

## Population assessment of the American crocodile, *Crocodylus acutus* (Crocodylia: Crocodylidae) on the Pacific coast of Costa Rica

Laurie A. Mauger<sup>1,6</sup>, Elizabeth Velez<sup>2</sup>, Michael S. Cherkiss<sup>3</sup>, Matthew L. Brien<sup>4</sup>, Michael Boston<sup>5</sup>, Frank J. Mazzotti<sup>3</sup> & James R. Spotila<sup>6</sup>

1. Department of Biology, Southern Utah University, 351 West University Boulevard, Cedar City, UT 84720, USA; lauriecotroneo@suu.edu
2. Kelonian Conservation Society, P.O. Box 473-3000, Heredia, Costa Rica; evbaulas@yahoo.com
3. University of Florida Fort Lauderdale Research and Education Center, 3205 College Ave, Davie, FL 33314, USA; mcherkis@ufl.edu, fjma@ufl.edu
4. Charles Darwin University, Casuarina 0810, Australia; crocmatt@hotmail.com
5. Casa Verde, 100 meters east of the Catholic Church, Puerto Jimenez, Puntarenas 8203, Costa Rica; mike@osaaventura.com
6. Department of Biology, Drexel University, 3141 Chestnut St, Philadelphia, PA 19104, USA; lcotroneo@gmail.com, spotiljr@drexel.edu

Received 11-X-2011. Corrected 30-IV-2012. Accepted 29-V-2012.

**Abstract:** The American crocodile, *Crocodylus acutus*, is widely distributed in the American neotropics. It is endangered throughout most of its range and is listed as vulnerable by the International Union for the Conservation of Natural Fauna and Flora (IUCN) and on Appendix I of the Convention for the International Trade in Endangered Species of Wild Flora and Fauna (CITES). Despite this listing, there are few published reports on population status throughout most of its range. We investigated the status of the *C. acutus*, at several locations along the Pacific coast of Costa Rica. We carried out spotlight and nesting surveys from 2007-2009 along the Costa Rican Pacific coast in four distinct areas, coastal areas of Las Baulas (N=40) and Santa Rosa (N=9) National Parks and the Osa Conservation Area (N=13), and upriver in Palo Verde National Park (N=11). We recorded crocodile locations and standard environmental data at each observation. Encounter rates, population structure, distribution within each area and data on successful nesting (presence of hatchlings, nests, etc) were determined. We attempted to capture all crocodiles to record standard morphometrics. A total of 586 crocodiles were observed along 185.8km of survey route. The majority of animals encountered (54.9%) were either hatchlings (<0.5m) or juveniles (0.5-1.25m). The average non-hatchling encounter rate per survey for the Pacific coast was 3.1 crocodiles/km, with individual encounter rates ranging from 1.2 crocodiles/km to 4.3 crocodiles/km in Las Baulas National Park and the Osa Conservation Area respectively. Distribution of size classes within the individual locations did not differ with the exception of Santa Rosa and Las Baulas National Parks, where hatchlings were found in water with lower salinities. These were the first systematic surveys in several of the areas studied and additional work is needed to further characterize the American crocodile population in Costa Rica. *Rev. Biol. Trop.* 60 (4): 1889-1901. Epub 2012 December 01.

**Key words:** American crocodile, *Crocodylus acutus*, Costa Rica, encounter rates, population surveys, size class distribution.

Crocodylians are keystone species that play an important role in biodiversity and maintenance of ecosystems (Mazzotti *et al.* 2009, Thorbjarnarson 2010). Effective management plans are critical to continued existence of crocodile populations and should

consider factors influencing a population, such as nesting and nursery habitat, feeding grounds, population structure and distribution and salinity levels (Kushlan 1988). Limited data on the population biology of many crocodylian species makes it crucial to gain a better understanding

of connections between different populations. The American crocodile, *Crocodylus acutus* (Cuvier 1807), is the most widely distributed of the New World crocodylians (Thorbjarnarson 2010). This species ranges from the extreme Southern tip of Florida, throughout the Caribbean and along the Pacific and Caribbean coasts of Central and Northern South America (Thorbjarnarson *et al.* 2006, Thorbjarnarson 2010). *Crocodylus acutus* is considered a coastal species, inhabiting lagoons and estuaries, areas with lower salinities and can also be found inland along major rivers and land-locked lakes (Kushlan & Mazzotti 1989a, Platt & Thorbjarnarson 2000, Thorbjarnarson *et al.* 2006, Mazzotti *et al.* 2009, Cherkiss *et al.* 2011). *Crocodylus acutus* can also be found in marine habitats (full-strength sea water) along offshore islands and atolls (Platt & Thorbjarnarson 2000).

Populations of *C. acutus* were severely depleted throughout the range during the 20<sup>th</sup> century due to hunting and over-harvesting (Thorbjarnarson *et al.* 2006). As a result, *C. acutus* was placed on the United States Endangered Species Act (1975) and Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1979 and is currently recognized as vulnerable by the International Union for the Conservation of Nature and Natural Resources (IUCN) Red Book (Baillie *et al.* 2004). The Florida population was down listed from endangered to threatened in 2007 (Mazzotti *et al.* 2007, Federal Register 72: 13027 2007). Availability of survey data for *C. acutus* is poor throughout much of its range with the exception of the Florida population (Ogden 1978, Dunson 1982, Gaby *et al.* 1985, Kushlan 1988, Kushlan & Mazzotti 1989a, Kushlan & Mazzotti 1989b, Mazzotti 1999, Mazzotti & Cherkiss 2003, Thorbjarnarson *et al.* 2006).

Establishing the status and ecology of *C. acutus* in Costa Rica is recognized as a high priority by the IUCN Crocodile Specialist Group (Ross 1998). Investigating the ecology of *C. acutus* throughout its range was further recognized as a moderate priority (Thorbjarnarson 2010). The population of *C. acutus* in

Costa Rica is considered one of the largest, with reports of healthy populations throughout the country (Ross 1998). However, suitable coastal habitat is more disjunct along the Pacific coast, which has resulted in a series of smaller, isolated populations of *C. acutus* (Thorbjarnarson *et al.* 2006). This makes the estuary system of the Pacific coast of Costa Rica an ideal place to study metapopulation structure of crocodiles. In Costa Rica, the Tempisque (2.28-11.1 crocodiles/km) and Tarcoles (10-35 crocodiles/km) rivers support very large, dense populations of *C. acutus* (Motte 1994, Sanchez *et al.* 1997, Sanchez 2001). While the status of the Tempisque River population is considered stable and increasing, the population in the Tarcoles River is declining due to pollution and alteration of habitat (Sanchez *et al.* 1997, Abadia & Orjuela 1998, Sanchez 2001). Metals and organochlorine pesticides have been found in measurable quantities in crocodiles scutes from the Tempisque and Tarcoles rivers (Rainwater *et al.* 2007). This shows that crocodiles accumulate environmental contaminants that are found in the Central Pacific region (Fuller *et al.* 1990). Reports of healthy populations around the country, along with an excellent infrastructure, make Costa Rica an ideal place to study the population structure of *C. acutus* for management and conservation.

