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Do individual crocodilians adjust their signaling to habitat structure?

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Do individual crocodilians adjust their signaling to habitat structure?

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All crocodilians use long-distance signals, composed of infrasound, vocal sounds and/or slaps. These components differ in their ability to carry information about the animal's location and status through air and water. It has been previously shown that signal composition differs between species and allopatric conspecific populations; species and populations living in fragmented aquatic habitats use more vocal signals and/or fewer slaps than species and populations living in continuous aquatic habitats, thus adjusting their signaling to habitat structure. There are two possible mechanisms for such adjustment: behavioral plasticity and evolved differences between species and populations. In the present study, it is shown (a) that individual yacare caimans (*Caiman yacare*) do not change the composition of their signals in response to changes in aquatic habitat continuity, and (b) that in areas where both continuous and fragmented aquatic habitats are available, American alligators (*Alligator mississippiensis*) and Nile crocodiles (*Crocodylus niloticus*) living in small bodies of water do not differ in signal composition from those living in large bodies of water. Therefore the previously found differences in signaling between species and between allopatric conspecific populations are evolved adaptations rather than behavioral responses by individual animals.

KEY WORDS: multimodal signaling, alligator, crocodile, caiman, acoustic, adaptation, plasticity, evolution.

INTRODUCTION

Multimodal signaling is often used by animals living in complex environments. One advantage of such signaling is that physically different signal components have different abilities to carry information through a particular environment, so by adjusting signal composition the animal can optimize its signal to the parameters of its habitat (GORDON & UETZ 2011). Here I present evidence that, unlike many other taxa for which such plasticity has been demonstrated, crocodilians do not adjust their signals

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by individually reacting to habitat parameters. This result means that in crocodilians, changes in signal composition are evolved.

All crocodilian species (alligators, caimans, crocodiles and gharials) have a particular category of signals used for long-distance communication. I refer to these signals collectively as advertisement calls (ACs), as in DINETS (2011a). These signals are performed predominantly during the mating season, and in most species include three major types of sound: vocal sounds (usually called "bellows" in alligators and "roars" in crocodiles and caimans, although in reality the sounds can be very similar and the terminology is not codified), slaps (produced in most species by slapping the head against the water surface), and infrasound vibrations.

Unlike hatchling vocalizations, which have been extensively studied (see BRITTON 2001), crocodilian ACs have received relatively little attention. The first detailed descriptions were published in the late 1970s (GARRICK & LANG 1977; GARRICK et al. 1978). Alligator signals were further studied by VLIET (1989) and WANG et al. (2007), but crocodile and caiman ACs were at best superficially described by later researchers (see DINETS 2011b for a bibliography and overview of ACs in all extant species). The present paper is based on two parts of a five-year study of crocodilian ACs, aimed at elucidating the mechanisms by which the evolution of crocodilian ACs is influenced by the environment.

The effectiveness of crocodilian communication can be increased by adjusting the composition of ACs to habitat structure. Vocal sounds are produced above the water surface, and are more effective for transmitting information about the animal's location and status through the air. Slaps are produced at the water surface, and are more effective for transmitting such information through the water (DINETS 2011a, 2011b).

Indeed, it has been shown that AC composition differs between species (DINETS 2011b) and allopatric conspecific populations (DINETS 2011a) depending on habitat parameters. Species and populations living in fragmented aquatic habitats use more vocal signals and/or fewer slaps than species and populations living in continuous aquatic habitats. These differences cannot be explained by climate, group size or population densities.

But how do such differences arise? There are two possible mechanisms. Individual crocodilians might be able to adjust the composition of their ACs to the structure of their aquatic habitat simply by reacting to their environment. Alternatively, such adjustments might be developed as evolved behavioral differences between species and populations.

The first mechanism can be expected to exist in crocodilians, as the ability of individual animals to adjust their signaling to habitat parameters has been found in many taxa. For example, male *Schizocosa ocreata* wolf spiders use more visual signals on substrates not conductive to seismic signals (GORDON & UETZ 2011); male great tits (*Parus major*) sing higher-pitched songs in urban areas with high levels of low-frequency background noise (SLABBEKOORN & PEET 2003); male anole lizards (*Anolis* spp.) speed up visual displays in noisy motion habitats (ORD et al. 2007); tree-hole frogs (*Metaphrynella sundana*) change the frequency of their songs in accordance with water depth to maximize transmission (LARDNER & BIN LAKIM 2002).

But in other cases even small differences in signaling are claimed to be genetically determined rather than produced by behavioral responses, and are used in systematics for splitting species based on vocal differences. This approach has been extensively used, for example, in owls (MARKS et al. 1999) with no sufficient scientific justification.

