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Use of diet and body condition assessments as intermediate indicators of translocation success in the Critically Endangered Philippine crocodile (*Crocodylus mindorensis*)

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Abstract

1. Intermediate metrics of translocation success are useful for long-lived, slow to mature species where survival and reproduction happen over decades.
2. With fewer than 150 individuals in the wild, the Critically Endangered Philippine crocodile (*Crocodylus mindorensis*) is one of the most threatened species on Earth. This study presents the first analysis of diet and body condition of wild Philippine crocodiles and headstarted (i.e. captive-reared) individuals released into the wild over the last decade, and uses these results to show how diet and body condition can be pertinent intermediate metrics of translocation success.
3. Analyses of stomach contents revealed 17 different aquatic and terrestrial invertebrate and vertebrate prey species. Interestingly, 70% of Philippine crocodiles showed snails to be the predominent prey type, followed by fish (36.7%), birds (33.3%) and reptiles (33.3%). More than 50% of crocodiles consumed the invasive golden apple snail, a leading agricultural pest. Regardless of crocodile history (wild vs. headstarted) or size class (juvenile vs. adult), no evidence was found for dietary differences in percentage occurrence, percentage composition or prey diversity.
4. Body condition was significantly higher in wild compared with headstarted individuals when analysed together in a pooled group, although neither group differed significantly from the standardized expectation, and headstarted individuals were not significantly different when body condition was derived independently for the two groups.
5. This study provides a working example of how assessing the convergence of diet and body condition between translocated and wild individuals can provide complementary monitoring parameters to demonstrate post-release establishment of translocated crocodylians. The congruent dietary composition and comparable body condition observed in this study suggest that headstarted crocodiles adapt well following release.

6. *Crocodylus mindorensis* survives in an agricultural landscape and is likely to play an ecologically important role by exploiting invasive species, reinforcing the importance of this species to local communities.

KEYWORDS
conservation, crocodylians, endangered, headstart, invasive species, Southeast Asia

1 | INTRODUCTION

Wildlife population declines are evident at a global scale (Dirzo et al., 2014) and management strategies involving conservation translocations are becoming increasingly vital for species recovery plans (Armstrong & Seddon, 2008). Following official guidelines defined by the 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). Evaluation of the success of such programmes requires post-release monitoring, often focusing on key parameters capable of demonstrating the establishment of a self-sustaining population (Armstrong & Seddon, 2008). Reviews of translocation projects globally have found generally low to average success rates for many taxa (Griffith et al., 1989; Dodd & Siegel, 1991; Fischer & Lindenmayer, 2000), a situation compounded by inadequate monitoring and difficulties inherent in the evaluation of long-term success (Germano & Bishop, 2009). To improve the probability of success for both continuing and future translocation efforts, programmes must incorporate rigorous long-term monitoring protocols and frequent dissemination of information throughout the course of the translocation effort (IUCN/SSC, 2013).

Headstarting – one form of translocation – has become a common management activity to reinforce threatened wild populations (Redford et al., 2011; McGowan, Traylor-Hozer & Leus, 2017). Headstart programmes aim to improve the survival rate of young by rearing them in captivity during early, more vulnerable life stages, and releasing individuals into the wild at a more advantageous size and age (Alberts, 2007). This strategy is expected to increase wild population numbers by counteracting high neonate and juvenile mortality (Alberts & Phillips, 2004). Since its initial conservation application in the 1970s for marine turtles (Pritchard, 1979), headstart programmes have continued to play an integral role in recovery of a diverse range of taxa (Seijas, 1995; Hudson & Alberts, 2004; van de Ven et al., 2009; Yang et al., 2018).

Despite the potential success of headstarting, questions have arisen concerning its efficacy (Dodd & Siegel, 1991; Seddon, Armstrong & Maloney, 2007; Escobar, Besier & Hayes, 2010). Captive conditions may decrease post-release survival rates through reduced health (Snyder et al., 1996) or wild behaviour incompetence (Alberts, 2007). For example, the inability to forage efficiently on natural food resources can have a detrimental impact on post-release behavioural and physiological processes (Brambell, 1977; Bowen, Conant & Hopkins-Murphy, 1994). Diet has been demonstrated to affect the growth, behaviour, reproduction and body condition of crocodylians (Lang, 1987; Delany, Linda & Moore, 1999; Platt et al., 2013), all of which are critical life history characteristics to understand when establishing effective management strategies (Saalfeld, Conway & Calkins, 2011). Therefore, diet (e.g. percentage occurrence, percentage composition or prey diversity) or health-based (e.g. body condition) metrics could provide suitable indicators of individual post-translocation success (Baker et al., 2021). Furthermore, non-reproduction-based metrics may be especially critical for long-lived species, whose reproductive success may take years or decades to assess, or when dealing with biologically time-sensitive scenarios (i.e. threats of extinction; Pinter-Wollman, Isbell & Hart, 2009).

Crocodylians (crocodiles, alligators, caimans and gharials) are long-lived species characterized by delayed sexual maturity (5–15 years; Ross, 1998; Grigg & Kirschner, 2015), iteroparity and high fecundity, but high egg and hatchling mortality (Briggs-Gonzalez et al., 2017). They comprise the proportionately most threatened Order, with 30.4% of extant species listed as Critically Endangered on the IUCN Red List (IUCN, 2020). Translocation programmes, in one phase or another, are critical conservation strategies for all seven Critically Endangered species: (i) Philippine crocodile (*Crocodylus mindorensis*) in the Philippines (van Weerd & van der Ploeg, 2008); (ii) Siamese crocodile (*Crocodylus siamensis*) in Thailand (Simpson & Bezuijen, 2010); (iii) Chinese alligator (*Alligator sinensis*) in China (Wang et al., 2011); (iv) gharial (*Gavialis gangeticus*) in India and Nepal (Whitaker & Basu, 1983; Maskey et al., 2006); (v) Orinoco crocodile (*Crocodylus intermedius*) in Venezuela (Muñoz & Thorbjarnarson, 2000); (vi) Cuban crocodile (*Crocodylus rhombifer*) in Cuba (Targarona et al., 2010); and (vii) West African slender-snouted crocodile (*Mecistops cataphractus*) in Côte d'Ivoire (M.H. Shirley, pers. comm.). Despite the longevity of some of these programmes, and available literature providing baseline data for non-reproduction-based metrics (e.g. diet; Rice, 2004; Platt et al., 2013), little effort has been made to use these metrics to evaluate translocation success (but see Elsey et al., 1992).

