2011-04-12

The Role of Habitat in Crocodilian Communication

Vladimir Dinets
University of Miami, dinets@gmail.com

Recommended Citation

Dinets, Vladimir, "The Role of Habitat in Crocodilian Communication" (2011). *Open Access Dissertations*. 570.
https://scholarlyrepository.miami.edu/oa_dissertations/570

UNIVERSITY OF MIAMI

THE ROLE OF HABITAT IN CROCODILIAN COMMUNICATION

By

Vladimir Dinets

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2011

UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

THE ROLE OF HABITAT IN CROCODILIAN COMMUNICATION

Vladimir Dinets

Approved:

Steven Green, Ph.D. Professor of Biology	Terri A. Scandura, Ph.D. Dean of the Graduate School
Richard Tokarz, Ph.D. Associate Professor of Biology	Keith D. Waddington, Ph.D. Professor of Biology
Carl Gerhardt, Ph.D. Curators' Professor of Biological Sciences University of Missouri	

DINETS, VLADIMIR (Ph.D., Biology)
The Role of Habitat in Crocodilian Communication (May 2011)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Steven Green.
No. of pages in text. (108)

All crocodilian species for which information is available have a particular category of signals, which are used as advertisement calls during the mating season. Each such call is a combination of a few components with different physical properties, such as body postures, vocal calls, headslaps or jawslaps, and infrasound vibrations. These components differ in their capacity to carry information about the animal's status and location, and their use can be expected to be adapted to habitat structure. In particular, vocal sounds should be used more in fragmented aquatic habitats where they are more effective, while slaps should be used more in continuous aquatic habitats. A comparison of signaling and preferred habitats by extant crocodilian species confirmed this prediction. Also, in species that are habitat generalists, animals in populations inhabiting only continuous aquatic habitats were found to use more slaps, while animals in populations inhabiting only fragmented aquatic habitats used more vocal sounds. But in populations inhabiting mixed habitats, individual animals did not adjust their signal composition to habitat parameters, so the observed differences between populations and species are evolved adaptations. In the course of the study, novel information on signaling was obtained for many crocodilian species, providing insights into their ecology and evolutionary history.

ACKNOWLEDGEMENTS

Many people have made this project possible, often going beyond what they were asked for, sharing their time, knowledge, experience, transportation, food, water, homes and campfires, issuing research permits, allowing access to private lands, tribal territories and research facilities. I can only name a selected few here, but am grateful to all of them.

My thanks to Eisha Alibasha (Ethiopia), Jamal Al-Jawari (Egypt), Chad Anderson (USA), Chief Asanka (Burundi), Balaqa Ashoba (Ethiopia), Brady Barr (USA), Mark Barrett (USA), Ben Bejtel (Namibia), Alex Bernstein (Kenya), Gaurav Bhatnagor (India), Tomas Blohm (Venezuela), Jesekiel Bomba (Uganda), John D. Brueggen (USA), Jaco Burger (Namibia), Gordon Burghardt (USA), John Burt (USA), Rick Cameron (Indonesia), Zilca Maria da Silva Campos (Brazil), Mariela Cardenas (Ecuador), Ada Castillo (Peru), Joseph Chadou (DRC), Michael Cherkis (USA), Jennifer Ciaccio (USA), John Clenn (Jamaica), Tommy Collard (Namibia), Steven Conners (USA), Steven Counsel (Mozambique), Paul van Damme (Brazil), Alla Dinets (Russia), Mitch Eaton (USA), Beniamin Eligulashvili (Israel), Henriette Engelbrecht (South Africa), Tamrat Fahid (Ethiopia), Carla Ferreira (South Africa), Bereket Gebretsadik (Ethiopia), Carl Gerhard (USA), Moses Gorongo (Kenya), Steven Green (USA), John Hall (Australia), Casey Handmer (Australia), Dabeer Hasan (India), Paolo Hatzfeld (Brazil), Sandra Hill (Kenya), Steve Irvin (Australia), Tim Isle (USA), Peter Jackson (Botswana), Tazz Jacobs (South Africa), Ramosh Jiah (Malawi), Zhao Xin Jiang (China), Leon Jooste (Namibia), Alan Karlon (USA), Polina Kaplan (Israel), Diana Kemp (Namibia), Michael L. Kipkeu (Kenya), Turner Kirk (USA), David Kledzik (USA), Ofer Kobi (Israel), Aaron Kortenhoven (USA), Michael Kosoy (USA), Boris Krasnov (Israel), Pavel Kvartalnov

(Russia), Jeronimo Dominguez Laso (Mexico), Mashera Leboma (Tanzania), Pauline Lindeque (Namibia), Pablo Lopez (Ecuador), Sarah Mackenzie (Zambia), Raul Marago (Bolivia), Erica Marce (Mexico), Edwin Matokwani (Zambia), Thaddeus McRae (USA), Diana, Edward & Melanie McTurk (Guyana), Krishna Kumar Mishra (India), Liz von Muggenthaler (USA), Mzwandile Mjadu (South Africa), Pedro Maria Montero (Colombia), Soham Mukherjee (India), Mary N. (Madagascar), David Naish (UK), Diego Navarra (Dominican Republic), Francois Ndele (Cameroon), Sunday Nelenge (Namibia), Jeremiah Newman (DRC), James C. Nifong (USA), Collin Ogden (South Africa), David Oudjani (France), Maria Oleneva (Mexico), Serverio Pachac (Ecuador), Luis Pacheco (Brazil), Richard Paper (Madagascar), Asy Patrysheva (Russia), Elena & Victor Pavlov (USA), SØe Pedersen (Denmark), Dietmar Posch (South Africa), Pradeep (India), Alfonso Llobet Querejazu (Bolivia), Devis Rachmawan (Indonesia), Eulalie Razoanantenaina (Madagascar), Patty & Allen Register (USA), Wang Renping (China), Sarit Reizin (Kenya), Mark Robinson (South Africa), James P. Ross (USA), Damian Rumiz (Brazil), Jorge Sanchez (Guatemala), William Searcy (USA), Genzap Sechen (Ethiopia), L. D. Sefu (Malawi), Mejangi Sfatau (Uganda), Kabir Sharma (India), Lorraine Shaunnessy (USA), Gopi Shindar (India), Victor M. Siamudaala (Zambia), Kesi Sinclair (USA), Allan Smale (South Africa), Adamm Smith (USA), Ralf Sommerland (Germany), Gerardo Susan (Mexico), Jievu Taljard (South Africa), Megan Taplin-Brandfield (South Africa), Peter Taylor (Guyana), Jean-Claude Toutondele-Louzolo (Congo), Asteraye Tsigie-Tesfahunegn (Ethiopia), John Thorbjarnarson (USA), Steve Thorley (Zimbabwe), Kevin Torregrosa (USA), Richard Tokarz (USA), Anastasiia Tsvietkova (USA), Ramon Vaquero (Venezuela), Mike Veitch (Indonesia), Eric

Villaume (Gabon), Kent Vliet (USA), Roland Vorwerk (USA), Keith Waddington (USA), Nikhil Whitaker (India), Romulus Whitaker (India), Christy Wolovich (USA), Wang Xianyan (China), Utai Youngprapakorn (Thailand), Tesfaye Zewdie (Ethiopia), and Stella !Nomxas (Namibia).

Research was partially financed by Grant-In-Aid of Research from Sigma Xi, The Scientific Research Society (2007) and by a Tropical Biology Fellowship from University of Miami (2008). The study was conducted under the University of Miami Institutional Animal Care and Use Committee, approval #06-053, issued to Steven Green, and Federal research permits EVER-2007-SCI-0026 and ARMLNWR SUP # 41560-06013.

TABLE OF CONTENTS

Page

Addendum

LIST OF FIGURES

LIST OF TABLES

Page

Table

CHAPTER 1. INTRODUCTION

> *"Respect the aged!"*
>
> *It was a thick voice – a muddy voice that would have made you shudder – a voice like something soft breaking in two. There was a quaver in it, a croak and a whine.*
>
> *"Respect the aged! O Companions of the River – respect the aged!"*
>
> *Rudyard Kipling.* The Undertakers.

1.1. The role of habitat in the evolution of communication

Crocodilian signaling is very old. If the term "living fossil" can be applied to a behavior, then crocodilian displays certainly deserve it. Most known forms of crocodilian communicatory behavior predate the separation of the alligatorid and crocodylid lineages, i. e. no more recent than in the Late Cretaceous (Senter 2008). Signals of crocodiles and alligators are still largely "mutually intelligible" (Garrick & Lang 1977).

It is unusual for signaling behavior to be so conserved. Closely related species, subspecies and populations often have surprisingly different communication systems. Their signaling can vary in complexity, signal structure and other parameters. High diversity of signaling in otherwise relatively uniform taxa has been found in birds (Barlein 2006), mammals (Gannon & Lawlor 1989), reptiles (Frankenberg & Verner 1992), amphibians (Narins et al. 2006), and insects (Desutter-Grandcolas & Robillard 2004). This diversity has been an obstacle in the studies of the role of habitat in the evolution of communication (Dawkins 1993).

The present study attempts to investigate the effects of habitat structure on communication by using crocodilians, a uniform group with a limited number of differences in life history and a relatively simple phylogeny. Crocodilians are a good choice for such a study for three reasons.

1. Crocodilians have a clear phylogeny.

With a few minor exceptions discussed below, crocodilian phylogeny is well understood, supported by an extensive fossil record, several molecular and morphological studies and some paleoecological data (see Neil 1971; Taplin & Grigg 1989; Densmore & White 2001; and Brochu 2003). Reliable phylogeny is critically important because even a minor error in presumed phylogeny might invalidate any analysis in which phylogeny is treated as the independent variable (Felsenstein 1983).

2. Crocodilians are an ancient, highly conservative lineage.

All 26 extant species of crocodilians are similar in habitat (water not far from shore), feeding and breeding behavior, and physiology (Neil, 1971; Brochu, 2003). The few known differences are largely independent of phylogeny. For example, habitat specialists (species living only in small or only in large bodies of water) and generalists (species inhabiting virtually any available body of water) exist in more than one subfamily (Neil 1971). The influences of habitat differences on communication should be easier to elucidate by a comparative study in conservative taxa than in more diverse and rapidly evolving taxa such as songbirds or iguanids.

3. Crocodilians have relatively simple signaling systems.

Crocodilian signaling systems are limited to a few acoustic (including infrasound, or sub-audible) and non-acoustic signals per species (Garrick & Lang 1977). This simplicity is important because comparative methods of studying evolving systems are most effective if rates of change are low, and the number of variables limited (Felsenstein 1983).

Unfortunately, signaling of many crocodilian species is poorly known. The present study attempts to solve this problem by obtaining original data and compiling available information (see Chapter 2).

1.2. Crocodilian communication

All crocodilian species have a category of signals characterized by several features. First, these signals are used mostly during the mating season (although out-of-season signals are sometimes observed). 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. Fourth, they are normally performed in head oblique tail arched (HOTA) posture, in which head and tail of the animal are raised (Garrick & Lang 1997).

I 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 (see Wells 1977, and Narins et al. 2006). Certain features of crocodilian ACs suggest that at least one of their functions is also long-range position signaling. Crocodilian ACs are the loudest signals in each species' repertoire, the only ones produced when no conspecifics are nearby, and the only ones produced at a certain time of day, usually in the morning, when environmental noise levels are minimum (Garrick & Lang 1997; see also Chapter 2.3).

Wermuth (1989) suggested for crocodilians that the "purpose of vocalization is attracting the opposite sex and acoustic marking of territory, similar to singing in birds." ACs may function as honest signals of status, because some of their parameters, such as the lowest frequency, depend on the size of the animal (Garrick et al. 1978).

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 is **infrasound**, non-vocal vibrations normally produced below the water surface at frequencies below the range of human hearing. Infrasound can be visually detected by the so-called "water dance" effect (Garrick & Lang 1977), apparently created by Faraday waves (Glynn 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).

1.3. Hypotheses and predictions

Advertisement calls of each crocodilian species have several components, with multiple components usually combined in the same AC. The benefit of having multiple components may be in their differing ability to spread through air and water, and to carry different kinds of information (Table 1.1).

Vocal sounds are produced above the water surface and spread well through the air, carrying information about the size and probably the condition of the animal. They do not spread well underwater (see Addendum 2.2). Note that crocodilian hearing is approximately as sensitive to low audible frequencies as human hearing (Beach 1944; Higgs et al. 2002).

Table 1.1. Comparison of crocodilian advertisement call components.

	signal properties					
	information carried about:		**range in:**		**ability to spread in aquatic habitat that is:**	
signal component	**size**	**direction towards source**	**air**	**water**	**fragmented**	**continuous**
vocal sound	potentially accurate	relatively accurate	long	short, if any	good	good
headslap/jawslap	probably difficult to interpret accurately	relatively accurate	long	long	good	very good
infrasound	potentially accurate	probably almost none	short, if any	very long	very limited	excellent
head oblique tail arched posture	accurate	accurate	within line of sight	none	very limited	variable

Slaps carry well through both water (see Addendum 2.1) and, to a lesser extent, air. They carry information about the existence and location of the animal (see Addendum 1) but are difficult to distinguish from a variety of other sounds (see Addendum 3.3), and the animal's size can only be estimated from the perceived loudness and distance. In turn, the distance to the signaling animal has to be estimated from the degree to which the sharpness of the slap is preserved.

Infrasound spreads over distances of many kilometers underwater (Hopp et al. 1998). Alligators produce infrasound as loud as 140 dB at 1 m (Todd 2007) and respond to infrasound by other individuals (Garrick & Lang 1977). However, infrasound can probably spread only through continuous aquatic habitat, as it is absorbed by the land barriers between isolated bodies of water (Berg & Stork 2005). Because the source of underwater infrasound is physically difficult to locate due to long wavelength, species that use infrasound for long-range signaling can be expected to accompany it with “direction beacons” – short, loud broadband sounds with very sharp onset, such as slaps. Producing infrasound involves rapidly displacing large volumes of water, so it might require considerable strength, large size, and a lot of energy. Therefore, it can also be used for honest condition signaling, but only within visibility range, when it is clear which animal is the source.

Head oblique tail arched posture is an honest signal of the animal's size (as both its tail and snout are clearly visible), but it works only within the line of sight, and only if the recipient's eyes are above the water. Animals that are completely out of the water can probably perceive HOTA posture at much longer distance than infrasound.

So **vocal sounds** are optimal for long-range advertising through the air; **slaps** combined with **infrasound** are optimal for long-range advertising through the water; **infrasound** by itself is useful for advertising to non-submerged recipients at close range, when the location of the animal producing it is obvious; finally, **HOTA posture** gives an honest indication of the animal's size at close range to signal recipients whose eyes are above the water surface. There is also evidence (Garrick & Lang 1977) of **odors** being yet another component of ACs, possibly carrying information about the animal's species, sex and sexual maturity (Weldon & Wheeler 2001). This component of ACs was not investigated in the present study.

As AC components differ in their ability to carry information through air and water, it was hypothesized that the effectiveness of crocodilian communication is optimized by adjusting the composition of ACs to habitat structure (Table 1.2). The following predictions stemming from this hypothesis were tested:

Prediction 1: Infrasound and HOTA posture are used by all animals to communicate with possible underwater/above-the-water recipients close by.

Prediction 2.1: Species inhabiting a wide range of habitats use both vocal sounds and slaps.

Prediction 2.2: Species living predominantly in fragmented aquatic habitat (i.e. habitat in which headslap-infrasound signals cannot spread further through the water than vocal sounds can spread through the air) use vocal sounds, but few, if any, slaps.

Prediction 2.3: Species living predominantly in continuous aquatic habitat (i.e. habitat in which headslap-infrasound signals can spread further through the water than vocal sounds can spread through the air) use slaps, but few, if any, vocal sounds.

Prediction 3. In species inhabiting a wide range of habitats, animals living in areas with only continuous aquatic habitat use slaps more often, and vocal sounds less often, than animals living in areas with fragmented aquatic habitat. Unlike predictions 2.1-2.3, testing this prediction is not confounded by the relatively small number of extant species in Crocodylia.

If any of these predictions were to be rejected, it would mean that the hypothesis is incorrect or requires modification, and/or that the assumptions about the function of the signal components are at least partially inaccurate.

Predictions 1 and 2 are examined in Chapter 2, and prediction 3 in Chapter 3.

Table 1. 2. Predicted use of advertising signal components by crocodilians under the hypothesis that signals are affected by habitat structure. Numbers in parenthesis correspond to predictions in the text (Chapter 1.3).

	species inhabiting aquatic habitats:				
	mostly fragmented	**mostly continuous**	**highly variable**		
			in the species' range	**in areas with one habitat type**	
signal component				**fragmented**	**continuous**
vocal sound	often (2.2)	rarely, if ever (2.3)	at least sometimes in some areas (2.1)	more often (3)	less often (3)
slap	rarely, if ever (2.2)	often (2.3)		less often (3)	more often (3)
infrasound	often (1)				
head oblique tail arched posture	often (1)				

CHAPTER 2. ADVERTISEMENT CALLS BY CROCODILIAN SPECIES

2.1. Overview

In the previous chapter, it was predicted (Table 1.2) that:

1. Infrasound and head oblique tail arched (HOTA) or similar posture are used by all crocodilian species in all habitats.

2.1. Species inhabiting a wide range of habitats use both vocal sounds and slaps.

2.2. Species living predominantly in fragmented aquatic habitat, in which slaps cannot spread further through the water than vocal sounds can spread through the air, use vocal sounds, but few, if any, slaps.

2.3. Species living predominantly in continuous aquatic habitat, in which slaps can spread further through the water than vocal sounds can spread through the air, use slaps, but few, if any, vocal sounds.

To test these predictions, the literature on signaling in crocodilians was reviewed, and individuals that work with crocodiles (zoologists, zoo curators, farm operators, protected area employees and hunters) were interviewed. Unfortunately, information on signaling behavior of most crocodilian species is very limited and often unreliable. For some species, only data on captive individuals are available, making it impossible to distinguish between long-range and close-range communication. Crocodilian behavior in captivity can be very different from natural behavior in the wild. For example, signaling rates of American alligators (*Alligator mississippiensis*) observed by Garrick et al. (1978) and Vliet (1989) in captivity were much higher than those observed in the wild in the present study (see Chapter 3.3). Saltwater crocodiles (*Crocodylus porosus*) roar frequently in captivity but seldom in the wild (Webb & Manolis 1998), while Australian freshwater crocodiles (*C. johnstoni*) kept in small groups sometimes do not produce ACs at all during the mating season (Compton, 1981). In the present study, observations on signaling were conducted on nine species in the wild, on seven species in the wild and in captivity, and on six species only in captivity.

2.2. Methods.

Study sites, habitat descriptions and observation periods are listed in Table 2.1. Observation periods were selected based on the timing of the mating season for each species. If possible, locations with little human disturbance were chosen.

Observation protocols for American alligators and Nile crocodiles (*Crocodylus niloticus*) are described in detail in Chapters 3 and 5, and for yacare caimans (*Caiman yacare*) in Chapter 4.

All broad-snouted caimans (*Caiman latirostris*) used in the study were observed simultaneously for one 28-hour period.

For species that are difficult to find in the wild, such as black (*Caiman niger*), Cuvier's dwarf (*Paleosuchus palpebrosus*) and Schneider's dwarf (*P. trigonatum*) caimans, Morelet's (*Crocodylus moreleti*) and Central African dwarf (*Osteolaemus tetraspis*) crocodiles, and the false gharial (*Tomistoma schlegeli*), 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 7 or 8 am until noon. All captive animals mentioned in this study, except for Chinese alligators (*Alligator sinensis*), were known to be males either from observed matings or from having been 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). If more than one vocal sound or more than one headslap were produced during the same AC (which always meant they were less than 10 seconds apart), they were counted as one vocal sound or one headslap, respectively. In Indian gharials (*Gavialis gangeticus*), which do not produce signals in HOTA posture (see below), all sounds were scored.

Body vibration was assumed to be a sign of infrasound production (Garrick et al., 1978). Tape recordings made during body vibrations (see Addendum 2 for equipment description) confirmed presence of infrasound for American alligators, yacare caimans, American (*Crocodylus acutus*), Morelet's, Orinoco and Nile crocodiles, but were not obtained for other species. It remains to be confirmed that such vibrations in very small species – the Chinese alligator, spectacled caimans (*Caiman crocodylus*) of Tobago population, dwarf caimans (*Paleosuchus*), dwarf crocodiles (*Osteolaemus*), and the Australian freshwater crocodile (*Crocodylus johnstoni*) – actually indicate infrasound production.

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 after one hour. For broad-snouted caimans, Indian gharials, saltwater crocodiles (*Crocodylus porosus*), and species observed in captivity, of which only small numbers of individuals were available, this restriction was relaxed to twenty minutes to minimize data loss.

No more than three ACs were recorded from any individual animal used in the study, except for American alligators and Nile crocodiles (see Chapters 3 and 5), yacare caimans (see Chapter 4), spectacled caimans (see Chapter 2.3.1), and captive animals.

Sounds produced without HOTA posture were usually produced in obvious close interactions with other animals; the few exceptions are listed below or in Addendum 3. Very few cases of infrasound production without accompanying vocal sounds and/or slaps were ever observed.

Lengths of animals mentioned in this and following chapters were visually estimated to the nearest 1/2 m, unless stated otherwise.

Each species was classified by its habitat preferences as described in available literature. Table 2.2 summarizes the available habitat information for each extant crocodilian species.

Table 2.1. Study sites and observation periods. 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. Altitudes above sea level rounded to the nearest 10 m. Species here and elsewhere listed in systematic order. NWR stands for National Wildlife Refuge, NP – for National Park.

Species	**Site**	**State, region or province/ Country**	**Latitude/ Longitude**	**Altitude, m a. s. l.**	**Aquatic habitat type and size/ Surrounding vegetation**	**Months/ years**
Alligator sinensis	Xuancheng Alligator Research Centre	Anhui/China	30°55'N/ 118°44'E	20	lakes 100 m^2-1 km^2/subtropical deciduous forest (semi-natural)	06/2009
Alligator mississippiensis	Ocala National Forest	Florida/USA	29°03-27'N/ 81°30-42'W	0	lake 150 km^2, ponds <1000 m^2/ dry pine forest	04-05/ 2008
	Fakahatchee Strand State Preserve		26°48-50'N/ 81°24-26'W		ponds up to 1000 m^2/ semi-dry tropical forest	04-05/ 2007-8
	Merritt Island NWR		28°37-48'N/ 80°45-51'W		brackish lagoons >75 km^2/ mangroves and salt marshes	04-05/ 2010
	Key Deer NWR		24°42'N/ 81°22'W		sinkholes and ponds 4-100 m^2/ semi-dry tropical forest	04/2010
	St. Augustine Alligator Farm Zoo		29°52'N/ 81°17'W		ponds up to 1000 m2/ bare-ground enclosure (captive)	04-05/ 2008-10
	Savannah NWR	Georgia; South Carolina/USA	32°11'N/ 81°20'W		rivers, canals, lakes 1-8km^2/ grassland, subtropical forest	04-05/ 2008-9
	Aransas NWR	Texas/USA	28°15'N/ 96°55'W		fresh and brackish lagoons 1-30 km^2/wet grassland	05/2009
	Anacoco Floodplain	Louisiana/ USA	31°24'N/ 93°24'W	30	ponds 25-100m^2/ deciduous temperate forest	06/2009
	Cat Island NWR		30°89'N/ 91°20'W	20	flooded river valley/ deciduous temperate forest	05-06/ 2009
	St. Catherine Creek NWR	Mississippi/ USA	31°22'N/ 91°42'W			05/2009
Caiman yacare	Pantanal	Mato Grosso/ Brazil	17°41-46'S/ 57°05-10'W	140	lakes 100m^2-10km^2/ tallgrass savanna	10-11/ 2007
	Noel Kempff Mercado NP area	Santa Cruz/ Bolivia	15°07-09'S/ 60°34-35'W	220		11-12/ 2007
Caiman latirostris	Itaipu Reservoir	Parana/ Brazil	25°14'S/ 54°14'W	400	shallow bay 0.01 km^2/ subtropical rainforest	01/2010
Caiman crocodylus	Homestead	Florida/USA	25°29'N/ 80°21'W	0	drainage canal 5-6 m wide/ shrubs and fallow fields	08/2010
	Alligator Adventure, Myrtle Beach	South Carolina/USA	33°49'N/ 78°44'W		pool 10m^2/ bare-ground enclosure (captive)	03/2011
Caiman niger	Karanambu Ranch	Region 9/ Guyana	3°45-49'S/ 59°17'W	110	blackwater river 25-90 m wide; oxbows 0.02-2 km^2/ flooded tropical rainforest	08/2008
	Yasuni NP	Orellana/ Ecuador	0°31'S/ 76°25-26'W	230	blackwater lake 1 km^2/ tropical rainforest	12/2010
	St. Augustine Alligator Farm Zoo	Florida/USA	29°52'N/ 81°17'W	0	pond 10 m^2/ grassy enclosure (captive)	03/2011
Paleosuchus palpebrosus	Iwokrama Rainforest	Region 8/ Guyana	4°20'N/ 58°48'W	60	overgrown blackwater creek/ flooded tropical rainforest	08/2008
	Yasuni NP	Orellana/ Ecuador	0°32'S/ 76°26'W	230	blackwater creek 1-3 m wide/ flooded tropical rainforest	12/2010
Paleosuchus trigonatum	Coitubo River	Amazonas/ Venezuela	5°32'N/ 67°35'W	80	blackwater river 5-15 m wide/ tropical rainforest	01/2009

(Continued on the next page.)

