross, 1998; van Weerd et al., 2016). Unfortunately, over the last century, the Philippines has suffered rates of environmental destruction exceeding those observed anywhere else in the world (Sodhi et al., 2004; Brown et al., 2013). The island nation now retains 4–8% of its original forest cover only (Catibog-Sinha and Heaney, 2006; Brown et al., 2013) and the range of *C. mindorensis* has been reduced to three localities only (northern Luzon Island, southwest Mindanao Island, and Dalupiri Island), occupying an area of less than 2,000 km² in total (van Weerd et al., 2016). Consequently, *C. mindorensis* survives in a predominantly agricultural landscape, often in close proximity to densely populated human settlements where it is perceived as a pest and occasionally killed (van Weerd and van der Ploeg, 2012).

Significant conservation measures for Philippine crocodiles began in 1999 after the discovery of a remnant population in the Municipality of San Mariano, Isabela Province, northern Luzon Island (Fig. 1; van Weerd, 2000; van Weerd, 2010). Shortly after the population’s discovery, the Mabuwaya Foundation (a local NGO) was established to protect Philippine crocodiles in the wild (van Weerd and van der Ploeg, 2004). To address threats facing *C. mindorensis*, Mabuwaya designed a long-term, *in-situ* conservation action plan with three key objectives: (1) mobilize

community support through various education and public awareness campaigns; (2) establish crocodile sanctuaries and buffer zones to protect vital nesting habitat around wetlands at the three remaining breeding sites of San Mariano (Fig. 1; Dinang Creek, Disulap River, and Dunoy Lake); and (3) improve the quality of life in the rural, impoverished communities of San Mariano by compensating barangays (local term for villages or small communities) for their support in crocodile conservation (van Weerd and General, 2003; Miranda et al., 2004; van der Ploeg and van Weerd, 2006). Because of these extensive, community-based conservation efforts, or otherwise known as CEPA programs (communication, education and public awareness: named by the IUCN Commission on Education and Communication), communities of San Mariano have adopted *C. mindorensis* as their flagship species and gained a more respectful appreciation for crocodile conservation, reducing crocodile killings throughout the municipality (van Weerd and van der Ploeg, 2004; van Weerd and van der Ploeg, 2008). However, despite the success of public education and outreach initiatives, the crocodile population in northern Luzon Island has remained small and fragmented, due primarily to high hatchling mortality rates and compounded by persisting anthropogenic pressures including the destruction of suitable nesting and hatchling habitats for agricultural expansion (van de Ven et al., 2009).

In 2005, Mabuwaya spearheaded a nest protection and headstart program in an effort to increase hatchling survival rates and to reinforce the wild population of northern Luzon Island (van Weerd and van der Ploeg, 2008). By training and hiring local farmers and fishermen as sanctuary guards to protect nests during the incubation period, Mabuwaya successfully collects wild hatchlings, raises them in captivity for 22–28 months, and then releases them back into the wild (van Weerd and van der Ploeg, 2008). Although rigorous monitoring efforts are still ongoing, limited studies exist on the progress and post-release performance of headstart individuals. Van Weerd and van der Ploeg (2008) reported that four headstart crocodiles had no

adaptation problems and survived for up to six months after release. Similarly, van de Ven et al. (2009) determined that 32 headstart crocodiles adjusted well to wild conditions, showing a 53% survival rate after one year. However, there is a notable absence of any studies on the diet of headstart crocodiles. And although there have been a handful of recent studies on the basic ecology of *C. mindorensis* (Manolo, 2008; Oliveros et al., 2005; Manolo et al., 2013; van de Ven et al., 2009; van Weerd et al., 2006), this conservation flagship species still remains one of the least studied crocodylians in the world with little information about key natural history traits, such as diet, critical for effective conservation action plans (van Weerd and van der Ploeg, 2012; Bohm et al., 2013).

In this study, we conduct the first analysis of stomach contents for *C. mindorensis*, characterizing the diet of wild Philippine crocodiles in Isabela Province of northern Luzon. In addition, we address concerns regarding captive-release programs by analyzing stomach contents and characterizing the diet of headstart crocodiles released into the wild over the last decade. We quantify dietary niche breadth and examine dietary differences of headstart and wild individuals. Our study of diet from a resident wild population acts as a robust, baseline comparison for evaluating the dietary habits of captive-released crocodiles and assessing their ability to forage efficiently and adjust to wild conditions. Finally, we provide the first calculation of a body condition index for *C. mindorensis* to provide baseline data for population monitoring and to examine any potential variability in condition between headstart and wild crocodiles. Not only is this study among the first to analyze crocodylian diet and body condition from captive-released individuals and wild conspecifics (see also Elsey, 1992; Elsey et al., 1992), but also, the conservation implications of our findings will be vital in guiding conservation management for *C. mindorensis*, a biodiversity hotspot, and continued improvement to global translocation efforts.

2. Methods

2.1. Study site

Field studies were conducted from February to October 2018 in the Municipalities of San Mariano and Divilacan in Isabela Province, Luzon Island, Philippines (Figure 1). Both municipalities are located in northeast Luzon Island along the northern Sierra Madre Mountain range. A large portion of the northern Sierra Madre is nationally protected within the Northern Sierra Madre Natural Park (NSMNP) (Figure 2). Outside of NSMNP, the region is intensely dominated by an agricultural landscape with an extensive stream network (Figure 3) (van Weerd and van der Ploeg, 2012). The climate is tropical with three distinct precipitation seasons: northeast monsoon (November–February), southwest monsoon (June–October), and dry (February–May). Frequent typhoons strongly influence precipitation, and annual average rainfall can vary across the Sierra Madre from 1,649 mm (Tuguegarao) in Cagayan Valley to 3,534 mm (Casiguran) along the Pacific Coast (Philippine Atmospheric, Geophysical and Astronomical Services Administration, 2005). Temperatures range from an average low of 19.0°C in January to an average high of 35.9°C in May (van Weerd and van der Ploeg, 2012). San Mariano covers an area of 1,469.5 km² in the foothills of the northern Sierra Madre along the NSMNP boundary in Cagayan Valley, and consists of a small-town center surrounded by 36 rural barangays and a human population that is estimated at 55,370 (38 inhabitants/ km²) (2015 Census, www.philAtlas.com).

We surveyed five primary sites within San Mariano: (1) Dunoy, (2) Narra, (3) Diwagden, (4) Dinang, (5) Baliao (Figure 4), and a sixth site located in Divilacan (5) Dication Lake. With the exception of Baliao, all sites are designated Philippine crocodile sanctuaries and have been used as release sites for the Mabuwaya headstart program since 2007. The first site, Dunoy, is found in the foothills of the protected NSMNP. The habitat around Dunoy is characterized by degraded forest, grasslands, bamboo groves, and interspersed corn and rice fields (van Weerd and van der Ploeg, 2012). Dunoy also contains several small ponds and lakes (i.e., Dunoy Lake, Dunoy Lake II) along the Catalangan River which are known historical nesting sites for *C. mindorensis* (Figure 5). Our second site, Narra, is on a plateau 1.5 km west of Dunoy but is located outside the NSMNP boundary. Surrounding habitat is dominated by agriculture, human settlements, and grasslands resulting from decades of slash-and-burn farming (Figure 6). The third site, Diwagden, is part of Barangay San Jose which is surrounded by the connecting stream network of Diwagden Creek and Disulap River. Diwagden lies in the bufferzone of the NSMNP, where the fast flowing Disulap River is characterized by alternating rapids and deep pools running between steep limestone cliffs (Figure 7). Our fourth site, Dinang, is in reference to Dinang Creek, a small tributary of the Ilaguen River in sitio Lumalog, Barangay Cadsalan. Although water levels fluctuate according to season, Dinang Creek has an average depth of approximately 0.56 m (van Weerd and van der Ploeg, 2005). Before draining into the Ilgauen River, Dinang Creek stretches for 11 km surrounded by farmlands and over 50 households from sitio Lumalog (Figure 8) (van de Ven, et al., 2009). Only the banks of the creek remain partially forested where a small buffer zone (1–5 m) of disturbed forest and bamboo groves remain. Our fifth site in San Mariano, Barangay Baliao, is located 7 km from Dinang Creek. Baliao is characterized by a network of small canals running between rolling hills completely dominated by agriculture (Figure 9). Land use around both Dinang and Baliao is defined by small agricultural plots with

irrigated rice fields in the valleys, banana plantations on steep slopes, and upland rice and yellow corn covering the hill tops (van Weerd and van der Ploeg, 2012). Finally, although our studies largely took place within San Mariano, we also briefly (July 2–8, 2018) surveyed a fifth site, Dicitian Lake, located outside of San Mariano. Dicitian Lake resides in the Municipality of Divilacan, situated along the eastern range of the Sierra Madre Mountains on the Pacific Coast of Luzon (Figure 10). Located within NSMNP, Dicitian is a 140,000 m² artificial lake (average water depth = 2.55 m) where the surrounding habitat is characterized by lowland dipterocarp forest (van Weerd and van der Ploeg, 2012).

2.2. *Data collection*

We visited all sites within San Mariano starting at the end of the 2018 northeast monsoon season (21 February 2018), continuing through the dry season, and concluding at the end of the southwest monsoon season (16 October 2018). Dicitian Lake was surveyed only at the beginning of the 2018 southwest monsoon season (3–8 July). Locations for crocodiles were determined by nighttime spotlight surveys, daytime snorkel surveys, and interviews with local farmers and fishermen to determine presence/absence of crocodiles in various aquatic habitats. We detected crocodiles at night using LED headlamps and hand-held flashlights via standardized spotlight survey methods developed by the Mabuwaya Foundation (van de Ven et al., 2009). Once crocodile presence was confirmed at a study site, individuals were primarily captured by nighttime baited trip-snare traps (Woodward and David, 1994), daytime snorkel surveys, or by hand captures if small juvenile crocodiles were encountered. Snare traps baited with chicken were set in the late afternoon or early evening, left overnight during the active foraging time for crocodiles, and checked at first daylight the following day (Woodward and David, 1994).

Daytime snorkel surveys typically involved two people snorkeling down river using waterproof LED lights to inspect underwater caves, crevices, and burrows for resting crocodiles. When crocodiles were discovered during snorkel surveys, they were immediately captured using 4–6 m of rope, a 1 m cable noose, and pilstrom tongs.

We measured all captured crocodiles for total length (TL), snout–vent length (SVL), tail girth (TG), neck girth (NG), head length (HL), tail length (Tail), mass, and sex following the standardized practices of Zweig et al. (2004). We determined if each crocodile was a newly caught wild individual, a wild recapture, or a headstart recapture via the unique caudal scute notching method used by the Mabuwaya Foundation since 2005. We permanently marked all newly captured wild crocodiles following this same method and, beginning in 2018, implanted all captured crocodiles with passive integrated transponder (PIT) tags subcutaneously on the mid-dorsal neck under the nuchal rosette. Following data collection, we released all crocodiles at the capture site within 12 h of capture. Both female and male Philippine crocodiles reach sexual maturity at approximately 1.5–2.1 m TL (Ross and Alcala, 1983; van Weerd and van der Ploeg, 2012). Crocodiles were classified as juveniles if they were less than 1.5 m TL, and adults if they were greater than 1.5 m TL.

2.3. *Diet analysis*

Stomach contents were extracted from crocodiles using the hose-Heimlich technique (Fitzgerald, 1989) as modified by Shirley et al. (2016). Flushing was repeated until only water was expelled from the stomach. Stomach flushing is a non-destructive and highly effective technique proven to recover >95% of prey, including most non-prey items, from crocodilian stomachs (Fitzgerald, 1989; Rice et al., 2005). Stomach contents were sorted, counted, digitally

photographed, and identified to the lowest taxonomic classification possible. We assigned each prey item to one of eight main prey categories (fish, birds, shrimp, snails, insects, mammals, reptiles, or amphibians), and non-prey items to three additional categories (gastroliths, vegetation, other). Non-prey items in the “other” category were not included in subsequent analyses.

Differential digestion of prey types is a common source of bias in crocodylian diet studies (Jackson et al., 1974; Garnett, 1985; Magnusson et al., 1987; Platt et al., 2013). For example, bone, flesh, and freshwater crustaceans are digested relatively quickly, whereas chitinous remains are more persistent (e.g., snail opercula, fish scales, hair, feathers, exoskeletons of invertebrates). To reduce this bias, we analyzed variation in diet within prey categories when making comparisons between wild and head-start crocodiles, and between juvenile and adult crocodiles, under the assumption that remains of different prey within any one prey category persisted in the stomach for similar periods of time (Magnusson et al., 1987; Thorbjarnarson, 1993; Tucket et al., 1996; Platt et al., 2013).

All statistical analyses were performed using R, and Shapiro-Wilk and Levene’s analyses were used to test for normality and homoscedasticity of the data (R Core Team, 2012). To address concerns of captive-release programs and assess the dietary habits of headstart and wild crocodiles, we estimated the percent occurrence of each prey category for headstart and wild crocodiles. Additionally, to obtain key natural history information for *C. mindorensis*, we combined our headstart and wild groups and estimated percent occurrence of each prey category for juvenile and adult crocodiles, and among all crocodiles. We define percent occurrence as the number of samples in which prey items occurred divided by the sample size per group (Rosenberg and Cooper, 1990; Platt et al., 2013). Following a study on food habits of *Alligator mississippiensis* by Saalfeld et al. (2011), we used a chi-square analysis to examine differences

of percent occurrence in prey presence/absence between headstart and wild crocodiles, and between juvenile and adult crocodiles. We then used a Wilcoxon rank sum test to analyze dietary differences in percent composition (the proportion [%] a single prey category comprised of the total number of prey categories within a diet sample) between headstart and wild crocodiles, and between juvenile and adult crocodiles.

Finally, we used the Shannon-Weiner diversity index (H') to estimate dietary niche breadth and the degree of dietary specialization (Schoener, 1968; Platt et al., 2013). As recommended by Platt et al. (2013), we standardized the index (H') on a scale of 0 to 1 using the evenness measure (J') estimated as: $J' = H'(\log n)^{-1}$, where n = number of prey categories (Krebs, 1989). A lower value of J' indicates more specialized feeding habits and therefore lower prey diversity (Schoener, 1968; Krebs, 1989; Platt et al., 2013). We used a Wilcoxon rank sum test to analyze differences in dietary diversity between headstart and wild crocodiles, and between juvenile and adult crocodiles.