Crocodylus mindorensis is one of the rarest vertebrates on Earth, with an estimated wild population of fewer than 150 mature individuals (van Weerd & van der Ploeg, 2008; van Weerd et al., 2016). It is a relatively small (maximum length 3.02 m) freshwater crocodylian endemic to the Philippine archipelago (Figure 1), where it is protected under Republic Act 9147 (van Weerd et al., 2016). Historically, with over 7,100 islands and a land mass of

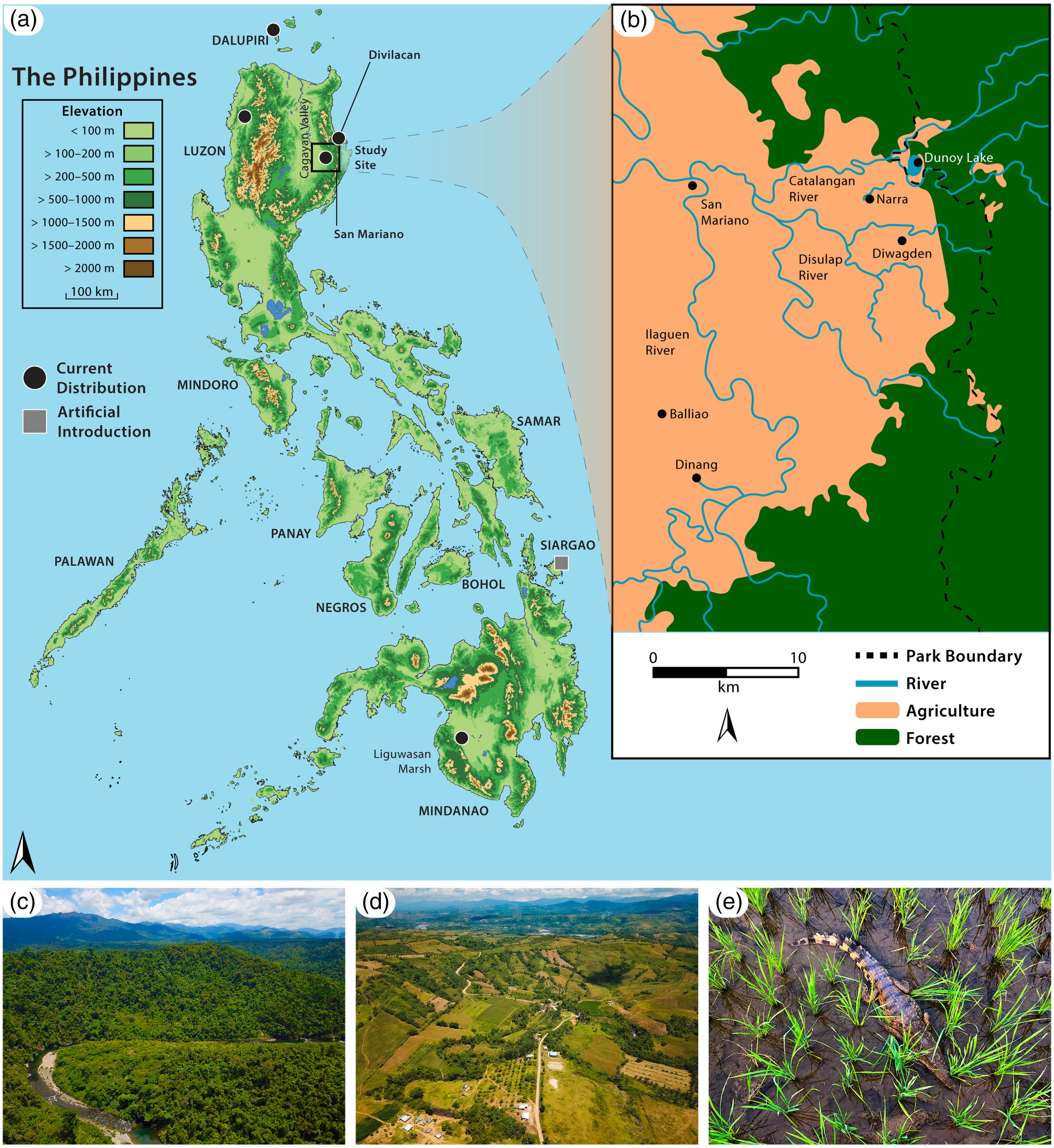

FIGURE 1 (a) Map of the Philippines showing current distribution records, along with an artificially introduced population, for *Crocodylus mindorensis*. (b) Map of study sites (Dunoy Lake, Narra, Diwagden, Dinang, and Balliao) in the Municipality of San Mariano in Isabela Province with orange shading highlighting agriculture habitat, dark green shading showing forest cover and the border of the Northern Sierra Madre Natural Park (NSMNP) indicated with a dashed black line for reference. (c) Aerial view of the Catalangan River running through more pristine habitat of the NSMNP in Isabela Province. (d) Agriculture-dominated landscape at Dinang study site in the Municipality of San Mariano showing a dirt road and the village of Lumalog (Barangay Cadsalan) in the centre and Dinang Creek hidden in the tree line to the left. (e) Image of *C. mindorensis* on a rice farm from Isabela Province, Philippines

