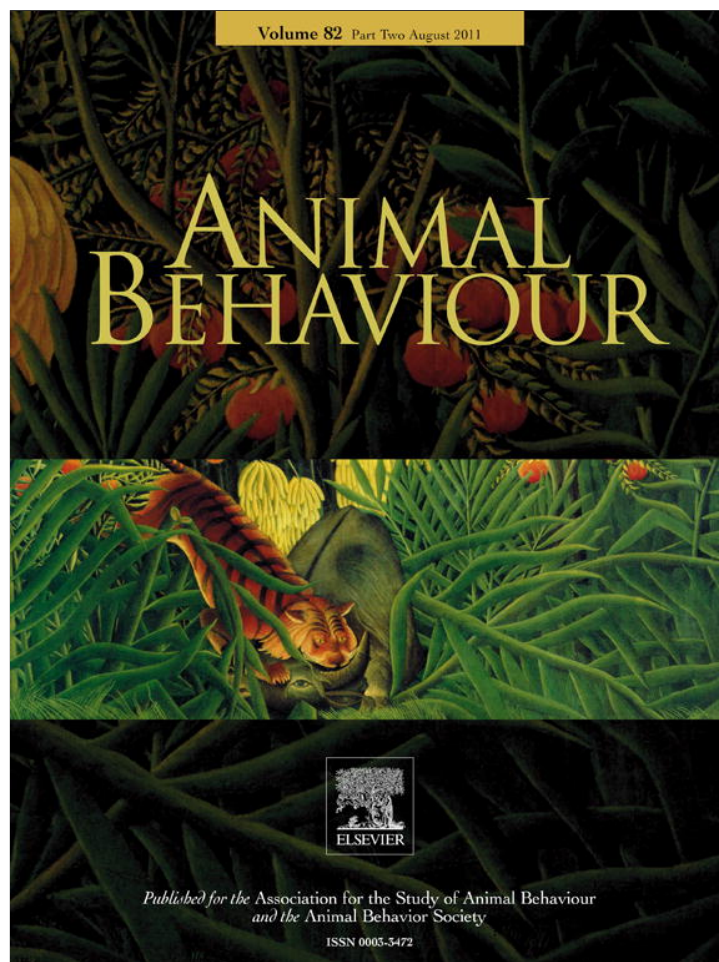


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## Effects of aquatic habitat continuity on signal composition in crocodylians

Vladimir Dinets\*

Department of Biology, University of Miami, Coral Gables, FL, U.S.A.

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All crocodylians use long-distance signals, composed of vocal sounds, head slaps or jaw slaps and infrasound in various combinations. These signal components differ in their ability to carry information about the animal's location and status through air and water. It can be predicted that animals living in fragmented aquatic habitats should predominantly use vocal sounds combined with infrasound, while those living in continuous aquatic habitats should predominantly use head slaps combined with infrasound. To test this prediction, I sampled signals of adult male American alligators, *Alligator mississippiensis*, and Nile crocodiles, *Crocodylus niloticus*, in geographical areas where each species inhabited only one type of habitat during the mating season. I found that American alligators used head slaps more often in areas with continuous aquatic habitat, but they bellowed frequently in all habitats. Nile crocodiles frequently used head slaps in all habitats, but they roared more often in fragmented aquatic habitats, whereas in areas with continuous aquatic habitat, their roars were reduced to quiet coughs and seldom used. This discrepancy might be due to some signal components having additional functions, such as bellows attracting participants to bellowing choruses in alligators. The ability of crocodylians to optimize their signalling to habitat parameters by adjusting signal composition might account for the evolutionary stability of their signalling systems, which are still very similar between crocodiles and alligators even after more than 70 million years of separation between these two lineages.

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Although crocodile and alligator lineages separated more than 70 million years ago (Neill 1971), their signalling is still very similar. Garrick et al. (1978) found that crocodiles and alligators generally 'understand' each other's signals. In fact, signalling is relatively uniform among all extant crocodylians (alligators, caimans, crocodiles, gharials; Dinets 2011).

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

Crocodylians have a relatively simple and uniform signalling system, limited to a few acoustic (including infrasound, or subaudible) and nonacoustic (Garrick & Lang 1977) signals per species. This simplicity makes them perfect for a study on the evolution of

signalling because comparative methods of studying evolving systems are most effective if rates of change are low and the number of variables limited (Felsenstein 1983).

Why does the crocodylian signalling system show such extreme longevity? Is it possible that it is so conservative because it can be easily adapted to changing environment without any substantial changes? In the present study, I attempted to answer this question by looking at particular kinds of signals that are used for long-distance communication and so should be most sensitive to the selective pressure of environmental conditions.

All extant crocodylian species have a category of signals used predominantly by adult animals during the mating season, such as roars, bellows and head slaps (Dinets 2011). I refer to these signals collectively as advertisement calls (ACs). The term 'advertisement call' is used in herpetology for amphibian calls used in long-range signalling (Wells 1977; Narins et al. 2006). Features of crocodylian ACs suggest that at least one of their functions is also long-range signalling: they are used mostly during the mating season, they are the only intraspecific signals used both by animals living in groups and those living in isolation, they are the loudest signals in each species' repertoire, and they tend to be produced at a certain time of day, usually in the morning, when environmental noise levels are minimal (Garrick & Lang 1977).

\* Correspondence and present address: 1705 Laurel Avenue, #2, Knoxville, TN 37916, U.S.A.

E-mail address: [dinets@gmail.com](mailto:dinets@gmail.com).

Crocodylian ACs 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. The second type is infrasound, nonvocal vibrations normally produced below the water surface at frequencies below the range of human hearing. It can be visually detected by the so-called 'water dance' effect, apparently created by Faraday waves (G. Holt, personal communication). The third type includes head slaps (sounds made by slapping the head against the water surface) and, in some species, jaw slaps (sounds made by slapping the jaws together at or below the water surface).

The benefit of having multiple components may be in their differing ability to spread and carry information through air and water. Vocal sounds are produced above the water surface, and spread well through the air. They do not spread well underwater (Dinets 2011). They may function as location indicators, and also 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). Slaps carry well through both water (Dinets 2011) and, to a lesser extent, air. They carry information about the existence and location of the animal, and it has been shown that crocodylians can locate their source underwater (Dinets 2011). Slaps have a very sharp onset, a feature known to make locating the source of the sound easier (Hopp et al. 1998). But slaps are difficult to distinguish from a variety of other sounds, and the animal's size can only be estimated from the perceived loudness of the signal and the distance to the source. In turn, the distance to the signalling animal has to be estimated from the degree to which the sharpness of the slap is preserved. Infrasound spreads over distances of many kilometres underwater (Hopp et al. 1998). However, infrasound can probably spread only through continuous aquatic habitat, as it would be reflected by water/ground surface. Since the source of underwater infrasound is physically difficult to locate, because of the high speed and long wavelength of these sounds, species that use infrasound for long-range signalling can be expected to accompany it with 'direction beacons', which are short, loud broadband sounds with very sharp onset, such as head slaps and jaw 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 signalling, but only within the visibility range, when it is clear which animal is the source, and only for partially submerged recipients.