2.4. *Body condition analysis*

Body condition factors are defined by a mass and length relationship and were developed as an index of relative fatness, health, or well-being (LeCren, 1951; Cone, 1989). Although condition indices were applied originally in fisheries research (LeCren, 1951; Cone, 1989), studies of crocodylian body condition often apply two particular indices: (1) Fulton's condition factor (K) (Rice et al., 2007; Fujisaki et al., 2009; Mazzotti et al., 2009; Mazzotti et al., 2012; Shirley et al., 2016); and (2) relative condition factor (K_n) (Brandt, 1991; Dalrymple, 1996; Barr, 1997; Leslie, 1997, Zweig, 2003). We calculated both condition indices for our study.

2.4.1. *Fulton's condition factor (K)*

Fulton's condition factor K (LeCren, 1951) is recommended by Zweig (2003) as the most appropriate body condition index when comparing groups of crocodylians. However, Fulton's K is quite limited in use due to the strict assumption of isometric growth (LeCren, 1951). Fulton's K can be written as:

$$K = \frac{W}{L^b} \times 10^n$$

where W = mass measurement, L = length measurement, n = a scaling factor that brings mean $K > 1$ (Cone, 1989), and b , which expresses the growth relationship between the two body dimensions, is equal to 3.0 for the cubic relationship of isometric growth in Fulton's K (Cone, 1989; Green, 2001).

To determine whether Fulton's K could be used for this study, we assessed the two strict assumptions that our focal species shows isometric growth ($b = 3.0$), and that its condition index (K) is independent of body length (L). We follow Zweig (2003) and Zweig et al. (2014) in calculating Fulton's K using $b = 3.0$, and two different length (SVL and HL) and mass (Mass and TG) measurements from our study, in which tail girth (TG) is considered a proxy for mass in crocodylians (Hurlburt, 1999). Thus, giving us a total of four different K values for each particular mass-length combination (Mass -SVL; Mass -HL; TG-SVL; and TG-HL). Total length was eliminated as an option for a length measurement to avoid measurement errors due to missing tail tips (Fujisaki et al., 2009). We assessed the assumption that body length (SVL or HL) is independent of K by running Pearson's correlations on the four K :length ratios. Mass-length combinations with correlations greater than 30% suggest a lack of independence (Zweig, 2003). We found that all four combinations (Mass -SVL [$r = 0.554$]; Mass -HL [$r = 0.765$]; TG-

SVL [$r = -0.859$]; TG-HL [$r = -0.877$] showed significant correlation ($> 30\%$) between condition (K) and their respective body length, indicating the length and mass measurements may not grow isometrically and thus would not permit a valid use of Fulton's K . These growth relationships were further invalidated since the regression slope (b) of each mass-length combination (i.e., Mass -SVL [$b = 3.286$]; Mass -HL [$b = 3.458$]; TG-SVL [$b = 1.146$]; TG-HL [$b = 1.206$]; see below for method of derivation) deviates significantly ($p < 0.05$) from the Fulton's K slope for isometric growth ($b = 3.0$). However, when the slope (b) value is close to three, the calculations for Fulton's K and relative condition factor are nearly equal (Mazzotti et al., 2012).

2.4.2. Relative condition factor (K_n)

Values of relative condition factor were obtained for all individuals as described by LeCren (1951). As the regression slope (b) of our Mass-SVL relationship ($b = 3.286$) is close to three, these mass-length measurements were used to calculate K_n and evaluate body condition of *C. mindorensis* in our study. Instead of assuming isometric growth, the mass-length relationship (b) of relative K_n is determined by empirical data and linear regression analysis (LeCren, 1951; Özer et al., 2016). The average K_n across all lengths and species is 1.0 (Anderson and Neumann, 1996), and thus K_n is constant across lengths. First, our Mass-SVL relationship was modelled by means of the power equation (Froese, 2006):

$$W = aL^b$$

where W = mass of crocodiles (in grams), L = SVL of crocodiles (in centimeters), and a and b are parameters estimated from sample data. The logarithmic form of this model was used to convert this relationship to the linear form so that the estimation of parameters a and b can be calculated by regression modelling with $\log(a)$ = intercept, b = slope terms (Özer et al., 2016). The predicted body mass for a given length ($W_e = aL^b$; LeCren, 1951) was calculated using the

estimated mass-length relationship curve, and then, relative condition factor was calculated, which corresponds to the ratio between the observed mass (W) and the predicted mass (W_e) as below (LeCren, 1951):

$$K_n = \frac{W}{W_e}$$

Values of estimated K_n were calculated for all individuals and Student t-test was used to examine how body condition (K_n) varied between wild and headstart crocodiles. In addition, mean values of estimated K_n were calculated for each group to compare these mean values with the standard value $K_n = 1$ by Student t-tests.

3. Results

3.1. Data collection

We collected stomach contents from 30 Philippine crocodiles (22 females, eight males) ranging in size from 71.0–264.5 cm TL (SVL = 14.1–143.0 cm, 1.01–106.4 kg) in Isabela Province of northern Luzon, of which most were collected in the Municipality of San Mariano ($N = 28$) and the remaining two individuals from the Municipality of Divilacan. Crocodiles were captured from February–October in 2018, with a majority taken in the months of February ($N = 10$), March ($N = 10$), and April ($N = 5$). We used baited trip-snare traps ($N = 22$), hand-catches ($N = 4$), and snorkel surveys ($N = 3$) (Figure 11). One additional individual was captured by a local farmer. Of the 30 *C. mindorensis* sampled, 20 were wild crocodiles (13 females, seven males) consisting of 14 adults and six juveniles ranging in length from 71.0–264.5 cm TL (SVL: 35.0–143.0 cm; $\bar{X} = 68.2 \pm 5.65$ cm); and 10 were headstart individuals (nine females, one male)

released into the wild over the last 10 years (mean time in the wild = 5.65 years). These included six juveniles and four adults ranging from 72.3–169.9 cm TL (SVL: 36.6–90.4 cm; $\bar{X} = 82.9 \pm 5.74$ cm). Comparatively, both groups were of similar length (SVL: $t = -1.62$, $p = 0.116$).

3.2. *Diet analysis*

Comparisons of stomach contents and dietary differences between headstart and wild crocodiles revealed no significant differences in the percent occurrence or percent composition of any of the eight prey categories and non-prey categories (Table 1 & Table 2). An analysis of dietary diversity (H') also revealed no significant difference between headstart and wild crocodiles ($p = 0.228$), in which both groups exhibited nearly the same degree of specialization (J') (Table 3). For percent occurrence, snails were the most prominent group of prey recovered for both headstart and wild crocodiles, occurring in 70.0% of stomach samples for both headstart and wild crocodiles (Table 2). Although not significantly greater, birds, reptiles, and mammals occurred more frequently in the stomachs of headstart than wild crocodiles (Table 1). In contrast, wild crocodile stomachs showed a slightly higher percent occurrence of fish, insects, and amphibians than headstart crocodiles, although a significant difference was not observed (Table 1). Despite an infrequent occurrence, crabs were observed in 20% of the stomach contents of both groups (Table 1). For non-prey items, gastroliths were recovered in almost equal proportions for both groups; however, vegetation was observed in the stomachs of nine wild crocodiles (45.0%) compared to one headstart individual only (10%) (Table 1).

Analysis of diet with combined headstart and wild crocodiles, showed no significant differences between juvenile and adult crocodiles for both percent occurrence and percent composition in any prey category (Table 4 & Table 5). Similar to our results above, snails were

the most prominent prey group for both juvenile (66.7%) and adult (72.2%) Philippine crocodiles. Insects were the second most common prey group for juvenile crocodiles (41.7%), whereas reptiles were the second most common prey group for adults (44.4%). For both juvenile and adult crocodiles, fish were the next most frequently observed prey group, occurring in 33.3% of juveniles and 38.9% of adults, in which adult crocodiles also consumed birds in exactly the same proportions (38.9%). The remaining prey groups for juvenile crocodiles, including crabs, birds, amphibians, and mammals occurred less frequently; however, all were observed equally in 25% of stomach samples (Table 4). The remaining prey groups for adult crocodiles, including mammals, insects, crabs, and amphibians, revealed an infrequent occurrence and were observed in less than 23% of stomach contents (Table 4).

For percent occurrence of all 30 crocodiles included in our study, snails were the most frequently consumed prey and were recovered from 70.0% of sampled individuals (Table 6). Only two snail species were observed: *Pomacea canaliculata*, an invasive species found commonly in irrigated rice farms (Naylor, 1996), and *Melanooides turricula*, a native species distributed widely throughout various aquatic habitats (Galan et al., 2015). *P. canaliculate* and *M. turricula* were recovered from 50% and 60% of all crocodile stomach contents, respectively. Snail remains typically consisted of bare opercula or opercula with flesh still attached, with whole snails observed in fewer samples. Overall, fish were the second most common prey group and the most frequently encountered vertebrate prey group (36.7%). Although fish remains often consisted of macerated scales and bone fragments, the recovery of intact skulls allowed us to identify two different species (Table 7). Birds and reptiles were both equally as common and were recovered from the stomachs of 10 crocodiles (33.3%). Reptiles were represented by at least five different species, recovered as freshly ingested intact snake and a lizard bodies, in addition to degraded chitinous remains of turtle scutes, lizard claws, and snake scales (Table 7).

For birds, no intact bodies were recovered, and all remains consisted entirely of bird feathers; however, we were still able to identify three species with confidence (Table 7). The remaining prey groups, including crabs, mammals, amphibians, and insects, were all represented in lower proportions of stomach contents (16–27%). All of these more infrequent prey observations were present as chitinous remnants of individual prey items, such as intact crab appendages, mammal hair, frog skulls, and insect exoskeletons typically from scarab beetles of the genus *Xylotrupes* (Table 7) In total, all 30 crocodiles contained at least one prey group with no empty stomachs observed.

Non-prey items, including gastroliths (small stones) and vegetation, were recovered in equal proportions between juvenile and adult crocodiles (Table 4). For non-prey items in the “other” category, these items consisted of two plastic bags recovered from the stomachs of two adult crocodiles, and a bullet/pellet recovered from the stomach contents of a third crocodile.

3.3. *Body condition*

Although we examined the stomach contents of 30 *C. mindorensis* for the analysis of diet, three individuals were excluded from the analysis of body condition, in which one was an outlier, and the two individuals collected from Divilacan were excluded to avoid any bias in relative K_n comparisons as Divilacan is considered a separate population from the San Mariano population. In total, we evaluated 27 crocodiles from San Mariano in northern Luzon, 17 were wild crocodiles with SVL 35.0–143.0 cm and mass 1.01–106.4 kg (12 adults, five juveniles; 12 females, five males), and 10 were headstart crocodiles with SVL 36.6–90.4 cm and mass 0.94–17.75 kg (four adults, six juveniles; nine females, one male). Regression analysis produced the logarithmic equivalent of the mass-length relationship of data with estimates $a = -2.088$ and

$b = 3.283$ indicating the overall regression equation of mass–length curve as $W = 0.008L^{3.283}$ with $R^2 = 0.9856$ and 95% CI of $a = (0.006; 0.011)$ and $b = (3.127, 3.438)$. This relationship allowed us to calculate the predicted body weight (W_e) and then the relative condition factor (K_n) as defined previously.

Body condition (K_n) was significantly higher in wild crocodiles than headstart crocodiles ($t = -2.88; p = 0.008$; (Figure 12). However, mean condition of the headstart group (mean $K_n = 0.93$) did not reveal any departure from the standard condition value of $K_n = 1.0$ ($t = -1.71, p = 0.121$; Table 8). In contrast, mean condition of the wild group (mean $K_n = 1.06$) was slightly higher than the standard condition value ($t = 2.38, p = 0.030$; Table 8). Overall, the values of K_n for wild crocodiles ranged from 0.86–1.26, whereas the headstart range was between 0.72–1.20.

4. Discussion

This study presents results from our three key objectives. First, we compared the stomach contents of headstart and wild Philippine crocodiles and found no evidence for dietary differences in percent occurrence, percent composition, and prey diversity. Our results indicate that captive-released crocodiles adjust well post-release and exhibit sufficient foraging behaviors compared to wild conspecifics. Second, our study of diet is the first analysis of stomach contents for *C. mindorensis*, from which we demonstrate the utilization of a wide diversity of 17 different aquatic and terrestrial invertebrate and vertebrate prey species across eight major prey categories (snails, fish, birds, reptiles, amphibians, mammals, crabs, and insects). Overall, 70% of Philippine crocodiles in our study showed snails as the prominent prey type, followed by fish (36.7%), birds (33.3%), reptiles (33.3%), insects (26.7%). A notable 50.0% of all crocodiles

consumed *Pomacea canaliculata* (the golden apple snail or golden kuhol)—an invasive species and the leading agricultural pest in the Philippines known to cost USD 28–45 million in losses for Filipino rice farmers in a single year (Naylor, 1996). Finally, our calculation of the first body condition index (K_n) for *C. mindorensis* indicates that wild crocodiles have higher condition scores than headstart individuals (Figure 12). However, the mean condition score of wild crocodiles was significantly higher than the average condition value ($K_n = 1.0$), whereas headstart crocodiles did not deviate from this average condition. As we discuss in greater detail below, our analysis of these three objectives provides valuable information for baseline ecological data, conservation management, and implications for the challenges that lie ahead in the Philippine archipelago.

4.1. Diet analysis of headstart and wild crocodiles

To our knowledge, Elsey (1992) is the only existing study which has assessed dietary habits between captive-released and wild crocodylians. But similar to our results, Elsey (1992) reported that farm-released *Alligator mississippiensis* (after being raised in captivity for the first two years of their life and then released into the wild) had similar diet and foraging habits compared to their wild counterparts. In contrast, Elsey (1992) noted that wild *A. mississippiensis* consumed two prey categories (fish and snails; $p < 0.05$) more frequently than captive-released *A. mississippiensis*; whereas our study demonstrates that all eight prey categories were consumed similarly between wild *C. mindorensis* and headstart individuals (Table 1). Although it is important to note that our analysis was limited by a small sample size, presumably our results reflect both the availability of prey within *C. mindorensis* habitat, and the ability of headstart crocodiles to adjust post-release and forage efficiently in the wild.

