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Scute Patterns as an Individual Identification Tool in an American Crocodile (*Crocodylus acutus*) Population on Coiba Island, Panama

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ABSTRACT.—Identification of individuals based on morphological patterns is a strategy used primarily in human forensics that has also been applied successfully in several wildlife scenarios. To date, no study has evaluated the potential of these techniques on American Crocodiles (*Crocodylus acutus*). We assessed whether the dorsal scute number and pattern of 110 American Crocodiles captured from the wild on Coiba Island, Panama could be used for individual recognition. We estimated scute variation using the number and position of scutes, testing both a binary and a coded assessment for scute presence and pattern, respectively. We analyzed scute patterns using 21 transverse scute lines (TSL) including the three most prominent scutes present on each side of the vertebral column axis. We found significant differences in the number of scutes per TSL and longitudinal scute lines (LSL) by individual. Based on both the binary and coded analyses, we identified all American Crocodiles assessed at the individual level, using only the first 13 and 10 TSL, respectively, in an anterior–posterior direction. This gave us a minimum probability of ≤ 0.0003 based on the coded analysis and $\leq 2.02 \times 10^{-5}$ based on the binary analysis to find pattern repetition (one out of 3,333 and one out of 49,504 American Crocodiles have the most-common scute pattern, respectively). Because the *C. acutus* total population of Coiba Island has been estimated as no more than 1,000 individuals, we could use this individual identification pattern recognition method (IIPR) to identify every American Crocodile inhabiting this island.

RESUMEN.—La identificación de individuos con base en patrones morfológicos es una estrategia usada principalmente en ciencias forenses, la cual ha sido también aplicada exitosamente en el estudio de vida silvestre. Sin embargo, a la fecha no existen estudios que hayan evaluado el potencial de estas técnicas en el cocodrilo americano (*Crocodylus acutus*). Este estudio evaluó la eficacia en el uso del número de escamas y patrones dorsales de escamaje como método para la identificación de individuos en *C. acutus*, con base en 110 animales colectados en la isla de Coiba, Panamá. Se estimó la variación en el escamaje usando el número y la posición de las escamas, evaluando de manera binaria y codificada la presencia/ausencia de escamas y patrones, respectivamente. Se analizaron un total de 21 líneas de escamas transversales (TSL) incluyendo las tres escamas más prominentes a cada lado de la columna vertebral. Se registraron diferencias significativas en el número de escamas por TSL y por línea de escamas longitudinales (LSL) por individuo. Con base en los dos análisis (binario y codificado) se identificaron todos los cocodrilos americanos evaluados en el presente estudio a nivel individual, usando solamente las primeras 13 y 10 TSL, respectivamente, en dirección antero-posterior. Se determinó una probabilidad mínima de repetir patrones ≤ 0.0003 con base en el análisis codificado y $\leq 2.02 \times 10^{-5}$ con base en el análisis binario (uno de 3,333 y uno de 49,504 cocodrilos americanos tendrá el patrón de escamaje más común, respectivamente). Para la isla de Coiba ha sido estimada una población total no mayor a 1,000 individuos, lo cual implica que el método propuesto en el presente estudio (patrones de reconocimiento para la identificación individual de animales con base en escamaje (IIPR) podría ser usado para identificar la totalidad de *C. acutus* que habitan esta isla.

American Crocodiles (*Crocodylus acutus*) are one of the largest crocodile species in the Americas and one of the more-threatened crocodylians in the Neotropics (Balaguera-Reina et al., 2015a). This species is widely distributed and occurs on the Pacific, Atlantic, and Caribbean coasts of North, Central, and South America, from Mexico to Peru and Florida (USA) to Venezuela (Thorbjarnarson, 1989). Being hunted for food and leather resources, persecution, and habitat modification are the major anthropogenic threats that this species has faced in the past century (Medem, 1981; Thorbjarnarson, 2010); however, after almost 40 yr of hunting bans across its range, countries such as the United States, Mexico, and Cuba have reported at least some population recovery (Thorbjarnarson et al., 2006). Nevertheless, the paucity of knowledge about the natural history of the species still limits the scope of actions needed to preserve the species (Balaguera-Reina et al., 2015b).

Historically, the individual identification of living crocodylians has been based on notching scales in the tail or on tagging (Chabreck, 1963), both requiring the capture and handling of the specimen. These techniques are time-consuming and expensive,

however, and compared to noninvasive methods can be dangerous for both researchers and crocodylians. Because of their threatened status (Thorbjarnarson, 2010), American Crocodiles are an elusive species in many countries where they are found. Furthermore, in some localities capture is complicated by their persecution by humans (Balaguera-Reina and González-Maya, 2010).

Identification of individuals based on morphological patterns is a strategy used primarily in human forensics that also has been applied successfully in several wildlife scenarios. Sea turtles (Schofield et al., 2008), whales (Hammond, 1990), and monk seals (Forcada and Aguilar, 2003) are examples of species where individual animals have been characterized. To put these pattern-recognition methods into practice, however, one must be confident that observed patterns are sufficiently variable to prevent pattern repetition. In the case of crocodylians, one simple way to distinguish individuals by pattern is to assess the scutellation (scute patterns) using conspicuous scutes on the dorsal surface. Those with osteoderms (bony elements embedded within many of the scutes, particularly dorsally) commonly bear conspicuous keels that are easy to distinguish with the naked eye from short distances (Grigg and Kirshner, 2015).