Thus, 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 partially submerged recipients at close range, when the location of the animal producing it is obvious. It can be hypothesized that the effectiveness of crocodylian communication can be optimized by adjusting the composition of ACs to habitat structure.

Species inhabiting predominantly fragmented aquatic habitat use vocal signals in their ACs, but they seldom or never use slaps, while species inhabiting predominantly continuous aquatic habitat use slaps, but they seldom or never use vocal signals, and their vocal signals (if present) tend to be reduced to quiet 'coughs' or 'grunts' (Dinets 2011). Species that are habitat generalists regularly use both slaps and vocal sounds. These differences are phylogeny independent and exist even between some closely related species.

The same differences can be predicted to exist between populations of habitat generalist species living in areas where only one type of aquatic habitat is available. Animals living in areas with only continuous aquatic habitat can be predicted to use slaps more often and vocal sounds less often than animals living in areas with fragmented aquatic habitat. Also, animals living in continuous

aquatic habitat might have their vocal signals reduced in loudness, as they are no longer important for long-distance communication. To test these predictions, I compared signalling behaviour of individuals living in fragmented and continuous aquatic habitat.

## METHODS

I compared signal compositions of conspecific populations of two species of crocodylians that inhabit a wide range of habitats 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 (1989): bellow(s) preceded by infrasound ('bellowing display') and head slap(s) preceded by infrasound ('head-slapping display'). Male Nile crocodiles, *Crocodylus niloticus*, use roars and head slaps (also preceded by infrasound) separately or within the same display (Garrick & Lang 1977).

### Study Sites

Study sites were selected in geographical areas where only one type of aquatic habitat (either fragmented or continuous) was used by the animals during the mating season. Hereafter, I refer to study sites with fragmented aquatic habitat as 'fragmented sites' and those with continuous aquatic habitat as 'continuous sites'.

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 acute as human hearing (Beach 1944; Higgs et al. 2002). Therefore, locations were 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.

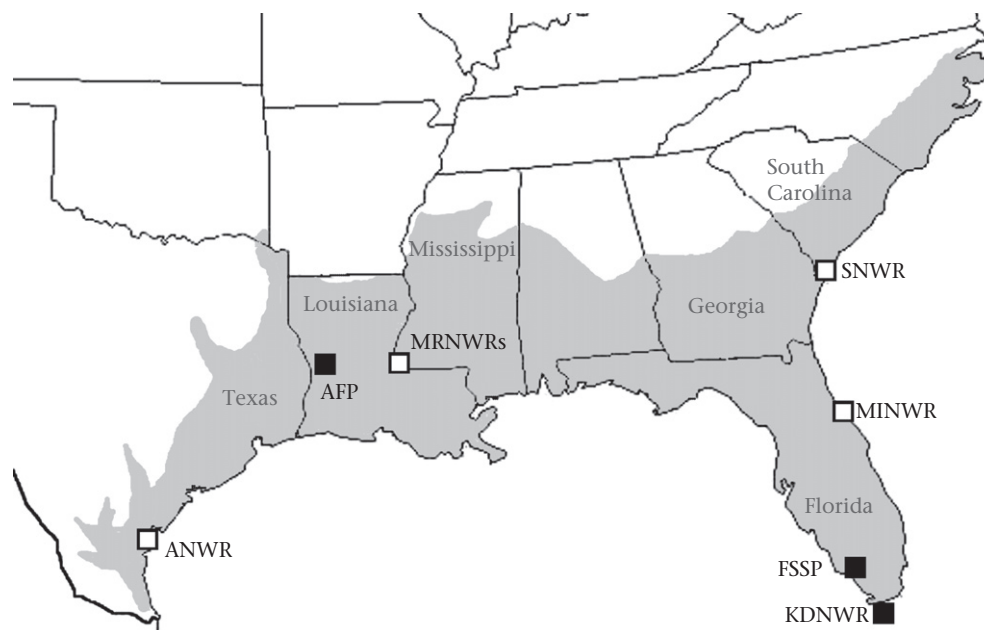
Continuous sites were those where all bodies of water inhabited by adult animals during the mating season (when the observations were conducted) were larger in at least one dimension than the maximum carrying distance of aerial signals. Alligator bellows and crocodile roars can be heard by a human observer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

American alligators were studied at four continuous and three fragmented sites (Fig. 1). One of the fragmented sites was not used in statistical analysis because of small sample size. The remaining six sites could be divided into three western and three eastern sites, or three northern and three southern sites, and in each case, each of the two groups included two continuous and one fragmented site.

### Continuous sites

(1) Cat Island National Wildlife Refuge, LA, U.S.A. (30°89'N 91°20'W) and St Catherine Creek National Wildlife Refuge, MS, U.S.A. (31°22'N 91°42'W). In these 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 harbouring adult alligators were found within 20 km of the refuges. These two wildlife refuges were considered a single study site (MRNWRs).

(2) Savannah National Wildlife Refuge (SNWR), GA and SC, U.S.A. (32°11'N 81°20'W). At this site, alligators inhabit large river



**Figure 1.** Geographical locations of American alligator study sites in the southeastern United States. Shaded area denotes the approximate range of the American alligator. Open squares: continuous aquatic habitat; filled squares: fragmented aquatic habitat. 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; SNWR: Savannah National Wildlife Refuge.

channels, deep canals and large lakes (over 1 km<sup>2</sup>). Although a few small bodies of water also exist in the area, they are dry or very shallow during the mating season, and no alligators longer than 50 cm were found in them during numerous night-time visits, when eyeshine would make any alligators easy to detect.

(3) Merritt Island National Wildlife Refuge (MINWR), FL, U.S.A. (28°40'N 80°48'W). At this site, alligators inhabit lagoons larger than 75 km<sup>2</sup> and a continuous network of tidal channels. Few small bodies of water exist in the area, and no alligators were found in them during repeated night-time visits, probably because all these small ponds contain sea water, in which alligators cannot live permanently (Neill 1971).

(4) Aransas National Wildlife Refuge (ANWR), TX, U.S.A. (28°15'N 96°55'W). At this site, alligators inhabit interconnected lagoons and lakes at least 1 km<sup>2</sup>. No small bodies of water existed in the area at the time of observations except for one pool that contained only juvenile alligators (less than 50 cm long).