Out of all eight major prey categories (snails, crabs, birds, fish, reptiles, amphibians, mammals, and insects) in our study, snails were the most prominent prey type for both headstart and wild crocodiles, consumed by precisely 70.0% of the individuals in both groups. In contrast, Elsey (1992) noted that snails were a minor component of *A. mississippiensis* diet, but wild alligators still consumed significantly more snails than captive-released individuals. In general, crocodylians are referred to as opportunistic predators, however, depending on the habitat, season, and availability of prey, they exhibit highly specialized foraging behaviors that allow them to exploit local prey inhabiting a variety of aquatic and terrestrial habitats (Magnusson et al., 1987). For example, as crocodylians increase in size they tend to shift diets from invertebrates (insects and crustaceans) to a more vertebrate (fish, mammals, birds, and reptiles) dominated diet (Thorbjarnarson, 1988). However, Balaguera-Reina et al. (2018) demonstrated that crustaceans and insects remain the most important prey for all age classes of *Crocodylus acutus* in Coiba Island, Panama, and suggested this prey preference is a result of the high abundance, diversity, and net energetic value of invertebrates in the surrounding coastal habitat. For our study, both headstart and wild crocodiles frequently consumed two aquatic snail species, *Pomacea canaliculata* (the golden apple snail or golden kuhol) and *Melanooides turricula* (fawn melania). Both of these snail species were observed in high abundance throughout our study sites, with *P. canaliculata* often occurring in agricultural wetlands and showing a preference for rice paddies (Naylor, 1996), and *M. turricula* distributed in a variety of disturbed wetlands and fast-flowing larger rivers (Galan et al., 2015).

Although the significance of snails in *C. mindorensis* diet is discussed in greater detail below, the high prevalence of snails in headstart crocodiles reflects fascinating insight on their behavioral competency to forage on pertinent prey resource which may be abundant in surrounding habitats. For example, Platt et al., (2006) observed *Crocodylus moreletti* in Belize

hunting snails underwater by crawling along the bottom and making frequent lateral head sweeps (a common foraging behavior for crocodylians), in which contact with a snail resulted in a snapping behavior for capture. Because crocodylians are known to have poor vision when submerged underwater (Fleishman et al., 1988; Platt and Brantley, 1991), it is believed that visual cues have minimal influence on underwater prey capture, but instead they rely on tactile and chemical cues to locate and capture prey (Platt et al., 2006). This theory on tactile cues was later confirmed by Letch and Cantania (2012), who demonstrated that highly specialized organs (integumentary sensory organs [ISOs]; Brazaitis, 1987) occurring on scales of the head, body, and limbs of all Crocodylidae (plus *Tomistoma* and *Gavialis*), while only on the head scales of Alligatoridae (Grigg and Kirshner, 2015), serve a mechanosensory function in relation to the detection, discrimination, and manipulation of certain prey. Taking into consideration that snails were clearly a dominant prey resource for both wild and headstart crocodiles, these results likely indicate the behavioral competency of headstart crocodiles to forage on an abundant aquatic prey type when vertebrate prey are presumably less available.

Similar to our results, Elsey (1992) reported that birds and mammals occurred more frequently in the stomach contents of captive-released individuals than wild individuals, although a significant difference was not observed (Table 1). Bird species recovered from headstart *C. mindorensis* include *Amauromis olivacea* (Philippine bush-hen) and *Gallinula chloropus* (common moorhen) of the Family *Rallidae*. Both *Rallidae* species we recovered from stomach contents can be observed often feeding along the waters-edge and emerging vegetation of Dunoy Lake, which overlaps habitat for all age classes of *C. mindorensis*. Notably, crocodylians are characterized as skilled predators (Grigg and Kirshner, 2015), often making calculated lunges and propelling themselves out of the water to capture birds flying above the water surface (Atwell, 1954; Platt et al., 2006), or, deliberately seeking out rookeries and nocturnal roosts to

prey upon nesting wading birds (McIlhenny, 1935; Hopkins, 1968; Nell et al., 2016). The results of our study indicate birds were a prominent prey resource for headstart *C. mindorensis*, which likely reflects their adept foraging behaviors similarly known from other wild crocodylians.

In contrast to Elsey (1992), and others (Thorbjarnarson, 1993; Platt et al., 2006; Wallace and Leslie, 2008; Balaguera-Reina et al., 2018), reptiles were a prominent prey resource for *C. mindorensis*, and even for headstart crocodiles (Table 1). For our study, reptiles (along with birds) were the second most common prey category and the most frequently encountered vertebrate prey of headstart crocodiles (Table 1). Reptile remains recovered from headstart crocodiles included digested chitinous remains of turtle scutes (*Cuora amboinensis*) and snake scales (likely from *Pytas luzonensis*), in addition to freshly ingested, intact snakes (*Coelognathus erythrurus manillensis*). *C. amboinensis* has been observed along rivers inhabited by *C. mindorensis* (personal observation), and in irrigation canals in flooded rice fields near disturbed secondary growth forest (Brown et al., 2013). However, *C. erythrurus manillensis* is a widely dispersed terrestrial snake species, where Brown et al., (2013) reported a late morning encounter with *C. erythrurus manillensis* as it was foraging on the ground in dry forest. Although it is definitely possible these snakes were captured by crocodiles near a local stream or lake, their common occurrence in dry forest possibly reflects the terrestrial foraging behaviors of *C. mindorensis* which should be investigated in future studies. Nevertheless, because the Philippines is distinctly recognized for its high abundance and diversity of reptile taxa (Brown et al., 2013), the recovery of these prey in headstart samples suggests a skillful foraging behavior and further supports their ability to exploit a local prey resource.

Fish and insects were the two prey categories in which wild *C. mindorensis* consumed a slightly greater (not significant) proportion than headstart crocodiles (Table 1). In contrast, Elsey (1992) reported that captive-released *A. mississippiensis* consumed more insects than wild

individuals, whereas fish were more frequently consumed by wild *A. mississippiensis*. For fish, analysis of stomach contents should be approached with caution since they are likely underrepresented due to rapid digestion in the stomach of crocodylians (Delany and Abercrombie, 1986). Most fish contents recovered from headstart *C. mindorensis* were unidentifiable remains of scales and macerated pieces of bone, but the recovery of one skull allowed us to confidently identify it as *Channa striata*, a bottom-dwelling eel-like fish commonly inhabiting flooded marshlands of rice paddies. Interestingly, Platt et al. (2006) noted that crocodiles likely depend on tactile cues to forage for bottom-dwelling fish in a similar manner (described above) they capture snails. Additionally, similar to our results for *Pomacea* snails, both the abundance of *C. striata* among rice paddies and their consumption by headstart *C. mindorensis* yields interesting insight on the behavioral competencies of headstart crocodiles and their ability to adjust to an agriculturally dominated landscape and exploit a local prey resource.

Crabs and amphibians both occurred infrequently, yet in similar proportions for both headstart and wild *C. mindorensis*. These results are as expected given that consumption of anurans by crocodylians is rare (Platt et al., 2006), and that crabs seem to be in low abundance throughout most of the *C. mindorensis* habitat we observed. Still, it is important to note that our study was limited by a small sample size, potentially underrepresenting these two groups.

For non-prey groups, vegetation was recovered from nine wild *C. mindorensis* and only one headstart individual. Vegetation is commonly recovered among crocodylian stomach contents and is likely ingested incidental to prey capture (Coulson and Hernandez, 1983). Interestingly, gastroliths (small stones) were recovered frequently from both headstart and wild *C. mindorensis* (Table 2). As discussed in greater detail below, small stones are deliberately consumed by crocodylians to facilitate the breakdown of prey (Platt et al., 2006), however, their presence in

the stomach contents of headstart crocodiles presumably reflects their ability to retain these natural behaviors even after being reared in captivity.

Studies of diet are essential to understanding a species' ecology (Rosenberg and Cooper, 1990), and as such for translocations, dietary studies of captive-released populations can yield valuable measures when assessing their ability to adjust and become established in the wild. By examining stomach contents and the utilization of a broad diversity of 17 different aquatic and terrestrial invertebrate and vertebrate prey species, our study provides evidence that headstart Philippine crocodiles exhibit no dietary differences when compared to their wild counterparts (Table 1). A captive-rearing effect related to incompetent foraging behaviors of released individuals remains a major concern for captive-release programs (Alberts, 2007), however, our study suggests that headstart crocodiles are able to forage and utilize a similar diversity of prey compared to wild conspecifics. Because of our focused monitoring methods, we were able to analyze the diet of wild crocodiles, gaining key natural history information on *C. mindorensis* dietary habits (see below), while employing these data as robust baseline comparisons against the behavioral performance of headstart crocodiles.

4.2 Diet analysis of *Crocodylus mindorensis*

Our study is the first to examine stomach contents of *C. mindorensis* from anywhere in its range, confirming that both juvenile and adult crocodiles consume a broad spectrum of prey inhabiting all types of habitat and consumption classifications (i.e., primary, secondary, and tertiary consumers) (Table 7). Most crocodylians are characterized as opportunistic predators that exhibit ontogenetic shifts in diet, in which smaller age classes rely on insects, aquatic invertebrates, and small fish, and such prey types decrease in importance as crocodylians

increase in size therefore utilizing larger vertebrate prey (fish, turtles, birds, and mammals; Thorbjarnarson, 1988; Ross, 1998; Wallace and Leslie, 2008). However, this characterization as “opportunistic” and these observed ontogenetic dietary trends are just broad generalizations. Crocodylians are known to have highly specialized foraging behaviors (Magnusson et al. 1987), and the dietary differences of different size classes are driven often by the habitat, and the diversity, abundance, and availability of prey (Delany and Abercrombie, 1986).

Prior to our stomach content analysis, the only existing natural history data on *C. mindorensis* diet was from anecdotal, direct observations of prey consumption (van Weerd and van der Ploeg, 2012). Van Weerd and van der Ploeg (2012) notably demonstrated that *C. mindorensis* utilize a variety of prey types, in which hatchling and small juveniles consume dragonflies, small fish, shrimp, and snails, with larger juveniles consuming shrimp, fish, frogs, small reptiles, and rodents, and then adult crocodiles taking larger vertebrates, including fish, civet cats, snakes, birds, and domestic pigs and dogs. Still, the diet of *C. mindorensis* was presumed to follow the generalized ontogenetic dietary trend encountered by many other crocodylians (Lang, 1987; Thorbjarnarson, 1988), with the diet of adult crocodiles primarily relying on larger vertebrates.

Although our study supports the general observations of diverse prey groups from van Weerd and van der Ploeg (2012); in contrast, our results indicate that both juvenile and adult Philippine crocodiles utilize a similar diversity of prey, from which small aquatic invertebrates, specifically snails, continue to play a more prominent role in the diet of adult Philippine crocodiles (Table 4). Out of all eight major prey categories in our study, snails were the most frequently encountered prey type for all *C. mindorensis* (70.0%) (Table 1). Similar to our results, dietary studies (Fogarty and Albury, 1968; Diefenbach, 1979; Thorbjarnarson, 1993; Platt et al., 2006) of other crocodylian species inhabiting tropical freshwater wetlands have indicated that snails are an

important prey resource for all size classes. For example, Platt et al. (2006) showed that *Crocodylus moreletti* in northern Belize progressively consume larger prey sizes as they grow from hatchlings to adults, but in particular, snail consumption increased with an increase in crocodile body size, where overall, snails were the most frequently consumed prey type by large adults. In contrast, previous studies found invertebrates to be important prey for smaller age classes but largely replaced by vertebrates in the diet of larger crocodiles (Saalfeld et al., 2011). However, optimal foraging theory (Stephens and Krebs, 1986) predicts individuals to select prey items that guarantee the highest energy intake per time unit (Coasta et al., 2015; Balaguera-Reina et al., 2018). But, when such beneficial prey categories are limited, an expansion of the trophic niche is expected and other prey categories can be exploited (Stephens and Krebs, 1986; Costa et al., 2015; Balaguera-Reina et al., 2018). Thus, our results presumably reflect the overall availability of both vertebrate taxa and snails in freshwater habitats around the Philippines, with further suggestions that larger crocodiles continue to supplement their diet with snails when more beneficial prey types are scarce.

Only two snail species were recovered from *C. mindorensis* stomachs in our study, *Pomacea canaliculata* (the golden apple snail or golden kuhol) and *Melanooides turricula* (fawn melania). *M. turricula* is an abundant native species in freshwater wetlands around the Philippines (Galan et al., 2015), while *P. canaliculata* is an invasive species also abundantly dispersed in wetlands. *P. canaliculata* specifically targets agricultural networks, invading rice-growing regions where it feeds on young rice seedlings (Naylor, 1996). Despite a wide infestation by *P. canaliculata* throughout Asian agricultural regions, no country has suffered greater economic damage (yield loss and costs of control) than the Philippines, where *P. canaliculate* ranks as one of the leading agricultural pest problems (Naylor, 1996). In our study, *P. canaliculate* was recovered from 50% of all *C. mindorensis*, in which the number of snails per crocodile ranged from 1– 85 (mean =

18.60). Although other studies have documented the consumption of *Pomacea* snails in crocodylians (Fogarty and Albury, 1968; Thorbjarnarson, 1993; Barr, 1994; Silveira and Magnusson, 1999; Platt et al., 2002), we provide the first report on the occurrence and importance of this prey item in Philippine crocodiles with our study. As noted above, many crocodylians exhibit ontogenetic shifts in diet, however, adult crocodylians may also supplement their diet with snails depending on habitat and prey availability (Magnusson et al., 1987). When considering the abundant infestation of *Pomacea* throughout Philippine rice farms, and that most (93.3%) of the crocodiles in our study were captured within or near adjacent rice paddies (Figure 13), our results indicate that Philippine crocodiles may be exploiting an abundant prey resource when more beneficial prey types are limited.

Reptiles were a prominent prey type for adult *C. mindorensis* in our study, occurring as the second most recovered prey category and the most frequently encountered vertebrate taxa (Table 6). Van Weerd and van der Ploeg (2012) also reported reptiles as a prey source for *C. mindorensis*, but because these data were based on general observations, they could not determine their overall dietary importance. Our study agrees with others (Delany and Abercrombie, 1986; Barr, 1997; Delany et al., 1999) that have found reptiles as an important prey item for larger size classes of crocodylians. However, the occurrence of reptiles consumed by adult crocodylians can vary widely depending on habitat, season, and prey availability (Rice, 2004). For example, Thorbjarnarson (1993) reported that fish, mammals, snails (*Pomacea*), and crabs were the predominant prey items depending on body size and wet/dry season during a study of *Caiman crocodilus* in Venezuela. While vertebrate prey consumption increased as caiman body size increased, reptiles were still infrequently used as a main prey item by caiman throughout the study (Thorbjarnarson, 1993).