300,000 km^2, the Philippines was >85% forested and *C. mindorensis* was distributed widely throughout the archipelago (Ross & Alcala, 1983; Brown et al., 2013). However, the Philippines has lost most of its natural wetlands, and retains only 4–8% of its original forest cover (Brown et al., 2013). *Crocodylus mindorensis* is now restricted to three localities (northern Luzon Island, Mindanao Island and Dalupiri Island), occupying a total area of less than 2,000 km^2 (Figure 1; van Weerd et al., 2016), where it survives in predominantly agricultural landscapes, often in close proximity to densely populated human settlements where they are sometimes killed out of fear and misinformed beliefs (van Weerd & van der Ploeg, 2012). Significant conservation measures began in 1999 after the discovery of a remnant population in San Mariano, Isabela Province, northern Luzon Island (Figure 1; van Weerd, 2010). Here, the Mabuwaya Foundation implements a long-term, *in-situ* conservation programme, including nest protection and headstarting (van Weerd & van der Ploeg, 2008). In addition to conservation efforts on Luzon Island, a population is also being introduced artificially on Siargao Island in the south-eastern Philippines as part of a new translocation programme (Rainier et al., 2016).

Despite rigorous conservation and monitoring efforts, and recent studies on the basic ecology of *C. mindorensis* (for a review, see van Weerd et al., 2016), only two published studies provide any assessment of post-release performance of headstarted individuals (van Weerd & van der Ploeg, 2008; van de Ven et al., 2009). Furthermore, there is a paucity of information on diet and body condition for naturally wild and headstarted Philippine crocodiles. This study proposes diet and body condition as monitoring metrics for Philippine crocodile headstarting success. To do this, the diet and body condition of both wild and headstarted *C. mindorensis* in northern Luzon are compared and implications for translocation monitoring discussed. This study is among the first to compare the diet and body condition of headstarted and wild crocodylians (see also Elsey, 1992; Elsey et al., 1992), which will both improve translocation standards for crocodylians globally and have additional application to *C. mindorensis* conservation programmes.

2 | METHODS

2.1 | Ethics declarations

All samples were collected in strict accordance with the regulations established by the University of Oklahoma's Institutional Animal Care and Use Committee (IACUC permit no. R18–001). Fieldwork was conducted under the Wildlife Gratuitous Permit Agreement Nos 2018-09 (Renewal) and 2019-04 (Renewal) between the Mabuwaya Foundation and the Philippine Department of Environment and Natural Resources.

2.2 | Study site

Field studies were conducted from the end of the 2018 north-east monsoon season (21 February 2018) through the dry season and concluded at the end of the south-west monsoon season (16 October 2018). Surveys were conducted at six sites, five in San Mariano Municipality (Dunoy Lake and Catalangan River, Narra, Diwagden, Dinang, and Baliao) and one in Divilacan Municipality (Dicatian Lake), Isabela Province. Both municipalities are located in north-east Luzon Island along the northern Sierra Madre mountain range (Figure 1). A large portion of the northern Sierra Madre is protected within the Northern Sierra Madre Natural Park. Outside the Natural Park, the landscape is intensely dominated by agriculture (Figure 1; van Weerd & van der Ploeg, 2012). With the exception of Baliao, all sites are designated Philippine crocodile sanctuaries (van der Ploeg et al., 2017) and have been used as release sites since 2007. Both wild and headstarted crocodiles were available for capture at all sites. Habitats ranged from seasonally fast-flowing rivers and small lakes surrounded by degraded forest, bamboo groves and interspersed corn and rice fields in the foothills of the Sierra Madre, to networks of small creeks and canals running between agriculture plots (Supplementary Data).

2.3 | Data collection

The presence or absence of crocodiles was determined using standard Mabuwaya Foundation nighttime spotlight surveys (van de Ven et al., 2009) and daytime snorkel surveys to search underwater caverns. Detected crocodiles were captured using baited snare traps deployed overnight (Woodward & David, 1994), manual snaring during snorkel surveys or by hand. All crocodiles were measured for total length (TL), snout–vent length (SVL), tail girth (TG), neck girth (NG), head length (HL), tail length (Tail), mass and sex following Zweig et al. (2014). Crocodiles were identified as wild or headstarted by the presence or absence of caudal scute notching (van Weerd & van der Ploeg, 2012). Newly captured wild crocodiles were caudal scute notched, and passive integrated transponder tags were implanted under the nuchal rosette of all captured individuals. Each individual was classified as juvenile (<1.5 m TL) or adult (≥1.5 m TL) (van Weerd & van der Ploeg, 2012). All crocodiles were released at the site of capture within 12 h of capture.

2.4 | Diet analysis

Stomach contents were extracted using the modified hose-Heimlich technique (Fitzgerald, 1989; Shirley et al., 2016). Stomach flushing is a non-destructive technique demonstrated to recover >95% of contents present in crocodylian stomachs (Fitzgerald, 1989; Rice, 2004; Rice et al., 2005). Contents were sorted, counted, digitally photographed and identified to the lowest possible taxonomic classification. Contents were then assigned to one of 11 categories: snails, crabs, insects, fish, amphibians, reptiles, birds, mammals, gastroliths, vegetation and 'other', which were excluded from subsequent analyses. To reduce bias from differential prey digestion rates (Jackson, Campbell & Campbell, 1974; Magnusson, da Silva & Lima, 1987; Platt et al., 2013), and under the assumption that prey within any one category digests at a consistent rate across crocodile type (Magnusson, da Silva & Lima, 1987; Thorbjarnarson, 1993; Tucker et al., 1996; Platt et al., 2013), variation in diet between wild and headstarted crocodiles was analysed within prey categories. Differences between groups (wild vs. headstarted) was tested for percentage occurrence (using chi-squared tests; Saalfeld, Conway & Calkins, 2011), percentage composition (using Wilcoxon rank sum tests) and dietary niche breadth and degree of specialization (using the Shannon–Weiner diversity index H'; Schoener, 1968; Platt et al., 2013). The Supplementary Data contains additional details.