#### Fragmented sites

(1) Fakahatchee Strand State Preserve (FSSP), FL (26°49'N 81°25'W). At this site, alligators inhabit ponds smaller than 1000 m<sup>2</sup> 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 one animal observed in 8 km of canals during night counts.

(2) Anacoco Floodplain (AFP), LA (31°24'N 93°24'W). At this site, alligators inhabit ponds known as 'gator holes', which are 25–100 m<sup>2</sup> 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. Such streams were considered fragmented for the purposes of this study because of their acoustic properties (Dinets 2011).

(3) Key Deer National Wildlife Refuge (KDNWR), FL (24°42'N 81°22'W). At this site, alligators inhabit tiny sinkholes (2–4 m<sup>2</sup>) and two artificial lakes about 2000 m<sup>2</sup> 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 statistical analysis.

Nile crocodiles were studied in three geographical regions (Fig. 2). In each region there was one continuous site and one fragmented site.

#### Southern region

(1) iSimangaliso Wetland Park (iSWP), South Africa (28°21'S 32°24'E), a continuous site where crocodiles inhabit a large (over 350 km<sup>2</sup>) river estuary with no small bodies of water nearby.

(2) North-central part of Kruger National Park (KNP), South Africa (23°46'S 31°33'E), a fragmented site where crocodiles inhabit small rivers that by the onset of the mating season break up into chains of pools smaller than 600 m<sup>2</sup>. No large bodies of water exist in the area.

#### Central region

(1) Mahango Game Reserve (MGR), Namibia (18°13'S 21°45'E), a continuous site where crocodiles inhabit a stretch of a large river with no tributaries and no small bodies of water nearby.

(2) Northwestern part of South Luangwa National Park (SLNP), Zambia (12°46'S 31°56'E), a fragmented site where crocodiles inhabit small creeks that by the onset of the mating season break up into chains of pools smaller than 100 m<sup>2</sup>. Although this area is not far from the large Luangwa River, it is separated from it by a steep escarpment with cataracts and waterfalls.

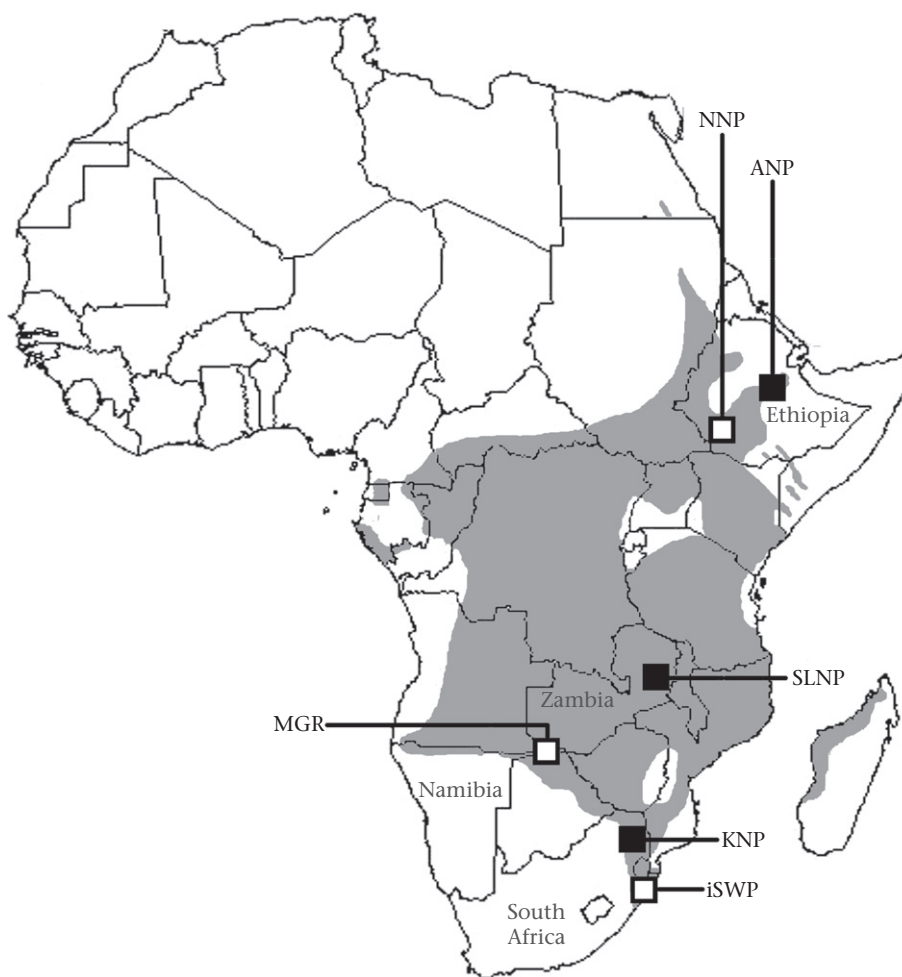
#### Northern region

(1) Nechisar National Park (NNP), Ethiopia (5°54'N 37°32'E), a continuous site where crocodiles inhabit two lakes, each larger than 500 km<sup>2</sup>. 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), Ethiopia (9°5'N 40°20'E), a fragmented site where crocodiles inhabit spring-fed ponds smaller than 1000 m<sup>2</sup>, with no large bodies of water in the area.

#### Choosing and Observing Focal Animals

Only males at least 2 m in total length (by visual estimate) were observed for the present study. Behavioural differences (see below) were used to sex the animals.



**Figure 2.** Geographical locations of Nile crocodile study sites. Shaded area denotes the approximate range of the Nile crocodile *sensu stricto*. Open squares: continuous aquatic habitat; filled squares: fragmented aquatic habitat. ANP: Awash National Park; iSWP: iSimangaliso Wetland Park; KNP: Kruger National Park; MGR: Mahango Game Reserve; NNP: Nechisar National Park; SLNP: South Luangwa National Park.

To locate focal male alligators, my assistants and I searched small ponds and the shores of large lakes and rivers on foot, by car or from a small boat, and we made note of particularly large animals. If more than one alligator larger than 2 m was visible from the same observation point, we watched them simultaneously until the next morning, when ACs usually occur. In American alligators, females produce ACs similar to those of males, but without infrasound (Vliet 1989). If an animal produced an AC with infrasound, it was considered a male, was designated the focal animal, and was observed by the same observer(s) daily from 0530 to 1030 hours ( $\pm 30$  min, depending on the location and time of year), until five ACs were recorded from it. Nonfocal animals at the same location were ignored. If no animal present 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 et al. 1978). All focal animals were at least 1 km from each other. This requirement was important because bellowing and head slapping are contagious behaviours in alligators (Garrick & Lang 1977; Vliet 1989). Observations at each site continued until five ACs were recorded from each of 10 alligators.