The frequent occurrence of reptiles in our study is not surprising since the Philippines is notably recognized as a biodiversity hotspot which is home to wide variety of nearly 300 reptile species (Brown et al., 2013). Furthermore, frequent typhoons, flash flooding, and seasonal fluctuations strongly influence water levels in the Philippines. Although limited studies exist on *C. mindorensis* movements (van de Ven., et al., 2009), van Weerd et al., (2006) noted that hatchling and juveniles typically reside in small ponds, lakes, and marshes year around, whereas adult crocodiles were observed to make frequent movements up larger rivers in the dry season when water levels are low, and then retreating to ponds and lakes during the wet season when water levels rise dramatically. A majority of the data collection for our study occurred at the end of the wet season and the beginning of the dry season, and since reptiles were still recovered more frequently than fish for adult *C. mindorensis*, these data may indicate that reptiles are a reliable prey resource when fish are more dispersed in the higher water levels.

The previous study by van Weerd and van der Ploeg (2012) reported that snakes were the only reptile taxa observed as prey items, however, our analysis of stomach contents revealed a variety of at least five different reptile taxa that occupy both terrestrial and semiaquatic habitats (Table 7). Although many of the stomach samples we examined consisted largely of chitinous remains for all prey categories, intact freshly ingested snakes were still sometimes recovered, possibly indicating a more frequent and regular prey resource. The remaining stomach samples containing reptiles were typically chitinous remnants of snake scales, turtle scutes, and *Varanus* claws. With an abundance of reptile diversity active throughout the year in the Philippines, presumably our results in part reflect both the availability of reptiles and the adept foraging behaviors of *C. mindorensis* in northern Luzon.

Similar to observations reported by van Weerd and van der Ploeg (2012), our results suggest that fish are an important prey for both juvenile and adult Philippine crocodiles. Still, fish were

likely under-represented in the diet due to the high digestive rates of most fish structures (Delany and Abercrombie, 1986). Previous diet studies of other crocodylian species highlight fish as prominent prey for both juvenile and adult age classes (Thorbjarnarson, 1988; Villegas and Schmitter-Soto, 2008; Wallace and Leslie, 2008). Furthermore, studies of crocodylian diet in relation to seasonal fluctuations have shown that fish are a more reliable prey resource during dry season drawdowns (Thorbjarnarson, 1993). Taking these previous studies into account, fish could presumably play a more prominent role in *C. mindorensis* diet during the dry season when water levels are much lower and fish populations are more concentrated. Fish remains mostly consisted of unidentifiable scales and macerated pieces of bone, but some intact bodies and skulls were recovered, including *Channa striata* (mud fish or snakehead). *C. striata* is a bottom-dwelling eel-like fish frequently found in the flooded rice paddies and marshlands that dominate the landscape of San Mariano. Since these flooded wetlands often serve as retreats for both hatchlings and juveniles, whereas adult crocodiles use them to move between the surrounding rivers and ponds, *C. striata* is likely an important prey for *C. mindorensis* in northern Luzon.

The results of our study and others (van Weerd and van der Ploeg, 2012) suggests that insects are an important prey for juvenile *C. mindorensis* and less so for adults; whereas in contrast, birds are a more reliable prey for adult crocodiles, and less important for juveniles (Table 5). For insects, these results are not surprising given that most dietary studies of crocodylians have found that aquatic and terrestrial insects are the primary prey type for smaller size class crocodylians (reviewed by Platt et al., 2006). With 440 native bird species (56% endemic; Brown et al., 2013), the Philippines is celebrated for its high bird diversity. However, due to widespread agriculture and local farmers commonly hunting native birds around most *C. mindorensis* breeding sites (Narra, Dinang, Balliao), the availability of birds as a prey resource is presumably much lower compared to the well-known breeding site of Lake Dunoy. Surrounded by both

agriculture and the nationally protected Northern Sierra Madre Natural Park (NSMNP), Lake Dunoy is a historical nesting site for *C. mindorensis* where we also observed an abundance of bird activity, particularly when they were feeding off the lake in the early morning and late evenings, an active foraging period for *C. mindorensis* (van Weerd and van der Ploeg, 2012). Since measures of percent occurrence can potentially minimize the importance of infrequently consumed larger prey that make a more beneficial energetic contribution to the diet (Rosenberg and Cooper, 1990), birds are likely a more prominent component of *C. mindorensis* diet than we observed for our study.

Other prey categories in our study, including crabs, mammals, and amphibians, occurred less frequently in the stomach contents of *C. mindorensis*. In contrast to our results, other studies (Thorbjarnarson, 1988; Villegas and Schmitter-Sotto, 2008) have found crustaceans to be an important prey for smaller size classes of crocodylians, whereas Platt et al. (2006) demonstrated that crustaceans were the most frequently recovered prey for adult *Crocodylus acutus* of coastal Belize. The occurrence of mammals in our samples consisted entirely of hair, likely from *Rattus tanezumi*, a rat species found in abundance around agricultural areas. Van Weerd and van der Ploeg (2012) reported *C. mindorensis* to consume *Paradoxurus hermaphroditus* (civet cat), however, we did not observe any identifiable remains of *P. hermaphroditus* in our samples. Even though the Philippines is known for an impressive diversity of 111 amphibian species (80% endemic; Brown et al., 2013), their infrequent occurrence is not surprising given that dietary studies of other crocodylians have determined that consumption of anurans is rare (Webb et al., 1982; Delany & Abercrombie 1986; Webb et al., 1991; Thorbjarnarson, 1993; Platt et al., 2006). Still, stomach content analyses regarding amphibians should be evaluated with caution given their rapid digestion in crocodylian stomachs, potentially resulting in an under-represented prey resource (Platt et al., 2006).

For non-prey items, both vegetation and stones (gastroliths) have been frequently recovered from the stomach contents of other crocodylian diet studies (Webb et al., 1991; Platt et al., 1990; Thorbjarnarson, 1993; Tucker et al., 1996; Shirley et al., 2016; Balaguera-Reina et al., 2018). In general, vegetation is assumed to be ingested incidental to prey capture (Coulson and Hernandez, 1983), whereas small stones are deliberately consumed by crocodylians and function as gastroliths to facilitate prey digestion (Davenport et al., 1990; Platt et al., 1990; Fitch-Snyder and Lance, 1993; Platt et al., 2013). Notably, gastroliths may be particularly important for smaller crocodylians that consume chitin-rich diets (Sokol, 1971; Davenport et al., 1990; Fitch-Snyder and Lance, 1993; Platt et al., 2013).

Overall, no empty stomachs were observed throughout our study, a similar result for most crocodylian dietary studies (Delany and Abercrombie, 1986; Webb et al., 1991; Platt et al., 2006). Although technically we observed no empty stomachs, it should be noted that the stomach contents of several crocodiles were based entirely on a few snail opercula, a chitinous prey structure which is resistant to digestion and commonly found to accumulate in crocodylian stomachs (Barr, 1997). Taking into consideration that many of the stomachs we examined for *C. mindorensis* were comprised entirely of chitinous remnants of various prey types, our results likely suggest that Philippine crocodiles feed at infrequent and lengthy intervals. This foraging strategy has been suggested to be common in crocodylians due to their low metabolic demands (Coulson and Hernandez, 1983) and high food conversion rates (Webb et al., 1991). Finally, it should be noted that even though percent occurrence has proven to be an efficient method to examine prey items in terms of relative abundance (Krebs, 1989; Fitzgerald et al., 1989; Platt et al., 2013; Balaguera-Reina et al., 2018), crocodylian digestion and gut retention times can potentially bias data due to an inflation of observed indigestible chitinous remains (e.g., snail opercula, crab carapaces, turtle scutes, fish scales, mammal hair, and feathers) compared to more

easily digested remains, such as bone and flesh (Jackson et al., 1974; Platt et al., 2013). Although it is possible the importance of snails in *C. mindorensis* diet is somewhat exaggerated, vertebrate remains are similarly resistant to digestion (Delany and Abercrombie, 1986; Janes and Gutzke, 2002) and would also be expected to accumulate and be over-represented if significant numbers of these taxa were being consumed (Platt et al., 2006). And because we analyzed dietary trends of our target groups (juvenile/adult, headstart/wild) within prey categories, any bias related to persistent prey remains is probably minimal (Magnusson et al., 1987; Thorbjarnarson, 1993; Platt et al., 2006). Finally, it is important to clarify that it was not our aim to demonstrate ontogenetic trends, but to obtain vital natural history information which has been lacking to date and is essential data for successful conservation management of *C. mindorensis*. Due to the critically endangered status and extremely low populations numbers of *C. mindorensis*, our analysis of diet was quite limited with a small sample size, and thus we chose the most appropriate groups as juveniles and sexually mature adults. However, given our limited sample size, the limited time scope of our study, the paucity of data on *C. mindorensis* movements, and the potential influence of seasonal fluctuations on prey availability in the Philippines, effective conservation management of *C. mindorensis* will be dependent on future studies of diet and movements for both headstart and wild crocodiles which span multi-year/seasonal durations.

Still, our study provides key natural history information suggesting that adult *C. mindorensis* continue to supplement their diet with aquatic invertebrates, exploiting an abundant prey resource which is also an invasive species and agricultural pest. Furthermore, these results also helped improve husbandry and captive-rearing protocols for the Mabuwaya headstart program. After learning that snails are a prominent prey type and given their high abundance throughout wetlands in northern Luzon, we were able to collect snails from the wild and effectively stock the captive-rearing ponds with snail populations at the Mabuwaya headstart facility. This

simultaneously provides (1) a live prey item which encourages natural foraging behaviors in captivity, and (2) an abundant, cost-effective food item for a conservation program that continuously faces challenges due to limited funding.

4.3 *Body condition*

The body condition (K_n) values we assessed for headstart and wild *C. mindorensis* provide conflicting results. We found that wild *C. mindorensis* had significantly higher body condition values compared to headstart individuals (Figure 12), in which these values suggest a state of well-being for these two groups. However, when comparing each group (headstart/wild) against the population average of $K_n = 1.0$, the mean body condition for wild crocodiles was significantly higher, whereas the headstart mean condition did not deviate from the average K_n value (Table 8). In regard to the significant difference in condition between these two groups, it is important to note that we did not observe any physical abnormalities or deficiencies for headstart crocodiles during our study. Although worrisome there is a difference in body condition between headstart and wild *C. mindorensis*, our results indicate that wild crocodiles have exceptionally high condition and headstart individuals are actually similar to what is expected given the overall population. As others have suggested, variation in body condition is influenced often by abiotic (location, water level, and temperature) and biotic (size, sex, and habitat) factors (Cone, 1989; Green, 2001; Rice, 2004; Mazzotti et al., 2012), however, the concerns expressed regarding captive-release programs introduces a complexity of additional factors that may impact an individual's condition.

To our knowledge, Elsey et al. (1992) is the only existing study to evaluate variation in body condition between captive-released and wild crocodylians. Contradictory to our results, Elsey et

al. (1992) reported that body condition factors were similar between wild *Alligator mississippiensis* and captive-released individuals in coastal Louisiana. However, there is a major difference between the captive-rearing conditions of *C. mindorensis* in our study and *A. mississippiensis* in Elsey et al. (1992) which should be taken into consideration. In the Philippines, wild *C. mindorensis* hatchlings are taken to a captive facility 15–20 km from their nest site, reared outdoors in semi-natural “soft-release” ponds where they are exposed to similar weather variables (e.g., temperature, precipitation, radiation, humidity) as their wild counterparts, and then offered a diet of chicken or fish approximately two times a week. Since *A. mississippiensis* is used for farming in the study by Elsey et al. (1992), eggs are collected from the wild, incubated and hatched in captivity (indoors), then are fed as much as possible and maintained at constant high temperatures to stimulate feeding and growth. As a result, Elsey et al. (1992) reports that farm-released individuals have greater mass and faster growth rates than wild *A. mississippiensis*, in addition to higher body condition for the first several months after release. These results raise some interesting questions, as captive-rearing strategies remain a topic of debate with some authors suggesting “soft-release” strategies help promote a greater range of coping strategies by exposing captive-reared individuals to natural conditions (Greenberg, 1976; Alberts, 2007), and others suggesting that optimal captive conditions, which enhance growth and body size upon release, could help buffer newly released animals from periods of environmental stress during the adjustment period (Pedrono and Sarovy, 2000; Knapp and Hudson, 2004). Nevertheless, Elsey et al. (1992) noted the high body condition of captive-released *A. mississippiensis* only took several months to lower and become similar with their wild counterparts. Taking this into consideration, along with the fact that headstart *C. mindorensis* in our study have been surviving in the wild for 1–10 years (mean = 5.65), their lower body condition is presumably the result of other factors affecting their current well-being.

As noted above, variation in body condition between headstart and wild crocodiles is likely influenced by a variety of abiotic and biotic factors. For instance, in northern Belize, Mazzotti et al. (2012) demonstrated that adult *Crocodylus moreletii* had higher body condition than juvenile/subadult crocodiles, and that seasonal fluctuations related to high water levels and warm temperatures caused an overall decrease in body condition. Similarly, adult *Alligator mississippiensis* in the Florida Everglades revealed significantly higher body condition in the dry season than in the wet season, in which juvenile/subadults revealed no difference in condition between seasons (Fujisaki et al., 2009). Interestingly, in both of these studies (Fujisaki et al., 2009; Mazzotti et al., 2012), water levels had a significant influence on body condition, in which higher water levels disperse prey and limit foraging opportunities, as opposed to the dry season when prey are more concentrated.

Given the pronounced wet-dry seasonality in the Philippines, it is possible that wild *C. mindorensis* may be more efficient at foraging during these seasonal fluctuations, resulting in less energetic cost, higher nutrient intake, and thus, higher body condition. In contrast, the lower condition of headstart crocodiles could indicate deficient foraging behaviors which result in greater movements and greater energy expenditure to capture prey. Notably, Mazzotti et al. (2012) suggest that variation in body condition between sexes of *A. mississippiensis* in the Florida Everglades is possibly due to behavioral differences, in which males have lower body condition as a result of increased energy costs from greater movements over a larger home range. For *C. mindorensis*, similar data on movements and home ranges for both wild and headstart crocodiles is lacking. Although the diet component of our study reveals a similar prey diversity between headstart and wild crocodiles, and clearly demonstrates the behavioral competency of headstart crocodiles to capture prey, we were not able to document specific foraging behaviors which definitely warrants future studies. In general, field observation of crocodylian foraging

activities is difficult due to their elusive behavior and nocturnal foraging activities (Magnusson et al., 1987; Thorbjarnarson, 1993; Platt et al., 1990), and similar to *C. mindorensis* in the Philippines, a paucity of data exists for most crocodylians on their behavioral patterns associated with hunting specific prey (Lang, 1987; Gans, 1989; Platt et al., 2006).