2.5 | Body condition analysis

Body condition indices, such as Fulton's condition factor (K) and the relative condition factor (K_n) (Le Cren, 1951), are regularly used as indicators of crocodylian health and well-being (Elsey et al., 1992; Rice, 2004; Fujisaki et al., 2009; Mazzotti et al., 2012; Shirley et al., 2016). *Crocodylus mindorensis* body condition was evaluated following Zweig et al. (2014). Philippine crocodiles did not exhibit isometric relationships between different lengths (e.g. TL, SVL, HL) and masses, indicating that Fulton's K would not be an appropriate body condition index (Supplementary Data). The relative body condition index K_n does not assume isometric relationships and was, therefore, used to evaluate body condition of *C. mindorensis* (Le Cren, 1951). The mass–length relationship (b) was determined via linear regression using empirical data (Le Cren, 1951). To obtain the K_n for each individual, the mass–SVL relationship was modelled over all individuals combined (i.e. both wild and headstarted) and also by treating the wild and headstarted groups as two separate populations. Relative K_n was calculated for each individual as the ratio of observed mass to theoretically expected mass ($K_n = W/W_e$), and a Student's t-test was used to test the difference between crocodile groups, and to test the mean values of estimated K_n for each group against the standard condition value $K_n = 1$ (Supplementary Data).

TABLE 1 Prey items, gastroliths, and vegetation observed among wild ($N = 20$), headstarted ($N = 10$) and all combined ($N = 30$) Philippine crocodiles from Isabela Province, Luzon Island, Philippines. Number of crocodiles (n) and percentage occurrence (%) for each prey category shown for wild and headstarted crocodiles, followed by the results of chi-square analysis of each stomach content category frequency among wild and headstarted animals. In cases where prey items were identifiable to genus or species, scientific and common names are provided below the respective prey category for reference

	Wild		Headstart		Total		Statistic	
Prey category	***n***	**%**	***n***	**%**	***n***	**%**	χ^2	***P*-Value**
Snails	14	70.0	7	70.0	21	70.0	0.00	1.00
Pomacea canaliculate (Golden apple snail)								
Melanoides turricula (Fawn melania)								
Crabs (unidentified)	4	20.0	2	20.0	6	20.0	0.00	1.00
Insects	6	30.0	2	20.0	8	26.7	0.02	0.88
Xylotrupes sp. (Scarab beetle)								
Anomala sp. (Scarab beetle)								
Gryllotalpa orientalis (Mole cricket)								
Fish	8	40.0	3	30.0	11	36.7	0.02	0.89
Channa striata (Striped snakehead)								
Clarias batrachus (Walking catfish)								
Amphibians	4	20.0	1	10.0	5	16.7	0.03	0.86
Limnonectes macrocephalus (Luzon fanged frog)								
Reptiles	5	25.0	5	50.0	10	33.3	0.92	0.34
Coelognathus erythrurus (Philippine rat snake)								
Ptyas luzonensis (Smooth-scaled mountain rat snake)								
Eutropis cumingi (Cuming's eared skink)								
Varanus marmoratus (Marbled water monitor)								
Cuora amboinensis (Amboina box turtle)								
Birds	5	25.0	5	50.0	10	33.3	0.92	0.34
Gallinula chloropus (Common moorhen)								
Amaurornis olivacea (Philippine bush-hen)								
Centropus bengalensis (Lesser coucal)								
Mammals	4	20.0	3	30.0	7	23.3	0.02	0.88
Rattus tanezumi (Asian house rat)								
Gastroliths	13	65.0	6	60.0	19	63.3	0.00	1.00
Vegetation (unidentified)	9	45.0	1	10.0	10	33.3	2.27	0.13

3 | RESULTS

3.1 | Data collection

Stomach contents were collected from 30 Philippine crocodiles (22 females, eight males) ranging in size from 71.0 to 264.5 cm TL (SVL = 14.1–143.0 cm, 1.01–106.4 kg), including 28 from San Mariano and two from Divilican. Of these, 20 were wild (13 females, seven males), including 14 adults and six juveniles ranging in length from 71.0 to 264.5 cm TL (SVL: 35.0–143.0 cm; $\bar{X}$ = 68.2 ± 5.65 cm). Ten were headstarted (nine females, one male), released an average of 5.65 years before capture, including six juveniles and four adults ranging in length from 72.3 to 169.9 cm TL (SVL: 36.6–90.4 cm; $\bar{X}$ = 82.9 ± 5.74 cm). Both groups were of similar length (SVL: $t = -1.62$, $P = 0.116$).

TABLE 2 Prey items, gastroliths and vegetation observed among juvenile ($N = 12$) and adult ($N = 18$) Philippine crocodiles from Isabela Province, Luzon Island, Philippines. Number of crocodiles (n) and percentage occurrence (%) for each prey category shown for juvenile and adult crocodiles, followed by the results of chi-square analysis of each stomach content category frequency among age classes

	Juvenile		Adult		Stat	
Prey category	*n*	%	*n*	%	χ^2	*P*-Value
Snails	8	66.7	13	72.2	0.00	1.00
Crabs	3	25.0	3	16.7	0.01	0.93
Insects	5	41.7	3	16.7	1.20	0.27
Fish	4	33.3	7	38.9	0.00	1.00
Amphibians	3	25.0	2	11.1	0.25	0.62
Reptiles	2	16.7	8	44.4	1.30	0.24
Birds	3	25.0	7	38.9	0.16	0.69
Mammals	3	25.0	4	22.2	0.00	1.00
Gastroliths	6	50.0	13	72.2	0.72	0.39
Vegetation	4	33.3	6	33.3	0.00	1.00

