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# Long-Distance Signaling in Crocodylia

Vladimir Dinets<sup>1</sup>

**Long-distance signals such as bellows, roars, headslaps, and infrasound pulses are important components of crocodilian behavioral repertoire, yet there is little or no published information on signaling for many species. Here, original data augmented with a compilation of published and unpublished sources are presented for 24 species of crocodilians. Their analysis shows that crocodilians adapt their signal composition to habitat structure by choosing physically different components. Flexible multi-component composition might partially explain the extraordinary evolutionary longevity of crocodilian signaling. Comparative analysis provides novel evidence for solving the long-standing debate about the phylogeny of the genus *Tomistoma*, supporting its affinities with crocodiles rather than true gharials. It also suggests that the absence of species with adult male length of less than 120 cm among extant crocodilians might be caused by the necessity of producing infrasound as an honest signal of status.**

CROCODYLIAN signaling is a behavioral “living fossil.” Most known forms of crocodilian communicatory behavior predate the separation of the alligatorid and crocodylid lineages, which has happened no later than in the Late Cretaceous (Senter, 2008).

Long-distance signaling is of particular interest, as it is most sensitive to habitat parameters and should be the least conservative as those parameters change over time. However, long-distance signals of crocodiles and alligators are still largely “mutually intelligible” (Garrick and Lang, 1977).

Unfortunately, while there was a lot of research on short-distance signaling such as courtship behavior and particularly parent–offspring interaction, long-distance signaling of crocodilians has not been studied much since the groundbreaking studies of Garrick and Lang (1977) and Garrick et al. (1978) on *Alligator mississippiensis*, *Crocodylus acutus*, and *C. niloticus*. Except for a few short notes scattered through the literature, all subsequent studies (Vliet, 1989; Wang et al., 2006, 2007) were on alligators, which include just two of 26 extant species. Without exception, all published studies on long-distance signaling have been done in captivity, where crocodilian signaling behavior differs markedly from that in the wild (Compton, 1981; Webb and Manolis, 1998; Dinets, 2011a). The paucity of records on long-distance signaling even for well-known species of crocodiles, caimans, and gharials is stunning. The only published description of a roar of *Crocodylus palustris* is in a 19<sup>th</sup> century children’s book of fiction (Kipling, 1895). Even detailed accounts of courtship produced by zoos and breeding facilities routinely skip all pre-courtship behavior. A handful of published overviews (Senter, 2008; Brazaitis and Watanabe, 2011) are mostly based on Garrick and Lang (1977).

For the present overview, data on all extant species, except for two recently split *Osteolaemus* spp. (see below) were gathered and analyzed. Of 24 species, 16 were observed in the wild (some also in captivity) and six only in captivity; for two more species published information was found.

**What is long-distance signaling in crocodilians?—**All crocodilian species have a category of signals characterized by the following features. First, these signals are used mostly during the mating season (although out-of-season signals are sometimes observed) and predominantly at a certain time of day, usually at night or in the morning, when environmental noise levels are minimum (Garrick and Lang, 1977). Second, they are the only intraspecific signals used both by

animals living in groups and those living in isolation. Third, they are the loudest signals used. I will refer to these signals collectively as advertisement calls (ACs). The term “advertisement calls” is used in herpetology for amphibian calls used in long-range signaling (Wells, 1977; Narins et al., 2006). The features of crocodilian ACs suggest that at least one of their functions is also long-range position and status signaling.

Advertisement calls can include three major types of sounds used in various combinations. The first type is a sound produced vocally above the water. It is traditionally called bellowing in alligators and roaring in crocodiles and caimans. The second type, produced only by males, is infrasound, non-vocal vibrations normally produced below the water surface at frequencies below the range of human hearing (~10 Hz). It can be visually detected by the so-called “water dance” effect (Vliet, 1989), apparently created by Faraday waves (G. Holt, pers. comm.). The third type includes headslaps (sounds made by slapping the head against the water surface) and jawslaps (sounds made by slapping the jaws together at or below the water surface). These slaps have a very sharp onset, a feature known to make locating the source of the sound easier (Hopp et al., 1998), and probably serve as location beacons, alone or combined with infrasound, which is difficult to locate underwater due to long wavelength.

Advertisement calls are produced in a particular posture which makes it easy to visually ascertain the size of the animal from afar. Garrick and Lang (1977) called it “head oblique tail arched posture” (HOTA). It has been found in all species except *Gavialis gangeticus*, in which it is replaced with a head-up posture (see Results). HOTA posture is probably an honest signal of size, addressed to animals observing it from above the water, while infrasound is addressed mostly to submerged or partially submerged animals.

There is evidence (Garrick and Lang, 1977) of odor being yet another component of ACs, possibly carrying information about the animal’s species, sex, and sexual maturity (Weldon and Wheeler, 2001). This component of ACs was not investigated in the present study.

## MATERIALS AND METHODS

Data were collected by observing crocodilians in the wild and in captivity, with the numbers of behavioral events of

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each kind (bellows/roars, slaps, infrasound pulses) scored. Study sites are listed in Table 1. Observation periods were selected based on the timing of the mating season for each species (see Dinets, 2011a for details). If possible, locations with little human disturbance were chosen for observations in the wild.