Due to the complexity of factors that may influence condition, and the difficulty in interpreting these results, condition indices remain a controversial way of assessing condition for populations (Cone, 1989; Green, 2001; Zweig, 2003). Additionally, condition indices should be evaluated with caution, as the basic assumption that heavier crocodylians are in better health can be misleading (Delany et al., 1999; Zweig, 2003; Rice, 2004). For example, when comparing condition between *Alligator mississippiensis* from three different lakes in central Florida, Rice (2003) found that alligators with the highest condition occurred in a highly polluted lake, from which the alligators foraged on a single abundant fish species and exhibited a low reproductive rate for nearly two decades prior. In contrast, body condition studies of crocodylians have shown to be both an effective and efficient means to track populations trends after initial baseline data is collected (Mazzotti et al., 2012), yielding key insights on the effects of environmental variables (Fujisaki et al., 2009; Mazzotti et al., 2012), diet (Santos et al., 1996; Delany et al., 1999), growth (Saafeld et al., 2008), and reproduction (Barão-Nóbrega et al., 2018).

Finally, it is important to note, because of the low population numbers and severely threatened status of *C. mindorensis*, our evaluation of body condition between headstart and wild crocodiles was ultimately limited by a small sample size. This limitation prevented any thorough analysis on numerous abiotic and biotic factors which may have influenced our results, but nevertheless raises pertinent questions on captive-release strategies, foraging behaviors, seasonal fluctuations in relation to prey availability, and *C. mindorensis* movements, all of which warrant future studies with larger sample sizes by both sex and age class. Furthermore, we believe

condition indices can be an effective and efficient tool to further assess translocated crocodylians for many of the endangered species involved in captive-release programs, especially since the morphological data required to calculate such indices are commonly already collected for most population monitoring programs. And since most crocodylian headstart programs are found in developing countries where they rely on limited funds for field studies, body condition indices provide a cost-effective and non-invasive tool to assess both population trends and the health of translocated individuals after release. Of course, these studies reveal greater inferential power with large sample sizes, and when data is analyzed over a long duration of time and baseline comparative data from a resident population of conspecifics is available. Because our study is the first to investigate condition for *C. mindorensis*, we provide imperative baseline data for continued monitoring that can be used to track population trends, address confounding factors potentially influencing population health, and importantly, facilitate management decisions for this severely threatened species.

4.4 *Conservation Implications*

Post-release monitoring remains a fundamental component for any translocation (IUCN/SSC, 2013), and specifically, this study emphasizes the importance of timely monitoring methods that grant an effective means to evaluate the behavioral performance of released individuals against a resident wild population. Although survivorship and fecundity are commonly measured to evaluate translocation success, we believe our focused methods on diet and body condition provide pertinent monitoring parameters to demonstrate post-release establishment and behavioral competencies of translocated crocodylians. These monitoring methods prove

especially useful for long-lived crocodylians whose reproductive success may take decades to assess, and when management decisions must be made rapidly.

In addition, we stress the importance of post-release monitoring for the identification of emerging threats which may jeopardize both long-term success and population recovery as a whole. For example, after over a decade of intensive community-based conservation efforts which have resulted in a transformative and optimistic community-wide support for crocodile conservation, it was believed that Philippine crocodiles were no longer deliberately killed in the Municipality of San Mariano (van der Ploeg et al., 2011). However, during our study we observed an unfortunate incident in which an adult Philippine crocodile, one of only a few remaining breeding males, was brutally killed as it was resting in a lake and became exposed as a local farmer was draining the lake dry to pump water to a nearby rice paddy. Even though the crocodile showed no attempt to attack the farmer, he still took the aggressive action of illegally killing it because he considered the crocodile a threat and pest to have on his property. Furthermore, as this lake was a critical environmental resource for breeding *C. mindorensis*, nesting birds, and countless other freshwater species, this single event highlights the persisting anthropogenic threats in the Philippines that need to be continually addressed. This was a devastating event nonetheless, however, the backlash of this farmer's actions resulted in a monumental community-wide revulsion, with their subsequent disclosure of the crime to the municipal government agencies, a rare feat for a rural community typically resistant of government affairs. Additionally, the killing itself was only witnessed by several elementary school kids. These same kids who had previously experienced years of Mabuwaya's in-school lectures specifically addressing the importance for wetland, wildlife, and crocodile conservation. After observing the illegal incident, the kids then directly reported the crime to community sanctuary guards and tribal leaders. As the news of this crime spread fast, the surrounding

community expressed an overwhelming opposition to the farmers actions, while notably showing empathy and compassion for the killing of an iconic flagship species. Historically, prior to the establishment of Mabuwaya's *in-situ* action plan, an event such as this would have been shrugged off and most likely ignored as just common practice. But, as a direct result of continuous conservation efforts investing in education campaigns and community capacity building, several impressive actions followed this unfortunate incident which give encouraging hope for the future. Still, this incident reveals the importance for an incessant monitoring program that can evolve adaptive management strategies and conservation efforts to counteract the continuous emerging threats from an ever-expanding agricultural landscape.

Overall, key factors which have been shown to influence the success of translocated populations have been summarized to be ecological factors, such as habitat quality and food availability, in addition to non-ecological factors, including public relations, education, and a long-term commitment to the translocation project (Fischer and Lindenmayer, 2000; Germano and Bishop, 2009). Additionally, success is greatly influenced when there is potential for the translocated species to cause human-wildlife conflict (Ewen et al., 2014), as such for the world's 27 crocodylian species which often are considered a threat to many indigenous people given the potential danger they represent. Although our study provides critical and encouraging evidence for key ecological factors by showing that headstart crocodiles are able to adjust post-release and forage on a wide diversity of prey similar to their wild counterparts. These data have little relevance from a local perspective where *C. mindorensis* survives among rural, impoverished communities and the fate of the species, like many endangered species, is ultimately dependent on the acceptance and support of conservation efforts by the local people. Rural poverty, weak governance, and scarce financial resources are the common denominators that hinder conservation efforts in most developing countries (van der Ploeg et al., 2011). But as Canessa et

al. (2016) demonstrated, if captive-release programs can help avoid extinction in the short-term, their real value lies in providing time for learning and developing effective, sustainable conservation actions for the long-term.

Thus, as we have learned, our study highlights the importance for a continued focus on key ecological factors discussed above, but also, on non-ecological factors related to community-based conservation and CEPA programs, and notably, an active investment in local people to be trained in restoration and conservation efforts. As a result of our study and Mabuwaya's extensive conservation efforts over the last 15 years, the most compelling conservation impacts have stemmed from the empowerment of local community members who are actively engaged in every step of the translocation process. In return, researchers acquire reliable, on-the-ground personnel to provide constant feedback throughout the course of a translocation, personnel which also serve as respected and trusted ambassadors when lobbying for change with reluctant neighbors and government agencies. While at the same time these local people, whose livelihoods depend on their farm and consequently often have an unsympathetic attitude towards biodiversity conservation, are able to (1) gain a more enriched, educated outlook for sustainable land and wildlife management, (2) foster a genuine sense of pride and self-worth in protecting their native wildlife, and (3) earn financial incentives which enhance the livelihoods for their families and the surrounding community. As human populations continue to grow, coinciding with unchecked agricultural expansion and habitat alteration, the long-term sustainability of all conservation programs, irrespective of translocations, will be dependent on a long-term commitment to both ecological monitoring and enhancing the capacity of in-country local communities.

Bibliography

- Alberts, A.C., 2007. Behavioral considerations of headstarting as a conservation strategy for endangered Caribbean rock iguanas. *Applied Animal Behaviour Science* 102, 380–391.
- Alberts, A.C., Phillips, J.A., 2004. Experimental strategies for the recovery of depleted populations of West Indian rock iguanas. In: Gordon, M.S., Bartol, S.M. (Eds.), *Experimental Approaches to Conservation Biology*. University of California Press, Berkeley, pp. 83–100.
- Alcala, A.C., Ross, C.A., Alcala, E.L., 1987. Observations on reproduction and behaviour of captive Philippine crocodiles (*Crocodylus mindorensis* Schmidt). *Silliman Journal* 34, 18–28.
- Armstrong, D.P., Seddon, P.J., 2008. Directions in reintroduction biology. *Trends Ecol. Evol.* 23, 20–25.
- Atwell, R.I.G. (1954). Crocodiles feeding on weaver birds. *Ibis* 96, 485–486
- Balaguera-Reina, S.A., Venegas-Anaya, M., Beltrán-López, V., Cristancho, A., Densmore III, L.D., 2018. Food habits and ontogenetic dietary partitioning of American crocodiles in a tropical Pacific Island in Central America. *Ecosphere* 9(9)
- Barão-Nóbrega, J.A.L., Marioni, B., Botero-Arias, R., Nogueira, A.J.A., Lima, E.S., Magnusson, W.E., Silveira, R.D., Marcon, J.L., 2018. The metabolic cost of nesting: body condition and blood parameters of *Caiman crocodilus* and *Melanosuchus niger* in Central Amazonia. *J Comp Physiol B* 188:127–140
- Barnosky, A.D., Matzke, N., Tomiya, S. et al., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
- Barr, B.R., 1997. Food habits of the American alligator, *Alligator mississippiensis*, in the southern Everglades. Ph.D. dissertation. University of Miami, Miami, FL.
- Barr, B.R. 1994. Dietary studies on the American alligator (*Alligator mississippiensis*) in southern Florida. Master's Thesis, University of Miami, Coral Gables, 73.
- Blake, D.K., Loveridge, J.P., 1975. The role of commercial crocodile farming in crocodile conservation. *Biol. Conserv.* 8, 261–272.
- Böhm, M. et al., 2013. The conservation status of the world's reptiles. *Biological Conservation* 157, 372–385.
- Bowen, B.W., Conant, T.A., Hopkins-Murphy, S.R., 1994. Where are they now? The Kemp's Ridley headstart project. *Conserv. Biol.* 8, 853–856.

- Brandt, L. A., 1991. Growth of juvenile alligators in Par Pond, Savannah River site, South Carolina. *Copeia* 1991, 1123–1129.
- Brazaitis, P. (1987). Identification of crocodylian skins and products. In *Wildlife Management: Crocodiles and Alligators* (ed. G. J. Webb, S. C. Manolis and P. J. Whitehead), pp. 373-86. Chipping Norton, NSW: Surrey Beatty & Sons.
- Briggs-Gonzalez, V., Bonenfant, C., Basille, M., Cherkiss, M., Beauchamp, J., Mazzotti, F., 2017. Life histories and conservation of long-lived reptiles, an illustration with the American crocodile (*Crocodylus acutus*), *Journal of Animal Ecology*.
- Brown, R.M., Siler, C.D., Oliveros, C.H., Welton, L.J., Rock, A., Swab, J., van Weerd, M., van Beijnen, E.J., Rodriguez, D., Jose, E., Diesmos, A.C., 2013. Evolutionary processes of diversification in a model island archipelago. *Annu. Rev. Ecol. Evol. Syst.* 444, 411–35.
- Burghardt, G.M., Layne, D.G., 1995. Effects of ontogenetic processes and rearing conditions. In: Warwick, C., Frye, F.L., Murphy, J.B. (Eds.), *Health and Welfare of Captive Reptiles*. Chapman and Hall, London, 165–185.
- Burghardt, G.M., Milostan, M.A., 1995. Ethological studies of reptiles and amphibians. In: Gibbons, Jr., E.F., Durrant, B.S., Demarest, J. (Eds.), *Lessons for Species Survival Plans*. State University of New York Press, Albany, NY, 187–203.
- Canessa, S., Genta, P., Jesu, R., Lamagni, L., Oneto, F., Salvidio, S., Ottonello, D., 2016. Challenges of monitoring reintroduction outcomes: insights from the conservation breeding program of an endangered turtle in Italy. *Biological Conservation* 204, 128–133.
- Catibog-Sinha, C.S., Heaney, L.R., 2006. *Philippine Biodiversity: Principles and Practice*. Quezon City: Haribon Found. Conserv. Nat. Resour.
- Chabreck, R.H. 1972. The foods and feeding habits of alligators from fresh and saline environments in Louisiana. *Proceedings Annual Conference of Southeastern Association of Game and Fish Commission*, 25, 117–124.
- Cone, R.S., 1989. The need to reconsider the use of condition indexes in fishery science. *Transactions of the American Fisheries Society* 118 (5), 510–514.
- Costa, A., Salvidio, S., Posillico, M., Matteucci, G., De Cinti, B., Romano, A., 2015. Generalisation within specialization: inter-individual diet variation in the only specialized salamander in the world. *Scientific Reports*. <https://doi.org/10.1038/srep13260>.
- Coulson, R. A. & Hernandez, T. (1983). *Alligator Metabolism: Studies on Chemical Reactions in Vivo*. London: Pergamon Press.
- Craighead, F.C., 1968. The role of the Alligator in shaping plant communities and maintaining wildlife in the Southern Everglades. *Florida Nat* 41 (2), 769–774.