3.2 | Diet analysis

No empty stomachs were observed in this study. For all crocodiles combined, snails were the most prominent prey group (70% occurrence), followed by fish (36.7% occurrence), birds and reptiles (33.3% occurrence each), while the remaining prey groups were all represented in 16–27% occurrence (Tables 1, 2). There was no significant difference in percentage occurrence (Table 1) or percentage composition (Table S1; Supplementary Data) of any prey category between wild and headstarted crocodiles. Dietary diversity (H') (wild = 0.89, headstart = 0.70) was not significantly different ($W = 73$, $P = 0.228$) and wild and headstarted crocodiles exhibited comparable specialization (J') (wild = 0.43, headstart = 0.34; Table S2). Gastroliths were recovered in almost equal proportions for both groups (65% wild, 60% headstarted; Table 1). Diet did not vary significantly between juvenile and adult percentage occurrence (Table 2) or percentage composition (Table S3; Supplementary Data).

3.3 | Body condition

Three individuals were excluded from the body condition analysis, including the two Divilacan individuals to avoid any bias in relative K_n resulting from comparing individuals from isolated populations, leaving 17 wild and 10 headstarted. When modelling the mass–SVL

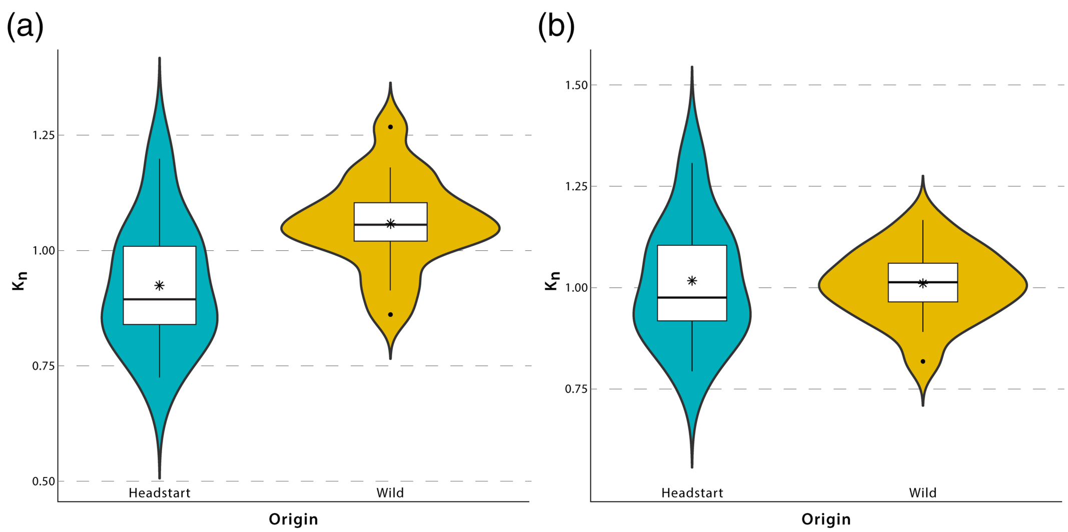

FIGURE 2 Results of body condition analyses represented by box plots within violin plots, showing (a) that wild *C. mindorensis* had significantly higher body condition values (K_n) compared with headstarted individuals when combining all individuals to calculate K_n, and (b) that there was no difference in body condition between wild and headstarted *C. mindorensis* when K_n was calculated separately for the wild and headstarted groups. The middle lines represent median values; asterisks represent means

relationship using all individuals combined, body condition (K_n) was significantly higher in wild than headstarted crocodiles ($t = -2.88$, $P = 0.008$; Figure 2). The mean condition of wild crocodiles ($K_n = 1.060$) was significantly higher than the standard condition value of $K_n = 1$ ($t = 2.38$, $P = 0.030$; Figure 2; Table S4), whereas the mean condition of headstarted crocodiles ($K_n = 0.925$) was not significantly different ($t = -1.71$, $P = 0.121$). However, when modelling the mass–SVL relationship as two separate populations (K_n wild $= 1.003$, K_n headstarted $= 1.010$) to obtain K_n, no differences in body condition were observed ($t = 0.13$, $P = 0.895$). No physical abnormalities or deficiencies were observed in headstarted crocodiles during the study.

4 | DISCUSSION

Post-release monitoring is fundamental to conservation translocations (IUCN/SSC, 2013). Timely and, most importantly, pertinent monitoring methods provide an effective means of evaluating programmatic and individual translocation success. Although survivorship and fecundity are commonly used success metrics, behavioural performance of released individuals compared with wild individuals (Pinter-Wollman, Isbell & Hart, 2009) can be critical metrics of intermediate success, especially for long-lived or species slow to mature. Diet and body condition can supplement or serve as proxies for long-term survival and reproductive success (Pinter-Wollman, Isbell & Hart, 2009). When compared with a resident wild population, diet and body condition can yield valuable metrics for assessing the ability of translocated animals to adjust to and become established at a new site or, in the case of headstarted individuals, in the wild (Richards & Short, 2003). In this way, regular monitoring of diet and body condition may be especially useful for long-lived, threatened vertebrates whose reproductive success may take decades to assess and when management decisions must be reached promptly. The need for such metrics is even greater for cryptic species with high capacity for long-distance dispersal, where recapture of translocated individuals is low frequency and often over considerable time (only 11 of 150 headstarted *C. mindorensis* were recaptured as part of this study). This study provides a working example of how assessing the convergence of diet and body condition between translocated and wild individuals can provide pertinent, and complementary, monitoring parameters to demonstrate post-release establishment of translocated crocodylians.