The primary objective of this study was to conduct population assessments in several estuaries, rivers and coastal lagoons along the Pacific coast of Costa Rica. *Crocodylus acutus* are hypothesized to live in isolated populations in small estuaries with minimal contact occurring between distant habitats. The data obtained during surveys were used with an ongoing study examining the genetic structure of crocodile populations in Pacific Costa Rica. Understanding linkages between these potential metapopulations is crucial in developing management plans for *C. acutus* within Costa Rica.

## MATERIALS AND METHODS

**Study Area:** We conducted spotlight surveys of *C. acutus* in four areas on the Pacific

coast of Costa Rica (2007-2009) including Las Baulas National Park (LB; 10°19.3'28.4" N - 85°49.5'42.32" W) in the Tempisque Conservation Area (ACT); Palo Verde National Park (PV; 10°19.6'28.1" N - 85°22'29.2" W), in the Arenal-Tempisque Conservation Area (ACA-T); Santa Rosa National Park (SR; 10°46.7' N-85°39.8' W) in the Guanacaste Conservation Area (ACG); and six areas throughout the Osa Conservation Area (ACOSA) including, Pejeperrito Lagoon (PTL; 8°26.1'17.6" N - 83°26'31.9" W), Pejeperrito Lagoon (PL; 8°24.1'46" N - 83°22.7'29.2" W), Río Esquinas (RE; 8°43.7'36.1" N-83°17.9'38.3" W), Río Coto (RC; 8°32.6'14.5" N-83°5.7'31.4" W), Río Sierpe (RS; 8°50.6' N-83°26.8' W) and the Parrot Bay Lodge area (PB; 8°32'18.9" N-83°17'59.2" W) in Puerto Jimenez. Localities ranged from large river systems (PV, RS, RE, RC), to estuaries (LB, SR) and coastal lagoons (SR, PL, PTL, PB). The rainy season began in late May/early June and reached its height in late September. The dry season in the Northern Pacific region (LB, PV, SR) extended from January to late May. The dry season in the South (ACOSA) is shorter and lasts two months on average.

Las Baulas National Park (LB), located in the ACT, was formed in 1990 and includes three beaches (Playa Ventanas, Playa Grande and Playa Langosta), two estuaries (Tamarindo and San Francisco) and extends 20km offshore. The Tamarindo Estuary is one of the largest mangrove swamps in dry Central America (Spotila & Paladino 2004) covering 440ha and was listed on the Ramsar list of wetlands of international importance (Boza & Cevo 2001). It has been named as one of the most important wetlands in the Guanacaste Province (Fuller *et al.* 2004). This brackish coastal environment is home to five species of mangrove trees, numerous bird and mammal species and the American crocodile.

Palo Verde National Park (PV), located in the ACA-T, contains the valley of the Tempisque River, the largest hydrological region of Guanacaste at 5 460km<sup>2</sup> (Frankie *et al.* 2004). Twelve different habitats exist in the park

including lagoons, freshwater and brackish swamps, mangrove forests, grasslands and dry forests (Boza & Cevo 2001). Palo Verde is an important area for resident and migratory birds and contained a large population of American crocodiles (Thorbjarnarson 2010). The Tempisque River, which passes through the park, is 144km long. Palo Verde National Park was formed in 1978 and has been an important Ramsar site since 1991.

Santa Rosa National Park (SR), located in the ACG, is on the Santa Elena Peninsula, the oldest (85 million years) and driest area of the country (Boza & Cevo 2001). SR was initially established to restore the dry forests in the area and to protect the neighboring rain forests, cloud forests and marine environments. Most of this park is on the Santa Rosa Plateau and includes a variety of habitats including grassland, deciduous forest, mesquite-nacasol swamps and mangrove swamps (Boza & Cevo 2001). The Naranjo Estuary and Laguna el Limbo are located on the beaches of Santa Rosa National Park in the Santa Rosa Sector. The lagoon was separated from the estuary by approximately 2km of beach and dry forest.

The Osa Peninsula and areas of the adjacent mainland in the southwest of Costa Rica (ACOSA) have extensive areas of wetland habitat that is ideal for *C. acutus*. Over 50%, approximately 20 254ha, of Costa Rica's mangrove wetlands are found in this area. The Terraba-Sierpe National Wetland is made up of the delta of the Terraba and Sierpe Rivers and is the most extensive mangrove swamp in the country (Boza & Cevo 2001). ACOSA also has 6 986ha of evergreen, broad-leaf swamp forest that is dominated by raffia palm (*Raphia taedigrea*), cerillo (*Symphonia globulifera*) and hog plum (*Spondias* sp.), and 822ha of freshwater, herbaceous swamps and lagoons. Open waterways and rivers also provide important habitat for *C. acutus*.