- Dalrymple, G.H. 1996. Growth of american alligators in the Shark Valley region of Everglades National Park. *Copeia* 1996, 212–216.
- Daltry, J.C., Starr, J.C.D.A., 2010. Development of a re-introduction and re-enforcement program for Siamese crocodiles in Cambodia, In: Soorae PS (Ed.) *Global Re-introduction Perspectives 2010: Additional Case Studies from Around the Globe*, IUCN/SSC Re-Introduction Specialist Group, Abu Dhabi, 118–123.
- Davenport, J., Grove, D.J., Cannon, J., Ellis, T.R. & Stables, R. (1990). Food capture, appetite, digestion rate and efficiency in hatchling and juvenile *Crocodylus porosus*. *Journal of Zoology* 220, 569– 592.
- Delany, M.F., Abercrombie, C.L., 1986. American alligator food habits in north central Florida. *Journal of Wildlife Management* 50, 348–353.
- Delany, M.F., Linda, S.B., Moore, C.T., 1999. Diet and condition of American alligators in 4 Florida lakes. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 53, 375–389.
- Diefenbach, C.O.D., 1979. Ampullarid gastropod - staple food of *Caiman latirostris*? *Copeia* 1979, 162–163.
- Dietz, M., 2004. Integrating animal behavior and conservation biology: a review. *End. Species Update* 21, 4–13.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the anthropocene. *Science* 345, 401–406.
- Dodd Jr., C.K., 2005. Amphibian conservation and population manipulation. In: Lannoo, M. (Ed.), *Amphibian declines: the conservation status of United States species*. University of California Press, Berkeley, California, USA, 265–274.
- Dodd Jr., K.C., Siegel, R.A., 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? *Herpetologica* 47 (3), 336–350.
- Elsley, R.M., 1992. Food habits of native wild and farm-released juvenile alligators. *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 46, 57–66.
- Elsley, R.M., Joanen, T., McNease, L., Kinler, N., 1992. Growth rates and body condition factors of *Alligator mississippiensis* in coastal Louisiana wetlands: a comparison of wild and farm-released juveniles. *Comparative Biochemical Physiology Part A: Physiology* 103, 667–672.
- Ewen, J.G., Armstrong, D.P., 2007. Strategic monitoring of reintroductions in ecological restoration programmes. *Ecoscience* 14, 401–409.
- Ewen, J.G., Soorae, P.S., Canessa, S., 2014. Reintroduction objectives, decisions and outcomes: global perspectives from the herpetofauna. *Anim. Conserv.* 17, 74–81.

- Ferguson, G.W., Brown, K.L., DeMarco, V.G., 1982. Selective basis for the evolution of variable egg and hatchling size in some iguanid lizards. *Herpetologica* 38, 178–188.
- Feroli, R.C, 1998. Distribution of *Crocodylus niloticus*. In: Britton, A., 1995–2010. *Crocodylians: Natural history and Conservation*. <http://www.flmnh.ufl.edu/cnhc/cnhc.html>.
- Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. *Biol. Conserv.* 96, 1–11.
- Fitch-Snyder, H. & Lance, V. (1993). Behavioral observations of lithography in captive juvenile alligators. *Journal of Herpetology* 27, 335–337.
- Fitzgerald, L.A. (1989) An evaluation of stomach flushing techniques for crocodylians. *J. Herpetol.* 23, 170–172.
- Fleischman, L. J., Howland, H. C., Howland, M. J., Rand, A. S. & Davenport, M. L. (1988). Crocodiles don't focus underwater. *Journal of Comparative Physiology* 163A, 441–443.
- Fogarty, M.J., Albury, J.D., 1968. Late summer foods of young alligators in Florida. *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions* 21, 220–222.
- Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *J. Appl. Ichthyol.* 22, 241–253.
- Fujisaki, I., Rice, K.G., Pearlstine, L.G., Mazzotti, F.J., 2009. Relationship between body condition of American Alligators and water depth in the Everglades, Florida. *Hydrobiologia* 635:329–338
- Galan, G. L., Ediza, M. M., Servasques, M. S., Porquis, H. C., 2015. Diversity of Gastropods in the Selected Rivers and Lakes in Bukidnon. *International Journal of Environmental Science and Development* 6(8), 615–619.
- Gans, C., 1989. Crocodylians in perspective! *American Zoologist* 29, 1051–1054.
- Garnett, S.T., 1985. The consequences of slow chitin digestion on crocodylian diet analyses. *Journal of Herpetology* 19,
- Germano, J.M., Bishop, P.J., 2008. Suitability of amphibians and reptiles for translocation. *Conserv. Biol.* 23, 7–15.
- Green, A.J., 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82 (5), 1473–1483.
- Greenberg, N., 1976. Observations of social feeding in lizards. *Herpetologica* 32, 348–352.

- Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool - status and strategy. *Science* 245, 477–480.
- Grigg, G., Kirschner, D., 2015. *Biology and evolution of crocodylians*. Ithaca, NY. Cornell University Press.
- Hall, P.M., 1989. Variation in geographic isolates of the New-Guinea crocodile (*Crocodylus novaeguineae* Schmidt) compared with the similar, allopatric, Philippine Crocodile (*Crocodylus mindorensis* Schmidt). *Copei*.
- Hartup, B.K., Olsen, G.H., Czekala, N.M., 2005. Fecal corticoid monitoring in Whooping Cranes (*Grus maricana*) undergoing reintroduction. *Zoo Biology* 24, 15–28.
- Heppell, S.S., Crowder, L.B., Crouse D.T., 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* 6, 556–565.
- Hopkins, M. (1968). Alligators in heron rookeries. *The Oriole* 33, 28–29.
- Hudson, R.D., Alberts, A.C., 2004. The role of zoos in the conservation of West Indian iguanas. In: Alberts, A.C., Carter, R.L., Hayes, W.K., Martins, E.P. (Eds.), *Iguanas: Biology and Conservation*. University of California Press, Berkeley, pp. 274–289.
- Hurlburt, G. 1999. Comparison of body mass estimation techniques, using recent reptiles and the pelycosaur *Edaphosaurus boanerges*. *J. Vert. Paleontol.* 19:338–350.
- Hutton, J.M., 1987. Growth and feeding ecology of the Nile crocodile, *Crocodylus niloticus* at Ngezi, Zimbabwe. *Journal of Animal Ecology* 56, 25–38.
- IUCN 2019. The IUCN Red List of Threatened Species. Version 2019-1. <http://www.iucnredlist.org>.
- IUCN/SSC (2013). *Guidelines for Reintroductions and Other Conservation Translocations*. Version 1.0. Gland, Switzerland: IUCN Species Survival Commission, viiii + 57 pp.
- Jackson, J. F., Campbell, H.W., Campbell, K.E., 1974. The feeding habits of crocodylians: validity of the evidence from stomach contents. *Journal of Herpetology* 8, 378–381.
- King, F.W., 1988. Crocodiles: keystone wetland species. In: Dalrymple, G.H., Loftus, W.F., Bernadino, F.S. (Eds.), *Wildlife in the Everglades and Latin American Wetlands*. Abstracts of the Proceedings of the First Everglades Nat. Park Symposium, Miami 1985, 18–19.
- Kleiman, D.G., Stanley-Price, M.R., Beck, B.B., 1994. Criteria for reintroductions. in P. J. S. Olney, G. M. Mace, and A. T. C. Feistener, editors. *Creative conservation: interactive management of wild and captive animals*. Chapman and Hall, New York. 287–303.
- Knapp, C.R., Hudson, R.D., 2004. Translocation strategies as a conservation tool for West Indian iguanas. In: Alberts, A.C., Carter, R.L., Hayes, W.K., Martins, E.P. (Eds.), *Iguanas: Biology and Conservation*. University of California Press, Berkeley, pp. 199–209.

- Krebs, C.J., 1989. Ecological methodology. Harper Collins, New York, New York, USA.
- Kushlan, J.A., Mazzotti, F.J., 1989. Population biology of the American crocodile. *Journal of Herpetology* 23, 7–21.
- Lang, J. W., 1987. Crocodilan behavior: implications for management. In G. J. W. Webb, S.C. Manolis, and P.J. Whitehead (eds.), *Wildlife Management : Crocodiles and Alligators*, pp. 273–294. Surrey Beatty and Sons, Ltd., Sydney, Australia.
- LeCren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology* 20:201–219.
- Leitch DB, Cantania KC (2012). Structure, innervation and response properties of integumentary sensory organs in crocodylians. *The Journal of Experimental Biology* 215, 4217–4230.
- Leslie, A.J., 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St. Lucia, Kwazulu/Natal, South Africa. Ph.D. dissertation. Drexel University, Philadelphia, PA.
- Magnusson, W.E., da Silva, E.V., Lima, A.P., 1987. Diets of Amazonian crocodylians. *Journal of Herpetology* 21,85–95.
- Manalo, R., 2008. Occurrence of *Crocodylus mindorensis* in the Cordillera Central. Abra Province, Luzon Island. *National Museum Papers* 14, 109–115.
- Manolo, R., Pomares, C., Mercado, V., Belo, W., Saljay, G., 2013. Philippine crocodile (*Crocodylus mindorensis* Schmidt 1935) population recorded in highlands of Lake Sebu, Southern Mindanao, Philippines. *Crocodile Specialist Newsletter* 32 (1), 15–17.
- Martins, E.P., 2004. Introduction: behavior and ecology. In: Alberts, A.C., Carter, R.L., Hayes, W.K., Martins, E.P. (Eds.), *Iguanas: Biology and Conservation*. University of California Press, Berkeley, 97–100.
- Maskey, T.M., Cadi, A., Ballouard, J.M., Fougeirol, L., 2006. Gharial conservation in Nepal: result of a population reinforcement program. *Proceedings of the 18th Working Meeting of the Crocodile Specialist Group*. France, 19–23.
- Mathews, F., Orros, M., McLaren, G., Gelling, M., Foster, R., 2005. Keeping fit on the ark: assessing the suitability of captive-bred animals for release. *Biological Conservation* 121, 569–577.
- Mazzotti, F.J., Best, G.R., Brandt, L.A. Cherkiss, M.S., Jeffery, B.M., Rice, K.G., 2009. Alligators and crocodiles as indicators for restoration of Everglades ecosystems. *Ecological Indicators* 9, S137– S149.

- Mazzotti FJ, Cherkiss M.S, Brandt LA, Fujisaki I, Hart K, Jeffery B, McTurry S.T, Platt, S.G, Rainwater TR, Vinci J (2012) Body condition of Morelet's crocodile (*Crocodylus moreletti*) from Northern Belize. *J Herpetol* 46:356–362.
- McGowan, P.J.K, Traylor-Hozer, K., Leus, K., 2017. IUCN guidelines for determining when and how *ex situ* management should be used in species conservation. *Conservation Letters*.
- McIlhenny, E. A. (1935). *The Alligator's Life History*. Boston: Christopher Publishing House
- Miranda, J.S.Q., van Weerd, M., van der Ploeg, J., 2004. Devolving crocodile conservation to the local level: the case of Philippine crocodile conservation in the Municipality of San Mariano, northeast Luzon, the Philippines. The 17th Working Meeting of the IUCN-SSC Crocodile Specialist Group, 309–316 in *Crocodiles*. IUCN: Gland.
- Mittermeier, R.A., Myers, N., Robles, P.G., Mittermeier, C.G., (Eds.), 1999. *Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecosystems*. Mexico City: CEMEX
- Munoz., M.C., Thorbjarnarson, J., 2000. Movement of captive-released Orinoco Crocodiles (*Crocodylus intermedius*) in the Capanaparo River, Venezuela. *Journal of Herpetology* 34 (3), 397–403.
- Muths, E., Bailey, L.L., Watry, M.K., 2014. Animal reintroductions: an innovative assessment of survival. *Biological Conservation* 172, 200–208.
- Naylor, R. 1996. Invasions in Agriculture: Assessing the Cost of the Golden Apple Snail in Asia. *Ambio*. 25(7):443–448.
- Nell, L.A., Frederick, P.C., Mazzotti, F.J., Vliet, K.A., Brandt, L.A., 2016. Presence of breeding birds improves body condition for a crocodylian nest protector. *PLoS ONE*. 11 (3); e0149572. doi:10.1371/journal.pone.0149572.
- Oliveros, C., Manalo, R., Coñate Sr., E., Tarun, B., Telan, S., van Weerd, M., 2005. Philippine crocodile recorded on Dalupiri Island. *Crocodile Specialist Group Newsletter* 24 (3), 14–15.
- Pauwels, O.S.G., Mamonekene, V., Dumont, P., Branch, W.R., Burger, M., Lavoué, S., 2003. Diet records for *Crocodylus cataphractus* (Reptilia: Crocodylidae) at Lake Divangui, Ogooué-Maritime Province, Southwestern Gabon. *Hamadryad*, 27, 200–204.
- Pedrono, M., Sarovy, A., 2000. Trial release of the world's rarest tortoise *Geochelone yniphora* in Madagascar. *Biol. Conserv.* 95, 333–342.
- Perez-Buirago, N., Garcia, M.A., Sabat, A., Delgado, J. Álvarez, A., McMillan, O., Funk, S.M., 2008. Do headstart programs work? Survival and body condition in headstarted Mona Island iguanas (*Cyclura cornuta stejnegeri*). *Endangered Species Research* 6: 55–65.
- Pinter-Wollman, N., Isbell, L.A., Hart, L.A., 2009. Assessing translocation outcome: comparing behavioral and physiological aspects of translocated and resident African elephants (*Loxodonta africana*). *Biological Conservation* 142, 1116–1124.

- Platt, S. G. & Brantley, C. G. 1991. Observations of foraging behavior in captive juvenile *Alligator mississippiensis*. *Herpetological Review* 22, 83–8.
- Platt, S. G., Brantley, C. G. & Hastings, R. H. 1990. Food habits of juvenile American alligators in the upper Lake Pontchartrain Estuary. *Northeast Gulf Science* 11, 123–130.
- Platt, S. G., Rainwater, T. R., Finger, A. G., Thorbjarnarson, J. B., Anderson, T. A., McMurry, S. T., 2006. Food habits, ontogenetic dietary partitioning and observations of foaging behavior of Morelet's Crocodile (*Crocodylus moreletii*) in northern belize. *Herpetological Journal* 16:281–290.
- Platt, S.G., Rainwater, T.R., McMurry, S.T., 2002. Diet, gastrolith acquisition and initiation of feeding among hatchling Morelet's Crocodiles in Belize. *Herpetological Journal* 12.
- Platt, S. G., Thorbjarnarson, J. B., Rainwater, T. R., Martin, D. R., 2013. Diet of the American Crocodile (*Crocodylus acutus*) in Marine Enviornments of Coastal Belize. *Journal of Herpetology* 47, 6: 1–10.
- Polet, G., Murphy, D.J., Lam, P.V., Mui, T.V., 2002. Crocodile conservation at work in Vietnam; re-establishment *Crocodylus siamensis* in Cat Tien national park. In: *Crocodiles: Proceedings of the 16th Working Meeting of the Crocodile Specialist Group*, 86–95.
- Redford, K.H., Amato, G., Baillie, J., et al., 2011. What does it mean to successfully conserve a (vertebrate) species? *Bioscience* 61, 39–48.
- Reinert, H.K., 1991. Translocation as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. *Herpetologica* 47, 357–363.
- Rice, A.N., Ross, J.P., Finger, A.G., Owen, R. 2005. Application and evaluation of a stomach flushing technique for alligators. *Herpetological Review* 36:400–401.
- Reynolds, M.H., Weiser, E., Jamieson, I., Hatfield, J.S., 2013. Demographic variation, reintroduction and persistence of an Island Duck (*Anas laysanensis*), *The Journal of Wildlife Management* 77 (6), 1094–1103.
- Rice, A.N., 2004. Diet and condition of American alligators (*Alligator mississippiensis*) in three central Florida lakes. Thesis. University of Florida.
- Rice, A.N., Ross, J.P., Woodward, A.R., Carbonneau, D.A., Percival, H.F., 2007. Alligator diet in relation to alligator mortality on Lake Griffin, FL. *Southeastern Naturalist* 6, 97–110.
- Rosenberg, K.V., Cooper, R.J., 1990. Approaches to avian diet analysis. *Sutudies in Avian Biology* 13:80–90.
- Ross, J.P., (ed). 1998. *Crocodiles. Status Survey and Conservation Action Plan*. 2nd Edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. Viii + 96pp.