Observation protocols for *A. mississippiensis* and *C. niloticus* are described in Dinets (2011b); for *Caiman yacare* in Dinets (2013). All *Caiman latirostris* used in the study were observed simultaneously for one 28-hour period. For species that were difficult to observe at study sites, such as *Melanosuchus niger*, *Paleosuchus palpebrosus*, *P. trigonatus*, *Crocodylus moreletii*, *Osteolaemus tetraspis*, and *Tomistoma schlegelii*, each wild animal judged from its size and published information to be adult was observed for as long as possible. Unless noted otherwise, observations of other species in the wild were conducted when possible rather than systematically by locating large individuals (likely to be males) and watching them from a distance of at least 10 m for caimans and alligators in the wild, at least 50 m for crocodiles and gharials in the wild, and at least 5 m for animals in captivity. For each species observed in the wild, continuous 24-hour observation was attempted in order to determine the approximate time of day when sound-producing behavior is most likely. After that time period was determined, observational effort was centered on it. For animals in captivity, nighttime observations usually were not possible, so each was observed from 0700 or 0800 hrs until noon. All captive animals mentioned in this study, except for *Alligator sinensis*, were known to be males either from observed matings or from being sexed by zoo personnel.

Hereafter, each behavior involving production of sound and/or body vibration in a continuous HOTA posture is called AC (advertisement call). Relative frequency of use was estimated by scoring observed behaviors. To avoid pseudo-replication, three restrictions were used when scoring behaviors. (1) If more than one vocal sound or more than one headslap were produced during the same AC (which always meant they were less than ten seconds apart), they were counted as one vocal sound or one headslap, respectively. In *Gavialis gangeticus*, which does not produce signals in HOTA posture (see below), all sounds were scored. (2) Unless specified otherwise, only ACs from animals in sight were recorded. In order to avoid inflated counts due to contagion (for example, in bellowing choruses), after an AC was produced by any animal within sight or hearing range of the observer, ACs from this or other animals were not counted until one hour has expired. For *C. latirostris*, *G. gangeticus*, *Crocodylus porosus*, and species observed in captivity, of which only small numbers of individuals were available, this restriction was relaxed to 20 minutes to minimize data loss. (3) No more than three ACs were scored from any individual animal, except for *A. mississippiensis* and *C. niloticus* (see Dinets, 2011b), *C. yacare* (see Dinets, 2013), *C. crocodilus* (see Results), and captive animals.

Body vibration was assumed to be a sign of infrasound production (Garrick et al., 1978). Tape recordings made during body vibrations confirmed presence of infrasound (always at the frequency of 9–11 Hz) for *A. mississippiensis*, *C. yacare*, *C. crocodilus*, *Crocodylus acutus*, *C. moreletii*, *C. intermedius*, and *C. niloticus* (Dinets, 2011b). Unlike HOTA posture, body vibrations were not considered a separate component of ACs. Although it is possible that they do serve

as visual signals, to date there are no data to support such a possibility.

Sounds produced without HOTA posture were usually emitted in obvious close interactions with other animals; the few exceptions are listed in Results. Very few cases of infrasound production without accompanying vocal sounds and/or slaps were ever observed. Lengths of animals were visually estimated to the nearest 0.5 m, unless stated otherwise.

## RESULTS

Table 2 lists original results and other available information on AC composition for all species for which such information could be obtained, as well as the amount of time spent observing each species in the present study. Note that loud vocal sounds produced by caimans and crocodiles are commonly called “roars,” while those produced by alligators are commonly called “bellows.”

**Family Alligatoridae.**—Alligators and caimans have two distinct types of ACs, both usually performed in HOTA posture: bellowing/roaring display and headslapping display. ACs of both types include infrasound in males, but not in females. *Alligator* spp. produce ACs mostly in the morning; *Melanosuchus niger* and *Paleosuchus* spp. do so at night (the former also at dawn); *Caiman* spp. produce them mostly in the morning, but may have a second peak during the last two hours before sunset. Both displays are highly contagious and performed by both sexes in *Alligator* and *Caiman*, but headslapping displays are rarely performed by females. There is no solid evidence of contagion or of females producing ACs in *Paleosuchus* and *Melanosuchus*. *Alligator* and *Caiman* bellowing displays are often performed in choruses (group displays joined by most adults within hearing range), and possibly serve a second function of attracting animals to sites of group courtship (Dinets, 2011b).

Advertisement calls of *A. mississippiensis* are described in detail by Garrick et al. (1978) and Vliet (1989). In a study described in Dinets (2011b), bellowing displays were produced almost daily by all adult males ( $n = 72$ ), and headslapping displays were produced almost daily by most males in some areas, but rarely in others.

*Alligator sinensis* produces bellowing displays similar to those of the American alligator (see Thorbjarnarson and Wang, 2010, for a detailed description). Bellows are given in HOTA posture (with rare exceptions) in a shallow area or even on shore (V. Dinets, pers. obs.; also Wang et al., 2007, based on extensive observations at the same location). Large males accompany their ACs with infrasound (Thorbjarnarson and Wang, 2010). Headslaps are used infrequently (none observed in the present study among more than 100 ACs). They are produced in HOTA posture and sometimes accompanied by short bellows (“chumphs”) and jawslaps (Thorbjarnarson and Wang, 2010).

*Caiman yacare* produces ACs generally similar to those of *A. mississippiensis*. In a study in Brazil and Bolivia (Dinets, 2013), the following differences between the two species were noticed: (1) Adult *C. yacare* ( $n > 100$ ) produce more roaring and headslapping displays per day than alligators (up to 12 ACs per caiman were observed in one day, as opposed to 1–3 in free-ranging alligators). (2) Unlike *A. mississippiensis*, which in the wild bellows almost exclusively in the morning, *C. yacare* produces ACs in the evening as well: all observed caiman ACs were produced either between

**Table 1.** Study Sites. All sizes for small bodies of water were visually estimated, and for large bodies of water obtained from maps or satellite images provided by GoogleEarth. Abbreviations: AA—Alligator Adventure in North Myrtle Beach, South Carolina; KWS—Kateraniaghat Wildlife Sanctuary; NP—National Park; NWR—National Wildlife Refuge; RCV—Rio Chajul Valley in Chiapas, Mexico; SAAFZP—Saint Augustine Alligator Farm Zoo in St. Augustine, Florida.