**Crocodile Surveys:** Crocodiles were surveyed in a mix of lagoons (SR, PTL, PL, PB), estuaries (LB, SR) and rivers (PV, RE, RC, RS) of different sizes and locations in Pacific

Costa Rica. We conducted nighttime spotlight surveys (Bayliss 1987) in LB, PV, SR, and ACOSA when waterways were accessible. An LED headlamp and a 12 000 candle power Pelican® Sabrelite 2000 spotlight were used to locate crocodiles by their eyeshine. Surveys were conducted at the beginning of the rainy season in SR (2007) and PV (2008-2009); throughout the year in LB (2007-2009) and during the end of the dry season in ACOSA (2008-2009). We conducted surveys by boat in all locations and by foot in some locations (SR, LB and PB). Walking surveys were conducted mainly to catch crocodiles that had been spotted during previous spotlight surveys. The entire navigable length of the estuaries in SR

and LB and the lagoons in SR, PB, PL and PTL were surveyed. Portions of the navigable length were surveyed at the other localities (Table 1). Surveys in SR were conducted in the Naranjo Estuary and the Laguna el Limbo roughly one kilometer to the South. One survey was conducted on Nancite Beach approximately one kilometer to the North. Survey lengths (Table 2) were calculated on ArcMap 9.3.1 using the start and end points of each survey as determined by GPS. Crocodiles were only counted during the survey and were not counted when returning after the survey. We conducted between 12 and 40 surveys in the four main areas studied on the Pacific coast (Table 2) with an average of 18 surveys per locality. We conducted a minimum

TABLE 1  
Summary of start and end points for crocodile surveys conducted along the Pacific coast of Costa Rica

Location	Number of Surveys	Start Point	End Point
Palo Verde* (2008)	8	10°20.3'26.5" N - 85°21.7'49.17" W	10°19.8'26.62" N - 85°22.4'32.84" W
Palo Verde* (2009)	2	10°19'52.9" N - 85°21'11.06" W	10°19'27" N - 85°21'20.35" W
Río Esquinas* (2008)	1	8°42.95' N - 83°19.35' W	8°44.3' N - 83°17.74' W
Río Esquinas* (2009)	1	8°44' N - 83°17'23.3" W	8°43'21.6" N - 83°19'25.2" W
Río Coto	2	8°32'14" N - 83°8.3'34.9" W	8°32.4'0.7" N - 83°4.62'16.4" W
Río Sierpe	2	8°50.1' N - 83°27' W	8°51.5' N - 83°28.3' W

\* Different areas of the rivers were surveyed in 2008 and 2009.

TABLE 2  
Summary of surveys for *C. acutus* performed along Pacific Costa Rica between 2007 and 2009

Habitat type	Las Baulas National Park (LB)	Palo Verde National Park (PV)	Santa Rosa National Park (SR)	Area of Conservation OSA (ACOSA)	Total
	Mangrove Estuary/Swamp	River	Mangrove Estuary/Swamp	Coastal Lagoons, Rivers and Swamps	
N.º surveys	40	11	9	13	73
<b>Survey distance</b>					
Total (km)	70	44.8	12.1	58.9	185.8
Mean (km/survey)	1.8	4.1	1.3	4.9	2.6
<b>Crocodile sightings</b>					
Non-hatchling	88	178	43	277	586
Mean (#/survey)	2.2	16.2	4.8	21.3	8
<b>Encounter rate</b>					
Per km	1.2	4	3.7	4.3	3.1
<b>Sex ratio</b>					
Non-hatchling (male: female)	4:9	2:3	1:2	4:11	21:44

of one and a maximum of three surveys per river or lagoon within ACOSA (Table 3) with an average of 2.2 surveys per location.

We recorded a location with a GPS, salinity (parts per thousand, ppt), and air and water temperatures (°C) for all crocodiles observed. Indication of nesting activity was recorded by either finding a nest or the presence of hatchlings in the estuary. Tide measurements were obtained from Port Quepos or Puntarenas (Central Pacific, Costa Rica). All boat surveys in the Naranjo Estuary (SR) were conducted during high tide when the waters were navigable. We conducted walking surveys in SR during low tide. Surveys were conducted during all tide cycles in LB, PV and ACOSA.

**Crocodile Capture:** We attempted to capture all crocodiles observed using the break-away snare method (Hutton *et al.* 1987, Hutton & Woodhouse 1989), snake tongs or by hand. Crocodiles were individually marked by removing caudal scutes in a numbered sequence (Mazzotti 1983, Richardson *et al.* 2002). This technique has been utilized in numerous studies and does not adversely affect crocodiles (Gaby *et al.* 1985, Kushlan & Mazzotti 1989a, Jennings *et al.* 1991, Leslie 1997, Davis *et al.* 2001, Dever & Densmore 2001). We measured

head length (HL; measured from the tip of the snout to the posterior edge of the supra-occipital bone), snout-vent length (SVL; measure from the tip of the snout to the posterior end of vent), total length (TL; measured from tip of snout to tip of tail), tail girth (TG; measured at the fourth whorl at the base of the tail) in centimeters, mass (grams), and determined sex of animals >0.75m TL. Crocodiles were released into the water at the capture site upon completion of measurements.

**Data Analysis:** Crocodiles were separated into four size classes: hatchlings (<0.5m), juveniles (0.5m-1.25m), sub-adults (1.25m-2.25m) and adults (>2.25m) (Kushlan & Mazzotti 1989a). The size class distribution was calculated as the percentage of crocodiles sighted or captured in each size class. Individuals that could not be placed into a size class were recorded as eyeshine only. We calculated encounter rates for each location as total number of non-hatchling crocodiles sighted per kilometer surveyed (Tables 2 and 3). Hatchlings were not included in encounter rates due to their high mortality rate. We compared the salinity of crocodile sightings and captures within and between sites using an analysis of variance (ANOVA).

TABLE 3  
Summary of surveys for *C. acutus* performed in the Osa Conservation Area (ACOSA) between 2008 and 2009

Habitat type	Pejeperrito Lagoon (PTL)	Pejeperro Lagoon (PL)	Río Coto (RC)	Río Esquinas (RE)	Río Sierpe (RS)	Parrot Bay Lodge (PB)	Total
	Coastal Lagoon	Coastal Lagoon	River	River	River	Coastal Lagoon/Swamp	
N.º surveys	3	1	2	2	2	3	13
<b>Survey distance</b>							
Total (km)	5	2	17.6	12	19.8	Under 0.5	58.9
Mean (km/survey)	1.7	2	8.8	6	9.9	0.2	4.5
<b>Crocodile sightings</b>							
Non-hatchling	72	18	87	40	57	6	277
Mean (#/survey)	24	18	43.5	20	28.5	2	21.3
<b>Encounter rate</b>							
per km	14.1	9	4.9	3.3	2.9	n/a	4.7
<b>Sex ratio</b>							
Non-hatchling (male: female)	0:4	3:1	0:2	0:1	0:1	1:2	4:11

## RESULTS

We conducted 73 crocodile surveys on the Pacific coast of Costa Rica covering 185.8km of crocodile habitat (Tables 2 and 3). 50% of surveys were conducted in the Tamarindo Estuary of Las Baulas National Park; the remainder of the surveys were spread between Palo Verde National Park (Tempisque River), Santa Rosa National Park (Naranjo Estuary and Laguna el Limbo) and the Osa Conservation Area (Tables 2 and 3). We observed crocodiles during all surveys.