The use of unmanned aerial vehicles (UAV; also called drones) in animal ecology has been growing in the last decade

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with the potential to revolutionize the way in which animals and habitats are monitored (Linchant et al., 2015). Before this technology can be applicable to collect absolute population numbers (number of individuals present), methods must be developed to accurately identify individuals. To date, no studies attempting to identify wild crocodylians based on external, conspicuous, genetically based characters such as scutes with osteoderms have been published. Natural patterns on the tail (black spots) have been used to identify individual Nile Crocodiles (*Crocodylus niloticus*) by Swanepoel (1996); however, this method has limitations because of the necessity of having the animal completely exposed (i.e., out of the water) to see the spots, the requirement of collecting photographs from both sides of the tail in the same individual every time an identification was needed, and a lack of assessment regarding potential ontogenetic changes of these marks as the animal grows.

Morphological studies on *C. acutus* specifically based on differences in scutellation have been previously described from museum specimens or individuals kept in captivity (Neill, 1971; Brazaitis, 1973; Garrick, 1982; Ross and Mayer, 1983). These baseline studies focused on the number of scutes present in the dorsal (post-occipital, nuchal, dorsal, and tail areas) and ventral (transversal and longitudinal lines) areas, identifying likely geographical variation in American Crocodile scutellation over its range (Garrick, 1982; Ross and Mayer, 1983). More-recent studies involving scute number suggest that scutellation patterns in this species show considerable variation among localities in the same country (Seijas, 2002; Garcia-Grajales et al., 2009) and among animals from different countries (Platt et al., 2010). Therefore, this level of variation might be enough to differentiate wild populations throughout the range of *C. acutus* (Platt et al., 2010).

Currently, variation in the dorsal scutellation of *C. acutus* has never been evaluated using both the number and position of scutes to identify individuals. Therefore, we assessed the dorsal scute patterns (in the post-occipital, nuchal, and dorsal regions; Fig. 1) per transverse scute line (TSL) and longitudinal scute line (LSL) of 110 American Crocodiles captured from the wild on Coiba Island, Panama, in 2013. We also estimated the variation in scute number and position and the likelihood of pattern repetition as an identification method based on both a binary and a coded assessment. Our major hypothesis was that the overall variation in number and position of the post-occipital, nuchal, and dorsal scutes per TSL among individuals would be sufficient to be useful for individual identification pattern recognition. We call this approach individual identification pattern recognition (IIPR).

MATERIALS AND METHODS

In 2013, we captured 110 American Crocodiles from El Maria and Playa Blanca beaches on Coiba Island, Panama. Every crocodile was marked (by notching scales in the tail following a numerical series to differentiate them), sexed (via cloacal probing), measured (total length, TL), dorsally photographed, and released at the original capture zone. We also assessed the dorsal scute patterns of these individuals based on 21 TSL found on the post-occipital (1 TSL), nuchal (3 TSL), and dorsal (17 TSL) regions (Fig. 1). This included the three most prominent scutes present on each side of the vertebral column axis (LSL designated here as Z, Y, and X, left or right, from the proximal to the distal part of the vertebral column axis; Fig. 1). We

defined the last TSL on the dorsal region (in an anterior-posterior direction) based on the joint between the leg and the tail.

These data were analyzed using two methods based on presence/absence of the scute (binary [1 = present, 0 = absent]) and presence/absence and position of the scute (coded [LSL: Z, Y, and X] left or right from the proximal to the distal part of the vertebral column axis; Fig. 1). Data were statistically analyzed based on the sum of values per TSL as well as the sum of values per LSL using R software (R Development Core Team, 2012). We determined whether scute variation was equal to or differed among TSL, LSL, individual, and age group (hatchling [<30 cm TL], juvenile [30–90 cm TL], subadult [91–180 cm TL], and adult [>181 cm TL; Platt and Thorbjarnarson, 2000]). We performed Shapiro-Wilk tests to determine the normality of the data and Kruskal-Wallis (H_{df}) tests to analyze their variability. We used Dunn's test for independent samples with a Bonferroni adjustment of P -values to determine pairwise differences of mean ranks when Kruskal-Wallis tests were significant ($P < 0.05$).

The binary and coded data were used to estimate the number of patterns and their representativeness (proportionally) per TSL per individual in the total scute combinations accounted for in all regions (post-occipital, nuchal, and dorsal). Based on these binary and coded determinations, we estimated the likelihood of finding two individuals with the same scute pattern and the necessary number of TSL needed for it (called minimum probability: minimum number of individuals needed to repeat a pattern). The IIPR analysis is based on simple comparisons of TSL patterns among individuals, increasing the number of lines used (from the anterior to the posterior part of the body) until only two individuals share the same pattern. At that point, we assessed the next TSL to define if it was different. If it was different, then we concluded that we had found the amount of TSL needed to differentiate each individual from this pool of animals. Therefore, we estimated minimum probability by multiplying the proportion of each scute pattern per TSL based on the total needed to differentiate individuals. For the two methods used in this study, we assumed that each of the TSLs per region were independent from one another (i.e., first nuchal transverse scute line was independent of the second nuchal transverse line scute and so on).

RESULTS

We collected complete data (information from all 21 TSL) from 102 individuals and partial information from 8 individuals (because of lack of definition or obstacles present in photos, e.g., ropes, which precluded clear recognition of presence/absence and/or number of scutes on TSL). Of the 110 animals, 69% (76) were hatchlings, 16% (18) juveniles, 13% (14) subadults, and 2% (2) adults. Regarding sex ratio, 10% (11) were females, 12% (13) males, and 78% (86) were undetermined (1 : 1.18; female : male ratio). All individuals had at least two scutes present in the post-occipital (L1), first (L2), and second (L3) nuchal TSL; however, only 53% of them had scutes in the third (L4) nuchal TSL. We found 17 TSL (from L5 to L21) in the dorsal region, of which 16 TSL (from L5 to L20) were present in all individuals with at least one scale. Only 42% presented a 17 TSL (L21) with at least 2 scutes.