Species	Site	Latitude, Longitude	Aquatic habitat
<i>Alligator sinensis</i>	Xuancheng Alligator Center, Anhui, China	30°55'N, 118°44'E	lakes 100 m <sup>2</sup> –1 km <sup>2</sup> (semi-natural)
<i>Alligator mississippiensis</i>	See Dinets, 2011b		
<i>Caiman yacare</i>	Pantanal, Mato Grosso, Brazil	17°41'–46'S, 57°05'–10'W	lakes 100 m <sup>2</sup> –10 km <sup>2</sup>
	Noel Kempff Mercado NP, Santa Cruz, Bolivia	15°07'–09'S, 60°34'–35'W	lakes 100 m <sup>2</sup> –10 km <sup>2</sup>
<i>Caiman latirostris</i>	Itaipu Reservoir, Parana, Brazil	25°14'S, 54°14'W	shallow bay 0.01 km <sup>2</sup>
<i>Caiman crocodilus</i>	Homestead, Florida, USA	25°29'N, 80°21'W	drainage canal 5–6 m wide (introduced)
	AA, South Carolina, USA	33°49'N, 78°44'W	pool 10 m <sup>2</sup> (captive)
<i>Melanosuchus niger</i>	Karanambu Ranch, Region 9, Guyana	3°45'–49'S, 59°17'W	river 25–90 m wide; oxbows 0.02–2 km <sup>2</sup>
	Yasuni NP, Orellana, Ecuador	0°31'S, 76°25'–26'W	lake 1 km <sup>2</sup>
	SAAFZP, Florida, USA	29°52'N, 81°17'W	pond 10 m <sup>2</sup> (captive)
<i>Paleosuchus palpebrosus</i>	Iwokrama Rainforest, Region 8, Guyana	4°20'N, 58°48'W	overgrown creek
	Yasuni NP, Orellana, Ecuador	0°32'S, 76°26'W	creek 1–3 m wide
<i>Paleosuchus trigonatus</i>	Coitubo River, Amazonas, Venezuela	5°32'N, 67°35'W	river 5–15 m wide
<i>Crocodylus acutus</i>	Everglades NP, Florida, USA	25°07'–09'N, 80°54'–89'W	brackish bays and channels
	Black River, St. Elizabeth, Jamaica	18°01'N, 77°50'W	brackish lagoon 27 km <sup>2</sup>
	Lago Enriquillo, Baoruco, Dominican Republic	18°30'N, 71°35'W	salt lake 265 km <sup>2</sup>
	RCV, Chiapas, Mexico	16°04'N, 90°57'W	oxbow lake 0.1 km <sup>2</sup>
	Isla de Salamanca NP, Magdalena, Colombia	11°56'N, 74°42'W	large brackish lagoons
	Moroccoy NP, Falcon, Venezuela	10°52'N, 68°13'W	brackish bays
	Manglares Churute Reserve, Guayas, Ecuador	2°25'–33'S, 79°36'–46'W	brackish channels
<i>Crocodylus intermedius</i>	Rio Capanaparo, Guarico, Venezuela	7°00'N, 68°19'W	oxbow lakes 1000–5000 m <sup>2</sup>
	Hato Masaguaral, Guarico, Venezuela	9°22'N, 67°41'W	pond 300 m <sup>2</sup> (semi-natural)
<i>Crocodylus moreletii</i>	RCV, Chiapas, Mexico	16°04'N, 90°57'W	oxbow lakes 0.03–0.05 km <sup>2</sup>
<i>Crocodylus rhombifer</i>	Zoo Miami, Florida, USA	25°36'N, 80°24'W	concrete pool 25 m <sup>2</sup> (captive)
	Gatorama (Palmdale), Florida, USA	26°55'N, /81°17'W	pond 16 m <sup>2</sup> (captive)
	Gatorland (Orlando), Florida, USA	28°21'N, 81°24'W	pond 20 m <sup>2</sup> (captive)
	SAAFZP, Florida, USA	29°52'N, 81°17'W	pond 10 m <sup>2</sup> (captive)
<i>Crocodylus novaeguineae</i>	SAAFZP, Florida, USA	29°52'N, 81°17'W	pool 8 m <sup>2</sup> (captive)
<i>Crocodylus siamensis</i>	SAAFZP, Florida, USA	29°52'N, 81°17'W	pool 25 m <sup>2</sup> (captive)
	AA, South Carolina, USA	33°49'N, 78°44'W	pool 12 m <sup>2</sup> (captive)
<i>Crocodylus niloticus</i>	See Dinets, 2011b		
<i>Crocodylus palustris</i>	KWS, Uttar Pradesh, India	28°21'N, 81°25'E	ponds 10–1000 m <sup>2</sup> ; river 100–300 m wide
	Sasan Gir NP, Gujarat, India	21°08'N, 70°47'E	ponds 100–1000 m <sup>2</sup> ; rivers 1–5 m wide
	Madras Crocodile Bank, Tamil Nadu, India	12°44'N, 80°14'E	concrete pond 100 m <sup>2</sup> (captive)
<i>Crocodylus porosus</i>	Sedangoli, North Maluku, Indonesia	0°51'N, 127°29'E	marine bay
	Tolire Besar, North Maluku, Indonesia	0°50'N, 127°18'E	crater lake 0.04 km <sup>2</sup>
	Sorong area, West Papua, Indonesia	0°54'S, 131°17'E	saltwater estuary
	Waigeo Island, West Papua, Indonesia	0°20'S, 130°59'E	shallow marine bay
<i>Crocodylus suchus</i>	SAAFZP, Florida, USA	29°52'N, 81°17'W	pond 10 m <sup>2</sup> (captive)
<i>Mecistops cataphractus</i>	SAAFZP, Florida, USA	29°52'N, 81°17'W	pond 8 m <sup>2</sup> (captive)
<i>Osteolaemus tetraspis</i>	Korup NP, Southwest, Cameroon	4°59'N, 8°50'E	pond 150 m <sup>2</sup> in a small stream
<i>Gavialis gangeticus</i>	KWS, Uttar Pradesh, India	28°21'N, 81°25'E	river 100–300 m wide
	Nandankanan Zoo, Orissa, India	20°23'N, 85°49'E	concrete pool 300 m <sup>2</sup> (captive)
<i>Tomistoma schlegelii</i>	Tanjung Puting NP, Kalimantan, Indonesia	2°57'S, 114°12'E	river 5–10 m wide
	AA, South Carolina, USA	33°49'N, 78°44'W	pool 12 m <sup>2</sup> (captive)