Evaluation of individual diets can be informative as an indicator of foraging patterns, particularly in the case of translocated and headstarted individuals where captive-rearing effects related to incompetent foraging behaviours of released individuals are of major concern (Jule, Leaver & Lea, 2008). Headstarted Philippine crocodiles exhibited no dietary differences compared with their wild counterparts (Table 1), strongly supporting their ability to forage on the expected natural prey base after release. The only prior existing information on *C. mindorensis* diet (van Weerd & van der Ploeg, 2012) suggested that *C. mindorensis* conformed to general expectations for crocodylian ontogenetic dietary trends (Lang, 1987; Thorbjarnarson, 1988). However, this study shows that both juvenile and adult Philippine crocodiles consume a wide diversity of 17 different aquatic and terrestrial invertebrate and vertebrate prey species. Snails, in particular, were the most frequently recovered prey type regardless of crocodile history (wild vs. headstart) or size class (Tables 1, 2), consistent with observations from other crocodylians (Diefenbach, 1979; Thorbjarnarson, 1993; Platt et al., 2006). It has been suggested that crocodiles rely on tactile and chemical cues to detect snails and bottom-dwelling eel-like fish under water (Platt et al., 2006). Such a common occurrence of these prey items in headstarted crocodile stomachs may reflect positively on their foraging competence despite spending the initial portion of their life being reared in captivity. In addition, the abundance and diversity of prey species from both agricultural habitats (e.g. invasive golden apple snail (*Pomacea canaliculata*), striped snakehead (*Channa striata*), walking catfish (*Clarias batrachus*) and Asian house rat (*Rattus tanezumi*)) and less disturbed habitats (e.g. Philippine bush-hen (*Amaurornis olivacea*), smooth-scaled mountain rat snake (*Ptyas luzonensis*) and Philippine rat snake (*Coelognathus erythrurus*)) suggests that headstarted *C. mindorensis* are exploiting a similar breadth of habitat and, thus, have foraging behaviours comparable with those of their wild counterparts.

To date, only one previous study compared dietary habits between captive-released and wild crocodylians (Elsey, 1992), which found that farm-released American alligators (*Alligator mississippiensis*; after being raised in captivity for 2 years) had similar diet and foraging habits to wild alligators (Elsey, 1992). The present study found similar results, but also illustrated that both juvenile and adult Philippine crocodiles consume a comparably broad spectrum of prey inhabiting a variety of habitats and trophic classes (Table 2). This suggests that dietary studies using percentage occurrence, percentage composition and prey diversity are suitable for assessing intermediate translocation success, for which data from a local (i.e. wild) or otherwise established population is essential (Figure 3). Because wild populations provide a valuable baseline for comparison, a convergence of these dietary measures between translocated and wild individuals, as this study observed, would indicate the extent to which translocated animals successfully adjust to wild conditions.

Body condition indices are an easily accessible metric of individual health; therefore, comparing the body condition of translocated individuals with baseline expectations from wild individuals provides a rapid assessment on how these individuals are adjusting to wild conditions. Although body condition values for the wild and headstarted Philippine crocodile groups showed a degree of overlap, wild *C. mindorensis* individuals were found to have statistically significant higher body condition compared with headstarted individuals when both groups were treated as the same population (Figure 2). However, the mean body condition for both groups either met or exceeded the standard condition value (i.e. $K_n \geq 1.0$; Table S4), suggesting that headstarted crocodiles still met the normal expectations for body condition in this population. Further, when these two groups were treated as separate populations as a means to achieve a ‘true’ baseline K_n (e.g. K_n for wild