Signalling behaviour differs between captive alligators kept in large and small groups (Vliet 1989). To minimize group size bias (large groups were more likely to be found at continuous sites),

alligators in groups of more than 10 were ignored. A group was defined as all animals at least 2 m long 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 because of 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 until the focal animal produced at least five ACs. All focal animals were separated by at least 50 m. This distance was considered sufficient because roaring and head slapping are less contagious in crocodiles than are bellowing and head slapping in alligators (Garrick & Lang 1977; J. Thorbjarnarson, M. Robinson & D. Kledzik, personal communication). Observations continued until at least five ACs were recorded from each of 10 crocodiles.

All observations at all sites were performed with the observer positioned at least 5 m from the water edge, at least 10 m from the focal animal, and concealed by vegetation or a portable blind, if

possible. If such concealment was impossible because of absence of vegetation and extremely hot weather (which happened only a few times), the observers tried to lie on the ground and move as little as possible. Disturbance to the animals was further reduced by arriving on site 30–60 min prior to the expected onset of signalling behaviour.

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.

#### Data Recording

Each behaviour involving production of sound and/or body vibration in a continuous arched-back posture (Garrick & Lang 1977) was counted as an AC. If more than one vocal sound or more than one head slap was produced during the same AC (which always meant that the behaviours were less than 10 s apart), they were counted as one vocal sound or one head slap, respectively. Body vibration was assumed to be a sign of infrasound production (Garrick et al. 1978). To avoid inflated counts due to contagion (for example, in bellowing choruses) or repetitive behaviour, after an AC was produced by any animal within sight or hearing range of the observer, no ACs were counted until 1 h had expired.

Alligator ACs were scored as belonging to one of the two AC types, namely a 'bellowing display' containing bellow(s) and infrasound, or a 'head-slapping display' containing head slap(s) and infrasound. All ACs by focal animals observed during the present study ( $N = 351$ ) belonged to one of the two types. No ACs composed only of infrasound or including both bellow(s) and head slap(s) were ever observed, although a few head-slapping displays included a quiet low growl (as described by Vliet 1989).

Crocodile ACs were scored as containing roars or head slaps, or roars and head slaps. All observed ACs ( $N = 306$ ) 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.

#### Interobserver Reliability Testing

Interobserver reliability studies for scoring alligator ACs 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 behaviours they considered to be ACs, and recorded the composition (infrasound, bellow and/or head slap) 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 behaviours were scored. All of these behaviours were considered ACs by both members of a team. Of these behaviours, 35 were scored as bellows with infrasound, 22 were scored as head slaps with infrasound and four were scored as bellows without infrasound (which were scored as produced by females and dropped from the study). The interobserver agreement in determining the presence of an AC, as well as in determining AC composition, was 100%.

Interobserver reliability studies for scoring Nile crocodile ACs were conducted in the same way at Crocoloco Crocodile Farm, Israel. 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 behaviours were scored. All of these behaviours were considered ACs by both members of the team. Of these behaviours, nine were scored as infrasound with head slaps and two were scored as infrasound with both roars and head slaps. The interobserver agreement in determining the presence of an AC, and in determining AC composition, was 100%.

#### Analysis

##### Alligators

All analyses used significance levels of 0.05 and two-tailed tests. Five ACs were recorded from each focal animal to ensure that each animal was weighted equally. I tallied the number of head-slapping displays for each animal, and I statistically compared the resulting counts.

(1) I compared tallies for animals at continuous ( $N = 40$ ) and fragmented ( $N = 20$ ) sites using Mann–Whitney  $U$  tests.

(2) I compared the prevalence of head-slapping displays for alligators that produced at least one head-slapping display among the five ACs recorded at fragmented ( $N = 30$ ) and continuous ( $N = 30$ ) sites using Fisher's exact test.

(3) The data on head-slapping and bellowing displays were not mutually independent because I constrained the number of scored ACs to exactly five per animal. To obtain fully independent data on the frequency of use of each signal type, I tallied ACs of each signal type produced within the first 2 days of observation by animals in fragmented and continuous sites separately, and I compared these values using Mann–Whitney  $U$  tests.

(4) I repeated steps 1–3 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.

##### Crocodiles

Only the first five ACs were scored from each focal animal, so that each animal was weighed equally.

I analysed the data for roars and head slaps separately, but in the same way. I tallied the number of ACs containing roars and the number of ACs containing head slaps for each animal, and statistically compared the resulting counts.

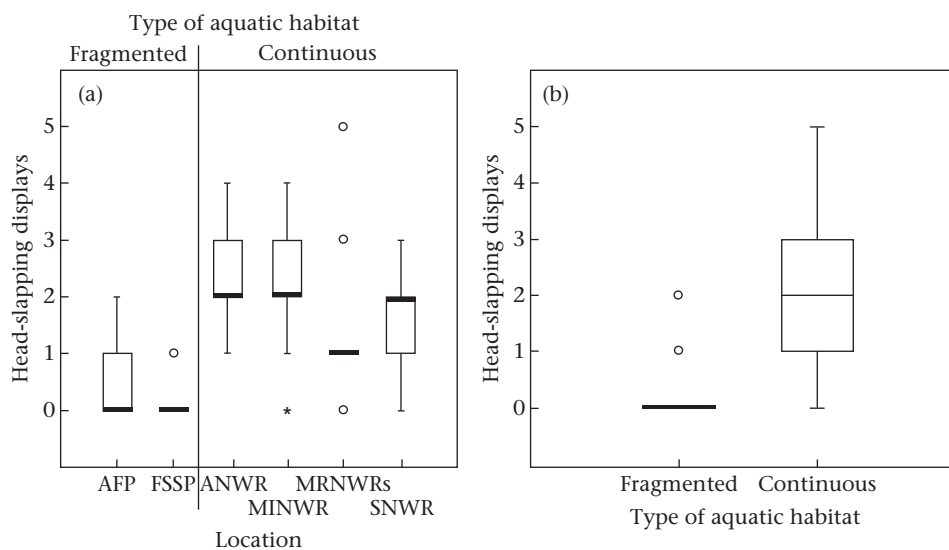
(1) I used ANOVA, with habitat type, geographical region and their interaction as factors. Since the distribution had an upper limit and was not normal, I applied arcsine transformation  $\arcsin(\sqrt{x})$ , and then used Levene's test for normality.

(2) I compared tallies of each AC component for animals at continuous ( $N = 30$ ) and fragmented ( $N = 30$ ) sites using Mann–Whitney  $U$  tests.

(3) I repeated step 2 for comparisons between the two sites ( $N = 10$ ) within each geographical area, and between the three geographical areas ( $N = 20$ ) using Kruskal–Wallis tests.

(4) I compared the prevalence of roars and head slaps among crocodiles between fragmented ( $N = 30$ ) and continuous ( $N = 30$ ) sites using Fisher's exact tests.