Table 2.1 (continued).

Species	Site	State, region or province/Country	Latitude/ Longitude	Altitude, m a. s. l.	Aquatic habitat type and size/ Surrounding vegetation	Months/ years
Crocodylus acutus	Everglades NP	Florida/USA	25°07-09'N/ 80°54-89'W	0	brackish bays and channels/ mangroves	02-03/ 2007-10
	Black River	St. Elizabeth/ Jamaica	18°01'N/ 77°50'W		brackish lagoon 27km^2/ mangroves and grassy marshes	01/2009
	Lago Enriquillo	Baoruco/ Dominican Republic	18°30'N/ 71°35'W	- 40	salt lake 265 km^2/ mangroves	02/2008
	Rio Chajul Valley	Chiapas/Mexico; El Quiche/Guatemala	16°04'N/ 90°57'W	190	oxbow lake 0.1 km^2/ tropical rainforest	03/2008
	Isla de Salamanca NP	Magdalena/ Colombia	11°56'N/ 74°42'W	0	large brackish lagoons/ mangroves	01/2007
	Moroccoy NP	Falcon/Venezuela	10°52'N/ 68°13'W		brackish bays/ mangroves	01/2007
	Manglares Churute Reserve	Guayas/Ecuador	2°25-33'S/ 79°36-46'W		brackish channels/ mangroves	12/2010
Crocodylus intermedius	Rio Capanaparo	Guarico/Venezuela	7°00'N/ 68°19'W	80	oxbow lakes 1000-5000 m^2/ savanna	01/2008
	Hato Masaguaral		9°22'N/ 67°41'W	90	pond 300 m^2/ shrubby enclosure (semi-natural)	01/2008
Crocodylus moreleti	Rio Chajul Valley	Chiapas/Mexico; El Quiche/Guatemala	16°04'N/ 90°57'W	190	oxbow lakes 0.03-0.05 km^2/ tropical rainforest	03/2008
Crocodylus rhombifer	Zoo Miami	Florida/USA	25°36'N/ 80°24'W	0	concrete pool 25 m^2/ grassy enclosure (captive)	03-04/ 2010
	Gatorama (near Palmdale)		26°55'N/ 81°17'W		pond 16 m^2/ grassy enclosure (captive)	03/2011
	Gatorland, Orlando		28°21'N/ 81°24'W		pond 20 m^2/ grassy enclosure (captive)	
	St. Augustine Alligator Farm Zoo		29°52'N/ 81°17'W		pond 10 m^2/ grassy enclosure (captive)	
Crocodylus novaeguineae					pool 8 m^2/ bare-ground enclosure (captive)	
Crocodylus siamensis					pool 25m^2/ bare-ground enclosure (captive)	
	Alligator Adventure, Myrtle Beach	South Carolina/USA	33°49'N/ 78°44'W		pool 12m^2/ bare-ground enclosure (captive)	
Crocodylus niloticus	Mahango Game Reserve	Caprivi/Namibia	18°12-15'S/ 21°45-46'E	950	river 30-100 m wide/ wet meadows, savanna woodland	08-09/ 2008
	South Luangwa NP	Northern/Zambia	12°46-47'S/ 31°56-57'E	1000-1050	ponds 10-100 m^2 in a dry river channel/miombo woodland	09/2008
	Kruger NP	Limpopo/ South Africa	23°45-47'S/ 31°31-35'E	280-310	ponds 10-1000 m^2 in a dry river channel/savanna woodland	10/2008
	iSimangaliso Wetland Park	KwaZulu-Natal/ South Africa	28°20-23'S/ 32°24-25'E	0	brackish lagoon 350 km^2/ tropical rainforest	10-11/ 2008
	Nechisar NP	Oromia/Ethiopia	5°54-55'N/ 37°32-33'E	1110	two lakes over 500 km^2 each/ savanna woodland	12/2008
	Awash NP	Afar/Ethiopia	9°4-7'N/ 40°0-45'E	1000-1100	lakes and ponds <1000 m^2/ dry savanna woodland	12/2008
	Oromo River Delta	Southern Nations/ Ethiopia	4°28-29'N/ 36°11-12'E	360	brackish lake 6400 km^2 and ponds <1000 m^2/tropical salt desert	11/2008
	Crocoloco Crocodile Farm	North/Israel (near Ir Ovot)	30°80'N/ 35°15'E	- 40	concrete pools 100-300 m^2/ bare-ground enclosure (captive)	11/2010-01/2011

(Continued on the next page.)

Table 2.1 (continued).

Species	Site	State, region or province/Country	Latitude/ Longitude	Altitude, m a. s. l.	Aquatic habitat type and size/ Surrounding vegetation	Months/ Years
Crocodylus palustris	Katerniaghat Wildlife Sanctuary	Uttar Pradesh/India	28°21'N/ 81°25'E	170	ponds 10-1000 m^2; river 100-300 m wide/dry tropical forest	03/2007
	Sasan Gir NP	Gujarat/India	21°08'N/ 70°47'E	160-200	ponds 100-1000 m^2; rivers 1-5 m wide/dry tropical forest	01/2007
	Madras Crocodile Bank	Tamil Nadu/India	12°44'N/ 80°14'E	0	concrete pond 100 m^2/ bare-ground enclosure (captive)	12/2006
Crocodylus porosus	Sedangoli	North Maluku/ Indonesia	0°51'N/ 127°29'E		marine bay/mangroves	08/2009
	Tolire Besar Lake		0°50'N/ 127°18'E	50	crater lake 0.04 km^2/ rocky cliffs, tropical rainforest	
	Sorong area	West Papua/ Indonesia	0°54'S/ 131°17'E	0	saltwater estuary/mangroves	
	Waigeo Island		0°20'S/ 130°59'E		shallow marine bay/mangroves	
Crocodylus suchus	St. Augustine Alligator Farm Zoo	Florida/USA	29°52'N/ 81°17'W		pond 10 m^2/grassy enclosure (captive)	03/2011
Mecistops cataphractus					pond 8 m^2/ grassy enclosure with shrubs (captive)	
Osteolaemus tetraspis	Korup NP	Southwest/ Cameroon	4°59'N/ 8°50'E	60	pond 150 m^2 in a small blackwater stream/tropical rainforest	04/2009
Gavialis gangheticus	Katerniaghat Wildlife Sanctuary	Uttar Pradesh/India	28°21'N/ 81°25'E	170	whitewater river 100-300 m wide/dry tropical forest	03/2007
	Nandankanan Zoo	Orissa/India	20°23'N/ 85°49'E	40	concrete pool 300m^2/ grassy enclosure (captive)	12/2006
Tomistoma schlegeli	Tanjung Puting NP	Central Kalimantan/ Indonesia	2°57'S/ 114°12'E	0	blackwater river 5-10 m wide/ peat swamp forest	07/2009
	Alligator Adventure, Myrtle Beach	South Carolina/USA	33°49'N/ 78°44'W		pool 12m^2/ bare-ground enclosure (captive)	03/2011

Most species were classified as inhabiting a broad variety of aquatic habitats. Two species of crocodiles that are known to inhabit coastal habitats, large rivers and large lakes, and both species of gharials that are known to inhabit exclusively rivers were classified as inhabiting mostly continuous aquatic habitats. One species of alligator that inhabits ponds and small lakes, and five species of crocodiles inhabiting small ponds, shallow forest streams and shallow swamps were classified as inhabiting mostly fragmented aquatic habitats.

Table 2.2. Habitat preferences of extant crocodilians. See Chapters 2.3.1-2.3.3 for information sources.

Species	**Habitat**	**Category in the present study**
Alligator sinensis	Ponds and small lakes	mostly fragmented
Alligator mississippiensis	Ponds, rivers and lakes of any size, marshes, lagoons	broad range
Caiman crocodylus	Lowland bodies of water of any type	broad range
Caiman yacare	Lowland bodies of water of any type	broad range
Caiman latirostris	Small ponds to rivers, mangrove lagoons and estuaries	broad range
Caiman niger	Large rivers, forest streams, oxbow lakes, flooded savannas	broad range
Paleosuchus palpebrosus	Small and medium-size rivers, flooded forests	broad range
Paleosuchus trigonatum	Small and medium-size rivers, flooded forests	broad range
Crocodylus acutus	Lagoons, estuaries, seashores, large rivers and lakes	mostly continuous
Crocodylus intermedius	Rivers and lakes of all sizes	broad range
Crocodylus moreleti	Forest ponds, small lakes, swamps	mostly fragmented
Crocodylus rhombifer	Shallow marshes	mostly fragmented
Crocodylus niloticus	Small ponds to large lakes, rivers and coastal lagoons	broad range
Crocodylus suchus	Mangrove channels, large rivers and lakes	mostly continuous
Crocodylus palustris	Small ponds to large rivers and coastal lagoons	broad range
Crocodylus porosus	Lagoons, estuaries, seashores, large rivers and lakes	mostly continuous
Crocodylus johnstoni	Rivers, lakes and ponds	broad range
Crocodylus siamensis	Rivers, lakes and swamps of various size	broad range
Crocodylus novaeguineae	Rivers, lakes and swamps of various size	broad range
Crocodylus mindorensis	Small lakes, ponds, freshwater marshes, shallow forest rivers	mostly fragmented
Osteolaemus tetraspis[1]	Small forest ponds, swamps and shallow streams	mostly fragmented
Mephistops cataphractus	Rivers, lakes, heavily vegetated streams and flooded forests	broad range
Tomistoma schlegeli	Rivers	mostly continuous
Gavialis gangheticus	Large rivers	mostly continuous

[1] *Osteolaemus tetraspis* has been recently split into three species (Eaton et al. 2009). There is no evidence of differences in habitat preferences among these three species. All available information on signaling refers to *O. tetraspis* sensu stricto.

Shallow bodies of water with abundant vegetation or fallen tree branches can be classified as fragmented aquatic habitats for the purpose of the present study due to their sound-transmitting properties (see Addendum 2.1).

2.3. Results and Discussion

Table 2.3. lists original results and other available information on AC composition for all species for which such information could be obtained.

Table 2.3. Use of advertisement call components by crocodilian species for which information is available. The last two 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 brackets are percentages of advertisement calls containing the component in cases when they were below 25%.

Species	**Aquatic habitats**	**Head oblique tail arched posture**	**Infra-sound**	**Vocal sounds**	**Headslaps/ jawslaps**	**N of animals observed producing advertisement calls**	**Duration of pers. obs., hours**
Alligator mississippiensis	broad range	yes	yes	yes	yes	>100	>1000[1]
Alligator sinensis	mostly fragmented	yes	yes	yes	rarely (<1%)	>20; also published data	14
Caiman yacare	broad range	yes	yes	yes	yes	>70	385[1]
Caiman crocodylus	broad range	yes	yes	yes	yes	2; also published and pers. comm. data	26
Caiman latirostris	broad range	yes	yes	yes	yes	2	28
Caiman niger	broad range	yes	yes	yes	yes	5; also pers. comm. data	95[1]
Paleosuchus palpebrosus	broad range	yes	yes	yes	yes	2; also pers. comm. data	59[1]
Paleosuchus trigonatum	broad range	yes	yes	yes	yes	2; also pers. comm. data currently in prep.	3.5
Crocodylus acutus	mostly continuous	yes	yes	rarely (10.9%)	yes	34	172[1]
Crocodylus intermedius	broad range	yes	yes	yes	yes	4; also published data	60
Crocodylus moreleti	mostly fragmented	yes	yes	yes	rarely (8.3%)	5	65
Crocodylus rhombifer	mostly fragmented	yes	yes	yes	rarely (9.1%)	3	48
Crocodylus novaeguineae	broad range	yes	yes	yes	yes	1	18[1]
Crocodylus niloticus	broad range	yes	yes	yes	yes	>80	>900[1]
Crocodylus suchus	mostly continuous	yes	yes	no data	yes	1	6
Crocodylus palustris	broad range	yes	yes	yes	yes	13	150
Crocodylus porosus	mostly continuous	yes	yes	rarely (6.2%)	yes	8	72
Crocodylus johnstoni	broad range	yes	yes	yes	yes	published data	no pers. obs.
Crocodylus siamensis	broad range	yes	yes	yes	yes	2; also pers. comm. data	16[1]
Crocodylus mindorensis	mostly fragmented	no data	no data	yes	no data	published data	no pers. obs.
Mecistops cataphractus	broad range	yes	yes	yes	yes	1; also pers. comm. data	18[1]
Osteolaemus tetraspis	mostly fragmented	yes	no data	yes	no data	1, also pers. comm. data	6
Gavialis gangeticus	mostly continuous	head-up posture	no	no	yes	10, also published data	48
Tomistoma schlegeli	mostly continuous	yes	yes	no	yes	2, also published and pers. comm. data	6

[1] observations by the author and 1-4 assistants, man-hours.

2.3.1. Species inhabiting a wide range of habitats.

Approximately half of all living crocodilians are habitat generalists and occupy both fragmented and continuous aquatic habitats. This group includes one of the two alligators, all six caimans, and seven crocodiles.

The American alligator (*Alligator mississippiensis*) inhabits small ponds, sinkholes, slow-moving rivers and lakes of any size, freshwater marshes, and coastal lagoons in southeastern USA (McIlhenny 1935). It has two kinds of ACs, described in detail by Garrick et al. (1978) and Vliet (1989). Bellowing displays involve HOTA posture, bellows and (in male ACs) infrasound. Headslapping displays involve HOTA posture, headslap(s) and (in male ACs) infrasound; sometimes also jawslap(s) and low growling sound. In studies described in Chapters 3 and 5, 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.

The spectacled caiman (*Caiman crocodylus*) inhabits virtually every type of low-altitude aquatic habitat from southern Mexico to the Amazon Basin (Espinosa 1998a; Gorzula & Seijas 1989). Its signaling behavior is similar to that of the American alligator and includes roaring and headslapping displays, both performed in HOTA posture and involving infrasound production (Alvarez del Toro & Sigler 2001; John Thorbjarnarson pers. comm.). (Note that loud vocal sounds produced by caimans and crocodiles are commonly called "roars", while those produced by alligators are commonly called "bellows"). In the present study, a 1.5 m long spectacled caiman from an introduced population in southern Florida, mostly of Colombian origin (Ellis 1980), produced 6 roaring displays and 2 headslapping displays in five mornings of observation. A captive

1.5 m long captive male of Tobago origin produced 1 roaring display and 2 headslapping displays (all within 30 min) in two days of observation. All displays were performed in HOTA posture and included infrasound. Both kinds of displays seemed identical to corresponding displays by the following species.

The yacare caiman (*C. yacare*) is closely related to the spectacled caiman, and inhabits a similar wide spectrum of habitat in south-central South America (Espinosa 1998b). Its signaling behavior (described in detail in Chapter 4.3.1) is generally similar to that of the American alligator and the spectacled caiman. During the study described in Chapter 4, focal yacare caimans (n=70) produced both roaring displays (HOTA posture, infrasound and roar) and headslapping displays (HOTA posture, infrasound and headslap) more than once a day, with very few exceptions.

The broad-snouted caiman (*C. latirostris*) occurs from Bolivia and eastern Brazil to Uruguay. Its habitats range from small ponds to rivers, coastal lagoons and mangrove estuaries, although in areas of sympatry with yacare caiman it is more common in smaller bodies of water (Medem 1983; Scott et al., 1990; Moulton 1993). In a group of six caimans observed simultaneously in the present study, two caimans (probably males) produced 3 roaring displays and 2 headslapping displays in one 28-hour period. Both kinds of displays seemed identical to corresponding displays by yacare caimans.

The black caiman (*Caiman niger*) inhabits a wide variety of habitats including large rivers and streams, oxbow lakes and flooded savannas in the Amazon Basin and the Guyanas (Thorbjarnarson 1998). Its signaling system is apparently similar to that of yacare caiman, and includes roaring and headslapping displays (see Addendum 3.2 for additional information). In the present study, three black caimans over 3 m long observed (for one night and one morning each) in Guyana produced 2 roaring displays and 4 headslapping displays, while one 3.5 m long black caiman observed for three nights and three mornings in Ecuador produced 1 roaring display and 2 headslapping displays. A 2.5 m long captive male produced 5 roaring displays (1 daily) and 3 headslapping displays in five mornings of observation. All displays were performed in HOTA posture and accompanied by infrasound.

Dwarf caimans (*Paleosuchus*), widespread in tropical South America, inhabit small and medium-size forest rivers and flooded forests; in areas where larger caiman species occur, they are confined to small forest streams, fast-flowing rivers and flooded forest (Medem 1981; Medem 1983). Captive Schneider's dwarf caimans (*P. trigonatum*) are known to produce barks and headslaps, as well as body vibrations (Colin Stevenson in prep.). Cuvier's dwarf caimans (*P. palpebrosus*) in Brazil also produce such vibrations (Zilca M. S. Campos pers. comm.). Only six ACs were observed during the present study. A Cuvier's dwarf caiman in Guyana produced 1 bark-like sound in HOTA posture during one night of observation. Another individual in Ecuador produced 1 bark and 1 headslap accompanied with body vibration suggesting infrasound production in HOTA posture during four nights of observation. A Schneider's dwarf caiman, which was observed for three hours starting 30 min before midnight, produced 1 loud bark and 1 headslap, both in HOTA posture. Another individual of this species was located at night by the sound of a headslap it had made.

The Nile crocodile (*Crocodylus niloticus*) inhabits a broad variety of habitats in Africa (except the western part) and western Madagascar, from small pools in desert canyons (De Smelt, 2004) to African Great Lakes, major rivers and coastal lagoons

(Pooley & Gans 1976; Pooley 1982b). Crocodiles differ from alligators in that only large territorial males produce ACs, and their ACs can sometimes include infrasound combined with *both* roars and headslaps (Garrick et al. 1978). Male Nile crocodiles (N=70) at seven locations in eastern and southern Africa produced headslaps almost daily, while frequency of use and loudness of roars differed between geographical areas (see Chapters 3 and 5).

The Orinoco crocodile (*Crocodylus intermedius*) inhabits a wide variety of habitat in the Orinoco river basin (Thorbjarnarson & Franz 1987). According to Thorbjarnarson & Hernandez (1993), signals given in HOTA posture and including infrasound, roars and headslaps are the typical signaling behavior in adult males, although occasionally roars and headslaps are produced while swimming in inflated posture. Four large Orinoco crocodiles (two captive, known to be males, and two wild) observed in the present study produced 8 ACs in 6 days of observation. All 8 ACs included infrasound and headslaps, and all except 2 included also roars.

The Mugger crocodile (*Crocodylus palustris*) inhabits a broad variety of habitats, from small ponds to large rivers, and even coastal lagoons, in southern Asia (Whitaker & Whitaker 1983). In the present study, muggers were observed in three regions of India. In Sasan Gir National Park, where muggers inhabit forest ponds and deep river pools that are isolated during the mating season, four muggers over 2 m long produced 8 ACs, of which 6 included infrasound and roar(s), and 2 included infrasound and a headslap, in seven days of observation. In Katerniaghat Wildlife Sanctuary, where muggers inhabit a large river as well as small forest ponds, eight muggers over 2 m long produced 8 displays consisting of infrasound followed by roars and 3 displays consisting of infrasound followed by headslaps in five days of observation. A 3 m long captive male in

Madras Crocodile Bank produced 1 infrasound followed by a roar in one day of observation. All animals produced no more than 2 ACs per day. See Addendum 3.5 for additional information.

The Australian freshwater crocodile (*Crocodylus johnstoni*) is a small species that inhabits rivers, lakes and ponds. During the mating season, it frequently produces roars (sounding like loud grunts), headslaps (sometimes jawslaps) and "low frequency sound" (it is unclear if infrasound is involved) produced by body vibration, all given in HOTA posture (Webb & Manolis 1998).

The Siamese crocodile (*Crocodylus siamensis*), almost extinct in the wild (Crocodile Specialist Group 1996), once inhabited slow rivers, lakes and swamps of various size in Indochina and Borneo (Smith 1919). During the mating season, this crocodile produces headslaps, roars and infrasound in HOTA posture (Pavel Kvartalnov pers. comm. for reintroduced animals in a lake in Cat Tien National Park, Vietnam; Soham Mukherjee pers. comm. for captive animals in Madras Crocodile Bank, India; Utai Youngprapakom pers. comm. for captive animals at Samutprakan Crocodile Farm, Thailand). A 2 m long captive male in Florida produced 12 roars and 5 headslaps (all separately in HOTA posture) in nine mornings of observation; all headslaps and 8 roars were accompanied with infrasound. A 2.5 m captive male in South Carolina gave 1 roar with infrasound in HOTA posture in two mornings of observation.

The New Guinea crocodile (*Crocodylus novaeguineae*) inhabits swamps, marshes, lakes and rivers of New Guinea (Hall & Johnson 1987, Solmu 1994). In the present study, a 2 m long captive male produced 1 AC in nine mornings of observation. It was infrasound followed with a high-pitched roar and a headslap, given in HOTA posture.

The slender-snouted crocodile (*Mecistops cataphractus*) inhabits rivers, lakes, pools, marshes and flooded forests of Western and Central Africa. Although often found in large rivers and lakes, it seems to prefer densely vegetated rainforest streams over much of his range (Pooley 1982a, Shirley 2010, Steel 1989, Waitkuwait 1989). Such streams are similar to fragmented aquatic habitats in terms of their sound transmission properties (see Addendum 2), so this species is probably best classified as a habitat generalist for the purpose of present study. A captive male in Madras Crocodile Bank, India, regularly produced roars and headslaps (Soham Mukherjee pers. comm.). In the present study, a 2.5 m long captive male produced 3 roars, 16 headslaps, and 3 roars combined with headslaps, all accompanied with infrasound and given in HOTA posture, in eight mornings of observation.

So, all species inhabiting a wide variety of habitat regularly produce ACs including infrasound (possibly low-frequency sound in Australian freshwater crocodile), vocal sounds and headslaps, given in HOTA posture. Vocal sounds and headslaps are used frequently, at least in some areas within range of each species.

2.3.2. Species inhabiting predominantly fragmented aquatic habitats.

Almost one third of extant crocodilian species inhabit predominantly fragmented aquatic habitats. This group includes one alligator and six crocodiles. At least some information on AC composition is available for five such species.

The Chinese alligator (*A. sinensis*) inhabits ponds and small lakes of lower Yangtze valley, although it is possible that it inhabited larger bodies of water prior to being driven almost to extinction by hunting and habitat loss. Alligators living in rivers move into ponds and small lakes during the mating season (Chen et al. 2003; Wang et al. 2006, 2007). The Chinese alligator produces bellowing displays similar to those of the American alligator. Bellows are given in HOTA posture (with rare exceptions) in a shallow area or even on shore (pers. obs.; see also Wang et al. 2007, based on extensive observations at the same location). Large males vibrate while bellowing, indicating possible infrasound production (Thorbjarnarson & Wang 2010). Headslaps are used infrequently (none observed in the present study among more than 100 ACs). They are produced in HOTA posture and accompanied by short bellows ("chumphs") and jawslaps at the water surface (Thorbjarnarson & Wang 2010).

Morelet's crocodile (*Crocodylus moreleti*) inhabits forest ponds, small lakes and swamps of southeastern Mexico and northern Central America. In larger bodies of water it is usually replaced by the American crocodile (*Crocodylus acutus*) (Alvares del Toro & Sigler 2001). In the present study, five large Morelet's crocodiles (one known to be a male as it was observed during mating) produced a total of 12 ACs in eight days of observation; all ACs included infrasound and a short, sharp roar (Fig. 2.1) Only 1 headslap (combined with a roar) was heard. Alvarez del Toro & Sigler (2001) describe headslaps as part of mating-season displays in captivity; it is possible that some weak headslaps can only be heard, or distinguished from roars, at close range.

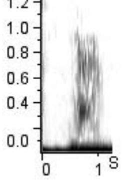


Figure 2.1. Spectrogram of a roar by a Morelet's crocodile (*Crocodylus moreleti*), recorded in Rio Chajul area on Mexican-Guatemalan border. See Addendum 2 for equipment information.

The Cuban crocodile (*Crocodylus rhombifer*) currently inhabits shallow marshes of western Cuba (Varona 1966). In the wild it frequently roars but rarely, if ever, headslaps (James P. Ross pers. comm.). In the present study, a captive male produced 6 ACs in seven days of observation. All ACs included a roar, but only 1 included also a headslap. In addition, on a rainy day (when the water temperature was probably low) that male produced four roars on land. Two captive males at other locations produced 1 roar in one morning of observation and 4 roars in three days of observation, respectively, but no headslaps (see Addendum 3.4 for additional information). All ACs performed in the water were given in HOTA posture and included body vibrations indicative of infrasound production.

The Philippine crocodile (*Crocodylus mindorensis*) inhabits small lakes and ponds, freshwater marshes and shallow forest rivers in the Philippines (Ross 1982). 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.

Dwarf crocodiles (*Osteolaemus* spp.) inhabit small forest ponds, swamps and shallow streams of Western and Central Africa (Waitkuwait 1989; Riley & Huchzermeyer 1999). In the present study, a Central African dwarf crocodile (*O. tetraspis*) was observed producing a moan-like sound preceded by a very brief, barely noticeable body vibration (it is unknown if any infrasound was actually produced) in HOTA posture. Rangers at Korup National Park (Cameroon) reported occasionally hearing dwarf crocodile "moans", but have never observed slaps.