**Table 2.** Use of Advertisement Call Components by Crocodylian Species for Which Information is Available. The last three columns refer only to animals that produced behaviors scored as advertisement signals. See text for sources of published and unpublished information other than original observations. In parentheses are percentages of advertisement calls containing the component among all scored advertisement calls in cases when these percentages are below 25%. HOTA stands for head oblique tail arched posture (Garrick and Lang, 1977); ACs stands for advertisement calls (see text). See Results for information sources and for notes on the systematics of *Crocodylus suchus* and *Osteolaemus* spp.

Species	Aquatic habitat	Signal components				<i>n</i> of animals observed	<i>n</i> of ACs observed	Pers. obs., man-hrs
		HOTA	Infra-sound	Vocal sounds	Slaps			
<b>Habitat generalists</b>								
<i>Alligator mississippiensis</i>	ponds, rivers and lakes of any size, marshes, lagoons (McIlhenny, 1935)	yes	yes	yes	yes	>100	>500	>1000
<i>Caiman yacare</i>	lowland bodies of water of any type (Espinosa, 1998a)	yes	yes	yes	yes	>100	>1000	385
<i>Caiman crocodylus</i>	bodies of water of any type (Gorzula and Seijas, 1989; Espinosa, 1998b)	yes	yes	yes	yes	2 <sup>a,b</sup>	11	26
<i>Caiman latirostris</i>	small ponds to rivers, mangrove lagoons and estuaries (Medem, 1983; Scott et al., 1990; Moulton, 1993)	yes	yes	yes	yes	4	7	28
<i>Melanosuchus niger</i>	large rivers, forest streams, oxbow lakes, flooded savannas (Thorbjarnarson, 1998)	yes	yes	yes	yes	6 <sup>b</sup>	18	95
<i>Paleosuchus palpebrosus</i>	small and medium-size rivers, flooded forests (Medem, 1981, 1983)	yes	yes	yes	yes	2 <sup>b</sup>	3	59
<i>Paleosuchus trigonatus</i>	small and medium-size rivers, flooded forests (Medem, 1981, 1983)	yes	yes	yes	yes	2 <sup>b</sup>	3	3.5
<i>Crocodylus intermedius</i>	rivers and lakes of all sizes (Thorbjarnarson and Franz, 1987)	yes	yes	yes	yes	4 <sup>a</sup>	8	60
<i>Crocodylus novaeguineae</i>	rivers, lakes and swamps of various size (Hall and Johnson, 1987; Solmu, 1994)	yes	yes	yes	yes	1	1	18
<i>Crocodylus niloticus</i>	small ponds to large lakes, rivers and lagoons (Pooley and Gans, 1976; T. Pooley, 1982; De Smelt, 2004)	yes	yes	yes	yes	>80	>500	>900
<i>Crocodylus suchus</i>	small ponds to large lakes, rivers and coastal lagoons (Waitkuwait, 1989; Kofron, 1992)	yes	yes	yes	yes	1	2	12
<i>Crocodylus palustris</i>	small ponds to large rivers and coastal lagoons (Whitaker and Whitaker, 1984)	yes	yes	yes	yes	13	20	150
<i>Crocodylus johnstoni</i>	rivers, lakes and ponds (Webb and Manolis, 1998)	yes	yes	yes	yes	published data; no pers. obs.		
<i>Crocodylus siamensis</i>	rivers, lakes and swamps of various size (Smith, 1919; Crocodile Specialist Group, 1996)	yes	yes	yes	yes	2 <sup>b</sup>	18	16
<i>Mecistops cataphractus</i>	rivers, lakes, heavily vegetated streams and flooded forests (A. C. Pooley, 1982; Steel, 1989; Waitkuwait, 1989; Shirley, 2010)	yes	yes	yes	yes	1 <sup>b</sup>	22	18
<b>Species inhabiting mostly continuous aquatic habitats</b>								
<i>Crocodylus acutus</i>	lagoons, estuaries, large rivers and lakes (Álvarez del Toro and Sigler, 2001)	yes	yes	rarely (10.9%)	yes	34	56	172
<i>Crocodylus porosus</i>	lagoons, estuaries, seashores, large rivers and lakes (Webb and Manolis, 1998; Messel and Vorlicek, 1989)	yes	yes	rarely (6.2%)	yes	8	13	72
<i>Tomistoma schlegelii</i>	rivers (Bezuijzen et al., 1997)	yes	yes	no	yes	2 <sup>a,b</sup>	2	6
<i>Gavialis gangeticus</i>	large rivers (Whitaker and Basu, 1983)	head-up posture	no	no	yes	5 <sup>a</sup>	7	48