An obvious way to test if individual crocodilians adjust their signal composition in response to habitat parameters would be to move some animals from fragmented to continuous aquatic habitat, or vice versa. But translocation of adult crocodilians is

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technically difficult and results in long-term stress (NEILL 1971). Two separate studies using different approaches were conducted instead.

STUDY 1. CHANGES IN ADVERTISEMENT CALL COMPOSITION AFTER A CHANGE IN HABITAT

One way to find out if individual crocodilians can adjust their advertisement call (AC) composition to habitat structure is to test if these animals change their AC composition 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*) inhabits 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) (DINETS 2011b). Caiman and crocodile vocalizations are usually called "roars" rather than "bellows", so caiman vocalizations preceded by infrasound will hereafter be called "roaring displays".

Yacare caimans were chosen for this study because they are easy to observe in the wild, can be individually identified (see below), and often 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.

Since roars are more effective for aerial communication, and headslaps are more effective for communication through the water, 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 the proportion of headslapping displays 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.

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METHODS (STUDY 1)

Study sites

Two sites were chosen for the study: the central-western part of the Pantanal in Brazil (17°41–46'S, 57°05–10'W) and the vicinity of Noel Kempff Mercado National Park (hereafter NKMNP) in Bolivia (15°07–09'S, 60°34–35'W). 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. The mating season of yacare caiman lasts from early October until late December (MEDEM 1981).

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, I chose six lakes with large numbers of caimans (20–60 animals larger than 1 m observed at night in each lake). Each lake was estimated to be 0.5–1 km^2 in size at the beginning of the study. Every day, two lakes were observed (each by one observer) from 4:00 until 9:00 and from 16:00 until 18:00. The next day, two other lakes were observed, and so on. In 9 days, each lake had been observed 3 times. The area was revisited after a 7-day gap in observations, by which time the water levels had dropped by 30 cm or more, and 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 8 days.

In NKMNP, I chose eight lakes with high numbers of caimans (approximately 10–40 animals larger than 1 m observed at night in each lake). 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 4:30 until 9:30 and the other from 16:00 until 19:00, all by the same observer. The next day, two other lakes were observed, and so on. In 4 days, each lake was observed once. The area was revisited after a 3-day gap in observations, by which time the entire floodplain containing all eight lakes became flooded to a depth of 50 cm or more. This continuous body of water was observed for 6 more days; then the observations had to be discontinued because caimans began to move widely, and finding known individuals became difficult.

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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 an inflatable kayak, 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 (7–15 × 35 and 10 × 42) were used when necessary.

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. 1, left column) and 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.).

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. 1, right column) was made, other individual markings noted, and total length estimated. If the conditions permitted, a photo or two were taken, 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.

Inter-observer reliability testing

A test of inter-observer reliability of animal identification was conducted at Fazenda Santa Clara in the Brazilian Pantanal (19°26'S, 57°04'W). The participants were the author and a volunteer previously unfamiliar with caimans.