So, all abovementioned species inhabiting fragmented aquatic habitat produce vocal sounds during the mating season. At least four out of five do so in HOTA posture. Use of slaps in ACs is rare in three species and possibly absent in two. Infrasound is used by at least three species; it is unknown if the remaining two species use it.

2.3.3. Species inhabiting predominantly continuous aquatic habitats.

Six crocodilian species inhabit predominantly continuous aquatic habitat. This group includes two crocodiles and both gharials.

The American crocodile (*Crocodylus acutus*) occurs from southern Florida and southwestern Mexico to coastal northern Peru and Venezuela, as well as on many Caribbean islands. It inhabits brackish lagoons, estuaries, large rivers and lakes, and protected seashores, especially with mangroves, although in some places it can also be found in smaller bodies of water (Alvares del Toro & Sigler 2001). Territorial males of this species produce infrasound followed by roars and/or headslaps, given in HOTA posture (Lang 1975, Garrick & Lang 1997). In the present study, American crocodiles 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 1 infrasound-only AC. No animal produced more than 2 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. In this area American crocodiles inhabit lakes and rivers of varying size, rather than large lakes and coastal lagoons as in other areas (Jeronimo D. Lazo pers. comm.). See Addendum 3.3 for additional information.

The saltwater crocodile (*Crocodylus porosus*) is an ecological counterpart of the American crocodile, occurring from Sri Lanka to the Philippines, Palau, Vanuatu and northern Australia. It inhabits protected seashores, mangrove lagoons, estuaries, and large rivers, although sometimes it can be found in smaller bodies of water and in the open sea (Webb et al. 1987; Messel & Vorlicek 1989). Roars by saltwater crocodiles are cough-like, very low sounds commonly called "growls" (Webb & Manolis 1998), audible to a human observer at no more than 100 m (pers. obs.). In the present study, saltwater crocodiles were observed producing infrasound and either headslap(s) or growls in HOTA posture. There were many more headslaps than growls: 6 headslaps vs. 1 growl in northwestern New Guinea (five animals), 1 headslap and 1 infrasound-only AC at Waigeo Island (one animal), 2 headslaps in Sedangoli at Halmahera Island (one animal), and 2 headslaps in Tolire Besar crater lake on Ternate Island (one animal). All animals produced no more than 2 ACs per day. Webb & Manolis (1998) also state that growls are seldom produced by saltwater crocodiles in the wild.

The West African crocodile (*C. suchus*), recently found to be a species distinct from the Nile Crocodile (Schmitz et al. 2003), inhabits mangrove channels, estuaries, large rivers and lakes in western and central-western parts of Africa (Waitkuwait 1985, Kofron 1992). In the present study, a 2.5 m long captive male produced (in HOTA posture) 2 headslaps accompanied with infrasound in four mornings of observation. This individual has never been heard roaring (David Kledzik pers. comm.)

The false gharial (*Tomistoma schlegeli*), which occurs in Malaysia and western Indonesia, is mostly a riverine species (Bezuijen et al. 1997). Captive false gharials produce headslaps in HOTA posture during the mating season (Trutnau & Sommerland 2006), but they produce vocal sounds only when physically provoked (Alan Karlon pers. comm., Utai 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 1 headslap accompanied with infrasound in two mornings of observation.

The Indian gharial (*Gavialis gangheticus*) currently inhabits large rivers in northern India and southern Nepal. Its signaling system is different from all other crocodilians for which information is available. Instead of HOTA posture, gharials often assume a head-up posture on land, which is believed to be a territorial and/or sex display (adult males and females differ strikingly in snout shape) (Singh & Rao 1990). This species is not known to produce infrasound. The only sounds associated with courtship are soft buzzes (Fig. 2.2), given in close proximity to other animals, and uniquely loud jawslaps, given by both males and females at or below (occasionally above) the water surface (Whitaker & Basu 1992). 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; 2 of these 5 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.

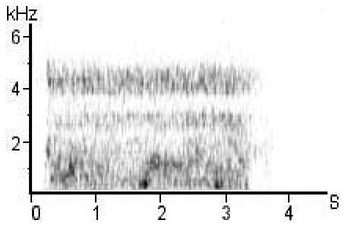


Figure 2.2. Spectrogram of a buzz by an Indian gharial (*Gavialis gangeticus*), recorded in Nandankanan Zoo, Orissa, India. Buzzes can last for 3-20 seconds. See Addendum 2 for equipment information.

So, all three abovementioned species of crocodiles produce headslaps, roars and infrasound in HOTA posture, but roars are never or rarely used, and are reduced to low growls in at least one species. The false gharial produces headslaps and infrasound in HOTA posture. Indian gharial's jawslaps probably serve a function similar to that of headslaps in other crocodilians. Due to its extremely narrow snout, this species can produce only very weak headslaps (Whitaker & Basu 1992). Its head-up posture probably serves a function similar to that of the HOTA posture in other crocodilians. None of the two gharials is known to produce loud vocal sounds.

2.3.4. Discussion

In most species (see Table 2.3 for a full list, and Table 2.4 for a summary), ACs by male crocodilians are produced in HOTA posture and virtually always include infrasound. The only known exception is the Indian gharial, which has a different signaling system. Very small species (the Chinese alligator, dwarf caimans, dwarf and Australian freshwater crocodiles) vibrate during ACs, but it is unknown if any infrasound is actually produced.

Table 2.4. Summary of the available data on use of advertizing signal components by crocodilian species.

signal component	**continuity of preferred aquatic habitat:**		
	highly variable	**mostly fragmented**	**mostly continuous**
head oblique tail arched or head-up posture	often		
infrasound	often, except in the Indian gharial		
headslap/jawslap	often, at least in some areas	never or rarely	often
vocal sound		often	rarely

Based on available information, all species inhabiting a wide range of habitats (n=14) frequently use both vocal sounds and slaps, at least at some locations; all species inhabiting predominantly fragmented aquatic habitats (n=5) use vocal sounds, but few or no slaps; all species inhabiting predominantly continuous aquatic habitat (n=5) use slaps, but rarely or never use vocal sounds.

So, the data match the predictions about signaling behavior by different crocodilian species. The predicted differences in behavior are seen even between very closely related species inhabiting different habitats (Table 2.2). For example, the Siamese, New Guinea and Philippine crocodiles are closely related to the saltwater crocodile (Oaks 2007); Cuban, Morelet's and Orinoco crocodiles are closely related to the American crocodile (Oaks 2007), and the Orinoco crocodile might be a distinct subspecies of the American crocodile (Venega-Anaya et al. 2007); the West African crocodile was until recently considered conspecific with the Nile crocodile.

All extant crocodiles are large reptiles. Only the smallest ones – Chinese alligators (Thorbjarnarson & Wang 2010), the Tobago population of spectacled caimans (Grenard 1991), Cuvier's dwarf caimans (Medem 1983), and dwarf crocodiles (Kofron & Steiner 1994) – can reach sexual maturity at less than 1 m length. However, full-grown males exceed 1.2 m in all of them: the Chinese alligator (Thorbjarnarson & Wang 2010); the Tobago spectacled caiman (pers. obs.); the Cuvier's dwarf caiman (Campos et al. 2010; length estimates adjusted for missing tail tips in all adults); and dwarf crocodiles (Mitch Eaton pers.comm.). These species are apparently capable of producing infrasound (Chapters 2.3.1 and 2.3.2). Male American alligators begin to accompany their bellows with infrasound at approximately the same length (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 crocodilians.

CHAPTER 3. ADVERTISEMENT CALL COMPOSITION IN AREAS WITH CONTINUOUS VERSUS FRAGMENTED AQUATIC HABITATS

3.1. Overview

In the previous chapter, it was found that crocodilian species inhabiting predominantly fragmented aquatic habitat use many vocal signals and few (if any) slaps in their advertisement calls (ACs), while species inhabiting predominantly continuous aquatic habitat use many headslaps and few vocal signals.

But do similar differences exist within species? Do animals of the same species differ in signaling behavior depending on the continuity of their aquatic habitat? In Chapter 1.3, it was predicted that in species inhabiting a wide range of habitats, individuals living in areas with only fragmented aquatic habitat use slaps less often and vocal sounds more often than those living in areas with only continuous aquatic habitat.

To test this prediction, signaling behavior was compared between individuals living in areas where only fragmented aquatic habitat was available, and individuals of the same species living in areas where only continuous aquatic habitat was available. Hereafter study sites with fragmented aquatic habitat will be called "fragmented sites", and those with continuous aquatic habitat will be called "continuous sites".

Such comparisons were performed on two species of crocodilians that inhabit a wide range of habitats (see Chapter 2.3.1) but have different ways of forming their ACs. Male American alligators (*Alligator mississippiensis*) use two distinct kinds of ACs, described in detail by Garrick et al. (1978) and Vliet (1980): bellow(s) preceded by infrasound (“bellowing display”) and headslap(s) preceded by infrasound (“headslapping display”). Male Nile crocodiles (*Crocodylus niloticus)* use roars and headslaps (also preceded by infrasound) separately or within the same display (Garrick and Lang 1977).

3.2. Methods

3.2.1 Choosing study sites

For this part of the study, geographical areas where only one type of aquatic habitat (either fragmented or continuous) is used by the animals during the mating season, and where anthropogenic disturbance is limited, were selected.

Fragmented sites were those where all bodies of water inhabited by adult animals during the mating season (when the observations were conducted) were smaller in all dimensions than the carrying distance of aerial signals. Alligator bellows and crocodile roars can be heard by a human observer at a distance of at least 100 m, and alligator hearing is approximately as sensitive as human hearing (Beach 1944; Higgs et al. 2002). So, locations where chosen where at the time of observations only bodies of water less than 100 m in any dimension were inhabited by adult animals, and the nearest large bodies of water inhabited by adult animals were at least 20 km away.

Continuous sites were those where all bodies of water inhabited by adult animals during the mating season (when the observations were conducted) were larger in at least one dimension than the maximum carrying distance of aerial signals. Alligator bellows and crocodile roars can be heard by a human observer from a distance of up to 1 km under ideal conditions. So, locations where chosen where at the time of observations all bodies of water inhabited by adult animals were larger than 1 km in at least one dimension, and any small bodies of water inhabited by adult animals were at least 20 km away.

3.2.2. Alligator study sites

American alligators were studied at four continuous and three fragmented sites (see Fig. 3.1 for map of locations, and Table 2.1 for location details and observation dates).

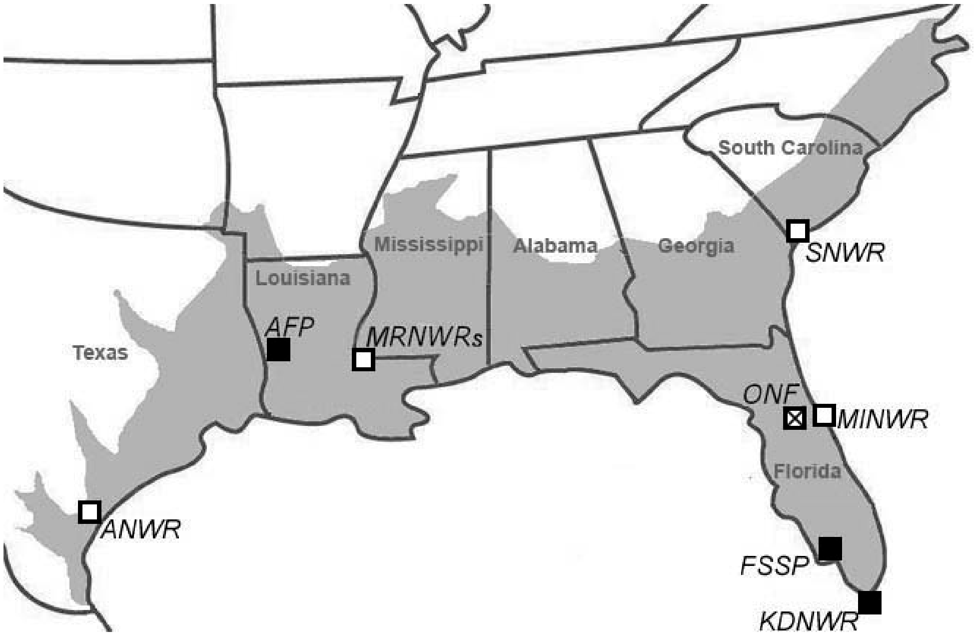


Figure 3.1. Geographic locations of American alligator study sites mentioned in chapters 4 and 5 in the southeastern United States. Shaded is the approximate range of the American alligator (Persival et al. 2000). Sites with continuous aquatic habitats are shown by empty squares, sites with fragmented aquatic habitats – by filled squares, and the site with both types of aquatic habitat – by a crossed square. Abbreviations: ANWR – Aransas National Wildlife Refuge, AFP – Anacoco Floodplain, FSSP - Fakahatchee Strand State Preserve, KDNWR – Key Deer National Wildlife Refuge, MRNWRs – Cat Island and St. Catherine's Creek National Wildlife Refuges, ONF – Ocala National Forest, SNWR – Savannah National Wildlife Refuge.

Continuous sites:

1) Cat Island and St. Catherine Creek National Wildlife Refuges. These two wildlife refuges were considered a single study site (MRNWRs). In these two adjacent areas, alligators inhabit parts of the Mississippi River valley that are continuously flooded at the time of the mating season (April-May). The surrounding uplands experience the

end of the dry season at that time of year, so no bodies of water that could be suspected of harboring adult alligators were found within 20 km of the refuges.

2) Savannah National Wildlife Refuge (SNWR). In this refuge, alligators inhabit large river channels, deep canals and large lakes (over 1 km^2). Although a few small bodies of water also exist in the area, they are almost dry or very shallow during the mating season, and no alligators longer than 50 cm were found in them during numerous nighttime visits, when eyeshine would make any alligators easy to detect.

3) Merritt Island National Wildlife Refuge (MINWR). In this refuge, alligators inhabit lagoons more than 75 km^2 in size and a continuous network of tidal channels. Very few small bodies of water exist in the area, and no alligators were found in them during repeated nighttime visits, probably because all these small ponds contain seawater in which alligators cannot live permanently (Neil 1971).

4) Aransas National Wildlife Refuge (ANWR). In this refuge, alligators inhabit interconnected lagoons and lakes at least 1 km^2 in size. No small bodies of water exist in the area, except for one pool less than 40 m^2 in size that contained only very small (less than 50 cm long) alligators at the time of observations.

Fragmented sites:

1) Fakahatchee Strand State Preserve (FSSP). In this preserve, alligators inhabit ponds less than 1000 m^2 in size during the mating season. Although a few irrigation canals run close to the area, adult alligators are virtually absent from them during the mating season, with only 1 animal observed in 8 km of canals during night counts.

2) Anacoco Floodplain (AFP). In this area alligators inhabit ponds, known as gator holes, which are 25-100 m^2 in size during the mating season. The only other bodies of water in the area during the mating season are shallow, heavily overgrown streams less than 2 m wide. Even if some adult alligators do live in these streams, such habitats can also be considered fragmented for the purpose of the study (see Addendum 2.1).

3) Key Deer National Wildlife Refuge (KDNWR). In this refuge, alligators inhabit tiny sinkholes (2-4 m^2) and two artificial lakes about 2000 m^2 each, located on three islands of the Florida Keys island chain. No larger bodies of fresh water exist on these islands. Data from KDNWR were limited and not used in any statistical analysis.

3.2.3. Crocodile study sites

Nile crocodiles were studied at three continuous and three fragmented sites, located in three geographical regions. In each region there was one continuous site and one fragmented site. See Fig. 3.2 for locations map, and Table 2.1 for location and habitat details and observation dates.

<u>Southern region:</u>

1) iSimangaliso Wetland Park (iSWP), a continuous site. In this park, crocodiles inhabit a large (over 350 km^2) river estuary with no small bodies of water nearby.

2) North-central part of Kruger National Park (KNP), a fragmented site. In this area, crocodiles inhabit small rivers that by the onset of the mating season break up into chains of pools less than 600 m^2 in size. No large bodies of water exist in the area.

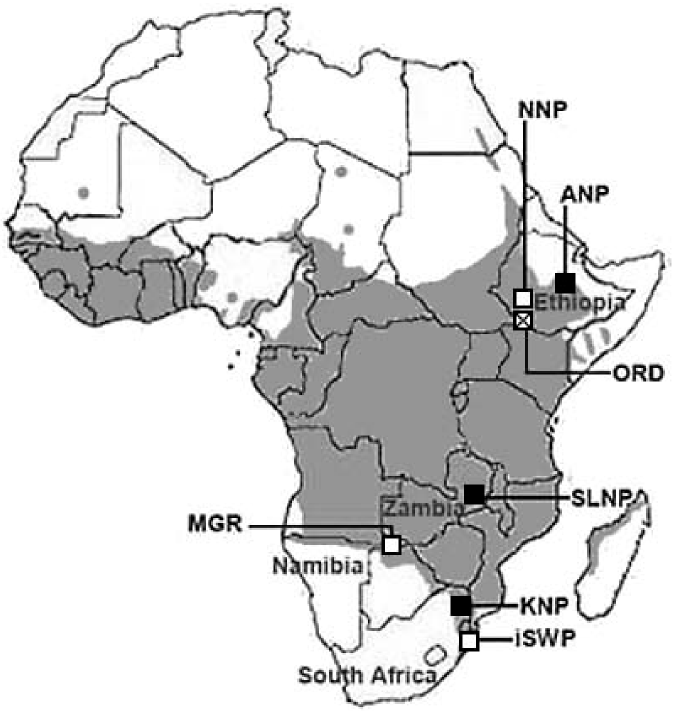


Figure 3.2. Geographic locations of Nile crocodile study sites mentioned in chapters 3 and 5. Shaded is the approximate range of the Nile crocodile (based on Ferioli 1998). Sites with continuous aquatic habitats are shown by empty squares, sites with fragmented aquatic habitats – by filled squares, and the site with both types of aquatic habitat – by a crossed square. Abbreviations: ANP – Awash National Park, iSWP – iSimangaliso Wetland Park, KNP – Kruger National Park, MGR – Mahango Game Reserve, NNP – Nechisar National Park, ORD – Oromo River Delta, SLNP – South Luangwa National Park.

Central region:

1) Mahango Game Reserve (MGR), a continuous site. In this reserve, crocodiles inhabit a stretch of a large river with no tributaries, no oxbow lakes (at least at the time of the study), and no small bodies of water nearby.

2) Northwestern part of South Luangwa National Park (SLNP), a fragmented site. In this area, crocodiles inhabit small creeks that by the onset of the mating season break up into chains of pools less than 100 m^2 in size. Although this area is not far from the large Luangwa River, they are separated by a steep escarpment with cataracts and waterfalls.

Northern region:

1) Nechisar National Park (NNP), a continuous site. In this park, crocodiles inhabit two lakes, each over 500 km^2 in size. The only small bodies of water in the area are small streams that are virtually dry during the crocodiles' mating season.

2) Northern part of Awash National Park (ANP), a fragmented site. In this area, crocodiles inhabit spring-fed ponds less than 1000 m^2 in size, with no large bodies of water in the area.

3.2.4. Choosing and observing focal animals.

Only males at least 2 m in total length were observed. Behavioral differences were used to determine sex of animals. Although males tend to be larger than females, and the largest animal in a group is likely to be a male, the only reliable way of sexing alligators and crocodiles without capturing them is to observe them either mating or producing ACs (Neil 1971; John Thorbjarnarson pers. comm.). In American alligators, females produce ACs similar to those of males, but without infrasound (Vliet 1989). In Nile crocodiles, only territorial males produce ACs (Garrick & Lang 1977).

To locate male alligators, small ponds and the shores of large lakes and rivers were searched on foot, by car or from a small boat, and particularly large animals were noted. They and conspecifics visible from the same observation point (if present) were then watched simultaneously until the next morning, the time of day when ACs usually occurred. If an animal produced an AC with infrasound, it was considered a male and was designated the focal animal. This focal male was observed by the same observer(s) daily from 0530 to 1030 hrs (± 30 min, depending on the location and time of year), until five ACs were recorded from it. Non-focal animals at the same location were ignored. If no animal produced an AC with infrasound during one morning of observation, or if there was only one animal larger than 2 m and it produced an AC without infrasound, the observer proceeded to search for other locations.

Presence of infrasound was determined by the "water dance" effect (Garrick & Lang. 1977). All focal animals were at least 1 km from each other. This requirement was important because bellowing and headslapping are known to be contagious behaviors in alligators (Garrick and Lang 1977, Vliet 1989). Observations at each site continued until 5 ACs were recorded from each of ten alligators.

Signaling behavior is known to differ between captive alligators kept in large and small groups (Vliet 1989), and thus can be expected to differ between wild animals found in large and small groups. To minimize group size bias (large groups were more likely to be found at continuous sites) alligators in groups of more than ten were ignored. A group was defined as all animals 2 m or more in length found within 50 m of the candidate focal animal during its initial observation.

Selecting focal animals after they produced an AC could create a selection bias towards individuals that produced ACs more often. However, during the mating season all adult male alligators produce ACs almost daily (Garrick & Lang 1977), so few, if any, adult males were ignored due to inactivity.

Crocodiles at all sites occurred in groups of 1-10 individuals (at NNP, a few larger groups were also present, but these were excluded from the study). All observed ACs were produced by the largest animal in the group. Only territorial males produce ACs in Nile crocodiles (Garrick & Lang 1977), so all AC-producing crocodiles were considered territorial males and were chosen as focal animals. Each observer watched one group (one or two groups at NNP) at a time, until each focal animal produced at least 5 ACs. All focal animals were separated by at least 50 m. This distance was considered sufficient because roaring and headslapping are less contagious in crocodiles than bellowing and headslapping in alligators (Garrick & Lang 1977; John Thorbjarnarson pers. comm., Mark Robinson pers. comm., David Kledzik pers. comm.). Observations continued until at least five ACs were recorded from each of ten crocodiles.

All observations at all sites were performed with the observer positioned at least 5 m from the water edge, and at least 10 m from the focal animal. The observer was concealed by vegetation or some kind of a portable blind. If such concealment was impossible due to absence of vegetation and extremely hot weather (which happened only a few times), the observer lay on the ground and moved as little as possible.

Disturbance to the animals was reduced by arriving on site 30-60 min prior to the expected onset of signaling behavior. Errors in identifying individual animals were possible, but if a focal animal was replaced by another one without the observer noticing the difference, the newcomer would be from the same geographical area, where only one type of habitat (either continuous or fragmented) was inhabited by adult animals. So the substitution would not invalidate the results.

3.2.5. Data recording

After each scored AC, new ACs from the same animal were ignored during the next hour to avoid over-counting in case of repetitive behavior. Alligators (Vliet 1989) and crocodiles (pers. obs.) often repeat their displays within 1-20 minutes.

Alligator ACs were scored as belonging to one of the two AC types, namely “bellowing display” containing bellow(s) and infrasound, or “headslapping display” containing headslap(s) and infrasound. All ACs by focal animals observed during the present study (n=351, plus 118 during the study described in Chapter 5) belonged to one of the two types. No AC composed only of infrasound or including both bellow(s) and headslap(s) was ever observed, although a few headslapping displays included a quiet low growl (as described by Vliet 1989).

Crocodile ACs were scored as containing roars, roars and headslaps, or headslaps. All observed ACs (306, plus 102 in the study described in Chapter 5) contained infrasound, except for two roars observed in SLNP which were produced by crocodiles on land (these two roars were excluded from the analysis). Infrasound-only ACs were never observed.

3.2.6. Inter-observer reliability testing

Inter-observer reliability studies for scoring ACs of American alligators were conducted at MINWR concurrently with regular observations. All observations at that site were performed by teams of two observers, one of them experienced and one inexperienced at the beginning of the study. Both team members watched the same focal animal from positions at least 5 m apart, independently scored all behaviors they considered to be ACs, and recorded the composition (infrasound, bellow and/or headslap) and time of each perceived AC following the protocol described above. Their records were compared at the end of each day.

A total of 61 behaviors were scored. All of them were considered ACs by both members of a team. Of these behaviors, 35 were scored as infrasound followed with bellow(s), 22 – as infrasound followed with headslap(s), 4 – as bellows without infrasound (from animals then dropped from the study as females). The inter-observer agreement in determining the presence of an AC, as well as in determining AC composition, was 100%.

Inter-observer reliability studies for scoring ACs of Nile crocodiles were conducted in the same way at Crocoloco Crocodile Farm, Israel (see Table 2.1 for site information). All observations at that site were performed by a team of two observers, both of them inexperienced at the beginning of the study.

A total of 11 behaviors were scored. All of them were considered ACs by both members of the team. Of these behaviors, 9 were scored as infrasound followed with headslap(s), and 2 – as infrasound followed with both roar(s) and headslap(s). The inter-observer agreement in determining the presence of an AC and in determining AC composition was 100%.

3.2.7. Analysis (alligators)

All analyses in this and following chapters used significance levels of 0.05 and two-tailed tests. SYSTAT Version 12 software was used for performing statistical tests and generating graphs in this and following chapters.

Box plots show the median and interquartile range, with whiskers that represent 1.5 times the interquartile range from the box ends. Outliers are represented by asterisks, far outliers (values beyond three times the interquartile range from the box ends) by open circles. The reported *U* is the Mann-Whitney *U*-test statistic.

Five ACs were recorded from each focal animal to ensure that each animal was weighed equally. The number of headslapping displays was tallied for each animal, and the resulting counts were subjected to statistical analysis.

1) Tallies for animals (n=40) observed at continuous sites were compared with tallies for animals (n=20) observed at fragmented sites using the Mann-Whitney *U*-test.