**Table 2.** Continued.

Species	Aquatic habitat	Signal components				<i>n</i> of animals observed	<i>n</i> of ACs observed	Pers. obs., man-hrs
		HOTA	Infra-sound	Vocal sounds	Slaps			
Species inhabiting mostly fragmented aquatic habitats								
<i>Alligator sinensis</i>	ponds and small lakes (Chen et al., 2003; Wang et al., 2006; Wang et al., 2007)	yes	yes	yes	rarely (<1%)	35 <sup>a</sup>	162	14
<i>Crocodylus moreletii</i>	forest ponds, small lakes, swamps (Álvarez del Toro and Sigler, 2001)	yes	yes	yes	rarely (8.3%)	5	12	65
<i>Crocodylus rhombifer</i>	shallow marshes (Varona, 1966)	yes	yes	yes	rarely (9.1%)	3	11	48
<i>Crocodylus mindorensis</i>	small lakes, ponds, freshwater marshes, shallow forest rivers (Ross, 1982)	no data	no data	yes	no data	published data; no pers. obs.		
<i>Osteolaemus tetraspis</i>	small forest ponds, swamps and shallow streams (Waitkuwait, 1989; Riley and Huchzermeyer, 1999)	yes	yes	yes	no	1 <sup>b</sup>	1 <sup>c</sup>	6

<sup>a</sup> also published data.

<sup>b</sup> also pers. comm. data.

<sup>c</sup> also more than 20 sound recordings provided by Elephant Listening Project.

0400 and 0930 hrs, or between 1600 and 1900 hrs. (3) All observed roaring displays of *C. yacare* consisted of one to three roars, while *A. mississippiensis* bellows are usually repeated more than eight times. (4) Alligators frequently bellow in choruses which last for up to ten minutes, while in caimans such choruses usually last less than a minute. (5) Caiman roars are sharp sounds shorter than 0.5 sec (alligator bellows usually last at least a second) and sound remarkably similar to the alarm calls of the barking deer (*Muntiacus* spp., V. Dinets, pers. obs.). (6) Roars of *C. yacare* were never heard by a human observer from more than 200 m away, while *A. mississippiensis* bellows can be heard from more than 500 m. Headslapping displays made up about a third of all observed ACs at both study sites.

*Caiman crocodilus* has signaling behavior similar to that of the *C. yacare* (Álvarez del Toro and Sigler, 2001; J. Thorbjarnarson, pers. comm., V. Dinets, pers. obs.), and roars of the two species look identical on sonograms (V. Dinets, pers. obs.). In the present study, wild *C. crocodilus* from an introduced population in southern Florida, mostly of Colombian origin (Ellis, 1980), and captive 1.5 m long male of Tobago origin produced roaring and headslapping displays, always between 0800 and 0900 hrs.

*Caiman latirostris* also produces signals similar to those of *C. yacare*. In a group of six caimans 1.5–2 m long observed simultaneously in the present study, four caimans produced five roaring displays and two headslapping displays in 28 hrs, all in the morning. Two of the roaring displays did not include infrasound and were produced by smaller individuals (probably females).

*Melanosuchus niger* produces roaring and headslapping displays similar to those of *Caiman* spp. (Dinets, 2011c). Roars of *M. niger* are louder and longer than those of *Caiman* spp., sound more like the loudest roars of *Crocodylus* spp. (below), and are seldom repeated more than once. HOTA posture of this species is distinct: the head is held horizontally, not at an angle as in other crocodilians (V. Dinets, pers. obs.). It is unclear if females of this species produce ACs: interpreting observations by other researchers

is difficult because in this species roars and slaps in HOTA-like posture are also used in threat displays (P. Taylor, pers. comm.; V. Dinets, pers. obs.).

Both species of dwarf caimans (*Paleosuchus*) produce bark-like roars and headslaps, as well as infrasound (C. Stevenson, unpubl.; Z. M. S. Campos, pers. comm.). In the present study, six *Paleosuchus* ACs were observed. Each of those ACs included infrasound and only one roar or slap. Roars of both species sound identical to a human observer, are very short in duration (less than 0.5 sec), and probably are not audible at more than 200 m.

**Family Crocodylidae.**—In most (probably all) species of *Crocodylus*, ACs are performed mostly by territorial (i.e., dominant) males. They are usually given in HOTA posture and include infrasound. Unlike in the previous family, ACs of at least some species can include roars and slaps at the same time, although headslaps are rare or absent in some species, while roars are rare or absent in some others. Females occasionally produce roars or slaps, but without infrasound and usually not in HOTA posture. In some (possibly all) species, headslapping displays also serve as signals of dominance, and can be performed by adult females kept in absence of males in captivity (Dinets, 2011b). Most species produce ACs in the morning, but *C. porosus* and *C. palustris* also do so at night. See accounts below for information on signaling by other genera. Unless specified otherwise, all described signals included infrasound and were given in HOTA posture.