We observed a total of 763 crocodiles (586 non-hatchling; Table 2) over the Pacific coast

with an average of 8 non-hatchling crocodiles per survey. The spectacled caiman, *Caiman crocodilus*, was encountered in the ACOSA making up 17% of all encounters with the remainder *C. acutus* or eye shine. Over 89% (n=548) of crocodiles for which a size could be estimated or directly measured were <2.25m (reproductive size; Table 4).

The mean encounter rate over all areas was 3.1 crocodiles/km with the highest encounter rate occurring in the ACOSA (4.3 crocodiles/km). Encounter rates differed between sites (ANOVA, F=13.845, p<0.01). The sex ratio over all locations was approximately 1:2 males to females (Table 2).

TABLE 4  
Size class distribution for *C. acutus* along Pacific Costa Rica

	LB (n=143)	PV (n=276)	SR (n=67)	ACOSA (n=277)	PTL (n=72)	PL (n=18)	RC (n=87)	RE (n=40)	RS (n=57)	PB (n=6)	TOTAL (n=763)
Hatchling (%)	38.5	35.5	35.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	23.2
Juvenile (%)	24.5	22.1	25.4	46.6	63.9	61.1	36.8	65.0	19.3	50.0	31.7
Subadult (%)	21.7	10.9	20.9	10.1	8.3	11.1	11.5	2.5	15.8	16.7	13.5
Adult (%)	7	9.4	6	7.9	8.3	5.6	6.9	0.0	15.8	33.3	8.1
Eyeshine Only (%)	8.4	22.1	11.9	35.4	19.4	22.2	44.8	32.5	49.1	0.0	23.5

**Las Baulas National Park (LB):** We conducted 40 surveys (54.5% of total) in LB covering 70km of crocodile habitat (Table 2). The majority of the surveys (39 out of 40) were conducted in the Tamarindo Estuary. One survey was conducted in the San Francisco Estuary to the South. Overall, we observed 88 non-hatchlings (1.2 crocodiles/km) with an average of 2.2 per survey. We classified over 60% (n=90) of the crocodiles as hatchlings or juveniles (Table 4). Crocodiles were not distributed in the estuary according to size class with the exception of hatchlings, who were only encountered in the right branch of the estuary moving upstream which had significantly lower salinity values. The average salinity value of hatchling observations was 9.4ppt which was significantly lower than the average salinity of all crocodile observations (21.8ppt, ANOVA, F=40.14, p<0.001).

Individuals captured ranged in size from hatchlings to adults (30.8cm-347cm). Hatchlings were 35.1±4.5cm in TL (n=31); juveniles were 76.7±28.2cm in TL (n=23); subadults were 186.8±25.3cm in TL (n=14); and adults were 238.0±8.7cm in TL (n=4). The largest adult encountered was 347cm. There was a bias towards catching smaller crocodiles in all locations due to the weariness of larger animals. The sex ratio of captured non-hatchling crocodiles was approximately 1:2 (males:females).

**Palo Verde National Park (PV):** We conducted 11 surveys (15.1% of total) on the Tempisque River covering 44.8km of crocodile habitat (Table 2). We observed 178 non-hatchling (4 crocodiles/km) with an average of 16.2 non-hatchlings per survey. The sex ratio of captured non-hatchling crocodiles was 2:3 (males: females).

Individuals ranged in size from hatchling to adult (30cm-314cm). Hatchlings were  $34.8 \pm 3.1$ cm TL (n=32); juveniles were  $79.1 \pm 15.1$ cm in TL (n=22); subadults were 166.5cm in TL (n=1); and adults were  $291.1 \pm 24.6$ cm in TL (n=3). Over 55% (n=159) of crocodiles observed were hatchlings or juveniles (Table 4). Crocodiles were not distributed in the river according to size class. The average salinity at all observations was 1.6ppt and did not differ between size classes (ANOVA,  $F=0.312$ ,  $p=0.82$ ).

**Santa Rosa National Park (SR):** We conducted 9 surveys (12.3% of the total) in SR covering 12.1km (Table 2). A large crocodile (approximately 3.5m) was known to live in the Nancite Estuary (Shaya Honovar, personal communication). This individual was not observed. We observed 43 non-hatchling crocodiles (3.7crocodiles/km) with an average of 4.8 non-hatchling crocodile per survey. Sex ratio of captured non-hatchling crocodiles was 1:2 (male: female).

Individuals ranged in size from hatchling to sub-adult (31.7cm-184.4cm). Hatchlings were  $32.6 \pm 0.6$ cm TL (n=13); juveniles were  $79.6 \pm 25.7$ cm TL (n=8); and subadults were  $144.0 \pm 23.5$ cm TL (n=5) with no adults captured. Two adults (approximately 2.5m and 3m) were observed but not captured. Over 60% (n=41) of the encountered crocodiles were hatchlings or juveniles (Table 4). No hatchlings were observed in the estuary. Juveniles were only encountered in the upper reaches of the estuary. All size classes were observed in the Laguna el Limbo, with hatchlings only being observed in the right branch. Hatchlings were found in lower salinities than other size classes (ANOVA,  $F=11$ ,  $p<0.001$ ). Average salinity of the estuary and lagoon were 5.2ppt and 0.9ppt respectively.

**Osa Conservation Area (ACOSA):** We conducted 13 surveys (17% of the total) in ACOSA covering 58.9km (Tables 2 and 3). We observed a total of 277 non-hatchling crocodiles (4.3 crocodiles/km). Individual encounter

rates ranged from 2.9 (RS) to 14.1 (PTL) crocodiles/km with non-hatchling observations ranging from 6 (PB) to 87 (RC) with an average of 21.3 non-hatchling crocodiles per survey. The sex ratio of non-hatchling crocodiles was approximately 4:11 (male: female).

Individuals ranged in size from juvenile to adult (50.2-273.7cm). Juveniles were  $71.6 \pm 17.1$ cm TL (n=35); subadults were  $150.5 \pm 21.3$ cm TL (n=3); and adults were 273.7cm TL (n=1). No observed individuals were classified as hatchlings and approximately 46% were classified as juveniles (n=133, Table 4).