2) The prevalence of headslapping display usage among alligators was compared between fragmented sites (n=30) and continuous sites (n=30) using Fisher's Exact test on the numbers of animals that produced at least one headslapping display among 5 ACs.

3) The data on headslapping and bellowing displays were not mutually independent due to constraining the number of scored ACs to exactly 5 per animal. To obtain fully independent data on the frequency of use of each signal type, ACs of each type produced within the first two days of observation were tallied. The tallies of headslapping displays produced by animals within the first two days of observation were compared between fragmented and continuous sites using the Mann-Whitney *U*-test. The same was done for the tallies of bellowing displays.

4) Steps 1-3 were repeated for comparisons between the three northern sites (SNWR, AFP and MRNWRs; n=30) and the three southern sites (FSSP, MINWR and ANWR; n=30), as well as between the three eastern sites (FSSP, MINWR and SNWR; n=30) and the three western sites (ANWR, AFP and MRNWRs; n=30). In each of these comparisons there were two continuous sites and one fragmented site in each group.

3.2.8. Analysis (crocodiles)

Only the first 5 ACs were scored from each focal animal to ensure that each animal was weighted equally. This rule did not cause substantial loss of data, because 6 or 7 ACs were recorded from only a few crocodiles.

The data for roars and headslaps were analyzed separately, but in the same way, as described below. The numbers of ACs containing roars and the numbers of ACs containing headslaps were tallied for each animal, and the resulting counts were subjected to the statistical analysis.

1) ANOVA was used, with habitat type, geographical region and their interaction as factors. Since the distribution had an upper limit and was not normal, arcsine transformation [arcsin (√x)] was applied and then Levene's test for normality was used.

2) Tallies of each AC component for animals (n=30) observed at continuous sites were compared with tallies for animals (n=30) observed at fragmented sites using the Mann-Whitney *U*-test.

3) Step 2 was repeated for comparisons between the two sites (n=10) within each geographical area, and among the three geographical areas (n=20, Kruskal-Wallis Test).

4) The prevalence of roar usage among crocodiles was compared between fragmented sites (n=30) and continuous sites (n=30) using Fisher’s Exact test. The same was done for the prevalence of headslap usage.

5) The data on headslaps and roars were not fully mutually independent due to constraining the number of scored ACs to exactly 5 per animal. To obtain fully independent data on the frequency of use of each signal component, ACs of each type produced within the first two days of observation were tallied. The tallies of headslap-containing displays produced by animals within the first two days of observation were compared between fragmented and continuous sites using the Mann-Whitney *U*-test. The same was done for the tallies of roar-containing displays. ANOVA was also used on these tallies, with habitat type, geographical region and their interaction as factors.

3.3. Results and Discussion

3.3.1. American alligators: AC composition

The American alligator has two kinds of signaling displays: headslapping displays and bellowing displays, described in detail by Garrick et al. (1978) and Vliet (1989) for animals in captive and semi-natural habitats.

Headslapping displays are produced frequently in areas with continuous aquatic habitat, but seldom in areas with fragmented aquatic habitat. The numbers of headslapping displays among 5 ACs by each alligator (n=10) at 6 study sites are shown in Fig. 3.3. The numbers of headslapping displays recorded in the first 2 days of observing each alligator (n=10) at 6 study sites are shown in Fig. 3.6. Results of statistical tests are listed in Table 3.1. The numbers of headslapping displays among 5 ACs recorded for each animal (Fig. 3.4), the prevalence of headslap use, and the numbers of headslapping displays produced by animals in the first 2 days of observation (Fig. 3.7) were all significantly higher at continuous sites than at fragmented sites. This difference cannot be explained by differences in latitude or longitude, since there were no such differences between northern and southern sites (Fig. 3.5.b), and no such differences between eastern and western sites (Fig. 3.5.a).

Alligators frequently produce bellowing displays in areas with continuous aquatic habitat as well as in areas with fragmented aquatic habitat. The prevalence of bellowing display use was close to or equaled 100% at all sites (only one animal did not use them). The numbers of bellowing displays produced by animals in the first 2 days of observation were not different between continuous and fragmented sites, between northern and southern sites, or between eastern and western sites.

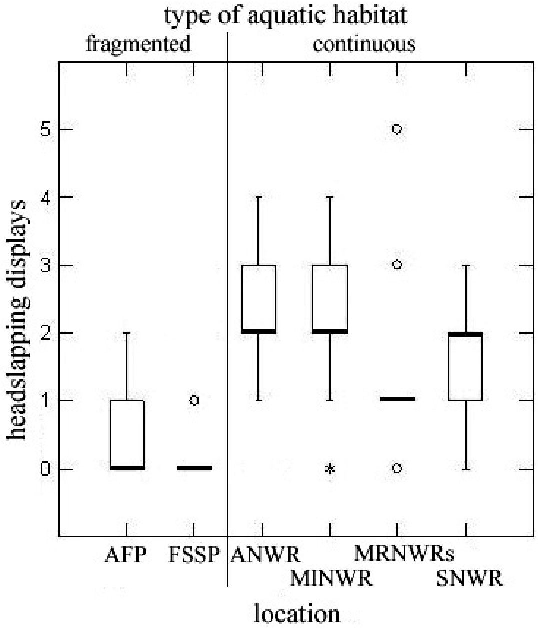


Figure 3.3. Box plots showing the numbers of headslapping displays among 5 advertisement calls by alligators (n=10) at 6 study sites (see Fig. 3.1 for map and list of abbreviations). Two of the boxes are collapsed because almost all alligators at those sites had the same number of headslapping displays.

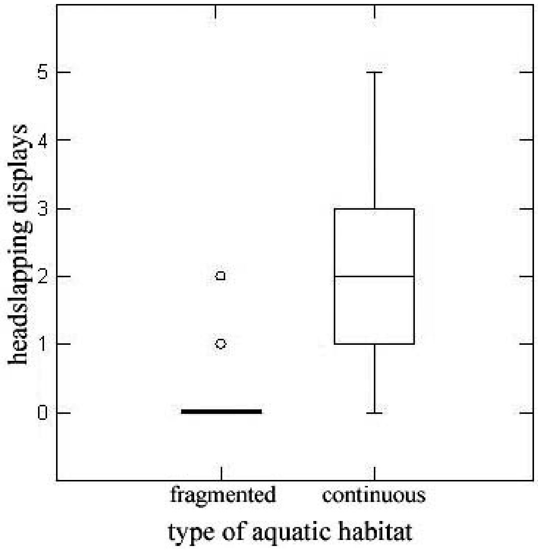


Figure 3.4. Box plot showing the numbers of headslapping displays among 5 advertisement calls by alligators from study sites with fragmented (n=20, 2 sites) and continuous (n=40, 4 sites) aquatic habitats. One of the boxes is collapsed because very few signals in fragmented aquatic habitats were headslapping displays.

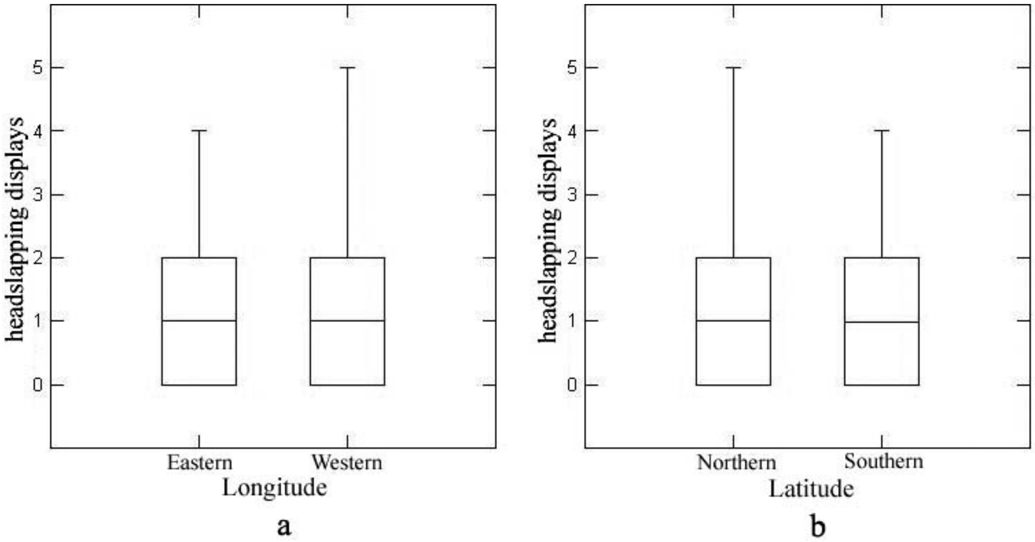


Figure 3.5. Box plots showing the numbers of headslapping displays among 5 advertisement calls by alligators from study sites divided into groups by longitude (a) and latitude (b). In each group there were two sites with continuous aquatic habitat (n=20) and one site with fragmented aquatic habitat (n=10).

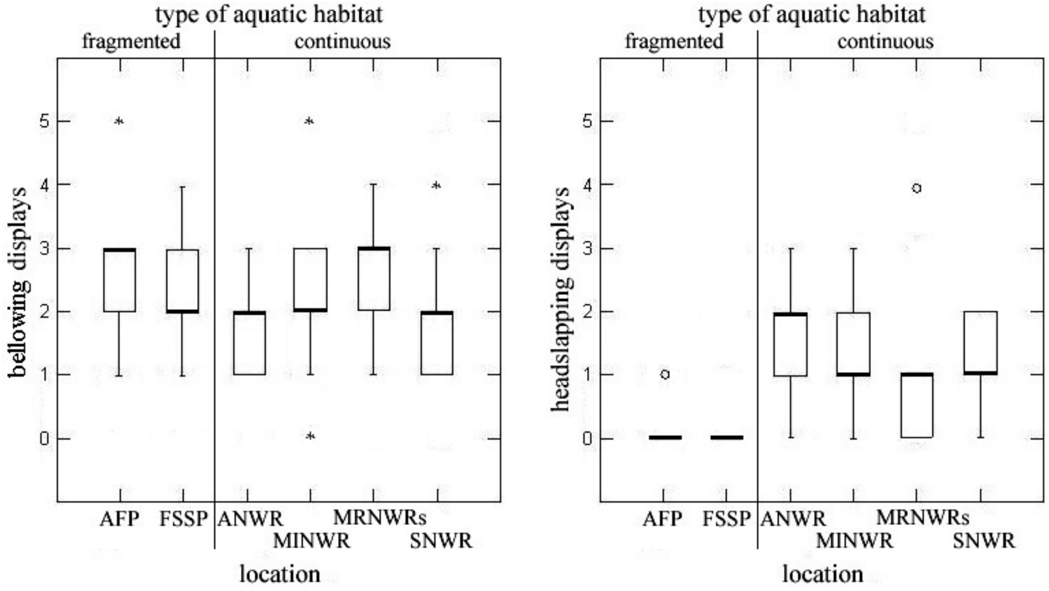


Figure 3.6. Box plots showing the numbers of bellowing (a) and headslapping (b) displays recorded in the first two days of observation of each alligator (n=10) at 6 study sites (see Fig. 3.1 for map and list of abbreviations). Two of the boxes are collapsed because no or almost no animals at those sites produced headslapping displays.

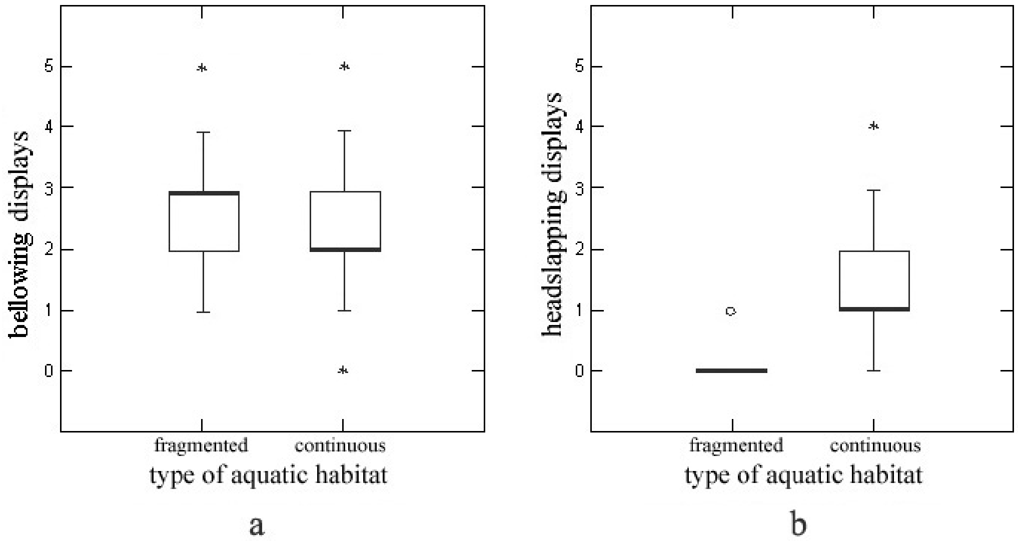


Figure 3.7. Box plots showing the numbers of bellowing displays (a) and headslapping displays (b) recorded in the first two days of observation of each alligator at study sites with continuous (n=40, 4 sites) and fragmented (n=20, 2 sites) aquatic habitats. One of the boxes is collapsed because almost all animals at those sites produced headslapping displays.

Table 3.1. Results of tests comparing headslapping displays (HD) and bellowing displays (BD) usage among American alligators at 6 study sites (4 sites with continuous aquatic habitat and 2 sites with fragmented aquatic habitat). At each site, 5 advertisement calls were recorded for each of 10 sampled animals. Results with $p<0.05$ highlighted in bold.

Comparison	**Number of HD**	**Prevalence of HD use**	**Prevalence of BD use**	**Number of HD in the first 2 days of observing each animal**	**Number of BD in the first 2 days of observing each animal**
Continuous aquatic habitat sites vs. fragmented aquatic habitat sites	$U = 725$ **$p < 0.001$**	**$p < 0.001$**	all animals except 1 used bellows	$U = 680$ **$p < 0.001$**	$U = 317$ $p = 0.1971$
3 northern sites vs. 3 southern sites[1]	$U = 513.5$ $p = 0.3524$	$p = 0.7846$		$U = 555$ $p = 0.1236$	$U = 394$ $p = 0.4122$
3 eastern sites vs. 3 western sites[1]	$U = 465$ $p = 0.8737$	$p = 0.5796$		$U = 345$ $p = 0.1236$	$U = 406.5$ $p = 0.5222$

[1] Two sites with continuous aquatic habitat and one site with fragmented aquatic habitat in each group (see Fig. 3.1). Data from Key Deer National Wildlife Refuge were not used in the analysis due to limited sample size.

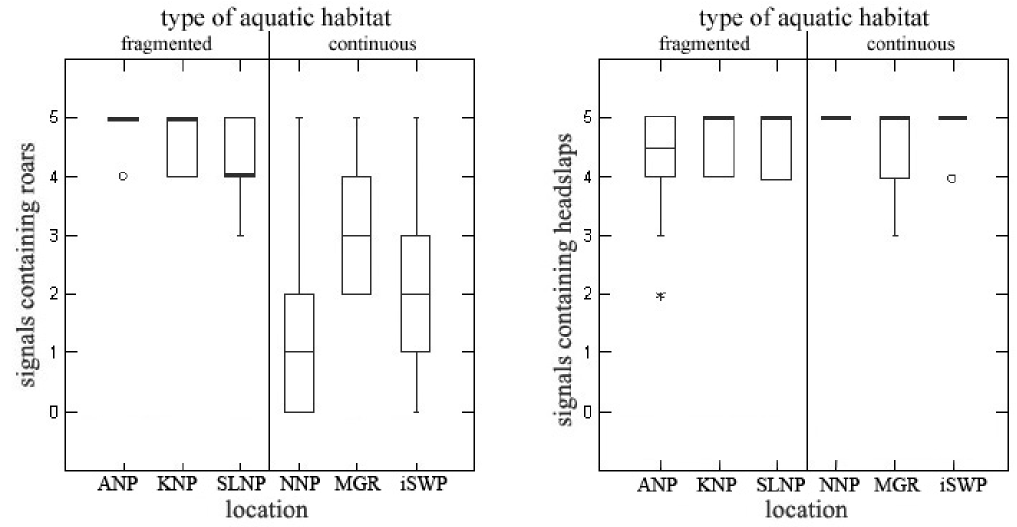
These results are reinforced by data from two other study sites. Two male alligators at KDNWR, an isolated fragmented site on three small offshore islands, produced 11 bellowing displays and no headslapping displays in 5 days of observation. In Ocala National Forest, an area with alligators inhabiting both continuous and fragmented aquatic habitats, the proportion of headslaps among ACs (5 ACs from each of 20 animals) was intermediate (0.14) between proportions of headslaps among ACs (5 ACs from each of 20 animals) observed in fragmented sites (0.02 and 0.08) and in continuous sites (0.22, 0.34, 0.42 and 0.48). See Chapter 5 for details on Ocala National Forest study.

3.3.2. Nile crocodiles: AC composition

Nile crocodiles produced headslaps and roars separately or combined within the same ACs. All these signals were produced in head oblique tail arched posture (Garrick & Lang 1977) and accompanied by infrasound, except for a few roars produced on land. With the exception of roars produced on land, all signals were produced in the morning between 1 hour before sunrise and 4 hours after sunrise, before the animals ordinarily leave the water for basking onshore.

Figure 3.8 shows the numbers of roars (a) and headslaps (b) among the 5 ACs recorded for each crocodile (n=10) at 6 study sites. The data for roars and headslaps were analyzed separately.

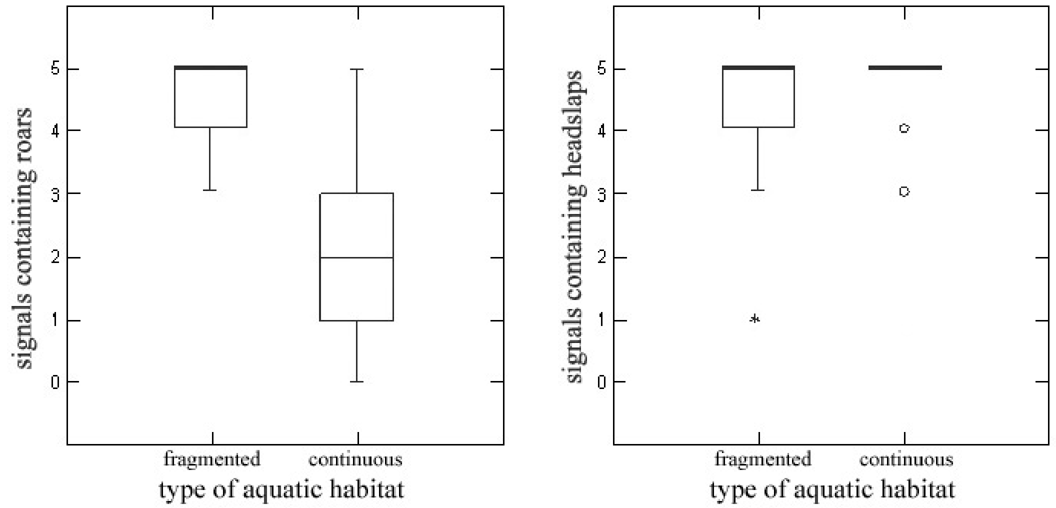
Nile crocodiles produce roars more frequently in areas with fragmented aquatic habitat than in areas with continuous aquatic habitat. The numbers of ACs containing roars among the 5 ACs recorded for each crocodile were higher at continuous sites than at fragmented sites (Fig. 3.9.a, Table 3.3). ANOVA revealed a significant effect of habitat-region interaction on the proportions of ACs containing roars (Table 3.2). The prevalence of roar use (the numbers of animals having at least one roar among the recorded ACs) was also greater at fragmented sites than at continuous sites (Table 3.3).



a

b

Figure 3.8. Box plots showing the numbers of advertisement calls containing roars (a) and headslaps (b) among 5 advertisement calls by crocodiles (n=10) at 6 study sites (see Fig. 3.2 for map and list of abbreviations). In (a) one of the boxes is collapsed because all except two signals in ANP contained roars. In (b) two of the boxes are collapsed because all signals in NNP and all except one in iSWP contained headslaps.



a

b

Figure 3.9. Box plots showing the numbers of advertisement calls containing roars (a) and headslaps (b) among 5 advertisement calls by crocodiles from study sites with continuous (n=30, 3 sites) and fragmented (n=30, 3 sites) aquatic habitats. In (b) one of the boxes is collapsed because almost all signals in continuous aquatic habitats contained headslaps.

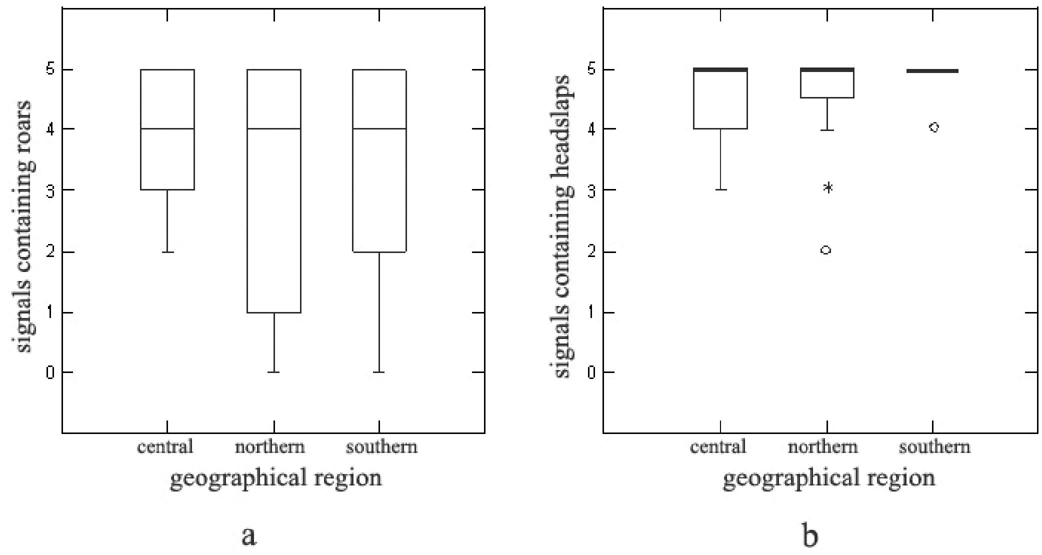


Figure 3.10. Box plots showing the numbers of advertisement calls containing roars (a) and headslaps (b) among 5 advertisement calls by crocodiles from study sites in central (n=20, 2 sites), northern (n=20, 2 sites) and southern (n=20, 2 sites) geographical regions (Fig. 3.2). In (b) one box is collapsed because almost all signals in the southern region contained headslaps.

Nile crocodiles frequently produce headslaps in areas with continuous aquatic habitat as well as in areas with fragmented aquatic habitat. The numbers of ACs containing headslaps among the 5 ACs recorded for each crocodile (Fig. 3.10.b) and the prevalence of headslap use did not differ significantly (Table 3.5). ANOVA revealed that only habitat type had a significant effect on the proportions of ACs containing headslaps among the 5 ACs recorded for each crocodile (Table 3.3).

Note, however, that the results for roars and headslaps are not independent because only a fixed number of ACs was scored for each animal. The observed difference in the numbers of animals with higher numbers of headslaps is probably an artifact of the much greater difference in the numbers of animals with higher roar usage. Analyzing independent sets of data for roars and headslaps (the numbers of roar- and headslap-containing ACs in the first two days of observing each animal) shows that the numbers of

ACs containing roars (Fig. 3.11) differ significantly between fragmented sites and continuous sites (Fig. 3.12), but the numbers of ACs containing headslaps do not (last columns in Tables 3.3 and 3.5). ANOVA shows significant effect of habitat type, but not of geographical region or habitat type-geographical region interaction, on the number of roar-containing ACs (Table 3.2), and no significant effect of any of the factors on the number of signals containing headslaps (Table 3.4).

Observed differences cannot be explained by differences in geographical location. Comparison of the three geographical regions (Fig. 3.10) shows no significant difference in the numbers of ACs containing roars (H=0.36, p=0.835) or headslaps (H=0.71, p=0.701) among 5 ACs recorded for each individual.

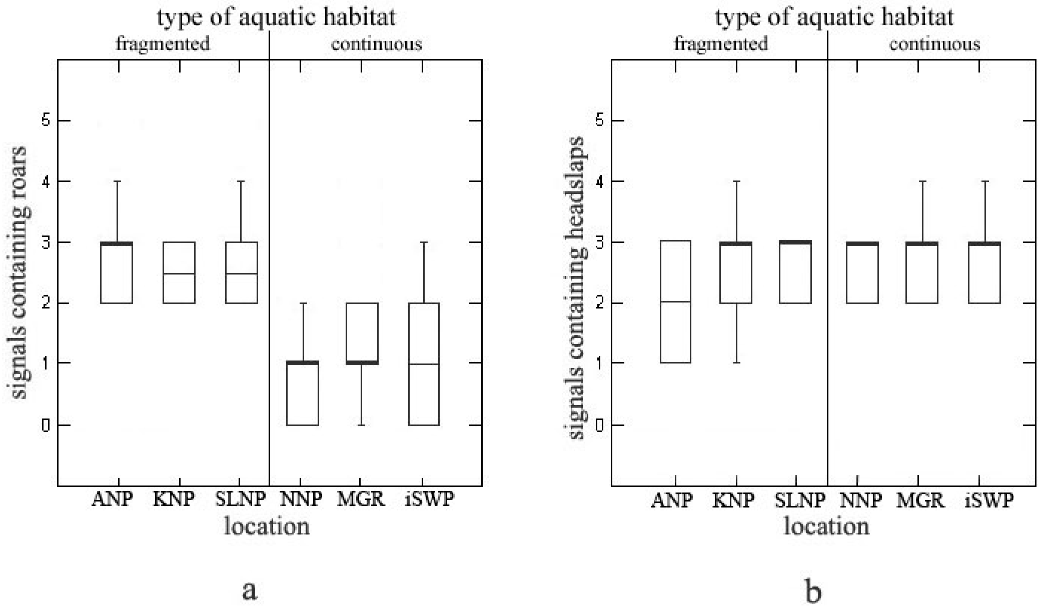


Figure 3.11. Box plots showing the numbers of advertisement calls containing roars (a) and headslaps (b) recorded in the first two days of observation of each crocodile (n=10) at 6 study sites (see Fig. 3.2 for map and list of abbreviations).