*Crocodylus niloticus* signaling was described in detail by Garrick et al. (1978). In the present study, male *C. niloticus* ( $n = 70$ ) at seven locations in eastern and southern Africa produced headslaps almost daily, while frequency of use and loudness of roars differed to a great extent between geographical areas (Dinets, 2011b). To a human observer, the louder roars sound similar to those of most other *Crocodylus* listed below, while quiet roars given in some areas are cough-like sounds resembling “growls” of *C. porosus* (see below), audible only at close range (V. Dinets, pers. obs.).

*Crocodylus suchus* was recently found to be a species distinct from *C. niloticus* (Hekkala et al., 2011). It frequently uses roars similar to those of *C. niloticus* (M. H. Shirley, pers. comm.). In the present study, a 2.5 m long captive male produced two headslaps and two roars in six mornings of observation.

*Crocodylus acutus* signaling has been described by Lang (1975) and Garrick and Lang (1977). In the present study, *C. acutus* were observed to produce headslaps much more frequently than roars: 23 headslaps vs. 3 roars in Florida; 7 headslaps vs. 1 roar in Colombia; 16 headslaps vs. 2 roars in Venezuela; 4 headslaps and no roars in Dominican Republic; 2 headslaps and no roars in Jamaica; and 13 headslaps vs. 1 roar in Ecuador. One male in Florida also produced one infrasound-only AC. No animal produced more than two ACs per day. In one area (the inland Rio Chajul Valley on Mexican-Guatemalan border) crocodiles had unusually low headslaps:roars ratio—8 headslaps vs. 3 roars. According to J. D. Lazo (pers. comm.) and my own observations, in this geographical area *C. acutus* inhabit lakes and rivers of varying size, rather than large lakes and coastal lagoons as in other areas; the importance of this distinction is discussed below. Although *C. acutus* is a large species, its roars are relatively quiet (audible to a human observer at up to 100 m under ideal conditions). The duration of sound is typically 0.5–1 sec (V. Dinets, pers. obs.).

*Crocodylus intermedius* signals include roars and headslaps, produced by adult males (Thorbjarnarson and Hernandez, 1993). Occasionally roars and headslaps are produced while swimming in inflated posture, rather than in HOTA posture (V. Dinets, pers. obs.; J. Thorbjarnarson, pers. comm.). In the present study, four large *C. intermedius* (two captive, known to be males, and two wild) produced eight ACs in six days of observation. All ACs included headslaps, and all except two included roars. Roars of this species are longer and louder than those of *C. acutus*: all observed roars lasted 1–2 sec, and one was clearly heard from 220 m away.

*Crocodylus moreletii* signals are known to include roars and headslaps in captivity (Álvarez del Toro and Sigler, 2001). In the present study, all ACs produced by five large *C. moreletii* (one known to be a male as it was observed during mating) included a loud, short (less than 1 sec long), sharp roar. One AC included also a headslap.

*Crocodylus rhombifer* frequently roars, but rarely, if ever, headslaps (J. P. Ross, pers. comm.). Roars of this species sound identical to those of *C. moreletii* (V. Dinets, pers. obs.). In the present study, captive males produced numerous ACs, all of which included a roar, but only one also included a headslap. In addition, on a rainy day (when the water temperature was probably low) one male produced four roars on land rather than in HOTA posture. See Dinets (2011d) for additional information.

Signals of *Crocodylus palustris* observed in the present study also included roars and headslaps. In Sasan Gir National Park, where *C. palustris* inhabits forest ponds and small river pools that are isolated during the mating season, four crocodiles over 2 m long produced eight ACs, of which six included roar(s) and two included a headslap, in seven days of observation. In Katarniaghat Wildlife Sanctuary, where *C. palustris* inhabits a large river as well as small forest ponds, eight crocodiles over 2 m long produced eight displays consisting of roars and three displays consisting of headslaps in five days of observation. A 3 m long captive male in Madras Crocodile Bank produced one roar in one

day of observation. Roars of this species are similar to those of *C. niloticus*, but louder (audible to a human observer at more than 1 km under ideal conditions) and longer (up to 5 sec in duration, as seen on spectrograms). All roars and headslaps were produced by animals more than 2 m long (by visual estimate), and never by animals known from mating observations to be females. All animals produced no more than two ACs per day. See Dinets (2011e) for additional information.

*Crocodylus porosus* roars are cough-like, very low sounds commonly called “growls” (Webb and Manolis, 1998), audible to a human observer at no more than 100 m (V. Dinets, pers. obs.). In the present study, *C. porosus* were observed producing either headslap(s) or growls. There were many more headslaps than growls: six headslaps vs. one growl in northwestern New Guinea (five animals), one headslap and one infrasound-only AC at Waigeo Island (one animal), two headslaps in Sedangoli at Halmahera Island (one animal), and two headslaps in Tolire Besar crater lake on Ternate Island (one animal). All animals produced no more than two ACs per day. Webb and Manolis (1998) also state that growls are seldom produced by saltwater crocodiles in the wild.

*Crocodylus siamensis* produces headslaps and roars (P. Kwartalnov, pers. comm. for reintroduced animals in a lake in Cat Tien National Park, Vietnam; S. Mukherjee, pers. comm. for captive animals in Madras Crocodile Bank, India; U. Youngprapakom, pers. comm. for captive animals at Samutprakan Crocodile Farm, Thailand). In the present study, captive males produced ACs including either one roar or one headslap, at a rate of 1–2 per morning.

*Crocodylus mindorensis* was not observed in the present study. A captive pair at a breeding facility at Negros Island (Philippines) exchanged “series of brief high-pitched groaning or bellowing sounds” (Alcala et al., 1987). There is no mention of HOTA posture, infrasound, or slaps in the description.