Based on the binary analysis (1 = present, 0 = absent), the smallest number of scutes was in line L4 and L21 (zero scutes); lines L14, L15, L13, and L8 had the highest scute number mean

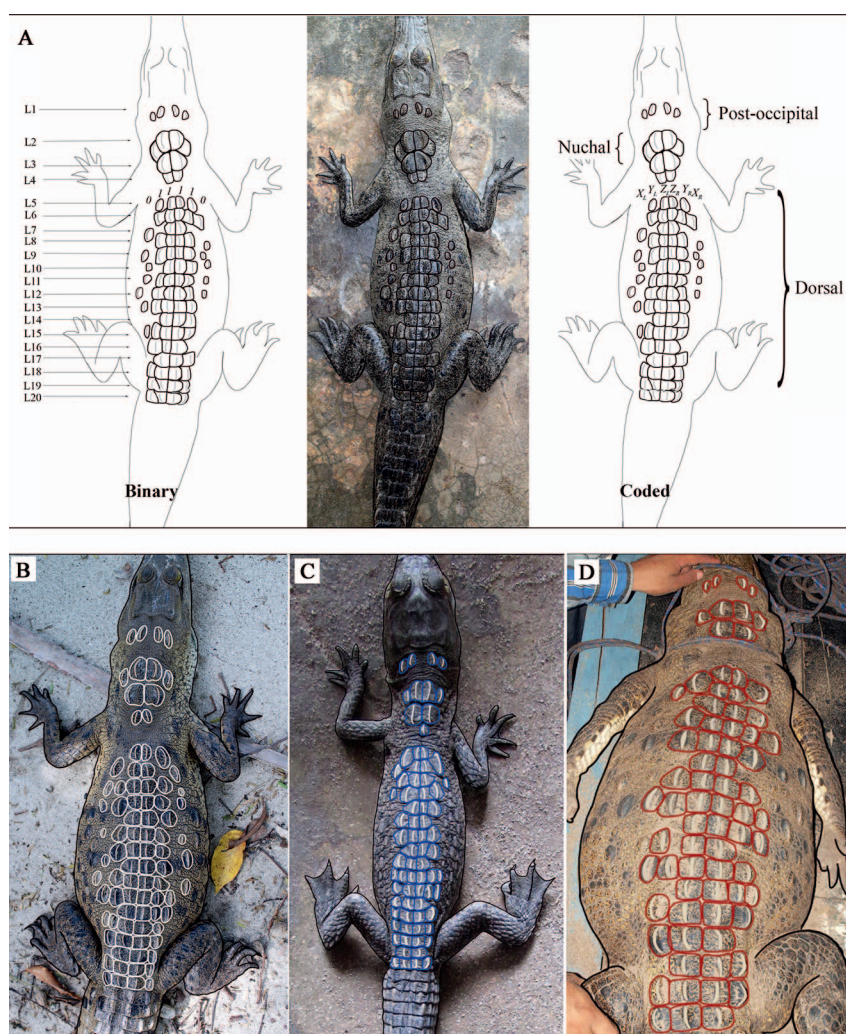


FIG. 1. (A) Vectorized photograph of an individual American Crocodile (ID91 female, subadult) captured in Coiba Island, Panama, describing the individual identification pattern recognition method (IIPR) based on the binary and coded assessments used to analyze the dorsal scute pattern of *Crocodylus acutus*. Notice the three scute regions (post-occipital, nuchal, and dorsal) and 20 instead of the 21 TSL because of the lack of L21 in this specific individual. Several examples of individuals and their scute patterns can be seen in (B) ID543 male subadult, (C) ID467 hatchling with 21 TSL, and (D) ID441 female adult.

(4.54, 4.33, 4.27, 4.02, respectively); lines L21, L14, L15, and L13 had the highest scute number variation (± 1.95 , 1.17, 1.15, 1.10, respectively); and lines L6, L7, L8, L9, L11, L12, L13, L14, L15, and L16 had the highest scute number range (from 2 to 6 scutes per line), all of these from the dorsal section (Table 1, Fig. 2). We found statistically significant differences among the summed number of scutes per TSL ($H_{20} = 737.82$, $P < 0.00$). The pairwise comparisons using Dunn's test showed that on average the majority of transverse lines were significantly different from each other ($P < 0.05$), the most-variable lines being L3, L4, L5, and L21 (nuchal and dorsal sections; Appendix 1). We also found statistically significant differences among individuals based on the total value of scutes per TSL ($H_{101} = 127.26$, $P = 0.03$). However, we did not find significant differences among age groups ($H_3 = 3.9$, $P = 0.27$).

Based on the number of the scutes present on each TSL, we found 7 scute patterns repeated throughout the 21 TSL (Figs. 2, 3). We obtained complete differentiation among individuals (i.e., no two individuals with the same pattern) using the first 13 TSL in an anterior–posterior direction [post-occipital (L1), nuchal (L2, L3, L4), and dorsal (from L5 to L13)]. Only two individuals (ID464 and ID513) shared the same scute pattern from L1 to L12,

but they differed in the pattern present in the TSL L13. Based on these results, and considering the proportion of each pattern per TSL (Fig. 3), the minimum probability of finding another individual with identical scute patterns as ID464 based on 13 TSL was 2.89×10^{-6} and as ID513 was 2.02×10^{-5} . Put another way, only one American Crocodiles out of 346,020 individuals will have the same number of scutes per TSL as ID464 and one individual out of 49,504 will have the same number of scutes per TSL as ID513 in the Coiba island population assessed (which is likely more individuals than we might have there). Based on the most-likely patterns per TSL we found in this study (Fig. 3), the minimum probability of obtaining the same number of scutes in two American Crocodiles from Coiba Island is 2.88×10^{-6} , meaning only one American Crocodile in a group of 347,222 individuals will have an identical scute number.