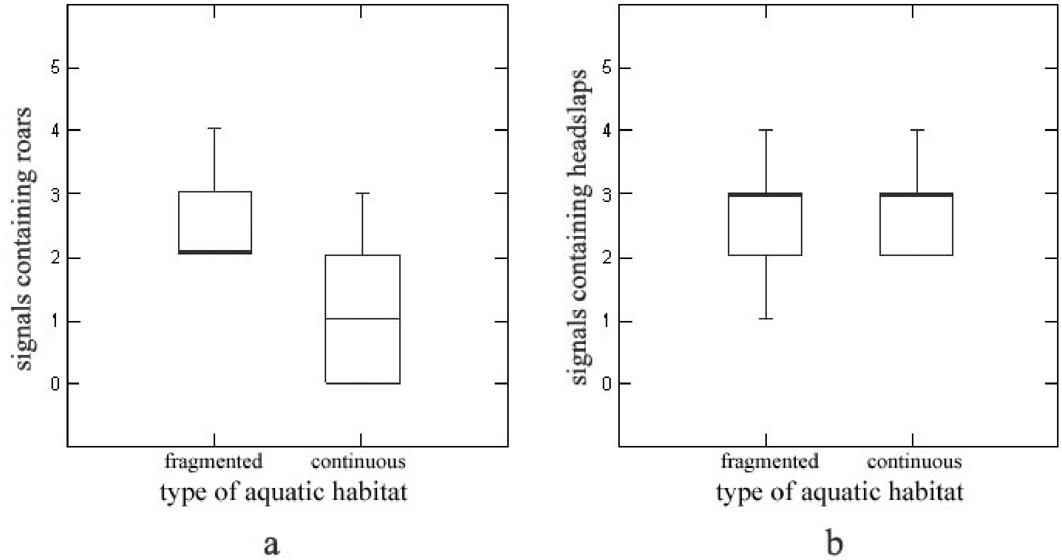


Figure 3.12. Box plots showing the numbers of advertisement calls containing roars (a) and headslaps (b) recorded in the first two days of observation of each crocodile at study sites with continuous (n=30, 3 sites) and fragmented (n=30, 3 sites) aquatic habitats.

Table 3.2. ANOVA results for advertisement calls containing roars in Nile crocodiles (n=10) at 6 study sites (one site with continuous aquatic habitat and one site with fragmented aquatic habitat in each of 3 geographical regions). Results with p<0.05 highlighted in bold.

Dependent variable	**Source**	**Type III SS**	**df**	**Mean squares**	**F-ratio**	**p-value**
Proportion of advertisement calls containing roars out of 5 advertisement signals[1]	Habitat type	10.109	1	10.109	41.442	**<0.0005**
	Region	0.048	2	0.024	0.099	0.906
	Habitat type * Region	1.553	2	0.777	3.184	**0.049**
	Error	13.173	54	0.244		
Number of advertisement calls containing roars in the first two days of observation[2]	Habitat type	36.817	1	36.817	68.320	**<0.0005**
	Region	1.900	2	0.950	1.763	0.181
	Habitat type * Region	1.433	2	0.717	1.330	0.273
	Error	29.100	54	0.539		

[1] These data passed Levene's test for normality (p=0.551) after arcsine transformation [arcsin (√x)] (see Chapter 3.2.8).

[2] These data passed Levene's test for normality (p=0.249) without a transformation.

Table 3.3. Results of tests comparing roar usage among Nile crocodiles at 6 study sites (one site with continuous aquatic habitat and one site with fragmented aquatic habitat in each of 3 geographical regions). At each site, 5 advertisement calls were recorded for each of 10 sampled animals. Results with p<0.05 highlighted in bold.

Comparison	**Proportion of advertisement calls containing roars**	**Prevalence of roar use**	**Numbers of advertisement calls containing roars in the first 2 days of observing each animal**
All sites with continuous aquatic habitat vs. all sites with fragmented aquatic habitat	*U* = 783 **p < 0.001**	**p = 0.024**	*U* = 748 **p<0,001**
Between 2 sites in the northern region	*U* = 94 **p < 0.001**	p = 0.087	*U* = 95.5 **p=0.001**
Between 2 sites in the central region	*U* = 78 **p = 0.045**	p = 1	U = 63 p=0.347
Between 2 sites in the southern region	*U* = 87 **p = 0.006**	p = 0.474	*U* = 84.5 **p = 0.010**

Table 3.4. ANOVA results for advertisement calls containing headslaps in Nile crocodiles (n=10) at 6 study sites (one site with continuous aquatic habitat and one site with fragmented aquatic habitat in each of 3 geographical regions). Results with p<0.05 in bold.

Dependent variable	**Source**	**Type III SS**	**df**	**Mean squares**	**F-ratio**	**p-value**
Proportion of advertisement calls containing headslaps out of 5 advertisement signals[1]	Habitat type	0.949	1	0.949	5.540	**0.022**
	Region	0.221	2	0.110	0.644	0.529
	Habitat type * Region	0.594	2	0.297	1.734	0.186
	Error	9.246	54	0.171		
Number of advertisement calls containing headslaps in the first two days of observation[2]	Habitat type	0.600	1	0.600	1.045	0.311
	Region	2.633	2	1.317	2.294	0.111
	Habitat type * Region	0.700	2	0.350	0.610	0.547
	Error	31.000	54	0.574		

[1] These data did not pass Levene's test for normality (p<0.001) after arcsine transformation.

[2] These data passed Levene's test for normality (p=0.223) without transformation.

Table 3.5. Results of tests comparing headslap usage among Nile crocodiles at 6 study sites (one site with continuous aquatic habitat and one site with fragmented aquatic habitat in each of 3 geographical regions). At each site, 5 advertisement calls were recorded for each of 10 sampled animals. Results with p<0.05 highlighted in bold.

Comparison	**Proportion of advertisement calls containing headslaps**	**Prevalence of headslap use**	**Number of advertisement calls containing headslaps in the first 3 days of observing each animal**
All sites with continuous aquatic habitat vs. all sites with fragmented aquatic habitat	*U* = 568.5 p = 0.082	All animals used headslaps	*U* = 358.5 p = 0.177
Between 2 sites in the northern region	*U* = 75 p = 0.06		*U* = 34 p = 0.242
Between 2 sites in the central region	*U* = 50 p = 0.968		*U* = 45.5 p = 0.764
Between 2 sites in the southern region	*U* = 60 p = 0.471		*U* = 42 p = 0.569

3.3.3. Nile crocodiles: roars vs. coughs

An unexpected result was the discovery of regional differences in the roars of Nile crocodiles. Such geographical variation has never before been described for any crocodilian.

At fragmented sites (KNP, SLNP, ANP) crocodiles produce sharp, loud roars (Fig. 3.13.a), clearly audible to a human observer at more than 100 m (up to 500 m under ideal conditions), or at approximately the same distance as headslaps. Such roars were first described by Cott (1961), who said that a roar of a crocodile in Victoria Nile, Uganda, is "a growling rumble, very deep in pitch, rattling, vibrant and sonorous, like distant thunder or the roll of a big drum which is protracted and may persist for six or seven seconds". Garrick and Lang (1977) described such roars as a part of mating-season display in a study of captive Nile crocodiles of unknown geographical origin. Pooley (1982b) described roars of Nile crocodiles in Ndumu National Park (South Africa) as pistol shot-like "chumpf" signals. Occasional observations and interviews with local hunters, game rangers and safari guides suggest that loud roars are also used by crocodiles in areas where they inhabit both large and small bodies of water: in Mamili National Park (Namibia), Lower Zambezi National Park (Zambia), and Kigosi Game Reserve (Tanzania). Loud roars are used in most ACs by crocodiles at Jerba Island Farm, Tunisia (David Oujani pers. comm). These crocodiles originate from northwestern Madagascar, where crocodiles inhabit both large and small lakes (pers. obs.).

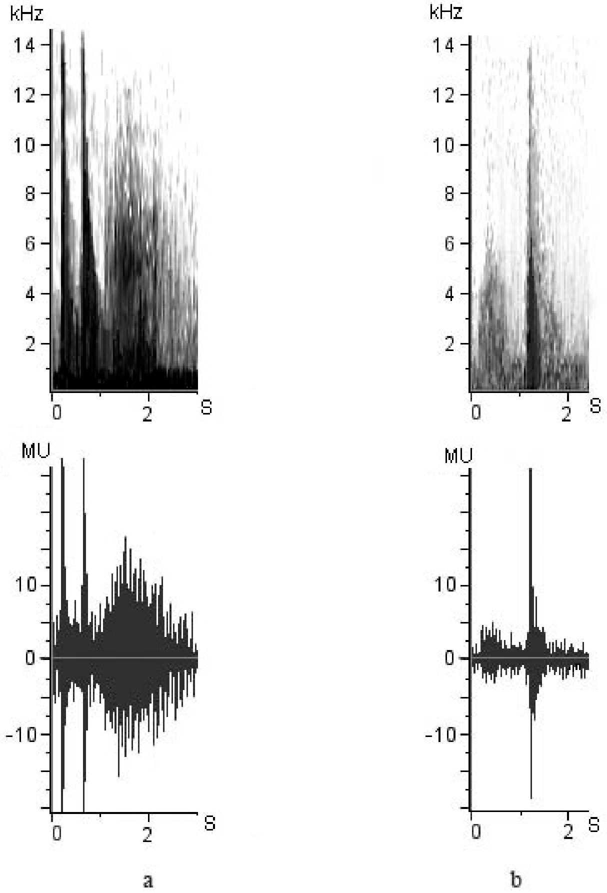


Figure 3.13. Spectrograms (top) and waveforms (bottom) of advertisement calls of Nile crocodiles: (a) two headslaps followed by a roar, South Luangwa National Park, Zambia; (b) a soft roar ("cough") followed by a headslap, iSimangaliso Wetland Park, South Africa. Infrasound is not visible on the waveforms because the recordings were obtained with an aerial microphone at more than 20 m from the source; the equipment used (see Addendum 2) could reliably record infrasound only at a very close range or with an underwater microphone.

At two out of three continuous sites (iSWP, NNP) crocodiles produce weak sounds (Fig. 3.13.b) similar to the so-called "coughs" of saltwater crocodiles (*C. porosus*) (pers. obs.). These coughs cannot be heard by a human observer at more than 100 m even under ideal conditions. Such weak signals are also produced in ORD area (see Chapter 5), where crocodiles inhabit small ponds as well as very large Lake Turkana, but the overwhelming majority of the population lives in the lake (there are estimated 14,000 crocodiles in Lake Turkana (Beard & Graham 1990), while the adjacent ponds of lower Oromo River Delta could not physically accommodate more than a few hundred). Vocal sounds in the ACs of Lake Turkana crocodiles are so quiet that a detailed description of local crocodiles' mating-season displays by Modha (1967) does not even mention them, although these animals are capable of loud roars and use them in other situations. At Crocoloco Crocodile Farm near Ir Ovot, Israel, where most Nile crocodiles originate from the Kenyan part of Lake Victoria and a few – from iSWP (Ofer Kobi pers. comm.), all observed roars were very quiet coughs (see Chapter 3.2.6). Interviews with local fishermen, park rangers and crocodile farm employees suggest that soft coughs are also used by crocodiles inhabiting lakes Nyasa (Malawi), Tana (Ethiopia), and Tanganyika, as well as by crocodiles living in Albert Nile and Lake Albert in Murchison Falls National Park, Uganda. A description of crocodilian courtship at Runde River in Botswana (Kofron 1991) mentions only headslaps.

Crocodiles at MGR produced vocal sounds intermediate in loudness between roars and coughs. Since all loudness estimates were done by ear in variable conditions, a detailed analysis of this aspect of AC variation was not possible. The numbers of roars used in MGR were higher than at two other continuous sites, although significantly lower than at any fragmented site (see Chapter 3.3.2). It is possible that available habitat at MGR is not completely limited to large bodies of water, because small ponds are formed in years with higher or lower water levels than during the year of the study. It is also possible that some crocodiles move between MGR and neighboring areas with small bodies of water. That might explain why MGR crocodiles are intermediate in AC composition and roar loudness between fragmented sites and the other two continuous sites.

In contrast with the Nile crocodile, no regional differences in the loudness of bellowing sounds were ever found in the American alligator. If such differences do occur, they could be detected by sampling alligators of different size under standardized recording conditions at different geographical locations.

3.3.4. Signaling differences and habitat: alligators vs. crocodiles

In both Nile crocodiles and American alligators, there are differences in signaling behavior between animals at fragmented and continuous sites (Table 3.4). These differences are not associated with geographical latitude or longitude.

In the Nile crocodile, neither the numbers of headslaps per AC per animal nor prevalence of headslap use among animals differed between fragmented and continuous sites. Crocodiles at continuous sites produced fewer vocal sounds per AC per animal and had lower prevalence of vocal sound use among animals than crocodiles at fragmented sites. In addition, vocal sounds produced by crocodiles at fragmented sites were noticeably louder than at continuous sites.

In the American alligator, alligators at fragmented sites produced fewer headslapping displays per AC per animal and had lower prevalence of headslapping display use among animals than alligators at continuous sites. This difference was due to animals at fragmented sites producing fewer headslapping displays, while bellowing displays were produced with the same frequency. No difference between sites in the average loudness of vocal sounds was ever noticed.

In both species, the observed differences in signaling behavior between animals at fragmented and continuous sites match the predictions (see Chapter 3.1), but not all predicted differences were observed. Why were the predicted differences observed only for one AC component in each species, and why the component for which these differences were observed was the headslaps in alligators but the vocal sounds in crocodiles? A possible answer is that headslaps in crocodiles and bellows in alligators have unique additional functions.

Wang et al. (2006, 2007) suggested that the main function of alligator bellows is not personal advertizing, but attracting more animals to bellowing choruses. It is now known that alligators engage in group courtship behavior, sometimes with dozens of participants, and these nighttime gatherings form in places with high concentrations of animals, where bellowing choruses naturally occur in morning hours (Dinets 2010). However, such courtship gatherings are rare and small in the northern part of American alligator's range, which includes AFP, MRNWRs and SNWR (Dinets 2010), most likely due to overall low population density (Ross 1998). Alligators bellow in all parts of their range, and animals living in isolation also bellow. Both headslaps and bellows by individuals attract animals of the opposite sex (Vliet 2001); bellowing by a male is often followed by aggression by another male, or by courtship attempts by females (Vliet 1989). It is likely that bellows have two functions: personal advertising and attracting more animals to choruses.

There are no headslapping choruses, and females seldom headslap (Garrick et al. 1978), although a few animals would sometimes headslap within a few seconds or minutes from each other. Probably alligators use headslaps only as personal advertising, and as such can be largely abandoned in areas with fragmented aquatic habitat, where bellows are more effective. But bellows cannot be abandoned in favor of headslaps in areas with continuous aquatic habitat, because bellows are used not only for personal advertizing, but also to attract other animals of either sex to chorus locations, thus increasing the size of courtship gatherings.

The opposite situation in Nile crocodiles can also be explained by headslaps having some additional function that roars do not have in this species. It has been suggested (Garnett 1989, Brazaitis & Watanabe 2011) that headslaps serve as signals of dominance in some species of crocodiles. Nile crocodiles are likely among these species (Brady Barr pers. comm.). Headslaps do not have that function in alligators (Vliet 1989).

3.3.5. Are the observed differences associated with population density?

Differences in signaling behavior between conspecific populations of reptiles have been demonstrated in studies of visual displays in *Crotaphytus* (McCoy et al. 2003) and *Anolis* (Bloch & Irschick 2006; Ord et al. 2007) lizards. These studies suggested that the observed differences in these lizards were associated with habitat structure, but failed to exclude population density as an alternative explanation or to treat it as a covariable.

Could differences in AC composition observed in the present study be associated with population density?

Among the six alligator study sites, the three northern sites (AFP, MRNWRs and SNWR) had much lower population density than the three southern sites (ANWR, FSSP and MINWR). At the southern sites, alligators occurred in groups of up to 30-40 individuals, and the arithmetic mean group size was more than 5 (the exact number was difficult to obtain as group sizes were constantly changing). In the northern sites, there were no groups of more than 5 individuals, and the arithmetic mean group size was less than 3. Note that alligators found in groups of more than 10 were not included in the present study to minimize group size bias (see Chapter 3.2.4). Although no exact measurements of distances between groups were taken, these distances were obviously larger in the northern sites. The typical population density in the northern part of American alligator range, where the three northern sites are located, is known to be more than 10 times lower than in the southern part, where the three southern sites are located (Neil 1971). However, there was no difference in AC composition between northern and southern sites (see Chapter 3.3.1).

Even though observed differences in signaling behavior were not associated with population density, there could still be density-dependent differences in alligator signaling. In the present study, the length of bellowing bouts and many other signal parameters were not recorded. Numerous differences between the behavior of wild alligators observed in the present study, and captive alligators studied by Garrick et al. (1978) and Vliet (1989), were noted. Wild alligators had limited use of bellowing on land (which was observed only twice in hundreds of hours of observation), a much lower rate of afternoon signaling (observed only once in approximately 30 hours of afternoon observations; this AC, a bellowing display, was not included in the analysis), and a lower overall rate of signaling (throughout the mating season, males seldom produced more than three displays of either kind in one day, counting each bellowing chorus as one display). These differences could be due to unnaturally high population density in captivity, although other explanations (such as long-term absence of unfamiliar animals, or abundance of energy due to overfeeding) can also be suggested. Vliet (1989) reported differences in signaling behavior between alligators kept in large and small groups.

As for Nile crocodiles, there was no obvious difference in average group size between study sites, although maximum group size was 17 in NNP and 8-10 at other sites (groups of over 10 were excluded from the study). Distances between groups were always less than 200 m at the two northern sites (ANP and NNP), but always more than 500 m at all other sites. Even though at the two central sites (MGR and SLNP, where many areas were inaccessible) some groups could remain unnoticed, AC composition did not differ between northern, central and southern sites (see Chapter 3.3.2).

Although further research is necessary to elucidate the role of population density in crocodilian signaling, it can be excluded as an alternative explanation for the differences in AC composition observed in the present study.

3.3.6. Are alligators "more vocal" than crocodiles?

Garrick & Lang (1977) found American alligators to be "much more vocal" than American (*C. acutus*) and Nile crocodiles, meaning that alligators produce many more bellows than crocodiles produce roars. The authors suggested that alligators rely more on sound communication "because of limited visibility in their marshy habitat".

This difference in habitat does exist between the American alligator and the American crocodile, but not between the American alligator and the Nile crocodile, as both species are habitat generalists with broad and widely overlapping habitat preferences (see Chapter 2). Both alligator and crocodile habitats used in the present study ranged from densely overgrown to extremely open.

In the present study, focal animals of all 3 species produced 1-3 ACs per day on more than 90% of all days of observation during the mating season, with 5 ACs being the maximum number of ACs observed in one day for both species. But in the American alligator, all but 2 observed vocal ACs were bellowing bouts as described by Garrick et al. (1978). Bouts were often repeated 2-3 times within 15-20 minutes (such repeats were not counted as separate ACs, see Chapter 3.2.5). Vocal ACs were produced by most or all adult animals present, including females.

Unlike alligators, crocodiles seldom repeated any components of their ACs more than twice, and the largest animal in each group (presumably the territorial male) was the only animal producing ACs. So the overall vocal activity by a group of alligators is much higher than vocal activity by a group of crocodiles. Each alligator in a group usually produces 10-70 separate bellows in one day, while fewer than 10 separate roars are produced by the entire group of crocodiles.

The difference between alligators and crocodiles in the number of vocal ACs produced by focal animals was far less pronounced (arithmetic means 0.7-1.5 per day per alligator in different study areas vs. 0.3-1.3 per day per crocodile). Crocodiles of both species produced more headslaps than alligators (arithmetic means 1.4-1.6 per day per crocodile in different study areas, compared to 0-0.7 in focal alligators).

The difference in overall vocal activity was thus due to alligators producing bellowing bouts and forming bellowing choruses. The other alligator species, Chinese alligator (*A. sinensis*), and some caimans also bellow or roar in bouts and form choruses (see Chapter 2). However, there is no evidence of long roaring bouts or roaring choruses in any species of crocodile, irrespective of habitat preferences. Apparently, higher vocal activity in alligators compared to crocodiles is best explained by phylogeny, not by differences in habitat.

3.3.7. Conclusion.

For both the American alligator and the Nile crocodile, AC composition differs between animals living at continuous and fragmented sites. These differences are achieved in alligators and crocodiles in different ways. In alligators, usage of vocal sounds does not differ, but usage of headslaps does. In crocodiles, usage of headslaps does not differ, but usage of vocal signals and their loudness does (Table 3.6). These differences are not associated with latitude, longitude or population density.

Table 3.6. Differences in signaling behavior between animals at sites with fragmented and continuous aquatic habitats.

Species	**Headslaps**	**Vocal sounds**	
	Frequency and prevalence of use	**Frequency and prevalence of use**	**Loudness**
Alligator mississippiensis	higher in continuous habitats	no difference	
Crocodylus niloticus	no difference	higher in fragmented habitats	

CHAPTER 4. CHANGES IN ADVERTISEMENT CALL COMPOSITION AFTER A CHANGE IN HABITAT.

4.1. Overview

Do individual crocodilians adjust the structure of their advertisement calls (ACs) to the size of their aquatic habitat? An obvious way to answer this question would be to move some animals into bodies of water of different size. But translocation of adult crocodilians is technically difficult and results in long-term stress (Neill 1971), so a better approach is to find out if animals change their AC structure as their habitat changes around them. Such habitat changes create a natural experiment that does not require any human disturbance of the animals.

The yacare caiman (*Caiman yacare*) is a medium-size crocodilian inhabiting a wide variety of habitats in tropical South America. Yacare caimans use the same two kinds of ACs as those described by Garrick et al. (1978) for the American alligator (*Alligator mississippiensis*): bellow preceded by infrasound (bellowing display) and headslap preceded by infrasound (headslapping display) (Alberto L. Querejazu pers. comm.). Caiman and crocodile vocalizations are commonly called "roars" rather than "bellows", so vocalizations preceded by infrasound will hereafter be called "roaring displays".

Yacare caimans were chosen for this part of the study for three reasons. First, they are easy to observe in the wild. In many parts of South America they are very tame, extremely abundant, and inhabit open landscapes (Espinosa 1998b). Second, yacare caimans can be individually identified (see below). Third, many populations of this species live in seasonally flooded savanna where water levels change dramatically over the duration of the caimans' mating season, either falling in the last weeks of the dry season, or rising at the onset of the rains (McClain 2002). As a result, some lakes inhabited by caimans either break into small ponds or merge into large flooded areas.

If roars are more effective for aerial communication, and headslaps are more effective for communication through the water, then it is expected that caimans will adjust their relative usage of the two kinds of ACs in response to changes in their habitat. The proportion of headslapping displays among caiman ACs should be different after large bodies of water turn into small ones, or vice versa. To maximize the number of caimans perceiving their signal, signaling caimans should decrease the proportion of headslapping displays when large lakes break into small ones, because this habitat change makes the receivers less likely to be in the same continuous body of water as the signaling animal. Signaling caimans should increase that proportion when small lakes become parts of a continuously flooded area, because this habitat change makes the receivers more likely to be in the same continuous body of water as the signaling animal.

4.2. Methods

4.2.1. Study sites

Two sites were chosen for the study (Fig. 4.1; see Table 2.1 for location details): the central-western part of Brazilian Pantanal and the vicinity of Noel Kempff Mercado National Park (hereafter NKMNP). Observations in the Pantanal were conducted on October 29-November 6 and November 14-22, 2007. Observations in NKMNP were conducted on November 27-30 and December 4-9, 2007.

Figure 4.1. Geographic locations of study sites in the Pantanal (1) and near Noel Kempff Mercado National Park (2).

At both sites, caimans inhabited lakes of all available sizes as well as small ponds and rivers. Some lakes or parts of lakes had very high caiman densities, often hundreds of animals in areas of less than 1 km^2. Local farmers were well aware of these areas of high density and claimed that they form only during the mating season, but not at the same locations each year.

In the Pantanal, six lakes with large numbers of caimans (20-60 animals larger than 1 m observed at night in each lake) were chosen. Each lake was estimated to be 0.5-1 km^2 in size at the beginning of the study (Fig. 4.2). Every day, two lakes were observed (each by one observer) from 0400 until 0900 hrs and from 1600 until 1800 hrs. Next day, two other lakes were observed, and so on. In nine days, each lake had been observed three times. The area was revisited after a seven-day gap in observations, by which time four lakes had broken into numerous small ponds. These four former lakes (now groups of ponds) were observed (two on odd days, the other two on even days) for eight days.