(5) The data on head slaps and roars were not fully mutually independent because I constrained the number of scored ACs to five per animal. To obtain fully independent data on the frequency of use of each signal component, I tallied ACs of each type produced within the first 2 days of observation by animals in fragmented and continuous sites separately, and I compared these values using Mann–Whitney  $U$  tests. I also performed ANOVAs on these tallies, with habitat type, geographical region and their interaction as factors.



**Figure 3.** Box plots showing the numbers of head-slapping displays among five advertisement calls by alligators. (a) Alligators ( $N = 10$ ) at six study sites (see Fig. 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 head-slapping displays. (b) 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 head-slapping displays.

**Ethical Note**

The study was conducted under the University of Miami Institutional Animal Care and Use Committee (approval number 06-053, issued to Steven Green) and Federal research permits EVER-2007-SCI-0026 and ARMLNWR SUP 41560-06013. Since it was a purely observational study of natural behaviour, we avoided disturbance of the study animals as much as possible.

**RESULTS AND DISCUSSION**

*American Alligators: AC Composition*

Head-slapping displays were produced frequently at continuous sites, but seldom at fragmented sites (Fig. 3a). The numbers of head-slapping displays among the five ACs recorded for each animal (Fig. 3b), the prevalence of head slap use and the numbers of head-slapping displays produced by animals in the first 2 days of observation were all significantly higher at continuous sites than at fragmented sites (Table 1). This difference cannot be explained by differences in longitude or latitude, since there were no such

differences between eastern and western sites, or between northern and southern sites.

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

In KDNWR, a fragmented site, two male alligators produced 11 bellowing displays in 5 days of observation. No head-slapping displays were observed at this site.

*Nile Crocodiles: AC Composition*

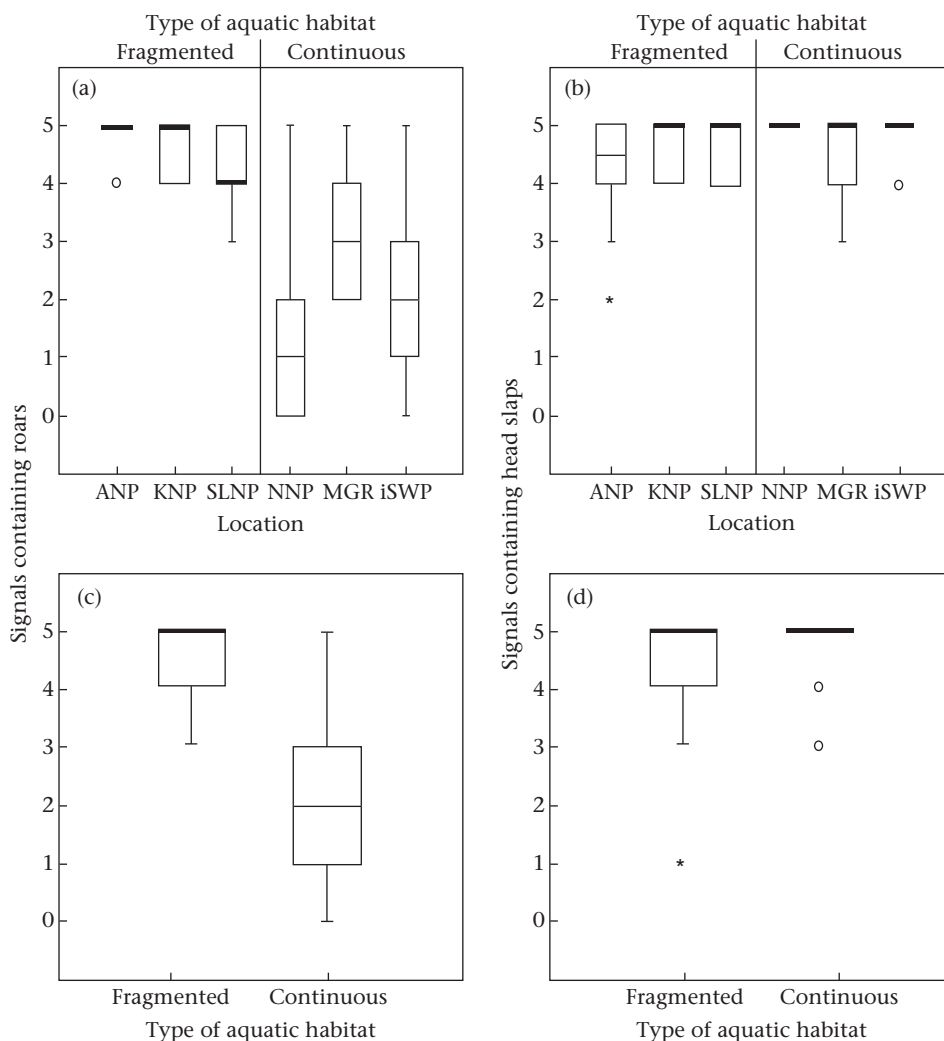
Crocodiles produced roars more frequently in areas with fragmented aquatic habitat than in areas with continuous aquatic habitat (Fig. 4a). The numbers of ACs containing roars among the five ACs recorded for each crocodile were higher at continuous sites than at fragmented sites (Fig. 4c, Table 2). ANOVA revealed a significant effect of habitat type, no effect of geographical region, and a significant habitat\*region interaction on the proportions of

**Table 1**  
Results of tests comparing use of head-slapping displays (HSD) and bellowing displays (BD) among American alligators

Comparison between aquatic habitat sites	Number of HSD	Prevalence of use		Number of displays in the first 2 days of observing each animal	
		HSD	BD	HSD	BD
Fragmented vs continuous sites	$U=725$ $N_1=40, N_2=20$ <b><math>P&lt;0.001</math></b>	<b><math>P&lt;0.001</math></b>	All animals except one used bellows	$U=680$ $N_1=40, N_2=20$ <b><math>P&lt;0.001</math></b>	$U=317$ $N_1=40, N_2=20$ $P=0.1971$
3 northern vs 3 southern sites*	$U=513.5$ $N_1=N_2=30$ $P=0.3524$	$P=0.7846$		$U=555$ $N_1=N_2=30$ $P=0.1236$	$U=394$ $N_1=N_2=30$ $P=0.4122$
3 eastern vs 3 western sites*	$U=465$ $N_1=N_2=30$ $P=0.8737$	$P=0.5796$		$U=345$ $N_1=N_2=30$ $P=0.1236$	$U=406.5$ $N_1=N_2=30$ $P=0.5222$

Data were compared between six study sites (four continuous and two fragmented aquatic habitat sites). At each site, five advertisement calls were recorded for each of 10 sampled animals. Significant values ( $P < 0.05$ ) are highlighted in bold.