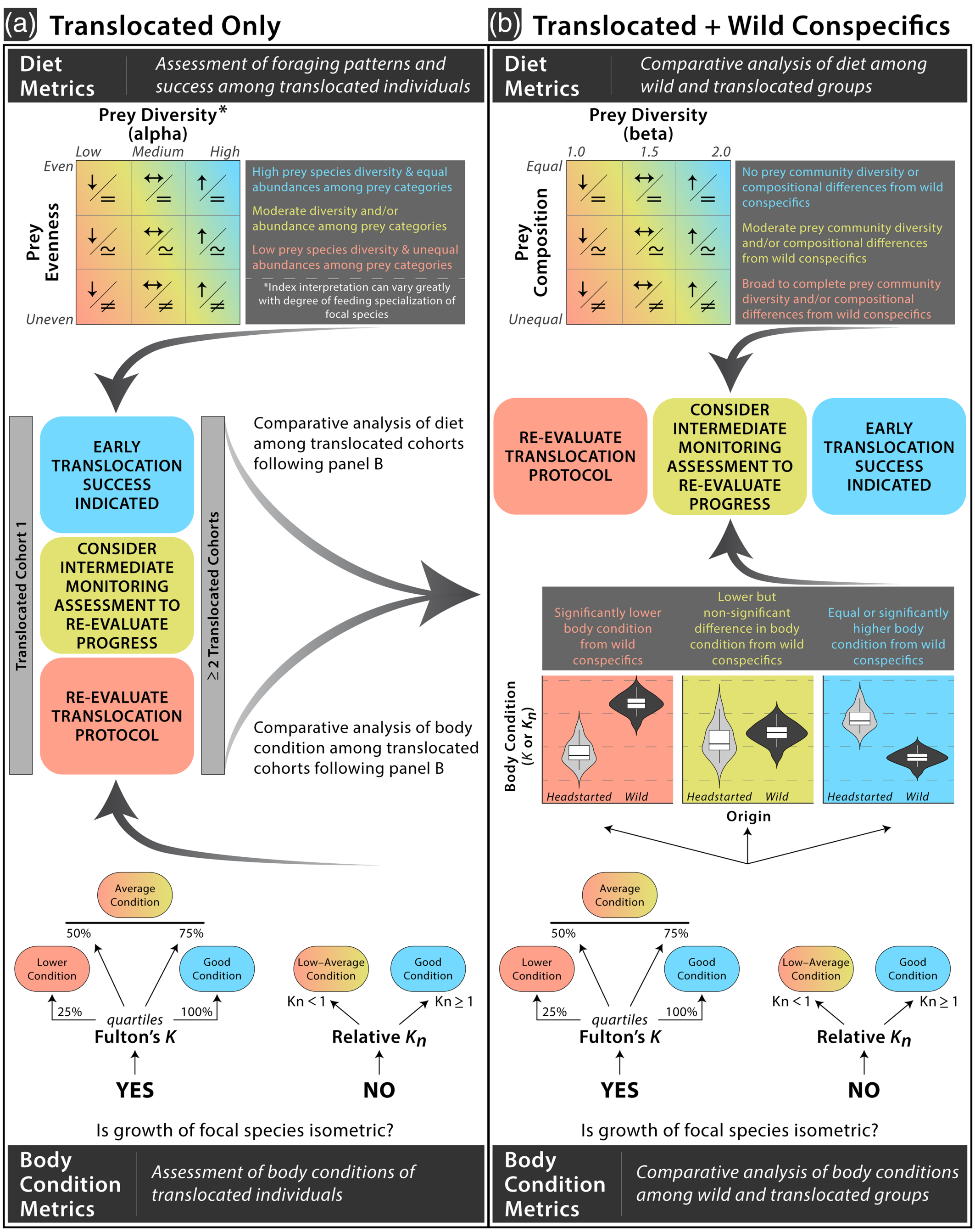

FIGURE 3 Guidelines for evaluating intermediate translocation success using diet and/or body condition-based metrics for cases without (a) and with (b) previously translocated cohorts or wild conspecifics available for comparison. These proposed guidelines should be adapted to species-specific cases and contexts and evaluated based on data from regular monitoring efforts. Conflicting conclusions from either metric should result in further investigations to identify underlying causes of the discrepancy

C. mindorensis) for comparison, no differences in body condition were observed. Body condition in crocodylians can be influenced by abiotic factors (location, water level and temperature) and biotic factors (size, sex and habitat), all of which change over time, often cyclically (Green, 2001; Rice, 2004; Mazzotti et al., 2012). Previous work on the effect of these factors, including comparison between demographic groups, has shown that body condition indices are effective and efficient indicators of crocodylian population health over time (Fujisaki et al., 2009; Mazzotti et al., 2012). Although a multitude of factors can influence individual body condition, when these data are collected regularly, they provide managers with an important means of tracking health trends for improved management decisions (Mazzotti et al., 2012). Owing to the limited sample size of this Critically Endangered species, further studies are needed for greater inferential insight of the confounding factors potentially influencing population health.

Overall, body condition comparisons using K_n are limited unless the slopes of the regression of the natural log of length on the natural log of mass are identical for all 'populations' (Murphy, Brown & Springer, 1990). Although previous crocodylian studies have used K_n (e.g. Dalrymple, 1996; Barr, 1997; Zweig et al., 2014), each employed a different variant of relative K_n, complicating comparisons using this specific body condition metric across disparate studies, including over time as part of regular monitoring. For *C. mindorensis*, it is as yet unclear how the limited sample size (as a result of small populations) affected the inference of non-isometric growth and more extensive sampling will be required to better understand growth relationships in this species, ideally enabling future use of Fulton's *K*. Although Fulton's *K* is limited by its assumption of isometric growth, it is advantageous because it can be used to make comparisons across space, time and populations – characteristics that are critical for long-term species monitoring (Fujisaki et al., 2009; Mazzotti et al., 2012).

Little work has been done to compare the body condition of wild and translocated crocodylians (but see Elsey et al., 1992); however, the results of this study, and previous work comparing populations under different environmental conditions (Delany, Linda & Moore, 1999; Brandt et al., 2016; Shirley et al., 2016) suggest that there is considerable potential for employing condition indices as indicators of intermediate translocation success (Figure 3). The condition indices Relative K_n (when growth is not isometric) and Fulton's *K* (when growth is isometric) could be used as benchmarks for body condition metrics of intermediate translocation success where baseline data from wild conspecifics is key for making effective evaluations (Figure 3). Application of Relative K_n could make comparisons against the standard body condition ($K_n = 1$), where significantly lower values ($K_n < 1$) among the translocated population would indicate a cause for concern, and values that meet or exceed null expectations ($K_n \geq 1$) would lend support to translocation success at the time of measurement (Figure 3). In addition, further insights could be obtained by making comparisons of K_n against the wild and translocated groups, and if both groups meet the appropriate assumptions, K_n values can be derived from treating the two groups as the same population (Figure 3). For systems that meet the assumptions of Fulton's *K*, and as suggested by Zweig et al. (2014), data could be partitioned into quartiles, with inferred body conditions and support for translocation success increasing from the bottom to top quartiles. Here, the top quartile may indicate good condition, the middle two average condition and the bottom quartile low condition, suggesting greater cause for concern for the success of the translocation programme in question (Figure 3). Not only does the application of body condition indices as metrics provide a more standardized grading system of intermediate and long-term programme success, but it also presents a pertinent assessment tool for long-lived species where reproductive success may take decades to assess and when rapid evaluation for management purposes is needed.

Beyond its use as a metric of translocation success, studies of diet are essential in understanding species ecology (Rosenberg & Cooper, 1990). This study found that *C. mindorensis* consumed a generalist diet reflective of the available prey items and habitat variability at the study sites (Tables 1, 2; Supplementary Data). It is both astonishing and encouraging that one of the world's rarest vertebrate species survives in a human-dominated landscape consuming mostly introduced species. However, this study highlights the remarkably adaptive capacities of crocodylians and suggests that if protected from hunting and with sufficient prey availability, *C. mindorensis* and other heavily threatened crocodylians are able to survive in heavily degraded habitats.