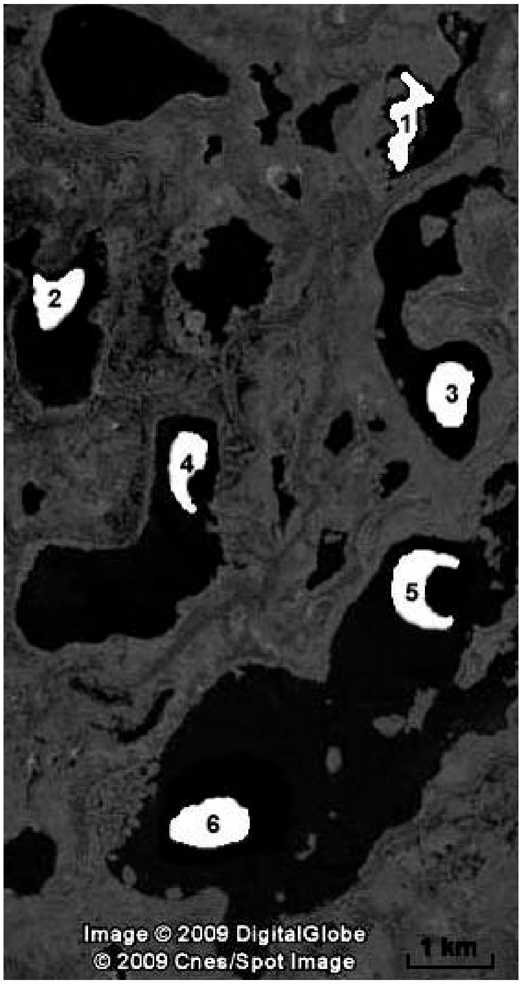


Figure 4.2. Satellite image of the study area in the Pantanal, Brazil (from GoogleEarth). Approximate shapes of six lakes where observations were conducted as they were at the beginning of the study are outlined in white. Observations on lakes 4 and 6 were later discontinued as these lakes failed to break up into small pools.

Figure 4.3. Satellite image of the study area near Noel Kempff Mercado National Park, Bolivia (from GoogleEarth). Eight lakes used in the study are shown as white circles (only lake 3 is large enough to be shown to scale).

In NKMNP, eight lakes with high numbers of caimans (approximately 10-40 animals larger than 1 m observed at night in each lake) were chosen (Fig. 4.3). Each lake was visually estimated to be within the size range of 100-3000 m^2 in size at the beginning of the study. Every day, two lakes were observed, one from 0430 until 0930 hrs and the other from 1600 until 1900 hrs, all by the same observer. The next day, two other lakes were observed, and so on. In four days, each lake was observed once. The area was revisited after a three-day gap in observations, by which time the entire floodplain containing all eight lakes became flooded. This continuous body of water was observed for six more days, then the observations had to be discontinued because caimans began to move widely, and finding known individuals became difficult.

4.2.2. Observing

In the Pantanal, all observations were made on horseback or on foot, with the observer at least 5 m from the water edge and at least 25 m from the nearest caiman. In NKMNP, the observations were made on foot, from trees, or from a small boat, with the observer at least 25 m from the nearest caiman. At this distance, no signs of the animals being disturbed by the observer were ever noticed. Binoculars (7-15x35 and 10x42) were used when necessary.

4.2.3. Choosing and identifying focal animals

Yacare caimans have facial markings (dark spots on the sides of their heads, especially on the jaws) which are highly variable (Fig. 4.4, left) and very useful for individual recognition. They are highly visible during the head oblique tail arched (HOTA) posture (Garrick & Lang 1977), which precedes ACs (see below), In old individuals, these markings sometimes become difficult to distinguish, but such animals tend to have other recognizable features (protruding teeth, missing scutes, scars, etc.).

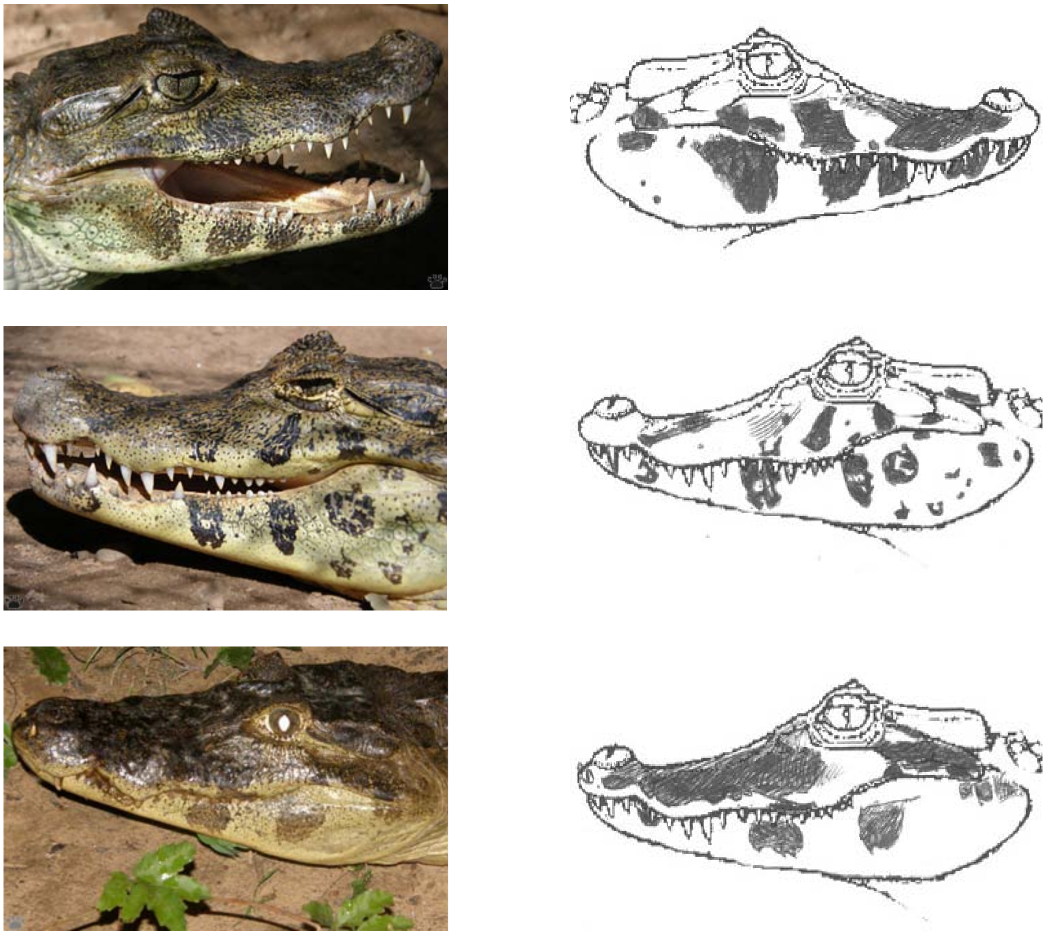


Figure 4.4. Sketches of facial markings of individual yacare caimans. Note that the bottom individual also has two lower teeth protruding through the upper jaw.

Every time a caiman was seen producing an AC for the first time, an identification card was filled for this animal. The cards had been printed in advance and showed outlines of caiman bodies and heads as seen laterally from both sides. As the card was filled, a sketch of the animal's facial markings (Fig. 4.4, right) was made, other individual markings noted, and total length estimated. If the conditions permitted, a photo or two were made, and later used in detailing the sketch. Identification cards proved to be highly effective: during later encounters, the animals could be easily recognized (using binoculars if needed) at distances of up to 250 m. Only in two cases was repeated identification considered uncertain by the observer; the two animals in question were dropped from the study.

4.2.4. Inter-observer reliability testing

A test of inter-observer reliability of animal identification was conducted at Fazenda Santa Clara in the Brazilian Pantanal ($19^o26`$S, $57^o04`$W) by the author and a volunteer previously unfamiliar with caimans.

The test was conducted on a remnant pond in a dry river channel, with a high concentration of caimans (no fewer than 160, as estimated by a rough night count). Only animals estimated to be 1 m or more in total length were used. To avoid disturbing the animals, the observers used only the immediately visible side of each caiman's head and made no attempt to see the other side (facial markings are asymmetrical and differ as much between left and right sides as between animals).

On the first day, both observers walked along the pond, and took turns making sketches of the caimans' facial markings, using pre-printed templates (Fig. 4.4., right column). No caiman was sketched twice. Each observer made 24 sketches – 12 of left sides of caimans' heads and 12 of right sides. All 48 sketches were shuffled, then numbered and copied, so that each observer had a full set.

On the second day the observers again walked around the pond. Every caiman they encountered was given a number. Then each observer went through his set of 48 sketches, looking for a match. He had to go through 24 sketches showing either left or right sides of caimans' heads, depending on which side was visible. If a match was found, the observer would still go through the rest of the set to avoid giving clues to the other observer. He would then silently write down the number given to the caiman, and either the number of the matching sketch or “0” if none was found.

Of 80 caimans checked this way, 58 were considered by both observers to have no matching sketches; 21 were matched to the same sketch number by both observers; one caiman was considered to have a corresponding sketch by one observer, but to have no such sketch by the other.

The percentage agreement on whether a particular caiman did or did not have a matching sketch was 98%. (During the actual study, the percentage agreement was probably even higher because both sides of each animal’s head were sketched.) Among the animals which had a matching sketch according to both observers, the percentage agreement on which sketch was the matching one was 100%.

Even if a few mistakes were made, they should not have much effect on the results because all animals would be from the same population.

For inter-observer reliability studies on scoring behaviors, see Chapter 3.2.6.

4.2.5. Data recording

All ACs observed for any particular animal were recorded as belonging to one of the two AC types: roaring displays that contain roar(s) and infrasound, or headslapping displays that contain headslap(s) and infrasound. All ACs observed during the study (over 500 total) belonged to one of the two types. An AC containing only infrasound or both roars and headslaps was never observed. Presence of infrasound was determined by the "water dance" effect (Garrick & Lang 1977). Roars not followed by infrasound were sometimes heard during close interactions between caimans (with two animals less than 2 m from each other). In these cases the roars were not preceded by HOTA posture, and were not recorded as ACs because there was no reason to consider them long-distance communication. Garrick & Lang (1977) described such roars in alligators as aggressive displays.

The observers attempted to record at least three ACs for each focal animal before and after the change in habitat, and to have as many animals with six or more observed ACs as possible. Animals for which fewer than three ACs had been recorded were not used in the study because there would be too much uncertainty in the proportion of headslaps for animals with only 1-2 ACs recorded. Setting the minimum number of required AC observations in each study period as four or more rather than three would have made it impossible to sample a sufficient number of animals within the duration of a mating season.

In the Pantanal, 88 caimans were observed producing ACs during the first observation period. Of them, 44 animals were used in the analysis. Others produced fewer than three observed ACs during one of the two observation periods, could not be found after the gap in observations, or were in lakes that failed to break into small ponds.

In NKMNP, 82 caimans were observed producing ACs during the first observation period. Only 26 of them were used in the analysis. Others produced fewer than three observed ACs during one of the two observation periods, or could not be found after the gap in observations.

4.2.6. Analysis

Data for caimans at each site were analyzed to find if the proportion of headslapping displays among the ACs was the same before and after the change in habitat. These proportions among all ACs recorded for each animal before and after the change were counted and analyzed as paired data points. Each animal had an increase, a decrease, or no change in the proportion of headslapping displays. A Sign Test was used to determine if there was a statistically significant change among all animals; this test was chosen because only the direction of change, and not the magnitude of difference, was of interest for the present study.

4.3. Results and Discussion

4.3.1. Behavior of yacare caimans

Although caiman ACs are generally similar to those described in detail by Garrick et al. (1978) and Vliet (1989) for the American alligator, a few differences were noted. Caiman roars are shorter than 0.5 sec (Fig. 4.5), while alligator bellows usually last at least a second. During the study, roars were never heard by a human observer from more than 200 m away, while alligator bellows can be heard from more than 500 m (Neil 1971).

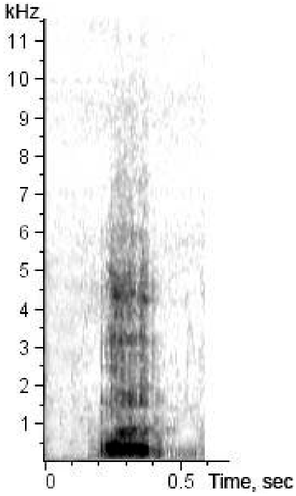


Figure 4.5. Acoustic spectrogram of a yacare caiman roar.

All observed roaring displays of caimans consisted of one to three roars, each roar preceded by infrasound, while alligator bellows are usually repeated more than eight times. In alligators, females often produce bellowing displays similar to those of males, but without infrasound; such displays have not been reported in female caimans. Unlike alligators, which in the wild bellow almost exclusively in the morning (see Chapter 3.3.1), yacare caimans produce ACs in the evening as well as in the morning. All observed caiman ACs were produced either between 0400 and 0930 hrs, or between 1600 and 1900 hrs. Caimans produce more ACs per day than alligators (up to 12 ACs per caiman were observed in one day, as opposed to 1-3 in free-ranging alligators, see next Chapter 3.3.5). Alligators frequently bellow in choruses (simultaneous displays by most adults in an area) which last for up to ten minutes). In caimans, such choruses usually last less than a minute.

As in alligators, roaring and headslapping displays by caimans are preceded by a HOTA posture, which can last from about 30 seconds to 3 minutes. HOTA posture gives an observer a useful sign of an upcoming AC, drawing his attention to the animal and often allowing him to take a photo with facial markings clearly visible.

4.3.2. Test results

In the Pantanal, the proportion of headslapping displays remained the same in 22 animals, increased in 11, and decreased also in 11 (Fig. 4.6). No test was needed since no net change was detected. Simulations show that with n=44 and 25-50% of ties, the difference between numbers of animals with an increase and those with a decrease would have had to be at least 12-14 to be significant ($p=0.05$).

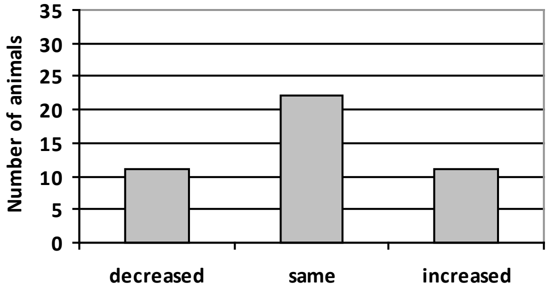


Figure 4.6. Numbers of yacare caimans (N=44) in which the proportion of headslapping displays among advertisement calls increased, decreased or remained the same after the change of their habitat in the Pantanal (Brazil) from large lakes to small ponds. The number of animals in which that proportion increased did not differ from the number of animals in which it decreased.

In NKMNP, the proportion of headslapping displays remained the same in 6 animals, increased in 8, and decreased in 12 (Fig. 4.7, p=0.503). Simulations show that with n=24 and 25-50% of ties, the difference between numbers of animals with an increase and those with a decrease would have had to be at least 8-10 to be significant.

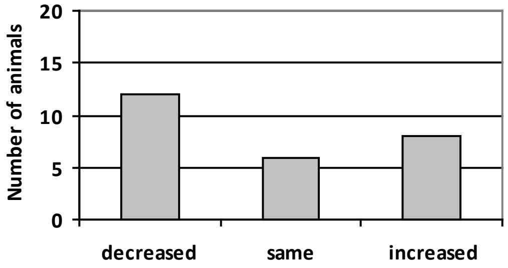


Figure 4.7. Numbers of yacare caimans (N=26) in which the proportion of headslapping displays among advertisement calls increased, decreased or remained the same after the change of their habitat near Noel Kempff Mercado National Park (Bolivia) from small lakes to water-covered floodplain. The number of animals in which that proportion increased did not differ significantly from the number of animals in which it decreased.

Neither the break-up of large lakes into small ones, nor merging of small lakes into a continuously flooded area was followed by a change in the relative usage of two types of ACs by caimans within the duration of the study.

CHAPTER 5. HABITAT-TO-HABITAT COMPARISONS OF ADVERTISEMENT CALL COMPOSITION WITHIN A GEOGRAPHICAL AREA.

5.1. Overview

In the previous chapter, it was found that the proportions of two call types among the advertisement calls (ACs) made by yacare caimans (*Caiman yacare*) before and immediately after changes in the size of their aquatic habitat did not differ.

It is possible, however, that if there are such differences, they are not apparent within weeks or months. Thus, it might be necessary to compare animals inhabiting large and small bodies of water in close proximity to each other in order to detect differences in relative usage of different AC types. Some of these animals would be those that have moved between habitats recently, but others would be long-term residents of either small or large bodies of water. Available data suggest that 80% or more of adult alligators (Chabreck 1965; Chen 1990; Morea et al. 2002) and crocodiles of most species (Brien et al. 2008; Cott 1961; van Hoven 2009; Hutton 1989; Modha 1967; Webb et al., 1983; Whitaker & Whitaker 1984) are philopatric in areas of less than 1.5 km^2, and usually in the same bodies of water, for many years. So, the majority of animals are long-term residents of a particular habitat type, and habitat-related differences in their ACs should be observable.

It is predicted that (1) headslaps, which carry further through water than through air, should be used more frequently by animals living in large bodies of water than by those living in small bodies of water, and (2) vocal sounds (commonly called "bellows" in alligators and "roars" in caimans and crocodiles), which are emitted above the water surface, should be used more frequently by animals living in small bodies of water than by those living in large bodies of water.

Comparisons of ACs were performed on the same two species of crocodilians that were used in the studies described in Chapter 3, for the same reasons.

5.2. Methods

5.2.1. Study sites

This part of the study was conducted at two sites: Ocala National Forest (ONF) in north-central Florida and the southeastern edge of Oromo River Delta (ORD) in Ethiopia (See Figures 3.1 and 3.2 for location maps, and Table 2.1 for location details and dates of observations).

In ONF, the American alligators chosen for the study inhabited slightly brackish Lake George (150 km^2) and small freshwater ponds in subtropical pine forest within 10 km of Lake George.

In ORD, the Nile crocodiles chosen for the study inhabited Lake Turkana (6400 km^2) and small ponds in a tropical salt desert within 1 km of Lake Turkana shoreline (as it was at the time of the study).

5.2.2. Choosing and observing focal animals and recording data.

Focal alligators and crocodiles were chosen and observed using the protocols described in Chapter 3.2.4.

Observations of alligators continued until 5 ACs were recorded from each of ten alligators in Lake George and ten alligators in small ponds, with each of 4 observers having observed 2-3 animals in each of the two habitat types.

Because of the difficulties in identifying alligators in the wild, some of the focal animals could have been replaced by similar-looking alligators during the observation period without the observer noticing the replacement event. However, the number of such events could not be high, because male alligators are known to be mostly philopatric (see Chapter 5.1). Even if animals were misidentified a few times, the results should be little influenced because the newcomers would most likely be animals from the same habitat.

Observations of crocodiles continued until five ACs were recorded from each of ten crocodiles in Lake Turkana and ten crocodiles in small ponds, with each of three observers observing 3-4 animals in each of the two habitat types.

Errors in identifying individual crocodiles were also possible, but if a focal animal was replaced by another one, it would be from the same habitat. Movement between Lake Turkana and the ponds at the time of observation would require crossing extensive mudflats, but neither crocodiles nor crocodile tracks were ever observed in the mudflats.

See Chapter 3.2.5 for data recording protocols, and Chapter 3.2.6 for inter-observer reliability studies.

5.2.3. Analysis

Only the first five ACs recorded from each focal animal were used in the analysis to ensure that each animal was weighted equally. This rule did not cause substantial loss of data, because six or seven ACs were recorded from only a few crocodiles.

For alligators, numbers of headslap displays out of five ACs were tallied for each animal. To test for statistical differences, the tallies for animals (n=10) observed in Lake George were compared with the tallies for animals (n=10) observed in small ponds using the Mann-Whitney *U*-test.

For crocodiles, the same tests were used, but numbers of ACs containing roars (with or without headslaps) and numbers of signals containing headslaps (with or without roars) were analyzed separately.

The prevalence of headslapping display usage among alligators (out of 10 in each habitat) was compared between Lake George and small ponds using Fisher's Exact test. The same was done for the prevalence of bellowing display usage.

The same comparisons of prevalence of headslap and roar usage were done for crocodiles in Lake Turkana and small ponds.

5.3. Results and Discussion

Results of statistical tests for alligators are listed in Table 5.1, for crocodiles – in Table 5.2.

There was no significant difference between alligators living in Lake George and in small ponds in the numbers of headslap displays among five ACs recorded for each individual (Fig. 5.1), indicating that these two samples were drawn from populations that did not differ in the likelihood of headslaps by individuals.

There was no significant difference between crocodiles living in Lake Turkana and in small ponds in the numbers of signals containing roars among five ACs recorded for each individual (Fig. 5.2.a), indicating that these two samples were drawn from populations that did not differ in the likelihood of using roars by individuals.

There was no significant difference between crocodiles living in Lake Turkana and in small ponds in the numbers of signals containing headslaps among five ACs recorded for each individual (Fig. 5.2.b), indicating that these two samples were drawn from populations that did not differ in the likelihood of using roars by individuals. In fact, all ACs except one (by an animal in Lake Turkana) contained headslaps.

For sample sizes of 10 used in the present study, the critical values of *U* are 23 and 77. For the likelihood of signal use to be significantly different, the numbers of animals with tallies at or below the common median would have to differ at least by 6.

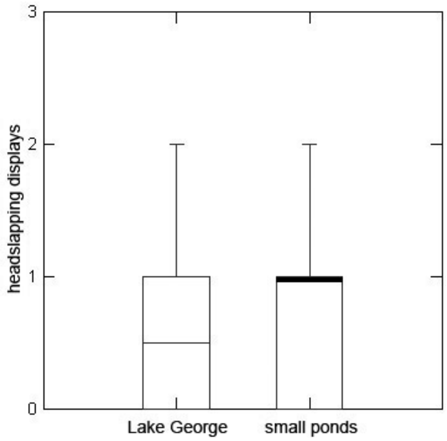


Figure 5.1. Box plot showing the numbers of headslapping displays among 5 advertisement calls by alligators living in large Lake George (n=10) and small forest ponds (n=10). Ocala National Forest, Florida.

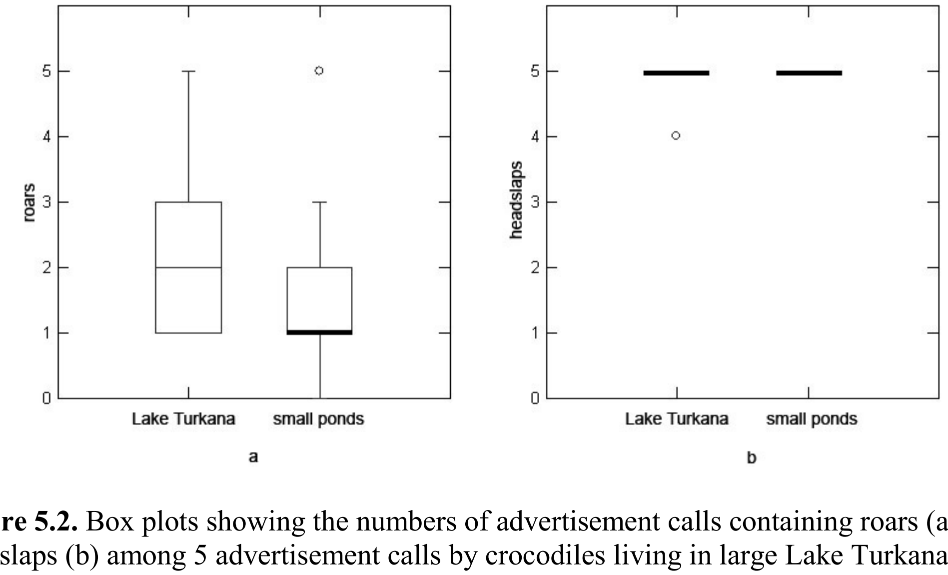


Figure 5.2. Box plots showing the numbers of advertisement calls containing roars (a) and headslaps (b) among 5 advertisement calls by crocodiles living in large Lake Turkana (n=10) and small desert ponds (n=10). In (b) the boxes are collapsed because all calls except one contained headslaps. Oromo River Delta, Ethiopia.

In both Lake George and small ponds, all alligators used bellowing displays. The numbers of animals having at least one headslap display among five recorded ACs were 5 out of 10 in Lake George and 4 out of 10 in small ponds.

In both Lake Turkana and small ponds, all crocodiles used headslaps. The numbers of animals having used at least one roar in five ACs were 10 out of 10 in Lake Turkana and 8 out of 10 in small ponds (p=0.474).

These results for both alligators and crocodiles indicate that the prevalence of use of headslaps and bellows/roars did not differ significantly between animals inhabiting large and small bodies of water. For the difference to be significant ($p<0.05$), the numbers would have to differ at least by 6.

Table 5.1. Results of tests comparing headslapping displays (HD) and bellowing displays (BD) usage among American alligators living in large Lake George and adjacent small ponds. At each habitat type, 5 advertisement calls were recorded for each of 10 sampled animals.

Comparison	Number of HD	Prevalence of HD use	Prevalence of BD use
Alligators in a large lake vs. alligators in small ponds.	*U* = 43 p = 0.642	p=1.0	all animals used bellowing displays

Table 5.2. Results of tests comparing roar and headslap usage among Nile crocodiles living in large Lake Turkana and adjacent small ponds. At each habitat type, 5 advertisement calls were recorded for each of 10 sampled animals.