\* Two sites with continuous aquatic habitat and one site with fragmented aquatic habitat in each group (see Fig. 1). Data from Key Deer National Wildlife Refuge were not used in the analysis because of limited sample size.



**Figure 4.** Box plots showing the numbers of advertisement calls containing roars and head slaps among five advertisement calls by crocodiles. (a) Calls containing roars and (b) signals containing head slaps in crocodiles ( $N = 10$ ) at six study sites (see Fig. 2 for map and list of abbreviations). In (a), one of the boxes is collapsed because all except two calls in ANP contained roars. In (b), two of the boxes are collapsed because all signals in NNP and all except one signal in iSWP contained head slaps. Signals containing (c) roars and (d) head slaps in crocodiles from study sites with continuous ( $N = 30$ , 3 sites) and fragmented ( $N = 30$ , 3 sites) aquatic habitats. In (d), one of the boxes is collapsed because almost all signals in continuous aquatic habitats contained head slaps.

**Table 2**  
Results of tests comparing roar usage among Nile crocodiles

Comparison between aquatic habitat sites	Proportion of ACs containing roars	Prevalence of roar use	No. of ACs containing roars in the first 2 days of observing each animal
Continuous vs fragmented sites	$U=783$ $N_1=N_2=30$ <b><math>P&lt;0.001</math></b>	<b><math>P=0.024</math></b>	$U=748$ $N_1=N_2=30$ <b><math>P&lt;0.001</math></b>
2 northern sites	$U=94$ $N_1=N_2=10$ <b><math>P&lt;0.001</math></b>	$P=0.087$	$U=95.5$ $N_1=N_2=10$ <b><math>P=0.001</math></b>
2 central sites	$U=78$ $N_1=N_2=10$ <b><math>P=0.045</math></b>	$P=1$	$U=63$ $N_1=N_2=10$ $P=0.347$
2 southern sites	$U=87$ $N_1=N_2=10$ <b><math>P=0.006</math></b>	$P=0.474$	$U=84.5$ $N_1=N_2=10$ <b><math>P=0.010</math></b>

Data were compared between six study sites (one continuous and one fragmented aquatic habitat site in each of three geographical regions). At each site, five advertisement calls (ACs) were recorded for each of 10 sampled animals. Significant values ( $P < 0.05$ ) are highlighted in bold.



**Table 3**  
ANOVA results for advertisement calls (ACs) containing roars in Nile crocodiles

Dependent variable	Source	Type III SS	df	Mean squares	F	P
Proportion of ACs containing roars (out of 5 ACs)*	Habitat type	10.109	1	10.109	41.442	<b>0.000</b>
	Region	0.048	2	0.024	0.099	0.906
	Habitat type × region	1.553	2	0.777	3.184	<b>0.049</b>
	Error	13.173	54	0.244		
No. of ACs containing roars in the first 2 days of observation†	Habitat type	36.817	1	36.817	68.320	<b>0.000</b>
	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		

ACs were sampled ( $N = 10$ ) at six study sites (one continuous and one fragmented aquatic habitat in each of three geographical regions). Significant values ( $P < 0.05$ ) are highlighted in bold.

\* These data passed Levene's test for normality ( $P = 0.551$ ) after arcsine transformation  $\arcsin(\sqrt{x})$  (see [Methods](#)).

† These data passed Levene's test for normality ( $P = 0.249$ ) without transformation.

ACs containing roars ([Table 3](#)). 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 2](#)).

Nile crocodiles frequently produced head slaps at all sites ([Fig. 4b](#)). The numbers of ACs containing head slaps among the five ACs recorded for each crocodile and the prevalence of head slaps did not differ significantly ([Table 4](#)). ANOVA revealed that only habitat type significantly affected the proportions of ACs containing head slaps among the five ACs recorded for each crocodile ([Table 5](#)).

However, the results for roars and head slaps were not independent because I scored a fixed number of ACs for each animal. Therefore, the difference in the numbers of animals with higher numbers of head slaps was probably an artefact of the much greater difference in the numbers of animals with higher roar usage. Analysing independent sets of data for roars and head slaps (the numbers of ACs with roars and head slaps per animal during the first 2 days of observation) showed that the numbers of ACs containing roars ([Fig. 5a](#)) differed significantly between fragmented and continuous sites ([Fig. 5b](#)), but the numbers of ACs containing head slaps ([Fig. 5c, d](#)) did not (last columns in [Tables 2 and 4](#)). ANOVA showed a significant effect of habitat type, but not of geographical region, and no habitat type\*geographical region interaction on the number of ACs containing roars ([Table 3](#), last row), and no significant effect of any of the factors on the number of signals containing head slaps ([Table 5](#), last row).

Observed differences cannot be explained by differences in geographical location. Comparison of the three geographical

regions showed no significant difference in the numbers of ACs containing roars ( $H = 0.36$ ,  $P = 0.835$ ) or head slaps ( $H = 0.71$ ,  $P = 0.701$ ) among the five ACs recorded for each individual.

#### Nile Crocodiles: Roars versus Coughs

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

At fragmented sites (KNP, SLNP, ANP), crocodiles produced sharp, loud roars ([Fig. 6a](#)), 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 head slaps. Such roars were first described as part of mating season displays by [Garrick & Lang \(1977\)](#) in a study of captive Nile crocodiles of unknown geographical origin, and by [Pooley \(1982\)](#), who 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 (D. Oujani, personal communication). These crocodiles originate from northwestern Madagascar, where crocodiles inhabit both large and small lakes (V. Dinets, personal observation).

At two out of three continuous sites (iSWP, NNP) crocodiles produced weak sounds ([Fig. 6b](#)) similar to the so-called 'coughs' of saltwater crocodiles (*Crocodylus porosus*) (V. Dinets, personal observation). These coughs cannot be heard by a human observer at more than 100 m even under ideal conditions. Such weak signals are also produced by crocodiles in Lake Turkana ([Dinets 2011](#)). Vocal sounds in the ACs of Lake Turkana crocodiles are so quiet that a detailed description of local crocodiles' mating season displays by [Modha \(1967\)](#) did not even mention them, although these animals use loud roars in aggressive interactions. At Crocoloco Crocodile Farm, Israel, where most Nile crocodiles originate from the Kenyan part of Lake Victoria and where a few originate from iSWP (B. Eli-gulashvili, personal communication), all observed roars were very quiet 'coughs'. 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 crocodylian courtship at Runde River, Botswana ([Kofron 1991](#)) mentions only head slaps.

