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RESPONSES OF JUVENILE AMERICAN ALLIGATORS (*ALLIGATOR MISSISSIPPIENSIS*) TO CONTACT CALLS

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Abstract.–Crocodylians are known for their ability to vocalize throughout their lives in a variety of social and ecological contexts, particularly during their vulnerable juvenile life stage. However, few studies have analyzed juvenile calls in laboratory settings, fewer still have analyzed them across large sample sizes or with respect to sex and body size, and no studies to date have analyzed crocodylian vocalizations with respect to human conditioning in captivity or animal personality profiles. This study tests juvenile American alligators' (*Alligator mississippiensis*) ability to respond via movement and callback vocalizations to pre-recorded conspecific contact calls across a large sample size (n=36), and tests for relationships between response rates and juvenile body size and sex. Seventeen and sixteen individuals out of a total of thirty-six responded via movement toward the source of pre-recorded vocalizations across the first and second experimental trials, respectively, whereas none responded through movement toward control sounds; 75% of juveniles who vocalized did so only in response to contact calls rather than controls (though the latter difference was not significant given that only four vocalized in Trial 1, and only a single animal vocalized in Trial 2); there was also no significant difference in movement toward recorded vocalizations across size or sex. However, one particularly vocal individual whose upbringing in captivity was known was identified as a possible unique personality profile given its propensity for callback vocalizations in comparison to its fellow study subjects.

Keywords: juvenile, crocodylian, vocalization, contact calls, social behavior

Crocodylians are unique among extant non-avian reptiles with regards to their dependence on vocalizations and parental care throughout all or much of their lives (Britton 2001; Vergne et al. 2009; Somaweera et al. 2013). Much like their bite-force and feeding morphology (Erickson et al. 2012), crocodylian vocalizations are highly conserved (Senter 2008) and used in a variety of contexts, most of which involve social displays, courtship, group hierarchical formations and cohesion, or parent-offspring communication (Vliet

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1989; Vergne et al. 2009; Roberto & Botero-Arias 2013). Detailed understanding of their acoustic ecology is still unfolding, and studies of the purpose, context, and extent of their vocalizations are relatively new (Wang et al. 2007; Vergne et al. 2009).

Juveniles and hatchlings display their own unique set of vocalizations (Britton 2001; Vergne et al. 2007), including (1) pre-hatching calls that coordinate clutch hatching rates within eggs and stimulate the mother to excavate the nest, (2) contact calls, which are thought to maintain group cohesion in pods and alert conspecifics to environmental discoveries (e.g. food), (3) distress calls, which may facilitate protection from a parent and warn siblings of predators, and may be analogous to the "screech" vocalizations made by birds when held by predators, and (4) threat calls, such as snarls or hisses, which are not dissimilar from adult hisses that also signal aggression.

The juvenile stage of all crocodylians is considered the most difficult to study given this stage's cryptic nature and vulnerability to predators (Brien et al. 2013; Somaweera et al. 2013). During the early parts of this life phase, juvenile crocodylians tend to congregate in sibling or neighbor groups called pods or crèches, and the extent to which they stay in these groups varies by species (Vergne et al. 2009; Somaweera et al. 2013; Brien et al. 2013). American alligators are known to maintain these crèches anywhere from one to three years (Somaweera 2013), and can include older siblings from previous clutches (Brien et al. 2013). A possible explanation for alligators' extended juvenile congregations is their sociable nature and high tolerance of conspecifics relative to other crocodylians (Brien et al. 2013). Alligators tolerate group-living conditions in captivity, are known to gather en masse frequently in the wild, and are among the least aggressive of all crocodylians. Species' aggressiveness and tolerance of conspecifics have been tied to dispersal rates among juveniles (Brien et al. 2013).

Fundamental to juveniles' intraspecific sociability and maintaining crèche stability are their use of contact calls, sometimes described as soft grunts by casual observers. Explored recently in black caimans (*Melanosuchus niger*), spectacled caimans (*Caimain crocodylus*), and Nile crocodiles (*Crocodylus niloticus*) by Vergne et al. (2007; 2009; 2011; 2012) based on earlier work by Campbell (1973) and Herzog & Burghardt (1977), the contact call is the primary vocalization through which juveniles communicate with each other and adults. Its acoustic parameters can be modulated into the similarly sounding distress call depending on environmental context, and its peak 1000 Hz frequency output in alligators (Young et al. 2014) corresponds to the most sensitive frequencies of adults' hearing range (100-8000 Hz in air) (Higgs et al. 2002; Bierman & Carr 2015).