Comparison	Proportion of advertisement calls containing roars	Prevalence of roar use	Proportion of advertisement calls containing headslaps	Prevalence of headslap use
Crocodiles in a large lake vs. crocodiles in small ponds.	*U* = 36 p = 0.474	p=0.474	*U* = 55 p = 0.734	All animals used headslaps

So, animals living in large and small bodies of water did not differ significantly in AC composition. It can be concluded that differences in signaling behavior between animals living in areas with continuous and fragmented aquatic habitats (see Chapter 3) are not a result of individuals changing their behavior in response to habitat structure.

The apparent inability of individual crocodilians to adjust their signaling to habitat structure is surprising. Such ability is possessed by male *Schizocosa ocreata* wolf spiders, which use more visual signals on substrates not conductive to seismic signals (Gordon & Uetz 2011); by male great tits (*Parus major*), which sing higher-pitched songs in urban areas with high levels of low-frequency background noise (Slabbekoorn & Peet 2003); and by male anole lizards, which speed up visual displays in noisy motion habitats (Ord et al. 2007).

CHAPTER 6. GENERAL CONCLUSION

6.1. Results overview

The data (Table 6.1) mostly match the predictions about habitat-driven differences in crocodilian signaling (Chapter 1.3). The predicted differences are seen even between very closely related species inhabiting different habitats (see Chapter 2 for details).

Table 6.1. Use of advertizing signal components by crocodilians: comparison of study results with predictions. Numbers in parenthesis correspond to predictions and relevant results in Chapter 6.1. Results in italics do not match the predictions.

signal component		species inhabiting aquatic habitats:				
		mostly fragmented	mostly continuous	highly variable		
				in the species' range	in areas with one habitat type	
					fragmented	continuous
head oblique tail arched posture	prediction	often				
	result	often (1)				
infrasound	prediction	often				
	result	often, except in Indian gharial (1)				
slap	prediction	rarely or never	often	at least sometimes in some areas	less often	more often
	result	never (2.2)	often (2.3)	at least sometimes in some areas (2.1)	rarely (alligators) *often* (crocodiles) (3)	often (3)
vocal	prediction	often	rarely or never	at least sometimes in some areas	more often	less often
	result	often (2.2)	rarely (2.3)	at least sometimes in some areas (2.1)	often (3)	*often* (alligators) rarely (crocodiles) (3)

Prediction 1. Infrasound and head oblique tail arched (HOTA) posture are used by animals in all habitats, with a possible exception of small species that might be physically incapable of producing infrasound.

Result 1. The data match the prediction. In most species (n=23), advertisement calls (ACs) by male crocodilians are virtually always produced in HOTA posture and include infrasound. The only known exception is the Indian gharial (*Gavialis gangheticus*), which has a very different signaling system. Even very small species – the Chinese alligator (*Alligator sinensis*), spectacled caimans (*Caiman crocodylus*) of Tobago population, dwarf caimans (*Paleosuchus*), dwarf crocodiles (*Osteolaemus*) and the Australian freshwater crocodile (*Crocodylus johnstoni*) – vibrate during ACs, although it is unknown if any infrasound is actually produced.

Prediction 2.1. Those species inhabiting a wide range of habitats use both vocal sounds and slaps.

Result 2.1. The data match the prediction. All species inhabiting a wide range of habitats (n=14) frequently use both vocal sounds and slaps, at least at some locations.

Prediction 2.2. Those species living predominantly in fragmented aquatic habitat (i.e. habitat in which headslap-infrasound signals cannot spread further through the water than vocal sounds can spread through the air) use vocal sounds, but few, if any, slaps.

Result 2.2. The data match the prediction. All species inhabiting predominantly fragmented aquatic habitats (n=5) use vocal sounds, but few or no slaps.

Prediction 2.3. Those species living predominantly in continuous aquatic habitat use slaps, but few, if any, vocal sounds.

Result 2.3. The data match the prediction. All species inhabiting predominantly continuous aquatic habitat (n=4) use slaps, but rarely or never use vocal sounds.

Prediction 3. In species inhabiting a wide range of habitats, animals living in areas with only continuous aquatic habitat use slaps more often, and vocal sounds less often, than animals living in areas with fragmented aquatic habitat.

Result 3. The data mostly match the prediction. In two species inhabiting wide range of habitats – the American alligator (*A. mississippiensis*) and the Nile crocodile (*Crocodylus niloticus*) – AC composition differs between animals living at sites with only continuous aquatic habitats and at sites with only fragmented aquatic habitats. However, not all predicted differences were observed (see Chapter 3 for details).

So, in general, crocodilians living in fragmented aquatic habitats differ in composition of their ACs from those living in continuous aquatic habitats. But is it because individual animals change their behavior in response to habitat structure? To answer this question, two more studies were conducted.

Result 4. In my study of yacare caimans (*Caiman yacare*) I found that they do not change the proportion of slaps in ACs immediately after a change in the continuity of aquatic habitat (see Chapter 4 for details).

Result 5. In both American alligators and Nile crocodiles inhabiting areas with a mix of continuous and fragmented aquatic habitats, animals inhabiting small ponds and large lakes did not differ in their signaling behavior (see Chapter 5 for details).

Therefore, the AC composition in crocodilians depends on habitat in the way predicted, but not due to changes in behavior of individual animals in response to habitat structure.

6.2. General discussion

The observed differences between species and between allopatric populations match the predictions (Chapter 1.3) about the role of habitat in their evolution. These predictions were based on the assumption that vocal sounds and slaps are used for long-distance advertising of the animal's position and status. Since most predictions are matched by the results of the present study, this assumption appears to be correct. However, in two cases the results do not fully match the predictions (Table 6.1). American alligators use bellows in all aquatic habitats, including continuous ones, and Nile crocodiles use headslaps in all aquatic habitats, including fragmented ones. Such discrepancies suggest that these signal components might have additional functions not shared with other signal components, and thus cannot be eliminated from the repertoire (see Chapters 3.3.4 and 3.3.5).

Individual crocodilians were found to maintain constant repertoires irrespective of habitat characteristics. Therefore the observed differences in signaling between species and populations probably evolved over time and do not reflect changes in behavior by individual animals.

The present study did not aim to estimate the time necessary for the evolution of these differences in signaling behavior, so relevant evidence was obtained only in one instance. The population of the saltwater crocodile (*C. porosus*) in Tolire Besar, a small crater lake in Indonesia, does not appear to differ from other populations in its signaling behavior (see Chapter 2.3.3) despite having been isolated from continuous aquatic habitat for more than 200 years (Gogarten 1918). Sample sizes obtained for saltwater crocodiles were too small to permit a statistical analysis of significance, but a more detailed study of this and other populations for which the length of time of isolation is known could provide data for estimating the rate of evolution of differences in signaling behavior.

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). 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.

The Indian gharial 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 (see Chapter 2.3.3). This system is probably an ancient adaptation to living only in continuous aquatic habitat and has evolved separately from the signaling of all other crocodilians.

The systematic position of the false gharial (*Tomistoma schlegeli*) is still a subject of controversy, with some data suggesting it has a common ancestry with the Indian gharial, but other data supporting the idea that it is an aberrant crocodile (Tarsitano et al. 1989; Brochu 2003; Janke et al. 2005; Piras et al. 2010). The results of the present study strongly support the second hypothesis, as the signaling system of the false gharial has nothing in common with that of the Indian gharial. Instead, the false gharial uses headslaps, infrasound, and HOTA posture, just like most other crocodilians, although unlike most other crocodilians, it makes no loud vocal sounds. Two evolutionary scenarios could lead to such a repertoire: either the vocal sounds were lost after false gharials had diverged from other crocodilians, 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 false gharial lineage. The first scenario (Fig. 6.1) seems more likely, because the false gharial is believed to have a recent (post-split) marine ancestor (Taplin & Grigg 1989).

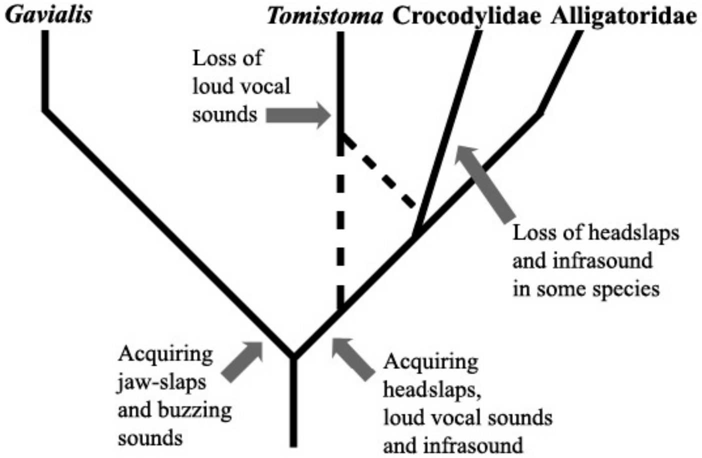


Figure 6.1. Possible sequence of events in the evolution of crocodilian signaling.

When did infrasound become a component of crocodilian signaling? It is used by all extant species except one, and is probably a limiting factor in the evolution of small size in extant crocodilians (Chapter 2.3.4). There are some very small fossil crocodilians, but the so-called "crown group", which includes all extant species (Brochu 2003) is conspicuously lacking such forms (Darren Naish pers. comm.). So it is likely that the use of infrasound as 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.

ADDENDUM 1. TESTING UNDERWATER SOUND LOCATING ABILITY IN CROCODILIANS

To determine if crocodilians show a directionally biased response to water-borne sounds, two experiments on American alligators were conducted.

A1.1. Experiments in canals

A1.1.1. Methods

The tests (n=30) were conducted during May 20-31, 2008, in artificial flood control canals in the Everglades, Florida, on sunny or partly cloudy days with air temperatures 24-28^{o}C. Three canals (two running east-west, 2-4 m wide, and one north-south, 10-12 m wide) were used. All tests were conducted in early morning, when most alligators were partially submerged and showed little overall activity.

Three observers moved upwind along a canal, testing animals or groups of no more than three, with at least 250 m between focal groups or solitary animals. Animals smaller than 1.5 m were ignored. While observer A was watching the animals from the closest point on the bank of the canal (Fig. A1.1.a), observers B and C positioned themselves neck-deep in the water (so that the animals could not see their movements) approximately 40 m from the animals, upwind and downwind along the canal.

Two minutes later, either observer B or observer C (in alternating order) produced a single sound underwater. In order to produce water-borne sounds with minimal airborne component, a small diving bell (a metal bucket weighted down with diving belts) was used. After submerging the bell, the water surface inside it was slapped with a plastic pad to produce a sound similar to an alligator headslap. The sound made underwater could not be heard by an above-water human observer at more than 3 m. Alligator hearing in audible frequencies is roughly as sensitive as human hearing (Beach 1944; Higgs et al. 2002), so at the distance of 30-50 m the animals could only hear the water-borne sound.

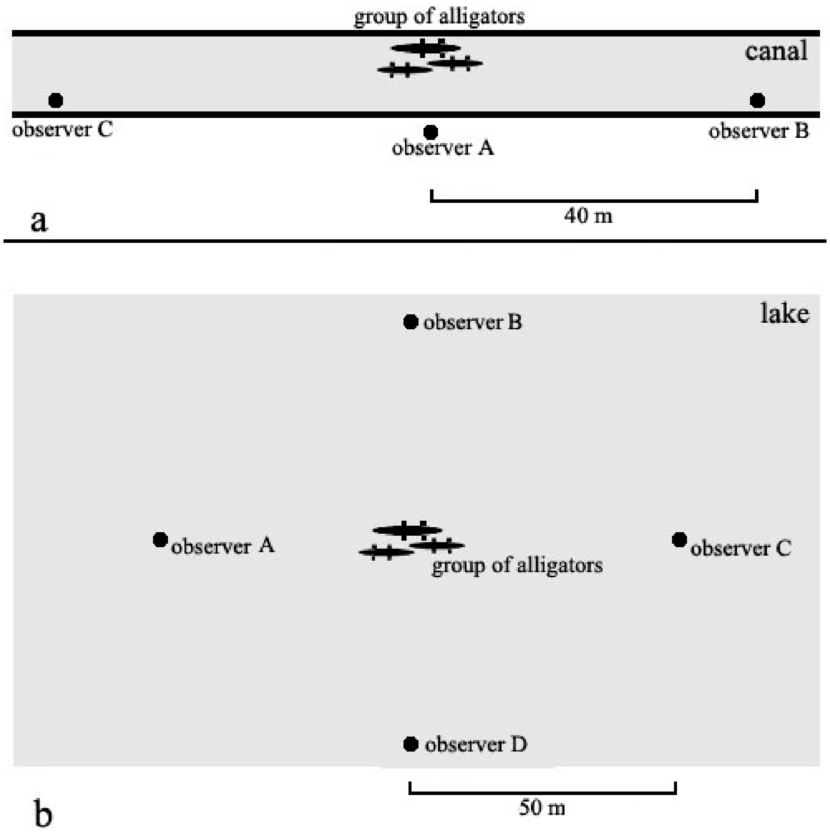


Figure A1.1. Setups used in sound source locating experiments. **a.** Setup used in canals. Sound was produced underwater by observer B or C in alternating order. **b.** Setup used in large lakes. Sound was produced by one of the observers, with compass directions used in consecutive order. Scale is approximate.

Movements of animals in the 1-minute periods before and after the slap were recorded; the before period was used as baseline. Movement was recorded as “1” if at least one animal in a group moved more than a body length in one direction. If the direction changed later, only the initial direction was recorded. If more than one animal in a group moved, only the movement of the first animal was counted. Movements within a

180^{o} arc of the direction towards the sound were then scored as movements towards the sound; all others – as movements away from sound. McNemar test (Markman 1978) was used to find if there was a significant change in the number of movements after the signal. The Binomial test was used to find if the proportion of movements towards the signal was significantly greater than expected by chance (½).

A1.1.2. Results

In 29 tests out of 30, the alligators were immobile during the 1-minute period before the sound. In 16 tests (11 out of 20 in canals running east-west, 5 out of 10 in a wider canal running north-south), at least one animal started swimming towards the source of the sound along the canal, and moved more than a body length. No movements away from the sound were observed. The number of animals that moved was significantly higher after the signal than before it ($p<0.001$ in McNemar test). The proportion of animals that moved towards the signal was significantly higher than expected by chance ($p<0.0001$ in Binomial Test).

A1.2. Experiments in large lakes

A1.2.1. Methods

A different set of tests ($n=27$) was performed in three large (larger than 1 km^2) lakes where animals could move in all directions. These tests were conducted in Savannah National Wildlife Refuge, Georgia and South Carolina, on June 3-10, 2008 ($n=12$) and April 24-May 9, 2009 ($n=9$), and at Lake Okeechobee, Florida, on April 01-03, 2010 ($n=6$). Tests were conducted in early morning, on sunny or partly cloudy days with air temperatures 20-26^{o}C.

Four observers in small boats moved across shallow portions of lakes 100-200 m from shore, testing animals in groups of 1-3, separated by at least 250 m. Animals smaller than 1.5 m were ignored. When a group was located, the observers positioned themselves in compass directions around it (Fig. A1.b), at a distance of approximately 50 m from it (estimated visually). One observer (compass directions used in consecutive order) submerged the diving bell, and two minutes later produced a single sharp slap inside it.

Movements of animals were recorded and analyzed in the same way as in the previous experiment, but the Binomial Test was performed with movements within a 90^o arc of the direction towards the sound counted as +, all other movements as –, and the expected ratio of 1:3.

A1.2.2. Results

In 25 out of 27 tests, the alligators were immobile during the 1-minute period before the sound. The number of animals that moved after the signal was 12 ($p<0.007$ in McNemar test). In 10 tests, at least one animal started swimming towards the source of the sound, and moved more than a body length. Animals that moved in other directions were observed twice. The proportion of animals that moved towards the signal was significantly higher than expected by chance ($p<0.004$ in Binomial Test).

A1.3. Conclusion

The experiments have shown that American alligators have a directionally biased response to water-borne sounds, which means they are capable of locating the source of a signal transmitted through the water. This ability must be important for them, as wild American alligators spend more than 30% of time submerged (James C. Nifong in prep.).

ADDENDUM 2. TESTING UNDERWATER TRANSMISSION OF CROCODILIAN SIGNALS

In order to obtain a rough estimate of the ability of crocodilian sound signals to transmit information underwater, sound recordings were obtained using Sony TCD-D8 digital audiotape recorder and Cannon XLR-3-50 microphone with Cannon XLR-3-11C connector cable. This recorder was chosen for its ability to record frequencies as low as approximately 5Hz (pers. comm. by Liz von Muggenthaler, president of Fauna Communication Research Institute). For underwater recordings, non-lubricated latex condoms were used to waterproof the microphone; they were stretched almost to the breaking point to minimize distortion, known to be significant if unstretched condoms are used (Liz von Muggenthaler pers. comm.). Microphone sensitivity was always set to Normal recording mode, recording level to 10, and sampling frequency to 44.1 kHz. Raven Light 1.0. software by Cornell Lab of Ornithology was used to generate spectrograms of recorded sounds.

A2.1. Headslaps.

Headslap tests were conducted in American alligator (*Alligator mississippiensis*) habitat in irrigation canals along Tamiami Trail Highway in southern Florida in April 2008. Imitation headslaps were produced using a Sevylor U142RED-00-000 plastic kayak paddle with aluminum shaft. Such imitations sounded identical to alligator headslaps to a human observer, and elicited approach from most adult alligators within 100 m distance. Tests were conducted in two canals: one 5 m wide and 2 m deep, with bottom vegetation about 0.5 m tall; the other 2 m wide and 50-75 cm deep, with bottom vegetation rising to the surface and large amounts of fallen tree branches in the water. Both canals had mud bottoms.

Spectrograms of recordings made above the water showed sharp onset and ending of headslap sounds at both 10 m (Fig. 2A.1.a) and 200 m (Fig. 2A.1.b) distance from the source. A spectrogram made at 500 m shows no sign of the sound (not illustrated); the sound was not audible to a human observer at such distance. Spectrograms of recordings made underwater show sharp onset and ending of headslap sounds at 10 m (Fig. 2A.1.c) and 200 m (Fig. 2A.1.d) in both canals. At 500 m, the spectrogram of recording made in the larger canal still shows sharp onset of the sound (Fig. 2A.1.e), but the spectrogram of recording made in the smaller canal does not (Fig. 2A.1.f).

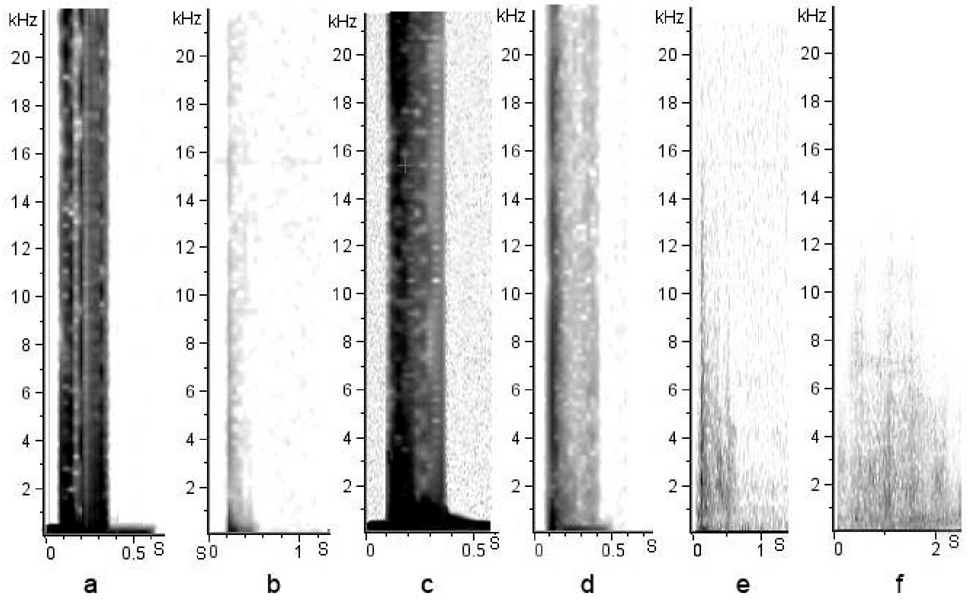


Figure A2.1. Spectrograms of slaps made on the surface of the water. (a) recorded in the air 10 m from the source; (b) recorded in the air 200 m from the source; (c) recorded underwater 10 m from the source in canal #2; (d) recorded underwater 200 m from the source in canal #2; (e) recorded underwater 500 m from the source in canal #1; (f) recorded underwater 500 m from the source in canal #2. Canal #1 was 5 m wide and 2 m deep, with bottom vegetation about 0.5 m tall; canal #2 was 2 m wide and 50-75 cm deep, with vegetation rising to the surface and large amounts of fallen tree branches.

These recordings show that headslaps can spread and carry information about the location of the source for hundreds of meters underwater, but their shape is changed in narrow, shallow channels with lots of obstructions. As travel in a direct line becomes impossible for sound waves, and more sound energy is transmitted by indirect routes, the sound loses its sharp onset and ending. For this reason, small forest streams and shallow forest swamps should be classified as fragmented aquatic habitats for the purpose of the present study.

A2.2. Bellows.

Bellows by two American alligators (known to be a male and a female, as mating had been observed) were recorded underwater at a distance of approximately 25 m at Chekika Lake (approximately 500 m^2 in size and more than 1 m deep) in Everglades National Park, Florida, in April 2010. The 3 m long male produced a bout of five bellows, each preceded with body vibration and "water dance" indicative of infrasound production (Garrick et al. 1978). The female produced one bellow with no indication of infrasound production just before the last bellow by the male. The spectrogram showed infrasound and low-frequency sounds produced by body vibrations immediately before the male bellows, but no male or female bellows.

Thus, bellows could not be recorded underwater at a distance of only 25 m, while the same equipment was able to record headslaps underwater at 500 m (see A2.1). This result indicates that bellows have very limited, if any, capability of spreading and carrying information underwater compared to headslaps.

ADDENDUM 3. MISCELLANEOUS NOTES ON SIGNALING IN CROCODILIANS

In the course of the present study, novel data on signaling were obtained for a few species of crocodilians. See Chapters 2-5 for methods, localities, time, numbers and durations of observations. Below is a summary of previously unpublished information that has not been included in previous chapters.

A3.1. The American alligator

During four nonconsecutive days of observing two large groups of captive American alligators (*Alligator mississippiensis*) at San Augustine Alligator Farm Zoo (USA) in April-May of 2008 and 2010, it was noted that on three days all animals longer than 1 m participated in numerous bellowing choruses, while only one animal produced a headslap. However, on the fourth day numerous headslapping displays were produced, but no bellows were observed. Such temporal separation of bellowing and headslapping displays has never been observed in the wild or described in available literature.

A3.2. The black caiman

The black caiman (*Caiman niger*) produces roaring and headslapping displays similar to those of yacare caiman (*C. yacare*, Peter Taylor pers. comm.). During the present study, observations of five individuals (three in Guyana, one in Ecuador and one in captivity in Florida) were obtained. All signaling in the wild was observed at night (from 1 hour after sunset until 20 min before sunrise); the captive caiman signaled during the first hour after sunrise (nighttime observations of this individual could not be performed). Black caiman roars are much louder than roars of yacare and broad-snouted caimans, and resemble American crocodile roars (see below) to a human observer. Body vibrations indicative of infrasound production accompanied all displays. Unlike all other crocodilians observed in the present study, signaling black caiman holds its head horizontally rather than with snout pointing upwards (Fig. A3.1).

Figure A3.1. Roaring black caiman (*Caiman niger*), St. Augustine Alligator Farm Zoo Park, Florida.

A3.3. The American crocodile

In the present study, signaling (Fig. A3.2.a) by American crocodiles (*Crocodylus acutus*) was found to be similar in many parts of their range, except that roars were much less common than headslaps in some areas, but only somewhat less common in others (see Chapter 2).

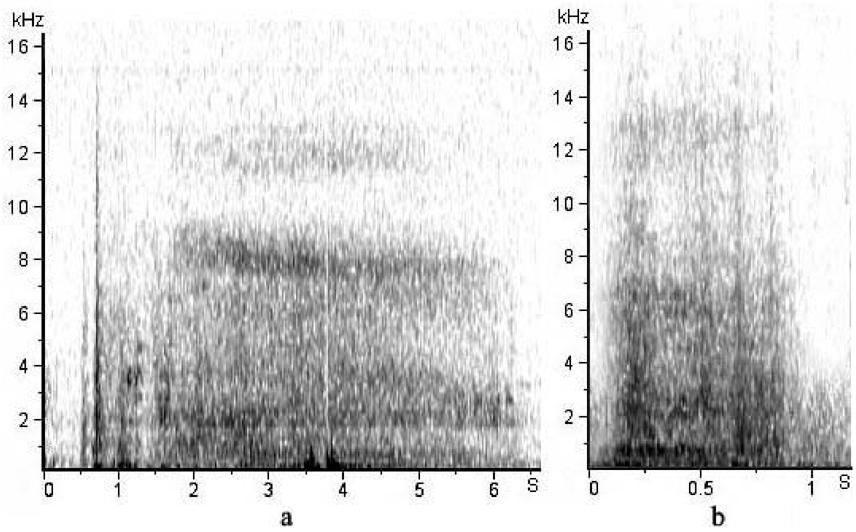


Figure A3.2. Spectrograms of crocodile signals: a) headslap and roar by an American crocodile (*Crocodylus acutus*), recorded in Everglades National Park, Florida, USA; b) roar by a mugger crocodile (*C. palustris*), recorded at Madras Crocodile Bank, Tamil Nadu, India. Roars by both species vary in length from less than 1 to 5 seconds.