Regarding the coded analysis, from a possible combination of 2,142 scutes per LSL (Z, Y, and X left and right $\times 102$ individuals $\times 21$ TSL), 93% (2,013) had a Z left scute (Z_L), 94% (2,017) a Z right scute (Z_R), 68% Y_L and Y_R scutes (1,466 and 1,472, respectively), 14% (319) an X_L scute, and 13% (287) an X_R scute. On average, we found 3.13 ± 2.01 scutes in X_L , 2.81 ± 2.07 in X_R , 14.37 ± 1.32 in Y_L , 14.43 ± 1.30 in Y_R , 19.74 ± 0.82 in Z_L ,

TABLE 1. Summary statistics per transverse scute line (TSL) of American Crocodiles assessed on Coiba Island, Panama based on the binary analysis ($n = 102$) highlighting the mean, standard deviation (SD), and minimum and maximum (Min–Max) of scales found.

Section	Line	Mean	SD	Min–Max
Post-occipital	L1	3.86	0.47	2–4
Nuchal	L2	3.80	0.60	2–4
Nuchal	L3	2.06	0.34	2–4
Nuchal	L4	0.93	0.94	0–2
Dorsal	L5	3.25	0.99	1–4
Dorsal	L6	3.92	0.94	2–6
Dorsal	L7	3.97	0.99	2–6
Dorsal	L8	4.02	0.91	2–6
Dorsal	L9	3.91	0.80	2–6
Dorsal	L10	3.71	0.75	2–5
Dorsal	L11	3.76	0.85	2–6
Dorsal	L12	3.90	0.91	2–6
Dorsal	L13	4.27	1.10	2–6
Dorsal	L14	4.54	1.17	2–6
Dorsal	L15	4.33	1.15	2–6
Dorsal	L16	3.81	0.93	2–6
Dorsal	L17	3.73	0.53	2–5
Dorsal	L18	3.55	0.59	2–4
Dorsal	L19	3.57	0.54	2–4
Dorsal	L20	3.64	0.59	2–4
Dorsal	L21	1.72	1.95	0–4

and 19.77 ± 0.84 in Z_R . We found statistically significant differences among the summed number of scutes per LSL ($H_5 = 547.34$, $P < 0.00001$). Pairwise comparisons revealed that on average the majority of LSL were significantly different from each other ($P < 0.05$), with the exception of the specular longitudinal axes ($X_L X_R$, $Y_L Y_R$, and $Z_L Z_R$; $P > 0.05$; Table 2).

We found 23 different scute patterns based on the number and position of scutes present on each TSL repeated throughout the 21 TSL (Fig. 4). The smallest number of patterns was in line L3 (2 patterns) and the greatest number in L6 and L7 (16 patterns on each, Fig. 5). The highest number of patterns was found between L5 and L15 (more than 10 in all cases), all present in the dorsal region. We obtained complete differenti-

TABLE 2. Pairwise comparisons using Dunn's test for independent samples between longitudinal scute lines (LSL) of all American Crocodiles captured in Coiba Island, Panama ($n = 102$). We only report data with significant pairwise comparison values ($P < 0.05$).

	X	X1	Y	Y1	Z
X1		-	-	-	-
Y	8.70E-15	3.50E-16	-	-	-
Y1	1.00E-14	4.30E-16		-	-
Z	<2e-16	<2e-16	4.10E-15	3.40E-15	-
Z1	<2e-16	<2e-16	1.20E-15	1.00E-15	

ation among individuals using only the first 10 TSL (post-occipital [L1], nuchal [L2, L3, L4], and dorsal [from L5 to L10]). Only two individuals (ID500 and ID531) shared the same scute pattern from L1 to L9, but they differed in the pattern present in the TSL L10. So, the minimum probability of finding another individual with identical scute patterns as ID500 on the basis of only the first 10 TSL was 0.0003 and as ID531 was 7.6×10^{-5} . Put another way, only one American Crocodile out of 3,333 individuals will have the same scute pattern as ID500 and one individual out of 13,157 will have the same scute pattern as ID531. Based on the most-likely patterns per TSL we found in this study (Fig. 4), the minimum probability of obtaining the same pattern in two American Crocodiles in Coiba Island is 6.98×10^{-8} , meaning only one American Crocodile in a group of 14,326,647 individuals will have an identical scute pattern.

DISCUSSION

This project represents the first effort to show a novel and practical method, individual identification pattern recognition (IIPR), to “fingerprint” American Crocodiles at the individual level using multiple scute dorsal patterns. Previous studies on *C. acutus* only measured variation in the number of scutes per TSL, taking only scute presence/absence into account (Seijas, 2002; Garcia-Grajales et al., 2009; Platt et al., 2010). Herein, we postulated and tested a method that included not only the