## DISCUSSION

There are few population assessments of *C. acutus* from Costa Rica, with those that have been undertaken having been conducted in Central and Northern rivers (Sasa & Chaves 1992, Bolaños *et al.* 1996, Porras 2004, Barrantes 2008). This study was the first to assess the population status of *C. acutus* in Las Baulas and Santa Rosa National Parks.

*Crocodylus acutus* encounter rates on the Pacific coast of Costa Rica were comparable to the majority of other population surveys on *C. acutus* populations (Table 5). These encounter rates support the hypothesis that *C. acutus* populations within Costa Rica are large (Ross 1998).

The American crocodile is known to prefer habitats of lower salinity (Kushlan & Mazzotti 1989a, Mazzotti *et al.* 2007). Crocodiles in this study were encountered in water with salinities ranging from 0ppt to over 50ppt. However, most (61%) encounters occurred in water with lower salinities (0-5ppt). Hatchlings were always encountered in lower saline environments than larger size classes with the exception of the Tempisque River in Palo Verde National Park where all size classes were in water of low salinity. All surveys on the Tempisque River were conducted further up river and salinity values of individual encounters did not differ significantly among size classes.

TABLE 5  
Summary of encounter rates (crocodiles/km) of *C. acutus* for comparison with this study

Location	Country	Survey method	Encounter rate	Habitat type	Population status	Reference
Biscayne Bay	USA	Day/Night	0-3.24	Coastline, mangrove	Increasing	Cherkiss <i>et al.</i> 2011
Turneffe and Lighthouse Atolls	Belize		0.28	Coastal		Platt & Thorbjarnarson 2000
Turneffe Atoll	Belize	Day/Night	1.2	Mangrove	Stable	Platt <i>et al.</i> 2004
Turneffe Atoll	Belize	Night/Nesting	0.34	Coastal/Mangrove	Declining?	Rainwater & Platt 2009
Osa Peninsula	Costa Rica	Day/Night	2.0-5.8	Rivers	Stable	Boston 2006
Isla de Salamanca	Columbia	Day/Night	2.56-7.78	Creeks, lagoons, marshes	Unstable	Balaguera-Reina & Gonzalez-Maya 2008
Río Tempisque	Costa Rica	Day/Night	2.8-11.1	River	Stable, increasing	Sanchez <i>et al.</i> 1997, Sanchez 2001
Río Bebedero	Costa Rica	Day/Night	4.5	River		Sanchez <i>et al.</i> 1997
Río Sierpe	Costa Rica	Day/Night	2.28	River	Stable	Bolaños <i>et al.</i> 1996
Río Rambla	Costa Rica	Day/Night	2.33	River		Bolaños <i>et al.</i> 1996
Nicoya Gulf	Costa Rica	Day/Night	1.93	Coastline		Bolaños <i>et al.</i> 1996
Río Tárcoles	Costa Rica	Day/Night/Aerial	Max: 10-35	River	Declining	Sasa & Chaves 1992, Abadía & Orjuela 1998, Sanchez 2001
Río Parrita	Costa Rica	Day/Night	6.6	River		Escobedo 2005
Río Paqueta	Costa Rica	Day/Night	0.95	River		Escobedo 2005
Río Tusubres	Costa Rica	Day/Night	3.86-5.58	River	Stable	Porras 2004



Crocodiles were encountered at different rates during our surveys (Tables 2 and 3) with the highest encounter rates within the ACOSA. These values may be skewed due to the large numbers of individuals encountered in the Pejeperrito and Pejeperro Lagoons and the timing of our surveys which coincided with nesting season (Table 3). These neighboring lagoons are small in size and had large numbers of crocodiles. This is possibly due to an abundance of food, protection from ocean currents and presence of suitable nesting habitat. The highest encounter rate within the Northwestern province of Guanacaste occurred in the Tempisque River (PV) which is known to have a large crocodile population (Ross 1998, Thorbjarnarson *et al.* 2006, Barrantes 2008). Since only a small number of surveys were conducted at each site, it is probable that the crocodile density along the Pacific coast of Costa Rica has been underestimated in this study, which has been shown during studies of other crocodiles (*C. porosus*; Stuebing *et al.* 1994). We recommend long term population monitoring of crocodile populations in different parks in Costa Rica.

The majority of all crocodiles encountered (54.9%) in each population were hatchlings and juveniles. Very few large adult animals (8.1%) were observed in this study. The smallest size classes were present in the highest numbers with frequencies decreasing as TL increased. The majority (86%) of the crocodiles captured during this study were smaller than 1.5m. Larger crocodiles are inherently more 'wary' and thus less likely to be observed (Messel *et al.* 1981, Ouboter & Nanhoe 1989). Therefore, they may be underestimated in this study. This low number of adults is consistent with the results of other studies (Webb *et al.* 1984, Kushlan & Mazzotti 1989a, Ouboter & Nanhoe 1989, Stuebing *et al.* 1994, Read *et al.* 2004, Cherkiss *et al.* 2011) and could be indicative of a recovering population (Ouboter & Nanhoe 1989). If hatchlings were excluded, roughly 40% of the entire coast and each of the Northern populations were composed of juveniles. Many of the sites in ACOSA were

close to or greater than 50% juvenile (Table 3). Therefore, further work is needed to determine the size structure and growth rates of *C. acutus* in Costa Rica to better understand the overall population structure and to ensure that good environmental conditions are maintained.

Distribution of the American crocodile populations in Florida are known to change seasonally for nesting, feeding or to find new territories, and individuals are known to have large overlapping activity areas (Kushlan & Mazzotti 1989a). Shoreline development and other anthropogenic effects may limit a crocodile's ability to find proper nesting and feeding areas along Pacific Costa Rica. The patchy distribution of suitable habitat within Costa Rica may make it necessary for crocodiles to move between areas. We noted during these surveys that some of the estuaries studied did not have suitable nesting habitat. Interviews with local fisherman also supported this observation. We hypothesize that crocodiles move between neighboring estuaries to fulfill different needs. For example, only large crocodiles have ever been observed in the San Francisco Estuary of Las Baulas Park. It is likely that adults from the larger Tamarindo Estuary to the North are moving to this estuary for feeding. Salinities are also higher in the San Francisco Estuary suggesting that this may not be suitable nursery habitat. However, we observed hatchlings in the Tamarindo Estuary so it appears to be the nesting area for this population. It is possible that a similar relationship exists between other estuaries and coastal lagoons along the Pacific coast of Costa Rica. Detailed studies investigating the migration of crocodiles among and between estuaries are needed to further understand this phenomenon.