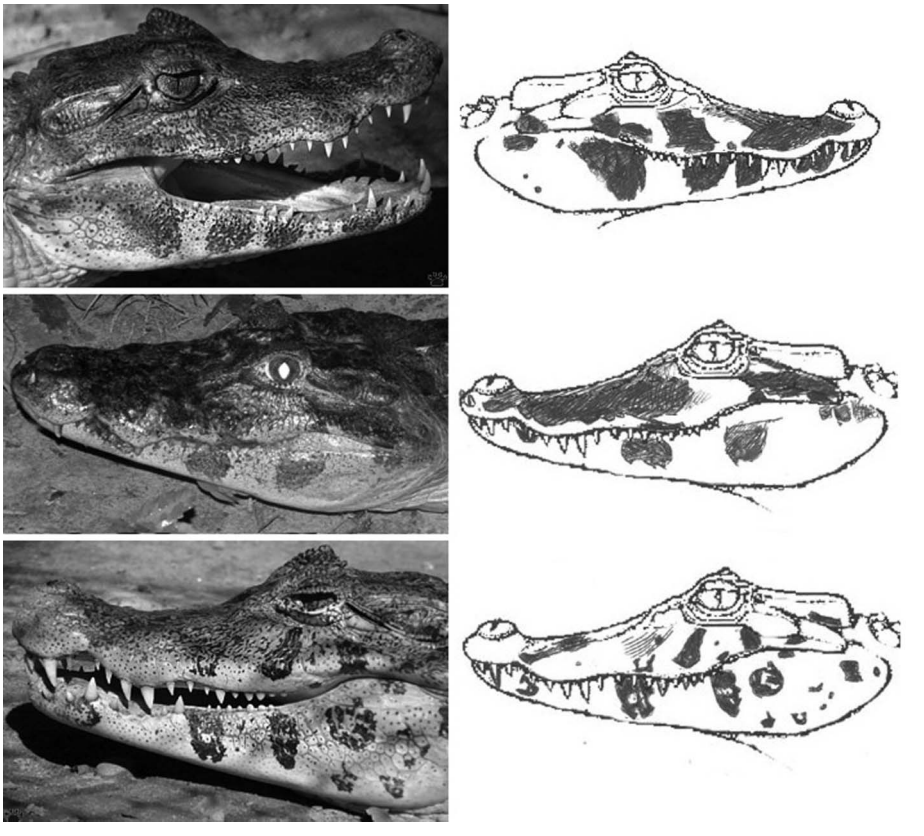

Fig. 1. — Facial markings of individual yacare caimans (left) and sketches of them made on pre-printed templates (right). Note that the bottom individual also has two lower teeth protruding through the upper jaw.

The test was conducted on a pond with a high concentration of caimans (no fewer than 160, as estimated by a rough night count). We used only animals estimated to be 1 m or more in total length. To avoid disturbing the animals, we 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, we walked along the pond, and took turns making sketches of the caimans' facial markings, using pre-printed templates (Fig. 1, 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 we again walked around the pond. Every caiman we 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.

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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; and 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 DINETS (2011a).

Data recording

ACs observed for any particular animal were scored 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 observed 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 these, 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.

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. In this and following sections, all analyses used significance levels of 0.05 and two-tailed tests. Statistical tests were performed using SYSTAT Version 12 software. Power analysis was performed using G*Power 3.1.4 software (FAUL et al. 2009), with power as (1-beta error) probability and β/α ratio of 1.

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RESULTS (STUDY 1)

In the Pantanal, the proportion of headslapping displays remained the same in 22 animals, increased in 11, and decreased also in 11. No test was needed since no net change was detected. The power of the test would be 0.75 for apriori effect size g = 0.15, and 0.94 for g = 0.25.

In NKMNP, the proportion of headslapping displays remained the same in 6 animals, increased in 8, and decreased in 12 ($P = 0.503$). The power of the test was 0.73 for apriori effect size g = 0.15, and 0.82 for g = 0.25.

For the two sites combined, the power of the test was 0.84 for apriori effect size g = 0.15, and 0.98 for g = 0.2.

It can be concluded that the caimans did not change the composition of their signals in response to the changes in aquatic habitat continuity. 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.

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STUDY 2. HABITAT-TO-HABITAT COMPARISONS OF ADVERTISEMENT CALL COMPOSITION WITHIN A GEOGRAPHICAL AREA

In the previous study, I 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 is 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.

I performed such comparisons of ACs on two species of crocodilians: the American alligator (*A. mississippiensis*) and the Nile crocodile (*Crocodylus niloticus*). The former species has two distinct AC types: bellowing display (bellows combined with infrasound) and headslapping display (headslap combined with infrasound, GARRICK & LANG 1977). The latter species can also use roars and headslaps within the same display (GARRICK & LANG 1977).

It has been found (DINETS 2011a) that American alligators inhabiting areas with only fragmented aquatic habitat use fewer headslapping displays than those living in areas with only continuous aquatic habitat; and that Nile crocodiles inhabiting areas with only continuous aquatic habitat use fewer roars than those living in areas with only fragmented aquatic habitat. If individual crocodilians can adjust their signal composition to habitat parameters, than it can be predicted that in populations of each species inhabiting both kinds of aquatic habitat, animals living in small bodies of water will differ in respectively similar ways from conspecifics living in large bodies of water.

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 American alligators (CHABRECK 1965; MOREA et al. 2002) and Nile crocodiles (COTT 1961; MODHA 1967; HUTTON 1989) are philopatric in areas of less than 1.5 km^2, and usually in the same bodies of water, for many years. Thus the majority of animals are long-term residents of a particular habitat type, and habitat-related differences in their ACs should be observable.

METHODS (STUDY 2)

Study sites

This study was conducted at two sites: Ocala National Forest (ONF) in north-central Florida (29°03–27'N, 81°30–42'W) and the southeastern edge of Oromo River Delta (ORD) in Ethiopia (4°28–29'N, 36°11–12'E). Observations in ONF were conducted in late April–mid-May 2008, and in ORD in November 2008. The mating season of the American alligator is from mid-April until late May (Neil 1971). For the Nile crocodile in Lake Turkana area it is from October until December (Modha 1967).

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 the Lake Turkana shoreline (as it was at the time of the study).