As in all other Neotropic crocodiles, roars and headslaps were produced 1-4 hours after sunrise, and were not observed after the animals left the water to bask. On one exceptionally cold morning in Everglades National Park (USA), when the air temperature at sunrise was only 12°C, a 3 m long male was observed to bask onshore for one hour, return to the water for 25 min, produce a headslap, then bask onshore for another hour, again return to the water and after 12 min produce a roar. Both the headslap and the roar were accompanied with infrasound and were produced in head oblique tail arched (HOTA) posture (Garrick & Lang 1977). A 2.5 m long female was present 30 m from the male, but not in his line of sight. She ignored the headslap, but immediately approached the male after the roar, and initiated courtship behavior (snout- and chin-touching). The male and the female then basked onshore side by side for at least five more hours. It is possible that the female ignored the headslap because at that time a large number of brown pelicans (*Pelecanus occidentalis*) were fishing in that area and produced loud splashes more than once per minute.

A3.4. The Cuban crocodile

A captive 2.2 m long male Cuban crocodile (*C. rhombifer*) in Zoo Miami produced roars (only one of them followed by a headslap) and body vibrations indicative of brief infrasound production in HOTA posture. Some of these displays were immediately followed by approaches and courtship behavior by the 1.7 m long female living in the same enclosure. Courtship by the female was sometimes followed by mutual courtship behavior and mating. The courtship behavior included not only snout- and chin-touching, but also rides around the pool by the female on the back of the male, which were observed on four occasions and lasted up to a minute (Fig. A3.3). On one rainy day (when the water temperature was probably lower than usual) the male produced four roars on land. Lengths of these two animals were known from measurements by zoo personnel.

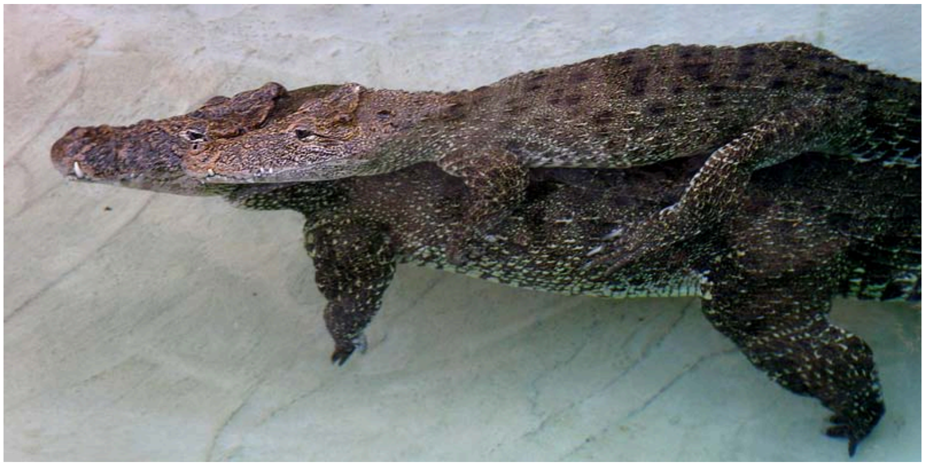


Figure A3.3. Female Cuban crocodile (*C. rhombifer*) riding on the male's back during courtship. Zoo Miami, Florida.

Two 2 m long captive males observed at other locations in Florida produced roars accompanied by body vibrations in HOTA posture, but no headslaps. No responses from females (present in both cases) were observed.

All described activity took place between two and four hours after sunrise.

A3.5. The mugger crocodile

Mugger crocodiles (*C. palustris*) produce signals similar to those of Nile crocodiles, but their roars (Fig. A3.2.b) are louder (audible to a human observer at more than 2 km under ideal conditions). Roars are apparently used more frequently than headslaps (unlike in the Nile crocodile). Roaring on land was not observed in wild individuals (in 12 days of observation), but a captive male at Madras Crocodile Bank was observed roaring on land (once in one day of observation). Two smaller crocodiles (probably females) immediately approached it and started courtship behavior (chin touching). In most cases, roars and headslaps were produced within one hour before or after sunrise, and before the animals left the water to bask on shore. The only exceptions were the abovementioned roar on land and one roar in the water, produced by a male in Sasan Gir National Park (India) three hours after sunrise, following two hours of basking on the shore on an exceptionally cold morning (minimum air temperature 11^{o}C). Another male at the same location once produced a roar without HOTA posture immediately after (and possibly in response to) a roar by a lion (*Panthera leo*) half an hour before sunrise. Interestingly, roars in response to other animals' sounds were never observed in Nile crocodiles, despite frequent occurrence at some study sites of lion roars, as well as trumpeting calls and belly rumbles accompanying infrasound production (Payne 1998) by African elephants (*Loxodonta africana*).

WORKS CITED

Alcala, A. C., C. A. Ross & E. L. Alcala. 1987. Observations on reproduction and behavior of captive Philippine crocodiles (*Crocodylus mindorensis* Schmidt). *Silliman J.* 34 (1-4): 18-28.

Alvarez del Toro, M. & L. Sigler. 2001. *Los Crocodylia de Mexico*. 1^{a} Edition. IMERNAR, PROFEPA, Mexico, 170 pp.

Barlein, F. 2006. Family Sylviidae (Old World Warblers). In: *Handbook of birds of the world*. Volume 11. del Hoyo, J., A. Elliott, and D. A. Christie (edit.). Lynx Edicions, Barcelona, Spain, pp. 492–578.

Beach, F.A. 1944. Responses of captive alligators to auditory stimulation. *Am. Nat.* 78: 481-505.

Beard, P. & A. Graham. 1990. *Eyelids of Morning*. Chronicle, San Francisco, 260 pp.

Berg, R. E. & D. G. Stork. 2005. *The Physics of Sound*. 3rd edition. Benjamin Cummings, San Francisco, 398 pp.

Bezuijen, M. R., P. Hartoyo, M. Elliot & B. Baker. 1997. *Second Report on the Ecology of the False Gharial* (Tomistoma schlegelii) *in Sumatera*. Wildlife Management International Pty. Ltd. mimeo report, 128 pp.

Bloch, N. & D. Irschick. 2006. An analysis of inter-population divergence in visual display behavior of the green anole lizard (*Anolis carolinensis*). *Ethology* 112: 370-378.

Brazaitis, P. & M. E. Watanabe. 2011. Crocodilian behavior: a window to dinosaur behavior? *Hist. Biol.* 23 (1): 73-90.

Brien, M. L., M. A. Read, H. I. McCallum & G. C. Grigg. 2008. Home range and movements of radio-tracked estuarine crocodiles (*Crocodylus porosus*) within a non-tidal waterhole. *Wildl. Res.* 35 (2): 140-149.

Brochu, A. C. 2003. Phylogenetic approaches towards crocodylian history. *Ann. Rev. Earth and Planetary Sc.* 31: 357-397.

Campos, Z., T. Sanaiotti & W. E. Magnusson. 2010. Maximum size of dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807), in the Amazon and habitats surrounding the Pantanal, Brazil. *Amphibia-Reptilia* 31(3): 439-442.

Cedeno-Vazquez, J. R., D. Rodriguez, S. Calme, J. P. Ross, L. D. Densmore III & J. B. Thorbjarnarson. 2008. Hybridization between *Crocodylus acutus* and *Crocodylus moreletii* in the Yucatan Peninsula: I. evidence from mitochondrial DNA and morphology. *J. Exp. Zool*. 309A: 661–673.

Chabreck, R. H. 1965. The movement of alligators in Louisiana. *Proc. Ann. Conf. of the Southeastern Association of Game and Fish Commissioners.* 19:102-110.

Chen, B. 1990. Preliminary studies of the home range of the Chinese alligator. In: *Crocodiles. Proceedings of the 10th Working Meeting of the Crocodile Specialist Group.* IUCN, Gland, Switzerland. pp. 43-46.

Chen, B. H., T. M. Hua, X. B. Wu & C. L. Wang. 2003. *Research on the Chinese Alligator*. Shanghai Scientific and Technological Education, Shanghai, 252 pp.

Compton, A. W. 1981. Courtship and nesting behavior of the freshwater crocodile (*Crocodylus johnstoni*) under controlled conditions. *Aust. Wild. Res*. 8(2): 443-450.

Cott, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Trans. Zool. Soc. Lond.* 29(4): 211-356.

Crocodile Specialist Group 1996. *Crocodylus siamensis*. In: IUCN 2010. *IUCN Red List of Threatened Species.* Version 2010.1.

Dawkins, M. S. 1993. Are there general principles of signal design? *Phil. Trans. R. Soc.* 340: 251–255.

Densmore, L.D. & P.S. White, 1991. The systematics and evolution of the Crocodilia as suggested by restriction endonuclease analysis of mitochondrial and nuclear ribosomal DNA. *Copeia* 1991: 602-615.

De Smelt, K. 2004. Status of the Nile crocodile in the Sahara Desert. *Hydrobiol.* 391: 81-86.

Desutter-Grandcolas, L. & T.Robillard. 2004. Acoustic evolution in crickets: need for phylogenetic study and a reappraisal of signal effectiveness. *Anais da Acad. Brasileira de Ciências* 76:132-142.

Dinets, V. 2010. Nocturnal behavior of American alligator (*Alligator mississippiensis*) in the wild during the mating season. *Herp. Bull.* 111: 4-11.

Eaton, M. J., A. Martin, J. Thorbjarnarson & G. Amato. 2009. Species-level diversification of African dwarf crocodiles (genus *Osteolaemus*): a geographic and phylogenetic perspective. *Mol. Phylogenet. Evol.* 50 (3): 496-506.

Ellis, T. M. 1980. *Caiman crocodylus*: an established exotic in Southern Florida. *Copeia* 1980 (1): 152-154.

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. *Am. Nat.* 139: 125–153.

Espinosa, E. (rev.). 1998a. *Caiman crocodylus*. In: Ross J. P. (ed.). 1998. *Crocodiles. Status survey and conservation action plan*. 2nd Edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK, pp. 14-17.

Espinosa, E. (rev.). 1998b. *Caiman yacare*. In: Ross J. P. (ed.). 1998. *Crocodiles. Status survey and conservation action plan*. 2nd Edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK., pp. 21-22.

Felsenstein, J. 1983. Parsimony in systematics: biological and statistical issues. *An. Rev. Ecol. Syst*. 14, 313-33.

Ferioli, R. C. 1998. Distribution of *Crocodylus niloticus*. In: A. Britton. 1995-2010. Crocodilians: Natural history and Conservation. *http://www.flmnh.ufl.edu/cnhc/cnhc.html*, accessed February 9, 2011.

Frankenberg, E. & Y.L. Werner. 1992. Vocal communication in the Reptilia: facts and questions. *Acta Zool. Lilloana* 41(0): 45-62.

Gannon, W. L. & T. E. Lawlor. 1989. Variation of the chip vocalization of three species of Townsend chipmunks (genus *Eutamias*). *J. Mamm*. 70: 740-753.

Garnett, S. 1989. *Crocodiles and alligators*. Checkmark Books, New York, 240 pp.

Garrick, L.D. & J.W. Lang. 1977. Social signals and behaviors of adult alligators and crocodiles. *Am. Zool*. 17: 225-239.

Garrick, L.D., J.W. Lang & H.A. Herzog, Jr. 1978. Social signals of adult American alligators. *Bull. Am. Mus. Nat. Hist*. 160: 153-192.

Gogarten E. 1918. *Die Vulkane der Nordlichen Molukken*. Zeit Vulk, 2: 1-298.

Gordon, S.D. & G.W. Uetz. 2011. Multimodal communication of wolf spiders on different substrates: evidence for behavioural plasticity. *Anim. Behav.* 81: 367-365.

Gorzula, S. & A.E. Seijas. 1989. The common caiman. In: *Crocodiles; their ecology, management and conservation. Special publication of the Crocodile Specialist Group of the Species Survival Commission of the International Union for the Conservation of Nature and Natural Resources* (edit. P. Hall), IUCN Publication New Series. pp. 308: 44-61.

Grenard, S. 1991. *Handbook of alligators and crocodiles*. Kruger Publishing Co., Malabar, Florida, 210 pp.

Hall, P. & D. R. Johnson. 1987. Nesting biology of *Crocodylus novaeguineae* in Lake Murray District, Papua New Guinea. *Herpetologica* 43: 249-258.

Higgs, D. M., E. F. Brittan-Powell, D. Soarez, M. J. Sousa, C. E. Carr, R. J. Dooling & A. N. Popper. 2002. Amphibious auditory responses of the American alligator (*Alligator mississippiensis*). *J. of Comp. Physiol.* A. 188: 217-223.

Hopp, S. L., M. J. Owren & C. S. Evans. 1998. *Animal Acoustic Communication: Sound Analysis and Research Methods*. Springer, Berlin & New York, 421 pp.

Hutton, J. M. 1989. Movement, home range, dispersal and separation of size classes in Nile crocodiles. *Am. Zool.* 29(3): 1033-1050.

Janke, A., A. Gullberg, S. Hughes, R. K. Aggrawal & U. Arnason. 2005. Mitogenomic analyses place the gharial (*Gavialis gangeticus*) on the crocodile tree and provide pre-K/T divergence times for most crocodilians. *J. Mol. Evol.* 61: 620-626.

Kipling, R. 1895. *The Second Jungle Book*. Macmillan & Co., London, 212 pp.

Kofron, C. P. 1991. Courtship and mating of the Nile crocodile. *Amphibia-Reptilia* 12: 39-48.

Kofron, C. P. 1992. Status and habitats of the three African crocodiles in Liberia. *J. Trop. Ecol.* 8: 265-273.

Kofron, C. P. & C. Steiner. 1994. Observations on the African Dwarf Crocodile, *Osteolaemus tetraspis*. *Copeia* 1994(2): 533-535.

Lang, J. W. 1975. The Florida crocodile: Will it survive? *Chicago (Field) Mus. Nat. Hist. Bull.* 46: 4-9.

Markman, E. M. 1978. Empirical vs. logical solutions to part-whole comparison problems concerning classes and collections. *Child Development* 49: 168-177.

McClain, M. E. 2002. *The Ecohydrology of South American Rivers and Wetlands.* International Association of Hydrological Sciences, USA, 210 pp.

McCoy, J. K., T. A. Baird & S. F. Fox. 2003. Sexual selection, social behavior and the environmental potential for polygyny. In: Fox, S. F., J. K. McCoy & T. A. Baird, eds. *Lizard Social Behavior.* The John Hopkins Univ. Press, Baltimore, pp. 149-171.

McIllheny, E. A. 1935. *The Alligator's Life History*. The Christopher Publishing House, Boston, 168 pp.

Medem, F. 1981. *Los Crocodylia de Sur America Vol. I*. Colciensias, Bogota, 354 pp.

Medem, F. 1983. *Los Crocodylia de Sur America Vol. II*. Colciensias, Bogota, 270 pp.

Messel, H. & G. C. Vorlicek. 1989. Ecology of *Crocodylus porosus* in northern Australia. In: *Crocodiles: Their Ecology, Management and Conservation*. IUCN, Gland, Switzerland, pp. 164-183.

Modha, M. L. 1967. The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *E. Afr. Wildl. J.* 5: 74-95.

Moulton, T. P. 1993. O programa sobre ecologia do Jacarféde-Papa-Amarelo (*Caiman latirostris*) no CEPARNIC, Ilha do Cardoso, São Paulo, Brasil. In: Verdade, L. M. (ed.), I. Packer, M. Rocha, F. Molina, P. Duarte & L.A.B.M. Lula. *Anais do III Workshop sobre Conservação e Manejo de Jacaréde-Papo-Amarelo (*Caiman latirostris*)*. ESALQ, Piracicaba, Brazil, pp. 133-134.

Morea, C. R., K. G. Rice, H. F. Percival, & S. R. Howarter. 2002. Home range and daily movement of the American alligator in the Everglades. In: *Crocodiles. Proceedings of the Working Meeting of the Crocodile Specialist Group.* IUCN, 15: 486-504.

Narins, P. M., A. S. Feng, R. R. Fay & A. N. Popper. 2006. *Hearing and Sound Communication in Amphibians*. Springer, New York, 362 pp.

Neill, W. T. 1971. *The Last of the Ruling Reptiles. Alligators, Crocodiles and their Kin*. Columbia University Press, New York and London, 468 pp.

Oaks, J. R. 2007. Phylogenetic systematics, biogeography and evolutionary ecology of the true crocodiles (Eusuchia: Crocodylidae: *Crocodylus*). M. S. thesis, Louisiana State University.

Ord, T. J., R. A. Peters, B. Clucas & J. A. Stamps. 2007. Lizards speed up visual displays in noisy motion habitats. *Proc. R. Soc. B.* 274: 1057-1062.

Payne, K. 1998. *Silent Thunder*. Simon & Schuster Inc., New York, 288 pp.

Percival, H. F., S. R. Howarter, K. G. Rice, C. R. Morea, C. L. Abercrombie, K. Portier & A. G. Finger. 2000. *Thermoregulation of the American Alligator in the Everglades*. Poster presented at the Greater Everglades Ecosystem Restoration Conference. *http://sofia.usgs.gov/geer/2000/posters/thermoreg_gator/*, accessed February 9, 2011.

Piras, P., P. Colangelo, D. C. Adams, A. Buscalioni, J. Cubo, T. Kotsakis, C. Meloro & P. Raia. 2010. The *Gavialis-Tomistoma* debate: the contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships. *Evol. & Development* 12(6): 568-579.

Pooley, A. C. 1982. The status of African crocodiles in 1980. In: *Crocodiles. Proceedings of the 5th Working Meeting of the IUCN/SSC Crocodile Specialist Group, Gainesville, Florida.* IUCN, Gland, Switzerland, pp. 174-228.

Pooley, T. 1982. *Discoveries of a Crocodile Man*. W. Collins Sons & Co. Ltd., Johannesburg, 213 pp.

Pooley, A. C. & C. Gans. 1976. The Nile crocodile. *Sci. Am*. 234: 114-124.

Riley, J. & F. W. Huchzermeyer. 1999. African dwarf crocodiles in the Likouala swamp forests of the Congo Basin: habitat, density and nesting. *Copeia* 1999(2): 313-320.

Ross, C. A. 1982. *Smithsonian Institution/World Wildlife Fund Philippine Crocodile Project*. Final Report WWF #1489. 34 pp.

Ross, J. P. (ed.). 1998. *Alligator mississippiensis*. In: *Crocodiles. Status survey and conservation action plan*. 2nd Edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK, pp. 10-11.

Scott Jr., N. J., A. Aquino & L. A. Fitzgerals. 1990. Distribution, habitats and conservation of the caiman (Alligatoridae) of Paraguay. *Vida Silvestre Neotropical* 2: 43-51.

Senter, P. 2008. Homology between and antiquity of stereotyped communicatory behaviors in Crocodilians. *J. Herp.* 42(2): 354-360.

Schmitz, A., P. Mansfield, E. Hekkala, T. Shine, H. Nickel, G. Amato & W. Böhme. 2003. Molecular evidence for species level divergence in African Nile crocodiles *Crocodylus niloticus* (Laurenti, 1786). *Comptes Rendus Palevol* 2(8): 703-712.

Shirley, M. H. 2010. Slender-snouted Crocodile *Crocodylus cataphractus.* In: *Crocodiles. Status Survey and Conservation Action Plan*. 3rd Edition. Crocodile Specialist Group, Darwin, pp. 74-78.

Singh, L.A.K. & R. J. Rao. 1990. Territorial behavior of male gharial *Gavialis gangeticus* in the National Chambal Sanctuary, India. *J. Bomb. Nat. Hist. Soc.* 87(1): 149-151.

Slabbekoorn, H. & M. Peet. 2003. Birds sing at a higher pitch in urban noise. *Nature* 424: 267.

Smith, L. A. 1919. *Crocodylus siamensis*. *J. Nat. Hist. Soc. Siam* 3: 217-222

Solmu, G. C. 1994. Status of *Crocodylus porosus* and *Crocodylus novaeguineae* populations in Papua New Guinea, 1981-1994. In: *Crocodiles. Proceedings of the 12th Working Meeting of the Crocodile Specialist Group.* IUCN, Gland, Switzerland, pp. 77-102.

Steel, R. 1989. *Crocodiles*. Christopher Helm Ltd., Kent, UK, 198 pp.

Taplin, L. E. & G. C. Grigg. 1989. Historical zoogeography of the Eusuchian crocodilians: a physiological perspective. *Am. Zool*. 29(3): 885-901.

Tarsitano F. E., E. Frey & J. Riess. 1989. The evolution of the Crocodylia: a conflict between morphological and biochemical data. *Am. Zool*. 29(3): 843-856.

Thorbjarnarson, J. B. (rev.). 1998. *Melanosuchus niger*. In: Ross J. P. (ed.). 1998. *Crocodiles. Status survey and conservation action plan*. 2nd Edition. IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland, pp. 23-28.

Thorbjarnarson, J. B. & R. Franz. 1987. Orinoco crocodile. In: *Catalog of American Amphibians and Reptiles.* 406.1-406.2. Society for the Study of Amphibians and Reptiles, pp. 26-34.

Thorbjarnarson, J. B. & G. Hernandez. 1993. Reproductive ecology of the Orinoco crocodile (*Crocodylus intermedius*) in Venezuela. II. Reproductive and social behavior. *J. Herp.* 27(4): 371-379.

Thorbjarnarson, J. B. & X. Wang. 2010. *The Chinese Alligator. Ecology, Behavior, Conservation and Culture*. J. Hopkins University Press, Baltimore, 265 pp.

Todd, N. 2007. Evidence for near-field hearing in crocodilian vocal communication: Intensity of the American alligator vocal display. Online publication by MARCSAL, *http://marcs.uws.edu.au/events/mmm/archive/2005/050606.htm*, accessed January 19, 2001.

Trutnau, L. & R. Sommerland. 2006. *Crocodilians: Their Natural History & Captive Husbandry*. Edition Chimaira, Frankfurt am Main, 648 pp.

Van Hoven, W. Nile Crocodiles in Flag Boshielo Lake. *http://www.t4cd.org/Resources/ICT_Resources/Projects/Pages/ICTProject_251.aspx*, accessed January 27, 2010.

Varona, L. S. 1966. Notas sobre los crocodilidos de Cuba y una descripcion de una nueva especie del Pleistoceno. *Poyeana* 16: 1-34.

Venega-Anaya, M., O. Sanjur, A. Escobedo & E. Bermingham. 2007. Phylogeny and systematics of *Crocodylus acutus*. In: *Materials of the Third International Workshop on Crocodilian Genetics and Genomics*. The Smithsonian Institute, USA, pp. 22-28.

Vliet, K. A. 2001. Courtship behavior of American alligators *Alligator mississippiensis*. In: G. C. Grigg, F. Seebacher & C. E. Franklin (eds.). *Crocodilian Biology and Evolution*. Surrey Beatty & Sons, Sydney, pp. 383-408.

Vliet, K. A. 1989. Social displays of the American alligator. *Am. Zool.* 29(3): 1019-1031.

Wang, X. Y., C. L. Wang, D. Wang, R. P. Wang & X. Wu. 2006. Congregative effect of the Chinese alligator's bellowing chorus in mating season and its function in reproduction. *Acta Zool. Sinica* 52: 663-668.

Wang, X. Y., C. L. Wang, D. Wang, R. P. Wang & X. Wu. 2007. Acoustic signals of Chinese alligators (*Alligator sinensis*): Social communication. *J. Acoust. Soc. Am.* 121 (5): 2984-2989.

Waitkuwait, W. E. 1989. Present knowledge on the West African slender-snouted crocodile, *Crocodylus cataphractus* Cuvier 1824 and the West African dwarf crocodile, *Osteolaemus tetraspis* Cope 1861. In: *Crocodiles. Their ecology, management and conservation*. IUCN, Gland, Switzerland, pp. 259-275.

Webb, G. J. W., R. Buckworth & S. C. Manolis. 1983. *Crocodylus johnstoni* in the McKinlay River Area, N. T. III. Growth, movement and the population age structure. *Aus. Wildl. Res.* 10: 383-401.

Webb, G. J. W. & H. Messel. 1978. Movement and dispersal patterns of *Crocodylus porosus* in some rivers of Arnhem Land, Northern Australia. *Aust. Wild. Res.* 5: 263-283.

Webb, G. J. W. & S. C. Manolis. 1998. *Crocodiles of Australia*. Reed New Holland, Sydney, 160 pp.

Weldon, P. J. & J. W. Wheeler. 2001. The chemistry of crocodilian skin glands. In: G. C. Grigg, F. Seebacher & C. E. Franklin (eds.). *Crocodilian Biology and Evolution*. Surrey Beatty & Sons, Sydney, pp. 286-296.

Wells, K.D. 1977. The social behavior of anuran amphibians. *Anim. Behav.* 25: 666-693.

Wermuth, H. 1989. Wie, wann und warum brüllen Krokodile? *D. Aquar.-Terr. Zeitsch.* 42: 553-555.

Whitaker, R. & D. Basu. 1982. The gharial (*Gavialis gangeticus*): a review. *J. Bomb. Nat. Hist. Soc.* 79(3): 531-548.

Whitaker, R. & Z. Whitaker. 1984. Reproductive biology of the mugger (*Crocodylus palustris*). *J. Bomb. Nat. Hist. Soc.* 81: 297-317.