**Conservation Implications:** Protection of the American crocodile and coastal habitat in Costa Rica is crucial to its continued survival. The central location of these populations within the species range makes them important in their regional management. The ability of individual crocodiles to migrate long distances (Webb & Messel 1978, Kushlan & Mazzotti 1989a, Kay

2004, Read *et al.* 2007) illustrates the importance of protecting all potential crocodile habitat. *Crocodylus acutus* habitats in Costa Rica are linked by gene flow (Cotroneo 2010), indicating that *C. acutus* populations exist as meta-populations along the Pacific coast of Costa Rica. Therefore, management of the American crocodile in Costa Rica should be aimed at protecting and conserving all populations

Hunting and habitat alteration have confined *C. acutus* populations to disjunct population centers throughout its range (Kushlan 1988, Thorbjarnarson *et al.* 2006) including Costa Rica. The largest potential threat to *C. acutus* in Costa Rica is habitat destruction and fragmentation (Thorbjarnarson *et al.* 2006, Thorbjarnarson 2010). Land use has increased exponentially in Costa Rica due to its growing urban and rural populations. It has especially intensified within the Central Valley and has expanded into more rural areas with deforestation being the key disturbance to the natural ecosystems (Veldkamp & Fresco 1997). Impacts of anthropogenic land use adversely affects biodiversity in Costa Rica (Dale *et al.* 1994, Daily *et al.* 2001). The Tarcoles River, which drains the urbanized central valley of Costa Rica, is one of the most polluted rivers in Central America (Fuller *et al.* 1990). Environmental contaminants have been found in the scutes of crocodiles captured in the Tarcoles and Tempisque Rivers (Rainwater *et al.* 2007, Rainwater *et al.* 2011). Our results indicate that the crocodile populations studied in Pacific Costa Rica are large, although they may be recovering from past reductions due to the large numbers of juveniles observed. It is important to maintain the environmental conditions necessary to ensure the continued survival of these populations.

#### ACKNOWLEDGMENTS

We would like to thank everyone that helped us in the field especially Bernal Cortes, Luis Fernando Lopez Lara, Juan Jose Victor Villalobos, Guillermo Briceo, Ademar Rosales, Fabricio Alvarez, Issac Ehresman, Gareth

Blakemore and Jim Tamarack. We would also like to thank the Ministerio del Ambiente, Energía y Telecomunicaciones (MINAET) and the Sistema Nacional de Áreas de Conservación (SINAC), especially Rodney Piedra, Jose Quiroz and Roger Blanco, for research permits. This work was largely supported by the Betz Chair of Environmental Sciences at Drexel University, and the Sophie Danforth Conservation Biology Fund from the Roger Williams Park Zoo in Rhode Island. The field research in Las Baulas National Park was partially supported by the Leatherback Trust. Research in the Osa Peninsula was also partially funded by the El Tigre Fund. The Leatherback Trust provided vehicles in Guanacaste, lodging at the Goldring Gund Marine Biology Station at Playa Grande, and a boat and motor for many of the crocodile surveys.

#### RESUMEN

El cocodrilo americano, *Crocodylus acutus*, se encuentra ampliamente distribuido en el neotrópico Americano y hay pocos estudios publicados sobre el estado de sus poblaciones en la mayor parte de su rango de distribución. Investigamos el estado del *Crocodylus acutus* en varias ubicaciones a lo largo de la costa del Pacífico de Costa Rica. Se realizaron muestreos nocturnos y de anidación a lo largo de la Costa Pacífica de Costa Rica en cuatro áreas en particular desde 2007-2009, áreas costeras en los Parque Nacionales de Las Baulas (N=40) y Santa Rosa (N=9), y en el Área de Conservación de la Osa (N=13) y en el curso alto del Parque Nacional de Palo Verde (N=11). Se registraron datos de la ubicación de los cocodrilos y datos ambientales estándar en cada observación. Se determinó la tasa de encuentros, estructura de la población, distribución dentro de cada área y evidencia de anidación exitosa (presencia de neonatos, nidos, etc.). Intentamos capturar todos los cocodrilos para registrar información morfológica estándar. En total, se observaron 586 cocodrilos a lo largo de 185.8km de ruta de muestreo. La mayoría de los animales encontrados (54.9%) fueron neonatos (<0.5m) o juveniles (0.5-1.25m). La tasa promedio de encuentros por muestreo de no-neonatos en la costa del Pacífico fue de 3.1 cocodrilos/km; con rangos de encuentro de individuos de entre 1.2 a 4.3 cocodrilos/km en el Parque Nacional de Las Baulas y el Área de Conservación Osa. La distribución por clases de tamaño no varió, a excepción de los Parques Nacionales de Santa Rosa y Las Baulas, donde se encontró a los neonatos en aguas con bajas salinidades. Estos fueron los primeros muestreos sistemáticos en varias de las áreas estudiadas y

son necesarios trabajos adicionales para caracterizar las poblaciones de cocodrilo Americano en Costa Rica.

**Palabras clave:** cocodrilo Americano, *Crocodylus acutus*, Costa Rica, promedio de encuentros, distribución por clases de tamaño.