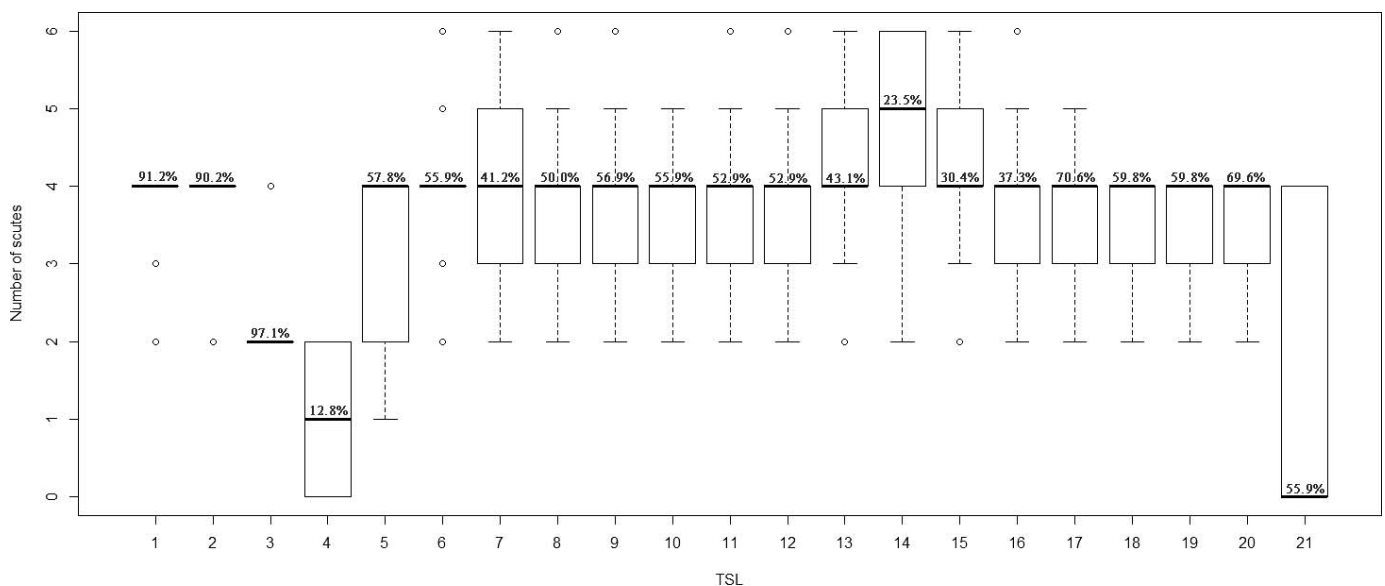


FIG. 2. Number of scutes found on each transverse scute line (TSL) from the anterior to the posterior part of the body (from L1 to L21) based on the binary analysis throughout the 21 TSL reported for American Crocodiles in Coiba Island, Panama ($n = 102$), expressed as median and quartiles with whiskers at minimum and maximum values. Outliers are represented as open circles. We also present the percentage of individuals that presented median values.

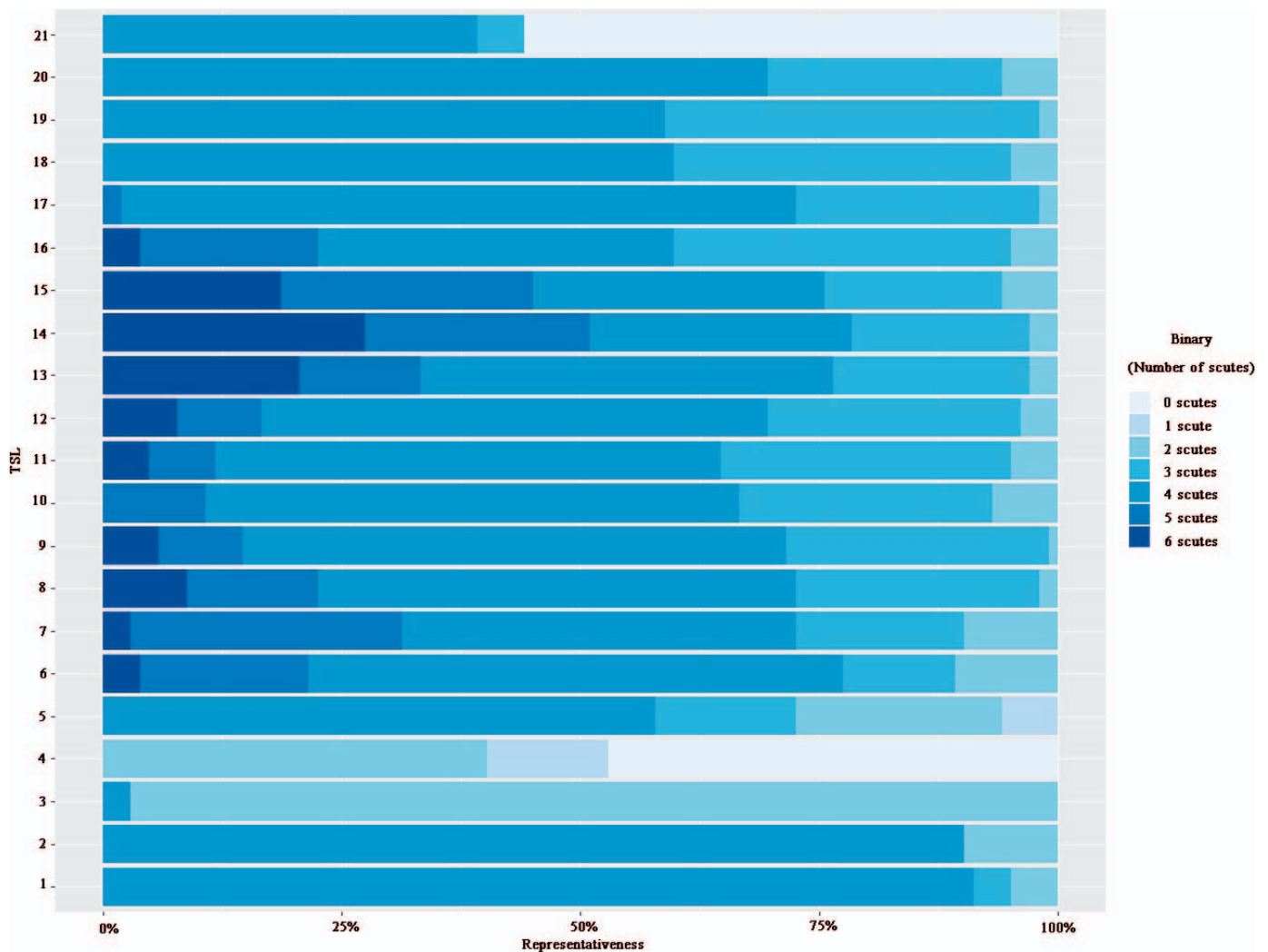


FIG. 3. Number of *Crocodylus acutus* scute patterns derived from the binary analysis in Coiba Island, Panama, highlighting all the scute patterns found per TSL as well as the number of individuals and its representativeness (percentage) based on the total sampling. Sample size per TSL oscillated between 102 and 110 because we included crocodiles with partial information.

number of scutes but also their relative position, defining the scute variation through the dorsal area of the species (post-occipital, nuchal, and dorsal regions) in a more comprehensive fashion.