*Crocodylus novaeguineae* signaling is still virtually unknown. In the present study, a 2 m long captive male produced one AC in nine mornings of observation. It was a high-pitched roar less than 1 sec long, followed by a headslap and body vibration indicative of infrasound production.

*Crocodylus johnstoni* was not observed in the present study. According to Webb and Manolis (1998), it frequently produces roars (sounding like loud grunts), headslaps (sometimes jawslaps), and “low frequency sound produced by body vibration” (apparently infrasound) during the mating season.

*Mecistops cataphractus* produces a lot of signals during the mating season. A captive male in Madras Crocodile Bank, India, regularly produced roars and headslaps (S. Mukherjee, pers. comm.). In the present study, a 2.5 m long captive male produced three roars, 16 headslaps, and three roars combined with headslaps in eight mornings of observation. Roars of this species sound similar to loud roars of many *Crocodylus* spp., and are 0.5–1 sec in duration (V. Dinets, pers. obs.).

*Osteolaemus tetraspis* has been recently split into three species (Eaton et al., 2009). All available information on signaling refers to *O. tetraspis sensu stricto*. In the present study, *O. tetraspis* was observed producing a groan-like sound preceded by a very brief body vibration in HOTA posture at night. Rangers at Korup National Park (Camer-

oon) reported occasionally hearing dwarf crocodile “moans,” but have never observed slaps. A captive male from Congo that lived for many years in Moscow Zoo, Russia, produced vocal sounds and body vibrations indicative of infrasound production, but no slaps (P. Kuchaev, pers. comm.). Recordings obtained in Evindo, Gabon, by the team of Elephant Listening Project contain numerous roars preceded by infrasound pulses, but no slaps (P. H. Wrese, pers. comm.).

*Tomistoma schlegelii* is a rare species, and its behavior is little known. Captive *T. schlegelii* produce headslaps in HOTA posture during the mating season (Trutnau and Sommerland, 2006), but they produce vocal sounds only when physically provoked (A. Karlon, pers. comm., U. Youngprapakom, pers. comm.). In the present study, a 3.5 m long animal was observed at night in the wild to assume HOTA posture for about nine seconds, as its body briefly vibrated, suggesting infrasound production. A captive 5 m long male produced one headslap accompanied with infrasound in two mornings of observation.

**Family Gavialidae.**—The signaling system of *Gavialis gangeticus* is different from all other crocodilians for which information is available. Instead of HOTA posture, *G. gangeticus* often assumes a head-up posture on land, which is believed to be a territorial display and a signal of sex and maturity (adult males have a huge bulbous growth called ghara on the tip of the snout), as suggested by Singh and Rao (1990). This species is not known to produce infrasound. The only sounds associated with courtship are soft buzzes, given in close proximity to other animals, and incredibly loud jawslaps, given by both males and females at or below (occasionally above) the water surface (Whitaker and Basu, 1983). In the present study, a stretch of a large (50–200 m wide) river with at least five males and ten females visible most of the time was observed for 32 hours. Jawslaps were seen twice and heard five more times; two of these five heard-only jawslaps were barely heard and probably were produced by animals outside that part of the river. In a captive group of 26 gharials (including five adult males), no jawslaps were heard in 16 hours of observation, although the animals were actively courting and buzzing. Jawslaps of *G. gangeticus* probably serve a function similar to that of headslaps in other crocodilians. According to Whitaker and Basu (1983), this species can produce only very weak headslaps due to its extremely narrow snout.

## DISCUSSION

**Why have so many signal components?**—Crocodilian ACs include up to five components (vocal sounds, slaps, infrasound, HOTA or head-up posture, and odor). As discussed in Dinets (2011b), the benefit of having multiple components may be in their differing ability to spread and carry information through air and water. Vocal sounds are optimal for carrying information about the location of the animal and its size through air, while slaps are optimal for carrying information about the location of the animal through water; HOTA posture and infrasound are honest signals of the animal’s size; infrasound is also a signal of sex as it is only produced by males. The head-up posture used by *G. gangeticus* is a signal of size, sex, and maturity. Together, all components form a robust and flexible signaling system.

**Signal composition versus habitat.**—If ACs containing loud vocal signals are better adapted for carrying information

through the air, while ACs containing headslaps are better adapted for carrying information through the water, then it can be expected that the former are used more in fragmented aquatic habitats, and the latter in continuous aquatic habitats.

In studies (Dinets, 2011b) of *A. mississippiensis* and *C. niloticus* such differences were found between allopatric populations of each species inhabiting different habitats. It was also found that roars by *C. niloticus* from populations living in large lakes and rivers are usually reduced to quiet “coughs.”

It can be predicted that species that are habitat generalists use both vocal signals and slaps; species inhabiting predominantly continuous aquatic habitats use slaps but few, if any, vocal signals; and species inhabiting predominantly fragmented aquatic habitats use vocal signals but few, if any, slaps.

Table 2 summarizes the available information on habitat and AC composition for extant crocodilian species. Most species inhabit a broad variety of aquatic habitats. All such species ( $n = 15$ ) frequently use both vocal sounds and slaps, at least at some locations. *Crocodylus acutus*, *C. porosus*, *G. gangeticus*, and *T. schlegelii* inhabit mostly continuous aquatic habitats. All these species ( $n = 4$ ) use slaps, but few or no vocal sounds, and in some species these sounds are reduced in loudness. *Alligator sinensis*, *C. moreletii*, *C. rhombifer*, *C. mindorensis*, and *O. tetraspis* inhabit mostly fragmented aquatic habitats. All these species ( $n = 5$ ) use vocal sounds, but few or no slaps. Note that shallow bodies of water with abundant vegetation or fallen tree branches, such as small forest streams, can be classified as fragmented aquatic habitats for the purpose of the present study because slap sounds rapidly lose their sharp onset and cannot carry location information over long distances in such habitats (Dinets, 2011a).