## REFERENCES

- Abadia, G. & M.F. Orjuela. 1998. *Crocodylus acutus* in the Tarcoles River, Costa Rica, p. 378. In Proceedings of the Fourteenth Working Meeting of Crocodile Specialist Group (eds.). IUCN - Gland, Switzerland.
- Baillie, J.E.M., C. Hilton-Taylor & S.N. Stuart. 2004. 2004 IUCN Red List of Threatened Species: A Global Species Assessment. IUCN, Cambridge, United Kingdom.
- Balaguera-Reina, S.A. & J.F. Gonzalez-Maya. 2008. Population structure, density, and habitat of *Crocodylus acutus* Cuvier 1807 in the Via Parque Isla de Salamanca, Magdalena Department, Columbia. *Herpetotropicos* 4: 59-63.
- Barrantes, L.D. 2008. Determinación de la variabilidad genética y flujo genético entre las poblaciones de cocodrilo (*Crocodylus acutus*) de los ríos Tempisque, Tárcoles y el complejo Terraba-Sierpe; con mención especial a la condición de la población del Río Tempisque. Tesis de Maestría, Universidad Nacional, Heredia, Costa Rica.
- Bayliss, P. 1987. Survey methods and monitoring within crocodile management programmes, p. 157-175. In G.J.W. Webb, S.C. Manolis & P.J. Whitehead (eds.). *Wildlife management: Crocodiles and alligators*. Surrey Beatty & Sons, Australia.
- Bolaños, J., L. Sánchez & L. Piedra. 1996. Inventario y estructura poblacional de cocodrilos en tres zonas de Costa Rica. *Rev. Biol. Trop.* 44/45: 283-287.
- Boston, M. 2006. Recent surveys of the American crocodile (*Crocodylus acutus*) in the Osa Peninsula Region (ACOSA) of southwestern Costa Rica: Justification for long term studies and conservation. Friends of the Osa Newsletter. (Available online: <http://www.southerncostaricamap.com/member-listing.php?ID=149&url=/articles.php&get=>).
- Boza, M.A. & J.H. Cevo. 2001. Costa Rica National Parks and other Protected Areas. Incafo Costa Rica, San José, Costa Rica.
- Cherkiss, M.S., S.S. Romanach & F.J. Mazzotti. 2011. The American crocodile in Biscayne Bay, Florida. *Estuar. Coast.* 34: 529-535.
- Cotroneo, L.A. 2010. Population genetics and conservation of the American crocodile, *Crocodylus acutus*, on the Pacific coast of Costa Rica. Ph.D. Thesis, Drexel University, Philadelphia, Pennsylvania, USA.
- Daily, G.C., P.R. Ehrlich & G.A. Sanchez-Azofeifa. 2001. Countryside biogeography: use of human dominated habitats by the avifauna of southern Costa Rica. *Ecol. Appl.* 11: 1-13.
- Dale, V.H., S.M. Pearson, H.L. Offerman & R.V. O'Neill. 1994. Relating patterns of land-use change to faunal biodiversity in Central Amazon. *Conserv. Biol.* 8: 1027-1036.
- Davis, L.M., T.C. Glenn, R.M. Elsey, H.C. Dessauer & R.H. Sawyer. 2001. Multiple paternity and mating patterns in the American alligator, *Alligator mississippiensis*. *Mol. Ecol.* 10: 1011-1024.
- Dever, J.A. & L.D. Densmore. 2001. Microsatellite's in Morelet's crocodile (*Crocodylus moreletti*) and their utility in addressing crocodilian population genetics questions. *J. Herpetol.* 35: 541-544.
- Dunson, W.A. 1982. Osmoregulation of crocodiles: salinity as a possible limiting factor to *Crocodylus acutus* in Florida Bay. *Copeia* 1982: 374-385.
- Escobedo, A.H. 2005. El lagarto amarillo (*Crocodylus acutus*, Crocodylia: Crocodylidae): su estado poblacional en dos ríos del Pacífico Central de Costa Rica. *Brenesia* 63/64: 113-120.
- Frankie, G.W., A. Mata & S.B. Vinson. 2004. Biodiversity conservation in Costa Rica: Learning the lessons in a seasonal dry forest. University of California, Los Angeles, USA.
- Fuller, C.C., J.A. Davis, D.J. Cain, P.J. Lamothe, T.L. Fries, G. Fernandez, J.A. Vargas & M.M. Murillo. 1990. Distribution and transport of sediment-bound metal contaminants in the Río Grande de Tárcoles, Costa Rica (Central America). *Wat. Res.* 24: 805-812.
- Gaby, R., M.P. McMahon, F.J. Mazzotti, W.N. Gillies & J.R. Wilcox. 1985. Ecology of a population of *Crocodylus acutus* at a power plant site in Florida. *J. Herpetol.* 19: 189-198.
- Hutton, J.M., J.P. Loveride & D.K. Blake. 1987. Capture methods for the Nile crocodile in Zimbabwe, pp. 243-247. In G.J.W. Webb, S.C. Manolis & P.J. Whitehead (eds.). *Wildlife management: Crocodiles and alligators*. Surrey Beatty & Sons, Australia.
- Hutton, J.M. & M.E. Woodhouse. 1989. Mark-recapture to assess factors affecting the proportion of a Nile crocodile population seen during spotlight counts at Ngezi, Zimbabwe, and the use of spotlight counts to monitor crocodile abundance. *J. Appl. Ecol.* 26: 381-395.
- Jennings, M.L., D.N. David & K.M. Portier. 1991. Effect of marking techniques on growth and survivorship of hatchling alligators. *Wildl. Soc. Bull.* 19: 204-207.
- Kay, W.R. 2004. Movements and home ranges of radio-tracked *Crocodylus porosus* in the Cambridge Gulf region of Western Australia. *Wildl. Res.* 31: 495-508.