- Ross, C.A., Alcalá, A.C., 1983. Distribution and status of the Philippine crocodile (*Crocodylus mindorensis*). Kalikasaan, Philippines. *Journal of Biology* 12, 169–173.
- Santos, S.A., Nogueira, M.S., Pinheiro, M.S., Campos, Z., Magnusson, W.E, Mourão, G.M., 1996. Diets of *Caiman crocodilus yacare* from different habitats in the Brazilian Pantanal. *Herpetol J* 6:111–117.
- Schoener, T.W., 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49, 704–726.
- Seddon, P. J., 1999. Persistence without intervention: assessing success in wildlife reintroductions. *Trends in Ecology & Evolution* 14, 503.
- Seijas, A.E., 1995. Captive breeding and rearing as conservation tool for the Orinoco crocodile. In: Bissonette, J.A., Krausman, P.R., (Eds.), *Integrating People and Wildlife for a Sustainable Future*. Proc. of the First International Wildlife Congress, The Wildlife Society, Bethesda, Maryland, 596–598.
- Shirley, M. H., Burtner, B., Oslisly, R., Sebag, D., Testa, O., 2016. Diet and body condition of cave-dwelling dwarf crocodiles (*Osteolaemus tetraspis*, Cope 1861) in Gabon. *African Journal of Ecology* 55, 411–422.
- Silveira, R.D., Magnusson, W.E., 1999. Diets of spectacled and black caiman in the Anavilhanas Archipelago, Central Amazonia, Brazil. *Journal of Herpetology* 33, 181–192.
- Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, S.B., Toone, W.D., Miller, B., 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10, 338–348.
- Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L., 2004. Southeast Asian biodiversity: an impending disaster. *Trends Ecol. Evol.* 19, 654–60.
- Sokol, O. 1971. Lithophagy and geophagy in reptiles. *Journal of Herpetology* 5, 67–71
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Sutherland, W.J., Armstrong, D., Butchart, S.H.M., Earnhardt, J.M., Ewen, J., Jamieson, I., Jones, C.G., Lee, R., Newbery, P., Nichols, J.D., Parker, K.A., Sarrazin, F., Seddon, F.J., Shah, N., Tatayah, V., 2010. Standards for documenting and monitoring bird reintroduction projects. *Conserv. Lett.* 3, 229–235.
- Targarona, R., Soberón, R.R., Tabet, M.A., Thorbjarnarson, J.B., 2010. Cuban Crocodile *Crocodylus rhombifer*. in *Crocodyles. Status Survey and Conservation Action Plan*. Third Edition, ed. by S.C. Manolis and C. Stevenson. Crocodile Specialist Group: Darwin. 114–118

- Taylor, J.A., 1979. The foods and feeding habits of subadult *Crocodylus porosus* Schneider in northern Australia. *Australian Wildlife Research* 6, 347–359.
- Temsiripong, Y., Ratanakorn, P., Kullavanijaya, B., 2004. Management of the Siamese crocodile in Thailand. In: *Crocodiles. The 17th Working Meeting of the IUCN-SSC Crocodile Specialist Group*. IUCN, Gland, Switzerland, 141–142.
- Thorbjarnarson, J. B., 1988. Status and ecology of the American crocodile in Haiti. *Bulletin of the Florida State Museum* 33, 1–86.
- Thorbjarnarson, J.B., 1993. Diet of the spectacled caiman (*Caiman crocodilus*) in the central Venezuelan Llanos. *Herpetologica*, 49 (1), 108–117.
- Tucker, A.D., Limpus, C.J., McCallum, H.I., McDonald, K.R., 1996. Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. *Copeia* 1996, 978–988.
- Van de Ven, W.A.C., Guerrero, J.P., Rodriguez, D.G., Telan, S.P., Balbas, M.G., Tarun, B.A., van Weerd, M., van der Ploeg, J., Wijtten, Z., Lindeyer, F.E., Iongh, H.H., 2009. Effectiveness of head-starting to bolster Philippine crocodile *Crocodylus mindorensis* populations in San Mariano municipality, Luzon, Philippines.
- Van der Ploeg J, Cauilan-Cureg M, van Weerd M, de Groot WT. 2011. Assessing the effectiveness of environmental education: mobilizing public support for Philippine crocodile conservation. *Conserv Lett.* 4(4):313–323.
- Van der Ploeg, J., van Weerd, M., 2006. A paradigm shift in Philippine crocodile conservation. *The 18th Working Meeting of the IUCN-SSC Crocodile Specialist Group: in Crocodiles*. IUCN: Gland. 164–186
- Van Weerd M., 2000. Update on Philippine crocodile occurrence in the Northern Sierra Madre Natural Park. *Crocodile Specialist Group Newsletter* 19, 12–14.
- Van Weerd, M., 2010. Philippine Crocodile *Crocodylus mindorensis*. in *Crocodiles. Status Survey and Conservation Action Plan. Third Edition*, ed. by S.C. Manolis and C. Stevenson. Crocodile Specialist Group: Darwin. 71–78
- Van Weerd, M., et al., 2006. Philippine crocodile conservation in northeast Luzon: an update of population status and new insights into *Crocodylus mindorensis* ecology. In: *Crocodiles. Proceedings of the 18th working meeting of the Crocodile Specialist Group*. IUCN-the World Conservation Union, Gland, Switzerland and Cambridge, UK, 306–321.
- Van Weerd, M., General, A.A., 2003. Conserving the Philippine crocodile in the northern Sierra Madre: the results of three years research and conservation action. In: *The Sierra Madre Mountain Range: Global relevance, local realities* edited by J. van der Ploeg, A.B. Masipiqueña and E.C. Bernardo. CVPED. Golden Press, Tuguegarao. 17–33
- Van Weerd, M., Pomaro, C., de Leon, J., Antolin, R., Mercado, V., 2016. *Crocodylus mindorensis*. *The IUCN Red List of Threatened Species*. e.T5672A3048281.

- Van Weerd M., van der Ploeg, J., 2004. Conservation of the Philippine crocodile, *Crocodylus mindorensis* in NE Luzon, the Philippines. An update. In: *Crocodyles*; Proceedings of the 17th working meeting of the Crocodile Specialist Group, IUCN, Gland, Switzerland pp. 277–28
- Van Weerd, M., van der Ploeg, J., 2008. Philippine crocodile hatchling head-start and re-enforcement program in San Mariano, Isabela Province, Luzon, the Philippines in *Global Re-introduction Perspectives: re-introduction case-studies from around the globe*. IUCN/SSC Re-introduction Specialist Group, Abu Dhabi, UAE. viii + 284
- Van Weerd, M., van der Ploeg, J., 2012. *The Philippine crocodile: ecology, culture and conservation*. Mabuwaya Foundation, Philippines.
- Wallace, K.M., Leslie, A.J., 2008. Diet of the Nile crocodile (*Crocodylus niloticus*) in the Okavango Delta, Botswana. *Journal of Herpetology* 42 (2), 361–368.
- Wallace, M.P., 2000. Retaining natural behavior in captivity for re-introduction programmes. In: Gosling, L.M., Sutherland, W.J. (Eds.), *Behaviour and Conservation*. Cambridge University Press, Cambridge, 300–314.
- Wang, Z.H., Yao, H., Ding, Y.Z., et al., 2011. Testing reintroduction as a conservation strategy for the critically endangered Chinese alligator: movements and home range of released captive individuals. *Chinese Sci. Bull.* 56, 2586–2593.
- Webb, G.J.W., Hollis, G.J., Manolis, S.C., 1991. Feeding, growth, and food conversion rates of wild saltwater crocodiles (*Crocodylus porosus*). *Journal of Herpetology* 25, 462–473.
- Webb, G.J.W., Manolis, S.C., Buckworth, R., 1982. *Crocodylus johnstoni* in the McKinlay River area, N.T.I. variation in the diet, and a new method of assessing the relative importance of prey. *Australian Journal of Zoology* 30, 877–899.
- Whitaker, R., Basu, D., 1983. The Gharial (*Gavialis gangeticus*): a review. *Journal of the Bombay Natural History Society* 79, 531–548.
- Wilson, B.S., Alberts, A.C., Graham, K.S., Hudson, R.D., Bjorkland, R.K., Lewis, D.S., Lung, N.P., Nelson, R., Thompson, N., Kunna, J.L., Vogel, P., 2004. Survival and reproduction of repatriated Jamaican iguanas. In: Alberts, A.C., Carter, R.L., Hayes, W.K., Martins, E.P. (Eds.), *Iguanas: Biology and Conservation*. University of California Press, Berkeley, 220–231.
- Wolf, C.M., Griffith, B., Reed, C., Temple, S., 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conserv. Biol.* 10 (4).
- Wolfe, J.L., Bradshaw, D.K., Chabreck, R.H., 1987. Alligator feeding habits: new data and a review. *Northeast Gulf Science* 9, 1–8.

Woodward, A.R., David, D.N., 1994. Alligators (*Alligator mississippiensis*). The Handbook: Prevention and Control of Wildlife Damage, 76.

Yang, Z., Gu, Xiaodong, G., Nie, Y., Huang, F., Huang, Y., Dai, Q., Hu, Y., Yang, Y., Zhou, Z., Zhang, H., Yang, Z., Wei, F., 2018. Reintroduction of the giant panda into the wild: A good start suggests a bright future. *Biological Conservation* 217, 181–186.

Zweig, C.L., 2003. Body Condition Index Analysis for the American Alligator (*Alligator mississippiensis*). M.S. Thesis, University of Florida, Gainesville.

Zweig, C.L., Rice, K.G., Percival, F., Mazzotti, F.J., 2014. Body condition factor analysis for the American alligator (*Alligator mississippiensis*). *Herpetol. Rev.* 45, 216–219.

Appendix

Table 1. Prey items, gastrolyths, and vegetation among wild (N = 20) and headstart (N = 10) Philippine crocodiles from Isabela Province, Luzon, Philippines. Percent occurrence (%) and number of crocodiles (*n*) containing a specified category within each group (wild/headstart), followed by Chi-square (x^2) and *p*-values resulting from chi-square analysis of each prey category frequency among wild and headstart crocodiles.

Prey Category	Wild		Headstart		Stat	
	<i>n</i>	%	<i>n</i>	%	x^2	<i>p</i>
Snails	14	70.0	7	70.0	0.00	1.00
Crabs	4	20.0	2	20.0	0.00	1.00
Birds	5	25.0	5	50.0	0.92	0.34
Fish	8	40.0	3	30.0	0.02	0.89
Reptiles	5	25.0	5	50.0	0.92	0.34
Amphibians	4	20.0	1	10.0	0.03	0.86
Mammals	4	20.0	3	30.0	0.02	0.88
Insects	6	30.0	2	20.0	0.02	0.88
Gastrolyths	13	65.0	6	60.0	0.00	1.00
Vegetation	9	45.0	1	10.0	2.27	0.13

Table 2. Wilcoxon rank sum test (w) and p values resulting from an analysis of percent composition (%) for each prey category between headstart (N = 10) and wild (N = 20) Philippine crocodiles from Isabela Province in the northern Philippines.

Prey Category	Headstart	Wild	Stat	
	%	%	W	p
Snails	32.6	42.5	73.00	0.23
Crabs	15.3	4.8	87.50	0.45
Birds	8.6	13.6	117.00	0.39
Fish	10.7	12.2	94.00	0.78
Reptiles	4.4	12.4	85.00	0.45
Amphibians	9.0	3.0	106.00	0.71
Mammals	7.2	6.4	83.00	0.33
Insects	12.1	5.1	89.50	0.57

Table 3. Shannon-Weiner diversity index (H') and evenness measure (J') for wild (N = 20), headstart (N = 10), juvenile (N = 12), and adult (N = 18) Philippine crocodiles sampled from Isabela Province in the northern Philippines.

	Wild	Headstart	Juvenile	Adult
Diversity (H')	0.89	0.70	0.85	0.81
Evenness (J')	0.43	0.34	0.41	0.39

Table 4. Prey items, gastrolyths, and vegetation among juvenile (N = 12) and adult (N = 18) Philippine crocodiles from Isabela Province, Luzon, Philippines. Percent occurrence (%) and number of crocodiles (n) containing a specified category within each group (juvenile/adult), followed by Chi-square (χ^2) and p-values resulting from chi-square analysis of each prey category frequency among juvenile and adult crocodiles.

Prey Category	Juvenile (12)		Adult (18)		Stat	
	n	%	n	%	χ^2	p
Snails	8	66.7	13	72.2	0.00	1.00
Crabs	3	25.0	3	16.7	0.01	0.93
Birds	3	25.0	7	38.9	0.16	0.69
Fish	4	33.3	7	38.9	0.00	1.00
Reptiles	2	16.7	8	44.4	1.30	0.24
Amphibians	3	25.0	2	11.1	0.25	0.62
Mammals	3	25.0	4	22.2	0.00	1.00
Insects	5	41.7	3	16.7	1.20	0.27
Gastrolyths	6	50.0	13	72.2	0.72	0.39
Vegetation	4	33.3	6	33.3	0.00	1.00

Table 5. Wilcoxon rank sum test (w) and p values resulting from an analysis of percent composition (%) for each prey category between juvenile (N = 12) and adult (N = 18) Philippine crocodiles from Isabela Province in the northern Philippines.

Prey Category	Juvenile	Adult	Stat	
	%	%	W	p
Snails	32.6	42.5	116.00	0.75
Crabs	15.3	4.8	95.50	0.47
Birds	8.6	13.6	123.50	0.45
Fish	10.7	12.2	114.50	0.77
Reptiles	4.4	12.4	139.00	0.12
Amphibians	9.0	3.0	91.50	0.30
Mammals	7.2	6.4	104.00	0.84
Insects	12.1	5.1	82.00	0.16

Table 6. Number of crocodiles (*n*) and percent occurrence (%) containing specified prey categories among all (N = 30) Philippine crocodiles sampled from Isabela Province in the northern Philippines.