Given their vulnerability to predation prior to sexual maturity (~ 1.85m in length for *A. mississippiensis*, Lance 2003), the difficulty of studying juvenile crocodylians in the wild, and the applicability of Crocodylia "order-specific" vocalization information across species (Britton 2001; Vergne et al. 2012), understanding the function of juvenile crocodylian vocalizations in general, and contact calls in particular, may be crucial to understanding the ecology of these keystone apex predators (Sergio et al. 2008; Mazzotti et al. 2009; Fujisaki et al. 2012). The goals of this experiment were to test whether juvenile alligators respond to pre-recorded contact calls in a laboratory setting, and if so, whether the rate or degree of response varied according to size, sex, or individual personality profiles. This study not only replicates certain aspects of similar studies (Campbell 1973; Herzog and Burghardt 1977; Vergne et al. 2012), but provides additional analysis regarding possible trends in juvenile response by way of a sizeable data set (*n* = 36). This experiment further raises questions regarding the influence of isolation on juvenile alligator responses to conspecific vocalizations, and provides the first analysis of a possible crocodylian personality archetype.

MATERIALS & METHODS

Study site and subjects.–This project was conducted at Gator Country, a privately owned alligator refuge and reptile pet rescue center outside of Beaumont, Texas. My test subjects were 36 juvenile American alligators (18 male, 18 female), ranging from 33-104 cm ($\bar{x}$ = 75.92 cm, median = 75.50 cm, *SD* = 12.65 cm). All juveniles were marked with Roman numerals for identification, 1 – 18 (i.e. I – XVIII), and colored by sex (blue for males, pink for females) with nail polish. All individuals were sexed on-site (Joanen & McNease 1978).

Time spent in captivity ranged from those who were bred on site to those who had been rescued from the wild as recently as a few months before the study began. Unfortunately, information was not available concerning how long each individual had been in captivity.

Living quarters and experimental area.–The juveniles lived indoors in a tank that measured approximately 2 m x 2 m x 1.5 m, filled with approximately 1 m^3 volume of water, with a 0.50 m^2 basking platform. Their test area was an enclosure housed in a separate room of the facility, measuring 2 m x 1 m x 1 m, utilizing two of the room's walls constructed by positioning a sheet of plywood and a plastic lid with observation holes against a sink counter. Thus, the testing enclosure was closed on all six sides.

Exemplar and control recordings.–Four different recordings, or exemplars, of juvenile alligator calls were used, one professionally recorded from the Cornell University Laboratory of Ornithology, and three amateur recordings from the video file-sharing website, YouTube.com. The professional recording and one of the YouTube recordings involved passive human handling of juveniles while they called, one amateur recording involved a stationary juvenile calling with no visible harassment or prompting, and the context of the remaining amateur recording was unknown. Two control audio samples were also used, one of Canada geese (*Branta canadensis*) calls from the Laboratory of Ornithology, and one of static “white noise” from YouTube.

Audio bitrate quality was not listed for any sources, but all three amateur samples’ frequency peaked at approximately 1000 Hz. The Lab of Ornithology sample’s frequency could not be analyzed, but qualitatively sounded comparable to the YouTube sources, if not of higher bitrate quality. All recordings were played at an identical volume (the device’s maximum output) from an Acer Aspire S7-391-6818 laptop computer with two Dolby Home Theater stereo speakers directly adjacent to the plastic wall of the experimental chamber.

Experimental protocol.–One randomly selected juvenile at a time was removed from their living enclosure and placed into the experimental enclosure and allowed to acclimate for 5 minutes. After this acclimation period, each individual was exposed to 2 one-min sessions of either a control sound or exemplar recording. The order of playing either exemplar or control first was determined randomly, as was the type of control played for each individual. Finally, a pre and post-exposure “buffer” period of 1 min was allowed before and after each stimulus.

Observations were carried out through the aforementioned observation holes, and each individual was returned to the living enclosure after experimentation. Because the experimental area was in an isolated section of the Gator Country facility and auditorily isolated from the animals’ living quarters, there was no possibility of individuals being conditioned to stimuli prior to testing. Observations were repeated over two trials (i.e. each alligator was tested two times, once per trial), with each trial carried out over two days, for a total of four days of testing. No individual was tested two days in a row.

Defining animal responses to stimuli.–Juveniles’ responses to either control or exemplar recordings were separated into four mutually exclusive categories: No Response, Movement, Movement

Toward Source, and Callbacks (the one exception being Callbacks did not exclude Movement Toward Source), which are described as:

> *No response*: Animal was stationary prior to, during, and immediately after stimuli.
>
> *Movement*: Animal was moving before, during, or after stimuli with no apparent response to stimuli; animal may have been perimeter-patrolling or moving in erratic, unpredictable patterns. The presence/absence of stimuli appeared to have no effect on degree of movement, either in speed or direction.
>
> *Movement toward source*: Animal was either stationary or moving in a direction away from stimuli, and subsequently changed position and moved directly toward stimuli *after* it was presented. Animal may also have attempted to push edge of pen or dig its way out in direction of stimuli.
>
> *Callbacks*: Animal vocalized during or immediately after, but not before, stimuli were presented. If calls were initiated before stimuli during 1-min pre-exposure period, and continued into exemplar/control exposure *without* pause, vocalizations were not categorized as callbacks.

Only the last two categories were analyzed as broader responses to stimuli. If the animal of interest showed no movement with regards to either control or exemplar or moved throughout exposure to pre-recorded stimuli with the recordings appearing to have no influence on movements, those trials were not recorded as "responses."