These differences in behavior are seen even between very closely related species inhabiting different habitats. For example, *C. siamensis*, *C. novaeguineae*, and *C. mindorensis* are closely related to *C. porosus* (Oaks, 2007); *C. rhombifer*, *C. moreletii*, and *C. intermedius* are closely related to *C. acutus* (Oaks, 2007), and *C. intermedius* might be a distinct subspecies of the latter (Venega-Anaya et al., 2007).

Although the extreme heterogeneity of available data prohibits meaningful statistical analysis at present, the match between what is known and the above predictions is remarkable.

**Evolutionary history of long-distance signaling.**—The fact that the signaling system of crocodilians, with its repertoire of physically different signals, can be easily adapted to diverse habitats simply by changing the usage of two signal components, might account for the preservation of this system since the Late Cretaceous (Senter, 2008). Although the signal composition is highly variable and can differ between closely related species and even between conspecific populations (Dinets, 2011b), the overall repertoire differs little between most species and appears to be extremely well conserved. This allows using the differences in signaling repertoire for reconstructing its evolutionary history. The most parsimonious scenario is that the common ancestor of crocodiles, alligators, and caimans was a habitat generalist and used both vocal signals and slaps, as well as infrasound and HOTA posture. If that common ancestor had been a habitat specialist, inhabiting



either only fragmented or only continuous aquatic habitats, one of the signal components (either slaps or vocal sounds) would have been lost instead of being inherited by all descendants of this common ancestor, as has evidently occurred in some descendant species with specialized habitat preferences.

*Gavialis gangeticus* has a different signaling system. It does not use infrasound or loud vocal sounds, only loud jawslaps. Instead of using HOTA posture in the water, it uses a head-up posture when onshore, and has a special morphological adaptation (the ghara) that makes this posture sex-specific. This system is probably an ancient adaptation to living only in continuous aquatic habitat, and has evolved separately from the signaling of all other extant crocodylians.

**The mystery of *Tomistoma*.**—The systematic position of *T. schlegelii* is still a subject of controversy, with some data suggesting it has a common ancestry with *G. gangeticus*, but other data supporting the idea that it is an aberrant crocodylid (Tarsitano et al., 1989; Brochu, 2003; Janke et al., 2005; Piras et al., 2010; Man et al., 2011). The results of the present study support stronger affinities with crocodylids, as the signaling system of *T. schlegelii* has little in common with that of *G. gangeticus*. Instead, *T. schlegelii* uses headslaps, infrasound, and HOTA posture, just like most other crocodylians, although unlike most other crocodylians, it makes no loud vocal sounds. Two evolutionary scenarios could lead to such a repertoire: either the vocal sounds were lost after *T. schlegelii* had diverged from other crocodylians, or the vocal signals are more recent in origin than infrasound and slaps, and were acquired by the common ancestor of true crocodiles, alligators, and caimans after its divergence from the *Tomistoma* lineage. The first scenario is more likely for two reasons. First, recent analyses suggest that alligators and caimans have diverged from crocodiles earlier than *Tomistoma* has (Man et al., 2011). Second, *T. schlegelii* is believed to have a recent marine ancestor (Taplin and Grigg, 1989), which makes secondary loss of vocal signals very likely.

**Infrasound and minimal size.**—All extant crocodiles are relatively large reptiles. Only the smallest ones—*A. sinensis* (Thorbjarnarson and Wang, 2010), the Tobago population of *C. crocodilus* (Grenard, 1991), *P. palpebrosus* (Medem, 1983), and *Osteolaemus* spp. (Kofron and Steiner, 1994)—can reach sexual maturity at less than 1 m length. However, full-grown males exceed 1.2 m in all of them: *A. sinensis* (Thorbjarnarson and Wang, 2010); the Tobago *C. crocodilus* (V. Dinets, pers. obs.); *P. palpebrosus* (Campos et al., 2010; length estimates adjusted for missing tail tips in all adults); and *O. tetraspis* (M. Eaton, pers. comm.). All these animals are apparently capable of producing infrasound when full-grown, and use it in their ACs. Male *A. mississippiensis* begin to accompany their bellows with infrasound at approximately the same length (V. Dinets, pers. obs.), so 1.2 m is likely the minimum size at which producing infrasound becomes physically possible. The importance of producing underwater infrasound, which can only be emitted by animals of sufficient size, could be a limiting factor in the evolution of small size in crocodylians.

When did infrasound become a component of crocodylian signaling? There are some very small fossil crocodylians, but the so-called crown group, which includes all extant species (Brochu, 2003) is conspicuously lacking such forms (D. Naish, pers. comm.). Thus it is likely that the use of

infrasound as an honest signal of sex and condition was acquired after the separation of the “crown group” from other lineages, and probably after the separation of true gharials, as it would be less parsimonious to consider its absence in the latter to be secondary. While other extant crocodylians appear to use at least two honest signals of size (infrasound and HOTA posture), *G. gangeticus* seems to use a handicap as a signal of fitness. Ghara, a huge growth on the snout tip of adult males, probably seriously interferes with fishing by rapid lateral movement of head, for which the narrow snout of gharials is an apparent adaptation (Whitaker and Basu, 1983).

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