Prey Category	<i>n</i>	%
Snails	21	70.0
Crabs	6	20.0
Birds	10	33.3
Fish	11	36.7
Reptiles	10	33.3
Amphibians	5	16.7
Mammals	7	23.3
Insects	8	26.7
Gastrolyths	19	63.3
Vegetation	10	33.3

Table 7. Prey items identified in the stomach contents of 30 Philippine crocodiles sampled in Isabela Province in the northern Philippines.

Category	Taxon
Snail	<i>Pomacea canaliculate</i> ----- (Goldend Apple Snail)
	<i>Melanoides turricula</i> ----- (Fawn Melania)
Insects	<i>Xylotrupes</i> ----- (scarab beetle)
	<i>Anomala</i> sp.----- (scarab beetle)
	<i>Gryllotalpa orientalis</i> ----- (Mole Cricket)
Fish	<i>Channa Striata</i> ----- (Mud fish)
	<i>Clarias batrachus</i> ----- (Walking Catfish)
Amphibians	<i>Limnonectes macrocephalus</i> (Luzon Fanged Frog)
Reptiles	<i>Coelognathus erythrurus</i> ---- (Philippine Rat Snake)
	<i>Pytas luzonensis</i> ----- (Smooth-scaled Mountain Rat Snake)
	<i>Eutropis cumingi</i> ----- (Cuming's Eared Skink)
	<i>Varanus marmoratus</i> ----- (Marbled Water Monitor)
	<i>Cuora amboinensis</i> ----- (Amboina Box Turtle)
Birds	<i>Gallinula chloropus</i> ----- (Common Moorhen)
	<i>Amaurornis olivaceus</i> ----- (Plain Bush-hen)
	<i>Centropus bengalensis</i> ----- (Lesser Coucal)
Mammals	<i>Rattus tanezumi</i> ----- (Oriental House Rat)

Table 8. Relative condition factor (K_n) and Standard Error (SE) with respect to Origin (Headstart/Wild) and individual T-test for the equality of K_n for each subgroup to the standard value of $K_n = 1$.

Origin	N	Mean K_n	SE	Significance for T-test ($H_0 : K_n = 1$)
Headstart	10	0.920	0.044	0.101
Wild	17	1.060	0.024	0.041*

Figure 1. Map of the Philippine archipelago showing our 2018 study sites in the Municipalities of San Mariano (orange) and Divilacan (yellow) in Isabela Province on the northeast island of Luzon.

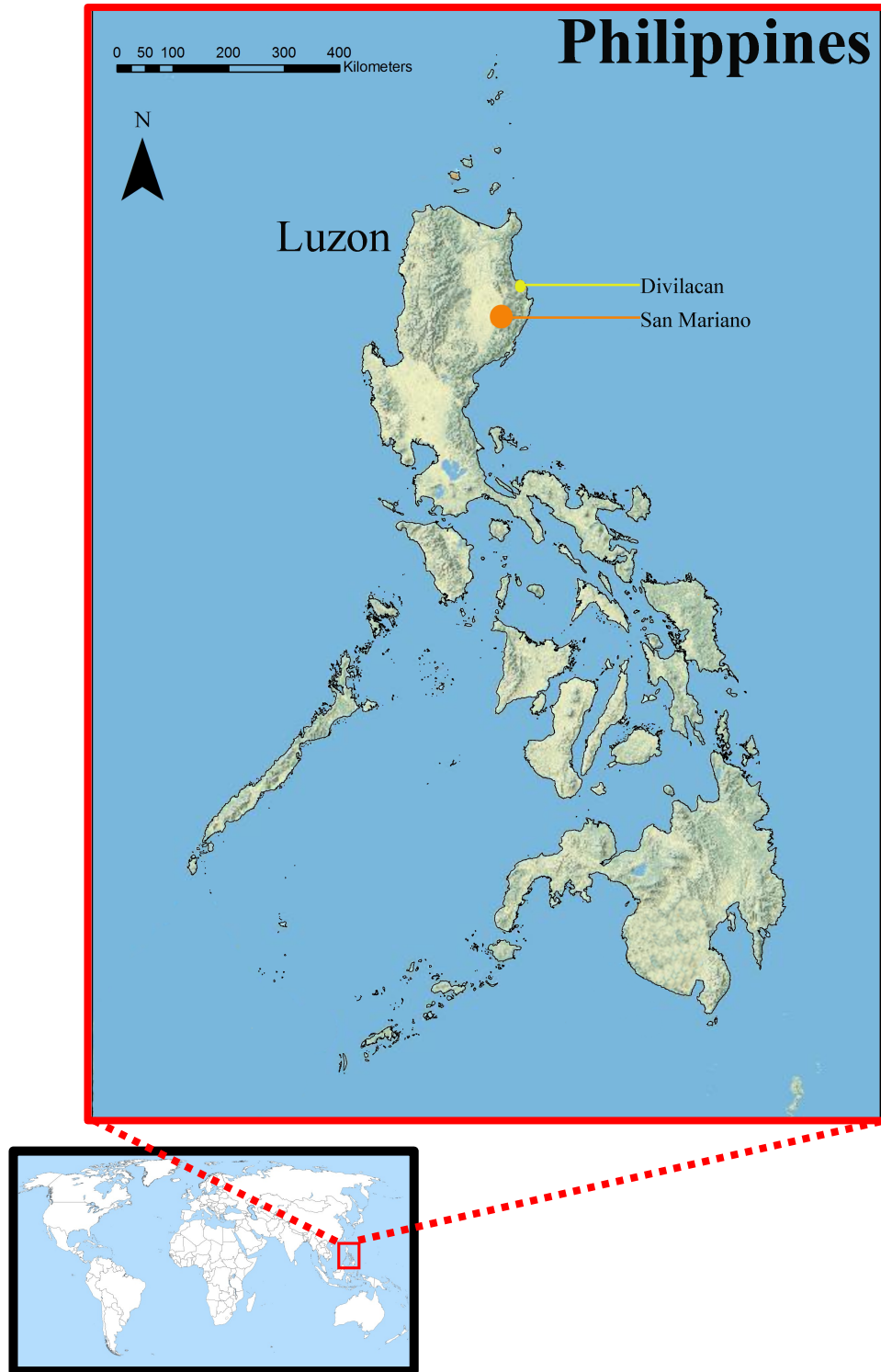


Figure 2. Aerial photograph highlighting the pristine habitat of the Sierra Madre mountain range within the nationally protected Northern Sierra Madre Natural Park (NSMNP) in Isabela Province of northeast Luzon Island. Shown below is the Catalangan River running through the NSMNP, approximately 8 km up river from our field site Dunoy.



Figure 3. An agricultural landscape dominates a majority of Philippine land cover and is one of the leading causes of habitat alteration and biodiversity population declines. Shown below is Philippine crocodile habitat around the Catalangan River in the Municipality of San Mariano of Isabela Province, located just outside the nationally protected Northern Sierra Madre Natural Park in northeast Luzon, Philippines.



Figure 4. A map of our study sites (Dunoy, Narra, Diwagden, Dinang, and Balliao) in the Municipality of San Mariano in Isabela Province, northeast Luzon, Philippines. Yellow shading of the map highlights agriculture habitat, whereas the dark green shading shows forest over and the black boundary line of the Northern Sierra Madre Natural Park.



Figure 5. The Catalanagan River (center) acts as the boundary line for the nationally protected Northern Sierra Madre Natural Park (NSMNP) at our study site Dunoy in San Mariano of northeast Luzon. This site contains one of the last remaining strongholds for the Philippine crocodile population throughout the archipelago. In the photograph below, to the left of the Catalanagan River is the beginning of an agricultural landscape which dominates the Municipality of San Mariano. To the right of the Catalanagan River are the foothills of the Sierra Madre Mountains and the beginning of the NSMNP.



Figure 6. Philippine crocodile habitat at our study site Narra in the Municipality of San Mariano in Isabela Province, northeast Luzon. Narra is dominated by agriculture, human settlements, and grasslands resulting from decades of slash-and-burn farming. Narra resides just outside the boundary line for the Northern Sierra Madre Natural Park and is located 1.5 km west of our study site Dunoy.



Figure 7. Researchers from the Mabuwaya Foundation sit alongside Diwagden Creek after conducting Philippine crocodile surveys at our study site Diwagden. Diwagden Creek and the connecting Disulap River are characterized by alternating rapids and deep pools with steep limestone cliffs and underwater caves running along the banks.



Figure 8. An agriculturally dominated landscape at our study site Dinang in the Municipality of San Mariano of Isabela Province in northeast Luzon. A dirt road and Barangay Cadsalan sit in the center of the photograph, with the Ilaguen River to the left of Cadsalan, and Dinang Creek (hidden in the tree line) to the right of Cadsalan. Dinang Creek stretches for 11 km surrounded by farmlands and over 50 households from Barangay Cadsalan before draining into the Ilaguen River. Dinang Creek is a known breeding site for Philippine crocodiles in San Mariano, with the surrounding tree line that acts as a buffer zone to protect critical nesting and hatchling habitat.



Figure 9. Philippine crocodile habitat at our study site Baliao in the Municipality of San Mariano of Isabela Province in northeast Luzon. Baliao is characterized by a network of small canals running between rolling hills completely dominated by agriculture. Land use is defined by small agricultural plots with irrigated rice fields in the valleys, banana plantations on steep slopes, and upland rice and yellow corn covering the hill tops.



Figure 10. Our study site at Dication Lake (center) with the Sierra Madre Mountains (left) and Pacific Ocean (right) in the background. Dication Lake resides in the Municipality of Divilacan, situated along the eastern range of the Sierra Madre Mountains on the Pacific Coast of Luzon Island, Philippines. Located within the Northern Sierra Madre Natural Park, Dication is a 140,000 m² artificial lake where the surrounding habitat is characterized by lowland dipterocarp forest.



Figure 11. A Philippine crocodile resting during the daytime in an underwater cave of the Catalangan River at our field site Dunoy. Daytime snorkel surveys revealed that *C. mindorensis* use underwater caves and crevices as daytime resting retreats.



Figure 12. Violin plot showing relative condition factor (K_n) values for headstart (N = 10) and wild (N = 17) Philippine crocodiles sampled in San Mariano, Isabela Province in northeast Luzon, Philippines. Statistical analysis revealed that body condition (K_n) for wild crocodiles (mean $K_n = 1.06$) was significantly higher than headstart crocodiles (mean $K_n = 0.93$).

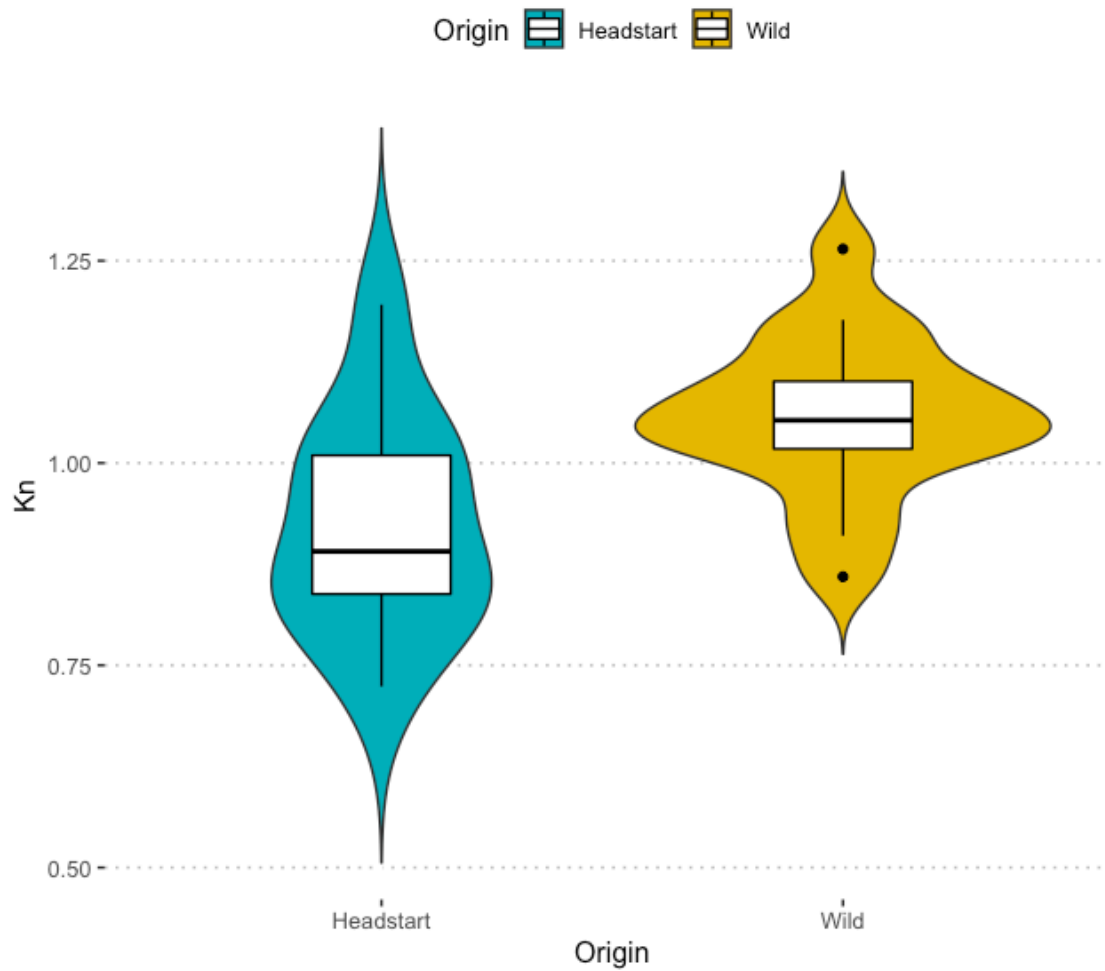


Figure 13. A Philippine crocodile resting within a rice paddy at our field site Dunoy. The local farmer who works these crops noted the crocodile living here for the past several years, routinely coming out to bask during the day time, yet quick to disperse into a nearby river whenever people come around. Snails were the most frequently recovered prey group for Philippine crocodiles in our study, with 50% of all crocodiles feeding on apple snails (*Pomacea canaliculate*). The invasive apple snail feeds on young rice seedlings and is the leading agricultural pest in the Philippines.