- Kushlan, J.A. 1988. Conservation and management of the American crocodile. *Environ. Manage.* 12: 777-790.
- Kushlan, J.A. & F.J. Mazzotti. 1989a. Population biology of the American crocodile. *J. Herpetol.* 23: 7-21.
- Kushlan, J.A. & F.J. Mazzotti. 1989b. Historic and present distribution of the American crocodile in Florida. *J. Herpetol.* 23: 1-7.
- Leslie, A.J. 1997. The ecology and physiology of the Nile crocodile, *Crocodylus niloticus*, in Lake St. Lucia, Kwazulu/Natal, South Africa. Ph.D. Thesis. Drexel University, Philadelphia, Pennsylvania, USA.
- Mazzotti, F.J. 1983. The ecology of *Crocodylus acutus* in Florida. Ph.D. Thesis, Pennsylvania State University, USA.
- Mazzotti, F.J. 1999. The American Crocodile in Florida Bay. *Estuaries* 22: 552-561.
- Mazzotti, F.J. & M.S. Cherkiss. 2003. Status and Conservation of the American Crocodile in Florida: Recovering an Endangered Species While Restoring an Endangered Ecosystem. University of Florida, Ft. Lauderdale Research and Education Center, Davie, Florida, USA.
- Mazzotti, F.J., L.A. Brandt, P. Moler & M.S. Cherkiss. 2007. American crocodile (*Crocodylus acutus*) in Florida: Recommendations for endangered species recovery and ecosystem restoration. *J. Herpetol.* 41: 121-131.
- Mazzotti, F.J., G. R. Best, L.A. Brandt, M.S. Cherkiss, B.M. Jeffery & K.G. Rice. 2009. Alligators and crocodiles as indicators for restoration of Everglades ecosystems. *Ecol. Indic.* 9: S137-S149.
- Messel, H., G.C. Vorlicek, A.G. Wells & W.J. Green. 1981. Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations. Monograph No. 1. Pergamon, Sydney, Australia.
- Motte, M. 1994. Abundancia, distribución e impacto de predación del cocodrilo (*Crocodylus acutus* Cuvier 1807) sobre el ganado vacuno en las fincas aledañas al río Grande de Tárcoles, Costa Rica. Tesis de Maestría, Universidad Nacional, Heredia, Costa Rica.
- Ogden, J.C. 1978. Status and nesting biology of the American crocodile, *Crocodylus acutus*, (Reptilia, Crocodylidae) in Florida. *J. Herpetol.* 12: 183-196.
- Ouboter, P.E. & L.M.R. Nanhoe. 1989. Notes on the dynamics of a population of *Caiman crocodius crocodilus* in Northern Suriname and its implications for management. *Biol. Conserv.* 48: 243-264.
- Platt, S.G. & J.B. Thorbjarnarson. 2000. Status and conservation of the American crocodile, *Crocodylus acutus*, in Belize. *Biol. Conserv.* 96: 13-20.
- Platt, S.G., T.R. Rainwater & S. Nichols. 2004. A recent population assessment of the American crocodile, *Crocodylus acutus*, Turneffe Atoll in Belize. *Herpetol. Bull.* 89: 26-32.
- Porras, L.P. 2004. Situación actual del cocodrilo Americano (*Crocodylus acutus*) en Ríos Jesús María, Tárcoles y Tusbres. Tesis de Maestría, Universidad Nacional, Heredia, Costa Rica.
- Rainwater, T.R., T.H. Wu, A.G. Finger, J.E. Cañas, L. Yu, K.D. Reynolds, G. Coimbatore, B. Barr, S.G. Platt, G.P. Cobb, T.A. Anderson & S.T. McMurry. 2007. Metals and organochlorine pesticides in caudal scutes of crocodiles from Belize and Costa Rica. *Sci. Total Environ.* 373: 146-156.
- Rainwater, T.R. & S.G. Platt. 2009. Possible decline of an American Crocodile (*Crocodylus acutus*) population in Turneffe Atoll, Belize. *Herpetol. Bull.* 107: 3-11.
- Rainwater, T.R., N.J. Millichamp, L.D. Barrantes, B.R. Barr, J.R. Bolaños, S.G. Platt, M.T. Abel, G.P. Cobb & T.A. Anderson. 2011. Ocular disease in American crocodiles (*Crocodylus acutus*) in Costa Rica. *J. Wildlife Dis.* 47: 415-426.
- Read, M.A., J.D. Miller, I.P. Bell & A. Felton. 2004. The distribution and abundance of the estuarine crocodile, *Crocodylus porosus*, in Queensland. *Wildlife Res.* 31: 527-534.
- Read, M.A., G.C. Grigg, S.R. Irwin, D. Shanahan & C.E. Franklin. 2007. Satellite tracking reveals long distance coastal travel and homing by translocated estuarine crocodiles, *Crocodylus porosus*. *PLoS ONE* 9: e949.
- Richardson, K.C., G.J.W. Webb & S.C. Manolis. 2002. Crocodile: Inside Out. Chipping Norton, Australia: Surrey Beatty.
- Ross, J.P. 1998. Crocodiles: an action plan for their conservation, IUCN/SSG Crocodile Specialist Group Publication. Oxford, Oxford.
- Sánchez, J.J., J. Bolaños & L. Piedra. 1997. Población de *Crocodylus acutus* (Crocodylia: Crocodylidae) en dos ríos de Costa Rica. *Rev. Biol. Trop.* 44: 835-840.
- Sánchez, J. 2001. Estado de la población de cocodrilos (*Crocodylus acutus*) en el río Tempisque, Guanacaste, Costa Rica. Unpublished Report, Área de Conservación Tempisque-Instituto Nacional de Biodiversidad (INBio), Heredia, Costa Rica.
- Sasa, M. & G. Chaves G. 1992. Tamaño, estructura y distribución de una población de *Crocodylus acutus* (Crocodylia: Crocodylidae) en Costa Rica. *Rev. Biol. Trop.* 40: 131-134.
- Spotila, J. & F. Paladino. 2004. Parque Marino Las Baulas: conservation lessons from a new national park and from 45 years of conservation of sea turtles in Costa Rica, p. 194-209. In G.W. Frankie, A. Mata & S.B. Vinson (eds.). Biodiversity conservation in Costa Rica: learning the lessons in a seasonal dry forest. University of California, Los Angeles, California, USA.

- Stuebing, R.B., G. Ismail & L.H. Ching. 1994. The distribution and abundance of the indo-Pacific crocodile *Crocodylus porosus* Schneider in the Klias River, Sabah, East Malaysia. *Biol. Cons.* 69: 1-7.
- Thorbjarnarson, J.B., F.J. Mazzotti, E. Sanderson, F. Buitrago, M. Lazcano, K. Minkowski, M. Muniz, P. Ponce, L. Sigler, R. Soberon, A.M. Trelancia & A. Velasco. 2006. Regional habitat conservation priorities for the American crocodile. *Biol. Cons.* 128: 25-36.
- Thorbjarnarson, J.B. 2010. American crocodile, *Crocodylus acutus*, p. 46-53. In S.C. Manolis & C. Stevenson (ed.). *Crocodyles. Status Survey and Conservation Action Plan*. Crocodile Specialist Group, Darwin, Australia.
- Veldkamp, A. & L.O. Fresco. 1997. Reconstructing land use drivers and their spatial scale dependence for Costa Rica (1973 and 1984). *Agr. Syst.* 55: 19-43.
- Webb, G.J.W. & H. Messel. 1978. Movement and dispersal patterns of *Crocodylus porosus* in some rivers of Arnhem Land, Northern Australia. *Aust. Wildl. Res.* 5: 263-283.
- Webb, G.J.W., S. Manolis, P. Whitehead & G. Lettis. 1984. A proposal for the transfer of the Australian population of *Crocodylus porosus* Schneider (1801), from Appendix I to Appendix II of C.I.T.E.S. *Cons. Comm. N.T. Tech. Rep.* 21.