Crocodiles at MGR produced vocal sounds intermediate in loudness between roars and coughs. The numbers of roars used in

**Table 4**  
Results of tests comparing head slap usage among Nile crocodiles

Comparison between aquatic habitat sites	Proportion of ACs containing head slaps	No. of ACs containing head slaps in the first 2 days of observing each animal
Continuous vs fragmented sites	$U=568.5$ $N_1=N_2=30$ $P=0.082$	$U=358.5$ $N_1=N_2=30$ $P=0.177$
2 northern sites	$U=75$ $N_1=N_2=10$ $P=0.06$	$U=34$ $N_1=N_2=10$ $P=0.242$
2 central sites	$U=50$ $N_1=N_2=10$ $P=0.968$	$U=45.5$ $N_1=N_2=10$ $P=0.764$
2 southern sites	$U=60$ $N_1=N_2=10$ $P=0.471$	$U=42$ $N_1=N_2=10$ $P=0.569$

All animals used head slaps. Advertisement calls (ACs) were sampled at six study sites (one continuous and one fragmented aquatic habitat in each of three geographical regions). At each site, five ACs were recorded for each of 10 sampled animals.

**Table 5**  
ANOVA results for advertisement calls (ACs) containing head slaps in Nile crocodiles

Dependent variable	Source	Type III SS	df	Mean squares	F	P
Proportion of ACs containing head slaps (out of 5 ACs)*	Habitat type	0.949	1	0.949	5.540	<b>0.022</b>
	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		
No. of ACs containing head slaps in the first 2 days of observation†	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		

ACs were sampled ( $N = 10$ ) at six study sites (one continuous and one fragmented aquatic habitat in each of three geographical regions). Significant values ( $P < 0.05$ ) are highlighted in bold.

\* These data did not pass Levene's test for normality ( $P < 0.001$ ) after arcsine transformation.

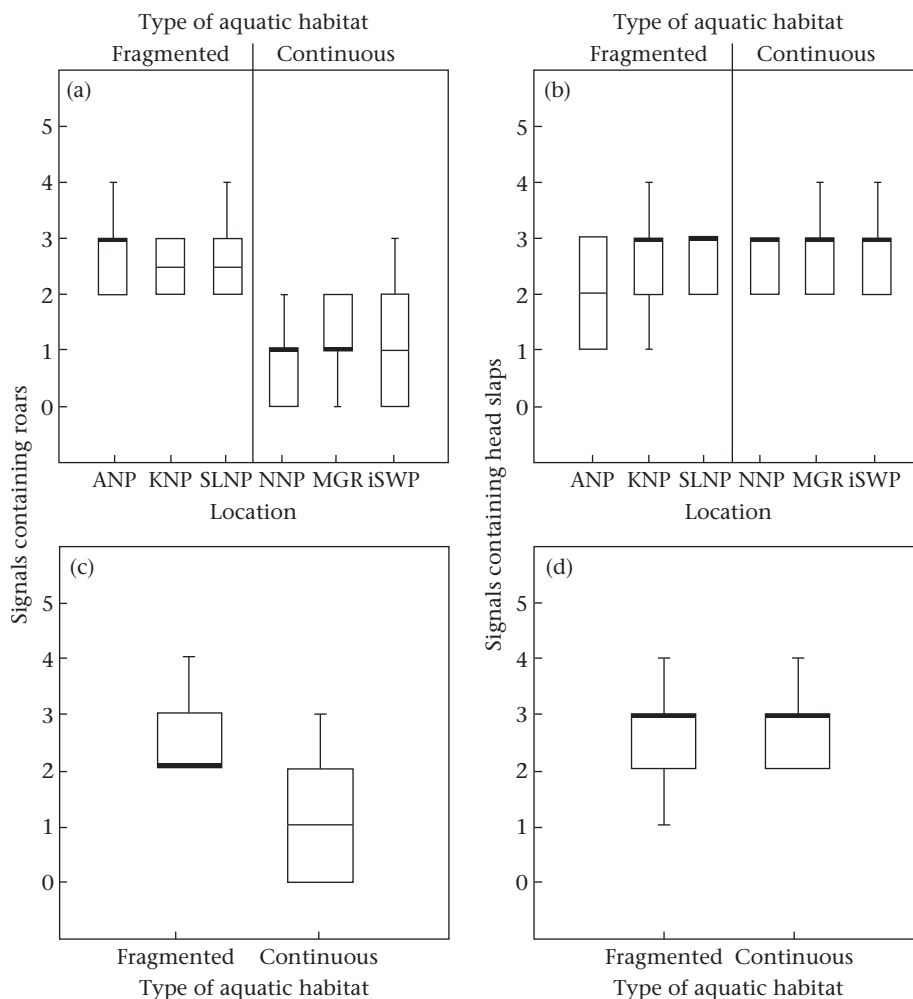
† These data passed Levene's test for normality ( $P = 0.223$ ) without transformation.

MGR were higher than at two other continuous sites, although significantly lower than at any fragmented site. It is possible that crocodile habitat at MGR is not always 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 neighbouring areas with small bodies of water.

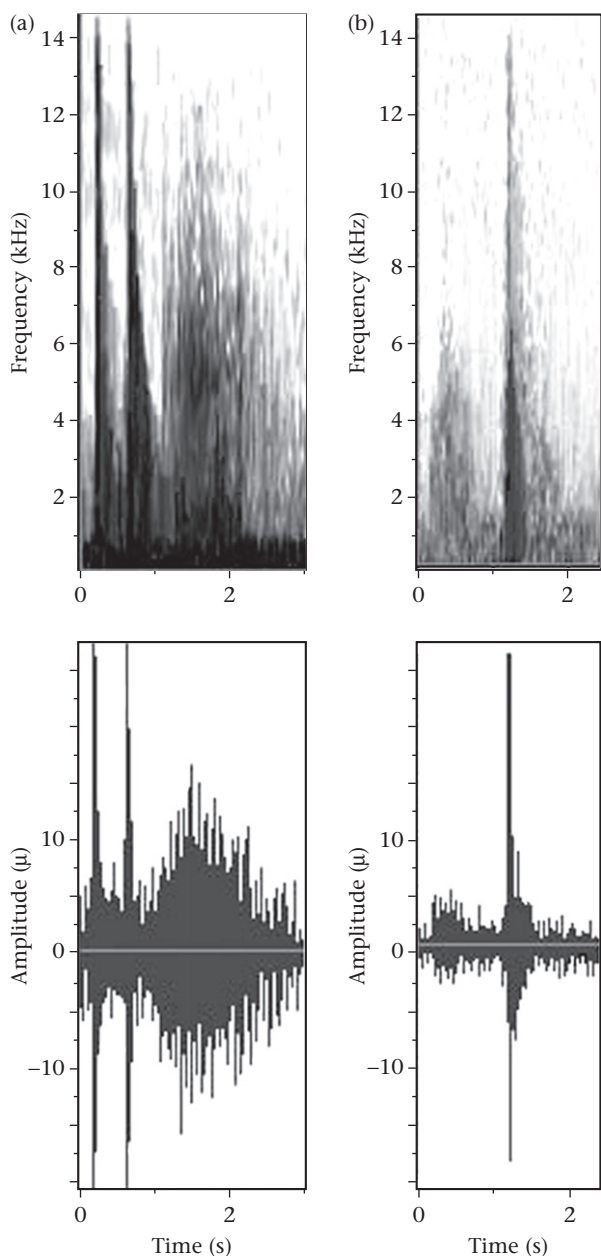
Crocodilian ACs are highly stereotypical behaviours with little, if any, evidence of grading. Roars by each animal show little variation;

in fact, an experienced observer can easily learn to recognize individual males by the sound of their roars (V. Dinets, personal observation), which differ in bottom frequency and loudness according to the size of the animal (Garrick et al. 1978). There was no overlap in the loudness of vocal signals between animals in 'roaring' and 'coughing' populations.