Using IIPR we found a high level of scute variation in both TSL and LSL through the post-occipital, nuchal, and dorsal regions based on both binary (presence) and coded (pattern) methods. Interestingly, TSL L4 in the nuchal region and L21 in the dorsal region were absent in a number of individuals (47% and 58%, respectively), contributing greatly to the overall scute pattern variation in this population. Regarding this matter, Brazaitis (1973) reported the presence of only two TSL (L2 and L3) in the nuchal region and 16–17 TSL (L5 to L20 or L21) in the dorsal region; however, he did not specify the origin (locality) of the individuals from which he collected this information. Populations assessed in Venezuela (Seijas, 2002), Mexico (García-Grajales et al., 2009), and Belize (Platt et al., 2010) also showed two TSL in the nuchal region (L2 and L3), differing only in the number of TSL in the dorsal region (15–16, L5 to L19 or L20 in Venezuela; 15–17, L5 to L19, L20, or L21 in Belize). We also documented a different range of post-occipital scutes per TSL (2–4 scutes) compared to the data from Brazaitis (1973; 4–6 scutes) and Seijas (2002; 3–5 scutes, Venezuela) but the same as

Platt et al. (2010; Belize). Something to highlight with respect to the study by Platt et al. (2010) is the uncertainty because of potential hybridization between American and Morelet's Crocodiles (*Crocodylus moreletii*) among the individuals sampled in Belize. Low levels of hybridization may not be detected by researchers without genetic studies (Ray et al., 2004) but could affect scute numbers and patterns.

We found statistically significant differences among the number of scutes per TSL and LSL as well as when they were assessed in a pairwise manner. Maximum variation was in the nuchal and dorsal regions (L3, L4, L5, and L21 TSL; Fig. 2, Appendix 1) and in all LSL with the exception of the specular longitudinal axes ($X_L X_R$, $Y_L Y_R$, and $Z_L Z_R$; Table 2). We also found significant differences among individuals based on the total number of scutes per TSL. These results are consistent with what was found by Seijas (2002) in Venezuela, reporting significant variation in scute patterns within American Crocodile populations across the country. Interestingly, we did not find statistical differences among age groups, which might support the idea that there are not ontogenetic changes of these attributes; however, specific studies to evaluate whether scute patterns vary as individuals grow must be performed.