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Choosing and observing focal animals and recording data

Focal alligators and crocodiles were chosen and observed using the protocols described in Dinets (2011a). See Dinets (2011a) also for inter-observer reliability test data.

Observations of alligators continued until five ACs were recorded from each of 10 alligators in Lake George and 10 alligators in small ponds, with each of four 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 above). 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 10 crocodiles in Lake Turkana and 10 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.

Analysis

I used only the first five ACs recorded from each focal animal 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 had been 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 reported U is the Mann-Whitney U-test statistic.

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.

RESULTS (STUDY 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 ($U = 43$, $P = 0.642$). This result indicates 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 ($U = 36$, $P = 0.474$). This result indicates 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 ($U = 55$, $P = 0.734$), 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. The power of the test for apriori effect size d = 1 is 0.8.

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 ($P = 1.0$; test power 0.49).

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 ($P = 0.474$; test power 0.89).

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.

It can be concluded that animals living in large and small bodies of water did not differ significantly in AC composition. Their signaling was remarkably uniform across both habitats.

DISCUSSION

In the first study, animals living in rapidly changing habitats were observed before and after the change in habitat continuity. There were no changes in the relative frequency of use of roars and slaps.

In the second study, signal composition was compared between animals living in small ponds and large lakes within the same population (no more than a few kilometers from each other). In the study of allopatric populations (Dinets 2011 a) where habitat-related differences in signal composition were found, animals living in small and large bodies of water were separated by hundreds of kilometers, and inhabited geographical areas where only one type of habitat was available.

For both crocodiles and alligators, the results of the present study were clearly opposite to those of DINETS (2011a).

In the present study, there was no significant difference between crocodiles living in Lake Turkana and in adjacent small ponds. However, in the study (DINETS 2011a) comparing crocodiles from six different populations using similar sample sizes and statistical tests, there were significant differences in roar use ($P < 0.045$ or less) between any two populations with different habitat types.

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In the present study, there was no significant difference between alligators living in Lake George and in adjacent small ponds. However, in the study (DINETS 2011a) comparing alligators from six different populations using similar sample sizes and statistical tests, there were significant differences in headslapping display use ($P < 0.01$ or less) between any two populations with different habitat types.

The results of the present study show that differences between populations found in DINETS (2011a) are not a result of behavioral plasticity. Individual crocodilians maintain constant repertoires irrespective of habitat structure. Therefore the observed differences in signaling between species (DINETS 2011b) and between allopatric conspecific populations (DINETS 2011a) are evolved adaptations.

This is a surprising result, not only because the ability of individual animals to adjust their signaling to habitat parameters has been found in various vertebrate and invertebrate taxa (ORD et al. 2007; GORDON & UETZ 2011), but also because crocodilians are known to modify their signaling in captivity (DINETS 2011b), which means that they are not totally incapable of such modifications in response to environmental parameters.

Adjusting one's signaling to make it more efficient in one's habitat would seem highly advantageous. So, why don't individual crocodilians do that? Answering this question would be of great interest for our understanding of the evolution of animal communication. One possible, and testable, explanation is that in each population, females have stereotyped expectations of the kinds and numbers of signals their prospective mates should produce, so all males have to adhere to the same fixed signaling pattern.

Knowing that signal composition in crocodilians is innate opens a possibility to obtain rough estimates of the rates of evolution of signal composition by comparing populations with known divergence times living in different habitats. Times of divergence can be estimated from molecular data, or, in some cases, be known from historical, geological or paleoecological data. Isolated populations of Nile crocodiles in African deserts and of saltwater crocodiles (*Crocodylus porosus*) in crater lakes are particularly interesting in this respect. For example, it would be informative to find out if the population of saltwater crocodiles in tiny Lake Tolire Besar on Ternate Island, Indonesia, which became completely isolated as a result of a nineteenth-century volcanic eruption (DINETS 2011b), already differs in signaling from other populations.

However, these findings cannot be used to justify taxonomic changes based on differences in vocalizations. Even in crocodilian species with innate signal composition and structure, otherwise similar populations can markedly differ in signal parameters (DINETS 2011a).

The present study found no evidence that individuals adjust the composition of their signals to habitat parameters. It shows that numerous opposite findings for many taxa, including reptiles (ORD et al. 2007), cannot automatically be generalized to include other groups.

It is somewhat counterintuitive to find such intelligent and overall "advanced" animals as crocodilians to be less flexible in some aspect of their behavior than relatively "primitive" jumping spiders (GORDON & UETZ 2011) and frogs (LARDNER & BIN LAKIM 2002). Perhaps this shows once again that our notions of taxa being more or less "intelligent", "advanced", or "evolved" are always subjective, oversimplistic and unreliable.

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