In contrast with the Nile crocodile, no regional differences in the loudness of bellowing sounds were ever noticed in the American alligator. At all sites, bellows by the largest males could



**Figure 5.** Box plots showing the numbers of advertisement calls containing (a) roars and (b) head slaps recorded in the first 2 days of observation of each crocodile ( $N = 10$ ) at six study sites (see Fig. 2 for map and list of abbreviations). Box plots showing the numbers of advertisement calls containing (c) roars and (d) head slaps recorded in the first 2 days of observation of each crocodile at study sites with continuous ( $N = 30$ , 3 sites) and fragmented ( $N = 30$ , 3 sites) aquatic habitats.



**Figure 6.** Spectrograms (top) and waveforms (bottom) of advertisement calls of Nile crocodiles: (a) two head slaps followed by a roar, South Luangwa National Park, Zambia; (b) a soft roar ('cough') followed by a head slap, iSimangaliso Wetland Park, South Africa. Infrasound is not visible on the waveforms because of equipment limitations. Recorded using Sony TCD-D8 digital recorder, Cannon XLR-3-50 microphone and Cannon XLR-3-11C connector cable.

be heard by a human observer at approximately 1 km under ideal conditions.

#### Signal Differences and Habitat: Alligators versus Crocodiles

In both Nile crocodiles and American alligators there were differences in signalling behaviour between animals at fragmented and continuous sites (Table 4). These differences were not associated with geographical latitude or longitude.

In the American alligator, alligators at fragmented sites used fewer head-slapping displays than alligators at continuous sites. There was no difference in use of bellowing displays. No difference between sites in average loudness of vocal sounds was ever noticed.

In the Nile crocodile, head slap use did not differ between fragmented and continuous sites. Crocodiles at continuous sites used fewer vocal sounds than crocodiles at fragmented sites. In addition, vocal sounds produced by crocodiles at fragmented sites were noticeably louder than those produced at continuous sites.

In both species, the observed differences in signalling behaviour between animals at fragmented and continuous sites matched the predictions (see above), but not all predicted differences were observed. Why were the predicted differences observed only for one AC component in each species, and why was the AC component for which these differences were observed the vocal sounds in alligators but the head slaps in crocodiles?

Wang et al. (2006, 2007) suggested that the main function of alligator bellows is not personal advertising, but attracting more animals to bellowing choruses. Alligators engage in group courtship behaviour, sometimes with dozens of participants, and these night-time gatherings form in places with high concentrations of animals, where bellowing choruses naturally occur in morning hours (Dinets 2010). However, alligators bellow in all parts of their range, including areas of low population density where large gatherings seldom or never occur (Dinets 2010), and animals living in isolation also bellow. Bellowing by a male is often followed by courtship attempts by females (Vliet 1989). Therefore, it is likely that bellows have two functions: attracting more animals to choruses and personal advertising.

Head slaps are apparently used only as personal advertising and can be largely abandoned in areas with fragmented aquatic habitat, where bellows are more effective. But bellows probably cannot be abandoned in favour of head slaps in areas with continuous aquatic habitat, because bellows appear to be used not only for personal advertising, 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 head slaps having some additional function that roars do not have in this species. It has been suggested (Garnett 1989; Vliet 1989; Brazaitis & Watanabe 2011) that head slaps serve as signals of dominance in some species of crocodiles, and probably in Nile crocodiles as well (B. Barr, personal communication). In alligators, head slaps do not have this second function (Vliet 1989).

#### Are the Observed Differences Associated with Population Density?

Differences in signalling behaviour 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 were associated with habitat parameters, but these studies 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 study sites (ANWR, FSSP and MINWR). However, there was no difference in AC composition between northern and southern sites.

Even though observed differences in signalling behaviour were not associated with population density, it does not mean that there are no density-dependent differences in alligator signalling. Numerous differences in signalling behaviour between wild alligators observed in the present study and in captive alligators studied by Garrick et al. (1978) and Vliet (1989) were noted (Dinets 2011), and could be due to unnaturally high population density in

captivity. Vliet (1989) reported differences in signalling behaviour between alligators kept in large and small groups.

As for Nile crocodiles, there was no obvious difference in average group size or population density between study sites (see Dinets 2011 for details). Evidently, population density can be excluded as an alternative explanation for the differences in AC composition observed in the present study.

#### Are Alligators 'More Vocal' than Crocodiles?

Garrick & Lang (1977) found American alligators to be 'much more vocal' than Nile crocodiles, and suggested that alligators rely more on sound communication 'because of limited visibility in their marshy habitat'. However, both these species are habitat generalists with broad and widely overlapping habitat preferences (Neill 1971).

In the present study, focal animals of both species produced one to three ACs per day on more than 90% of all days of observation during the mating season, with five being the maximum number of ACs observed in 1 day for both species irrespective of habitat. The difference in overall vocal activity was due to alligators producing bellowing bouts and forming bellowing choruses. The Chinese alligator, *Alligator sinensis*, and some caimans also bellow or roar in bouts and form choruses (Dinets 2011). However, there is no evidence of long roaring bouts or roaring choruses in any crocodile species, irrespective of habitat preferences. Higher vocal activity in alligators compared to crocodiles is best explained by phylogeny, not by differences in habitat.

#### Conclusion

Crocodylians can optimize the ability of their signals to carry information by adjusting the signal composition to habitat structure. Such adjustment is made easy by the fact that each signal is a combination of components with different physical properties. This flexibility is a possible reason for the evolutionary success of the crocodylian signalling system.

Multimodal signalling systems are common in animals: elephants use infrasound to increase the range of their acoustic communication (Payne 1998); rodents use ultrasound (Anderson 1954), most likely to avoid detection; some bird species living along noisy mountain rivers partially replace songs with visual displays (Desutter-Grandcolas & Robillard 2004). But a dynamic intraspecific system of adjusting signal composition towards the components that are optimal for a particular habitat has never been described before.

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