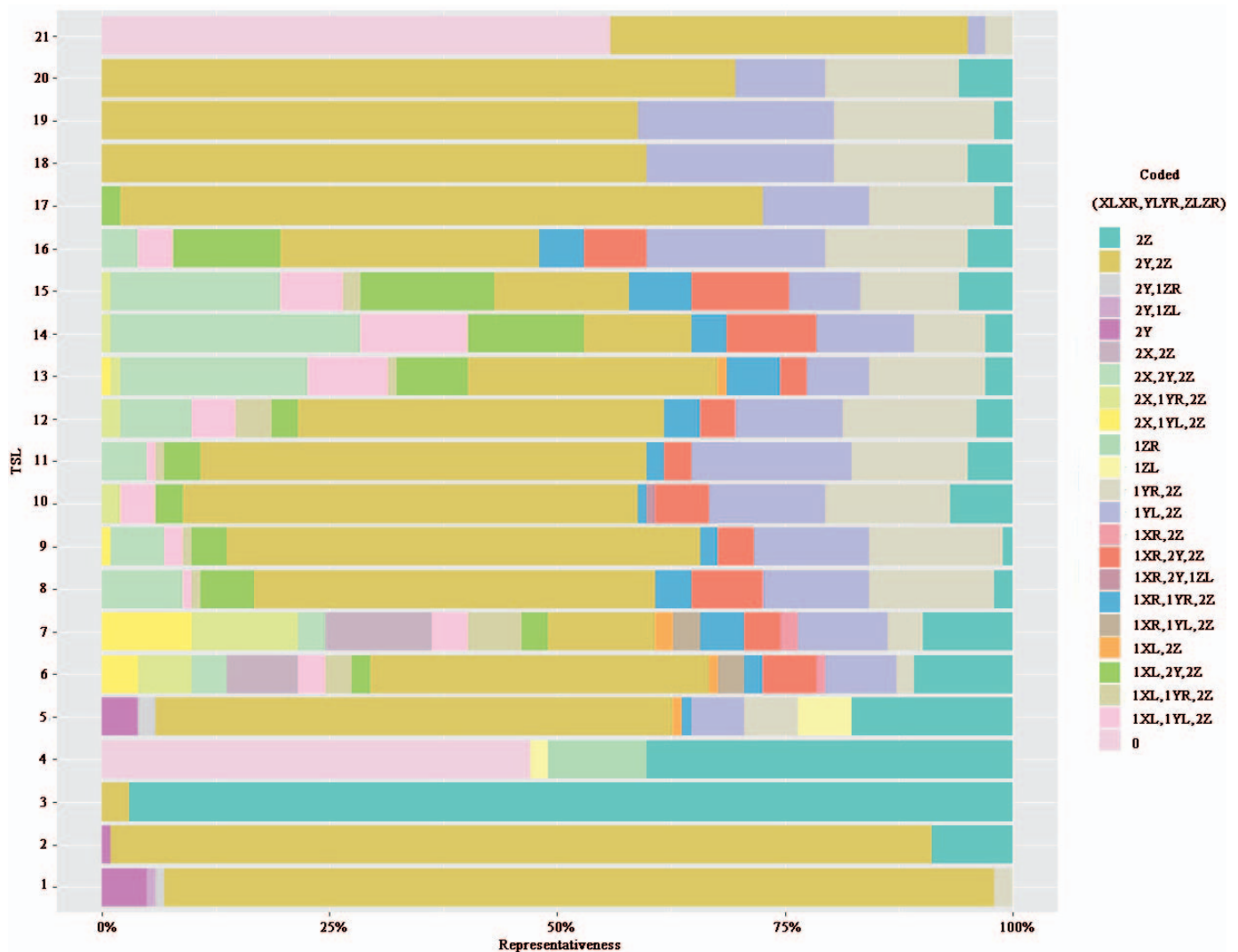


FIG. 4. Scute patterns derived from the coded analysis in Coiba Island, Panama, highlighting all the scute patterns found per TSL as well as the number of individuals and its representativeness (percentage) based on the total sampling. Sample size per TSL oscillated between 102 and 110 because we included crocodiles with partial information.

This high level of variation in the number of the scutes per TSL and LSL present on the post-occipital, nuchal, and dorsal regions reported through the *C. acutus* range in areas such as Jamaica (Garrick, 1982), Belize (Platt et al., 2010), Mexico (Garcia-Grajales et al., 2009), and Venezuela (Seijas, 2002) reflects just how variable are scute patterns and implies how useful they can be as potential means to identify individual crocodiles. Combining a numerical approximation (number of scutes per TSL) with the position of each scute (coding them) in IIPR analysis, we increased the detectable variability of scute patterns in a way that provides an efficient tool to characterize American Crocodiles. Prior to the present study, only Seijas (2002) and Garcia-Grajales et al. (2009) attempted to define patterns per TSL on the post-occipital and nuchal regions based on the number of scutes, assigning a numerical value and codes to each scale present. Using that method, Seijas (2002) recorded 7 scute patterns on the post-occipital region and 19 patterns in the nuchal region, concluding that the patterns were significantly different throughout the areas assessed across Venezuela. In contrast, Garcia-Grajales et al. (2009) defined 33 patterns combining the post-occipital and nuchal regions; however,

neither study assessed the potential of these patterns as markers to identify animals at the individual level.

We rejected the null hypothesis that no discernible patterns exist among TSL on the post-occipital, nuchal, and dorsal regions per individual, based on the coded and binary IIPR analyses, because we found and quantified several scute patterns (23 and 7, respectively) repeated throughout the 21 TSL, with the highest variation found in the dorsal region. This allowed us to identify all individual crocodiles among the 110 animals evaluated using just 10 (in the coded case) and 13 (in the binary case) out of the 21 TSL. We found only two individuals using both methods sharing the same scute pattern from L1 to L9 (ID500 and ID531, coded) and L1 to L12 (ID464 and ID513, binary), differing only in the pattern present in line L10 and L13, respectively. This gave us a minimum probability of ≤ 0.0003 based on the coded analysis and $\leq 2.02 \times 10^{-5}$ based on the binary analysis to find pattern repetition. Put in another way, we would need to have 3,333 American Crocodiles to find one individual with the most-common scute pattern based on 10 TSL using coded analysis and 49,504 American Crocodiles to find one individual with the most-common number of scutes based on 13 TSL using binary

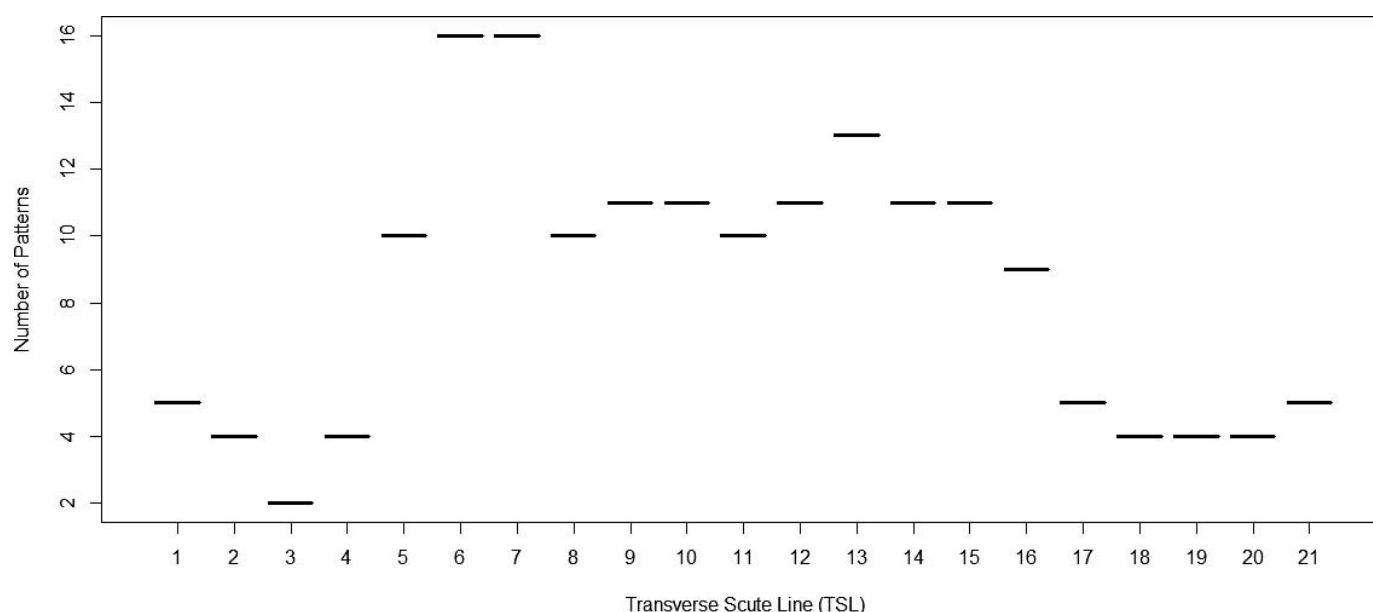


FIG. 5. Number of patterns of *Crocodylus acutus* found on each transverse scute line (TSL) from the anterior to the posterior part of the body (from L1 to L21) based on the coded analysis throughout the 21 TSL reported for American Crocodiles in Coiba Island, Panama ($n = 102$).