Both prey snail species, the golden apple snail (*P. canaliculata*) and fawn melania (*Melanoides turricula*), were observed in high abundance throughout the study sites, although the invasive *P. canaliculata* seemed to occur more frequently in agriculture-dominated habitats, whereas *M. turricula* appeared to occur in a variety of disturbed wetlands and fast-flowing rivers. These results suggest that Philippine crocodiles may be exploiting an abundant prey resource opportunistically as other prey types are less available owing to the extensive habitat loss in the country. For example, despite general expectations of crocodylian ontogenetic dietary trends, snails were prominent in the diet of adult *C. mindorensis*. Reliance on the invertebrate prey base has been previously hypothesized to result from their high abundance and diversity in the environment, as well as their net energetic value (Balaguera-Reina et al., 2018). Digestion rates and gut retention times can bias stomach content data owing to inflated observability of chitinous remains that have longer digestion times (e.g. snail opercula, crab carapaces, turtle scutes, fish scales, mammal hair and feathers; Jackson, Campbell & Campbell, 1974; Platt et al., 2013), suggesting that even the relative importance of these prey today must be interpreted cautiously. However, vertebrate remains are similarly resistant to digestion (Delany & Abercrombie, 1986; Janes & Gutzke, 2002) and therefore would also be expected to be over-represented if significant numbers of these taxa were being consumed (Platt et al., 2006). Because dietary trends were analysed within prey categories, any bias related to the accumulated persistence of specific prey remains is expected to be minimal (Magnusson, da Silva & Lima, 1987; Thorbjarnarson, 1993; Platt et al., 2006). In addition, the absence of stomach content data from *C. mindorensis* before widespread habitat declines in the Philippines prevents firm conclusions about resultant changes in diet over time. Data on snails in stomach contents should therefore be interpreted cautiously to avoid potentially overestimating their natural/historical importance in *C. mindorensis* diets.

Nevertheless, these observations could have potential applications beyond monitoring translocation success, including potentially improving husbandry and captive-rearing protocols for *C. mindorensis*. Snails added to captive-rearing settings as live prey may encourage natural foraging behaviours in captivity (Alberts, 2007). Snails are also an abundant, cost-effective food source with secondary advantages (e.g. dietary mineral supplementation from the snail shells; White et al., 2007). However, investigation of the relative nutritional value of snails compared with more traditional captive diets, and observations of growth and body condition in captive-held young crocodiles with snail-supplemented diets, are needed before conclusions about the long-term benefits of adding snails to the captive diet can be reached.

For non-prey items, both vegetation and gastroliths have been recovered frequently from the stomach contents of other crocodylians (for a review see Platt et al., 2013). Whereas vegetation is assumed to be ingested incidental to prey capture (Coulson & Hernandex, 1983), gastroliths are thought to be consumed deliberately by crocodylians either for better buoyancy control (Grigg & Kirschner, 2015) or improved digestive function, especially smaller crocodiles that consume chitin-rich diets such as snails (Davenport et al., 1990; Fitch-Snyder & Lance, 1993; Platt et al., 2013). Interestingly, the observation that headstarted crocodiles also consumed gastroliths, and in similar numbers compared with wild individuals, presumably reflects their ability to function naturally even after periods in captivity.

Translocation success can be challenged when there is potential for the translocated species to cause human–wildlife conflict (Ewen, Soorae & Canessa, 2014), a global crocodylian conservation issue. *Crocodylus mindorensis* today inhabits waterways within rural, impoverished communities, where the fate of the species is ultimately dependent on acceptance and support by local residents – in particular rural farmers. The invasive golden apple snail is considered an agricultural pest because it feeds on young rice seedlings and, in the Philippines alone, *P. canaliculata* invasions result in losses of US $28–45 million annually (Naylor, 1996). Most (93.3%) of the crocodiles captured in this study were within or near adjacent rice paddies, and 50% of individuals had *P. canaliculata* remains in their stomachs. Regardless of the reason why they are being consumed, and whether or not snails were historically an important part of the diet of *C. mindorensis*, this information could be promoted in environmental outreach campaigns, convincing local communities about the conservation value of this Critically Endangered species for controlling agricultural pests. The argument could be augmented with similar data on crocodile consumption of *R. tanezumi*, an agricultural pest and transmitter of disease in the Philippines (Tujan, Fontanilla & Paller, 2016), *C. striata* and *C. batrachus*, two introduced invasive fish species (Guerrero, 2014) and *Rhinella marina*, an introduced invasive toad species (Groffen et al., 2018). The absence of remains of domesticated animals (dogs, pigs) in examined crocodiles is also noteworthy, as farmers and politicians often claim that Philippine crocodiles mainly prey on livestock (Cureg et al., 2016). Future community outreach efforts by the Mabuwaya Foundation could consider incorporating such information.

Continued post-release monitoring remains critical for identifying emerging threats that may jeopardize the long-term success of translocations (Fischer & Lindenmayer, 2000), and future efforts should work to improve an understanding of the factors that result in reintroduction failures. For example, despite more than a decade of intensive community-based conservation efforts by the Mabuwaya Foundation that have been shown to have resulted in transformative community-wide support for crocodile conservation (Cureg et al., 2016; van der Ploeg et al., 2017), both wild adult and headstarted juvenile individuals were intentionally killed by community members during this study period. Although headstarted crocodiles are shown to be capable of successfully integrating into wild environments, only 11 headstarted individuals were recaptured out of 150 crocodiles that have been reintroduced to date. Future efforts should be devoted to understanding the factors that lead to individual reintroduction failures and improving the survival of released individuals. In addition, translocation success also depends on non-ecological factors (i.e. community engagement and education outreach; Fischer & Lindenmayer, 2000; Germano & Bishop, 2009). As human populations continue to grow, the long-term sustainability of all translocation programmes will depend on local, regional and national commitments among communities, government departments and conservation agencies.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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