analysis. The American Crocodile population in Coiba has been estimated as no more than 1,000 individuals (Thorbjarnarson et al., 2006; Venegas-Anaya et al., 2015), which means one should be able to identify all American Crocodiles (with no pattern repetition) inhabiting this insular area. Because of the gene flow reported between Coiba and Montijo Gulf (Venegas-Anaya, unpubl. data), applying these numbers to continental areas in Panama should also be plausible. First though, these hypotheses must be tested by sampling different areas in Coiba Island as well as populations from the Montijo Gulf, analyzing how the minimum probability varies as well as the number of TSL needed for individual identification.

Noninvasive methods for individual identification of crocodylians such as IIPR are very promising with the advancement of technology, opening new ways to monitor and assess American Crocodile populations. Devices such as UAVs could be used to map large areas inhabited by American Crocodiles by using high resolution photography, thus providing optimal data (dorsal high resolution imagery from American Crocodiles) to estimate population sizes and demographic structure as well as some other relevant population attributes. This method might also be applied to other species from the Crocodylidae family such as Morelet's Crocodiles, Nile Crocodiles, Cuban Crocodiles (*Crocodylus rhombifer*), Orinoco Crocodiles (*Crocodylus intermedius*), and Salt-Water Crocodiles (*Crocodylus porosus*) because they also exhibit irregular dispositions of the dorsal scutellation (Grigg and Kirshner, 2015); however, species-specific studies must be completed to test these hypotheses.

One important question that needs to be addressed regarding the value of these methods is, "Do the number and/or position of scutes change through the lifespan of American Crocodiles?" To our knowledge, no such studies have been attempted that can answer this question on American Crocodiles or any other crocodylian species. Studies of *Alligator mississippiensis* dermal bone formation during embryogenesis, however, have shown that osteoderms have a delayed development, i.e., they do not appear until hatching and then appear in an asynchronous

fashion across the body, first dorsally adjacent to the cervical vertebrae and later in caudal and lateral positions (Vickaryous and Hall, 2008). In contrast, dorsally conspicuous scutes composed mainly of β -keratin can be recognized immediately after hatching in almost all crocodylians (Grigg and Kirshner, 2015). This implies that scute patterns can be recognized almost immediately after hatching, but resolution improves over time as individuals and osteoderms grow.

In conclusion, the coded and binary analyses employed in IIPR appear to be feasible methods to determine individual identification of American Crocodiles based on the number and position of the scutes per TSL in the dorsal area. The coded analysis showed an overall higher variation per TSL than did the binary analysis, reaching the minimum probability using fewer TSL. This could be important when one wants to use this method as an indirect mark-recapture strategy (e.g., using drones or dorsal pictures of animals), requiring fewer TSL to visualize and achieve confident results. This provides a new and less-expensive method for population assessments based on IIPR in combination with UAV to collect highly relevant population attributes from inaccessible areas.

The minimum probability of repeating a pattern in Coiba Island using both coded and binary analyses was sufficiently high (one American Crocodile in 14,326,647 individuals and one in 347,222, respectively) to allow a complete, individual identification of several *C. acutus* populations throughout its range. The likelihood of identical scute patterns, however, as well as the number of TSL needed to identify an individual, might change depending on the patterns described in different populations. Nevertheless, the considerable variability present in these three regions over the dorsal area of American Crocodiles demonstrated by this and previous studies (Brazaitis, 1973; Garrick, 1982; Seijas, 2002; Garcia-Grajales et al., 2009; Platt et al., 2010) provide solid support to continue using and testing IIPR as a way to characterize individual *C. acutus*. Finally, additional studies throughout the range of *C. acutus* should be done using this approach to further assess both its scope and limitations.

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APPENDIX 1. Pairwise comparisons using Dunn's test for independent samples between transverse scute lines (TSL) of all American crocodiles captured in Coiba Island, Panama ($n = 102$). We only report data with significant pairwise comparison values ($P < 0.05$).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
2		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	0	0		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	0.01	0.03	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6			0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7			0	0	0		-	-	-	-	-	-	-	-	-	-	-	-	-	-
8			0	0	0			-	-	-	-	-	-	-	-	-	-	-	-	-
9			0	0	0.05				-	-	-	-	-	-	-	-	-	-	-	-
10			0	0						-	-	-	-	-	-	-	-	-	-	-
11			0	0							-	-	-	-	-	-	-	-	-	-
12			0	0								-	-	-	-	-	-	-	-	-
13			0	0	0								-	-	-	-	-	-	-	-
14			0	0	0				0.04	0	0	0.02		-	-	-	-	-	-	-
15			0	0	0					0.03	0.03				-	-	-	-	-	-
16			0	0										0		-	-	-	-	-
17			0	0										0	0.03		-	-	-	-
18			0	0									0	0	0			-	-	-
19			0	0									0	0	0				-	-
20			0	0									0.05	0	0					-
21	0	0	0.05	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0