RESULTS

All response rates to exemplars were compared to response rates to control sounds through chi-square tests. I found a significant difference between responses through movement toward stimuli of recorded juvenile contact calls and control sounds. Seventeen of 36

Table 1. An analysis of the response rate of juveniles via movement and callbacks to different exemplars of pre-recorded contact calls. Each exemplar was played for each individual (18) for a total of 72 sessions. There was a significant difference in the rate of movement response across exemplars (trial mean, $\chi^2 = 9.45$, $df = 3$, $P < 0.05$).

Exemplar No.	Type of Response	No. Responses/72 Sessions
Exemplar 1	Movement toward Source	15
	Callbacks (Vocalization Response)	2
Exemplar 2	Movement toward Source	5
	Callbacks (Vocalization Response)	1
Exemplar 3	Movement toward Source	10
	Callbacks (Vocalization Response)	0
Exemplar 4	Movement toward Source	3
	Callbacks (Vocalization Response)	2

animals responded by way of movement to playback calls in Trial 1 ($\chi^2 = 22.26$, $df = 1$, $P < 0.005$), while 16 of 36 animals responded through movement in Trial 2 ($\chi^2 = 20.57$, $df = 1$, $P < 0.005$). All responses to exemplars are listed in Table 1. Not one animal responded by movement toward controls in either trial (Fig. 1).

However, there was also a significant difference in movement response rate among exemplars, with juveniles responding 15 times to Exemplar 1, 5 times to Exemplar 2, 10 times to Exemplar 3, and 3 times to Exemplar 4 across both trials, (trial mean, $\chi^2 = 9.45$, $df = 3$, $P < 0.05$). Much of this difference may be explained by the quality of recordings, with Exemplar 1 being the professionally recorded juvenile contact calls, and Exemplars 2-4 being amateur recordings and thus, in theory, being of inferior audio quality.

No significant difference between vocalization (callback) responses to control and exemplars was found (trial mean, $\chi^2 = 1.391$,

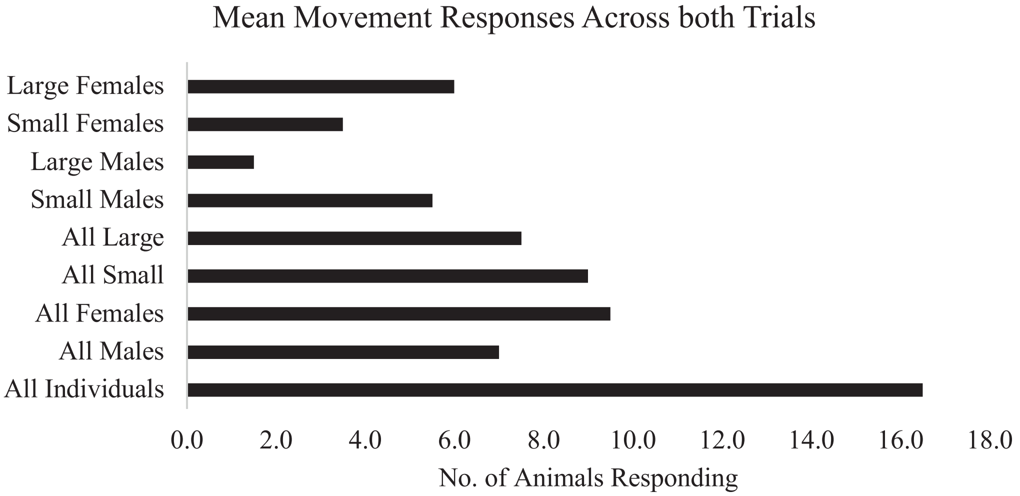

Figure 1. The mean number of juveniles responding to pre-recorded contact calls via movement across both trials. Size classifications: large = 76 – 104 cm; small = 33 – 75 cm. No juveniles responded via movement to control sounds.

df = 1, *P* = 0.238), nor was there any significant difference in movement responses between sexes (trial mean, $\chi^2 = 0.699$, *df* = 1, *P* = 0.403) or across size (categories defined as small = 33 – 75 cm, large = 76 – 104 cm; trial mean, $\chi^2 = 0.252$, *df* = 1, *P* = 0.617). Only four animals vocalized in response to contact call playbacks in Trial 1, while one responded to a control, whereas only one animal vocalized to playbacks and no animals vocalized to control sounds in Trial 2. There was, however, a noticeably more vocal individual, Female no. 18 (dubbed “Tiny”) who responded with almost as many callbacks (*n* = 14) as the other three individuals who vocalized (*n* = 15). Tiny was also the only individual who vocalized in both trials.

DISCUSSION

The purposes of this experiment were to further test juvenile American alligators’ ability to recognize and respond to conspecific contact-calls within a laboratory environment, to identify if responses varied by sex or size, and to establish if individuals exhibited identifiable personality profiles. The significance of crocodylians’ acoustic ecology to their survival is widely recognized (Vliet 1989; Britton 2001; Wang et al. 2007; Vergne et al. 2009; Dinets 2011), particularly for a species as vocal as the American alligator (Vliet 1989; Wang et al. 2007). Given alligators' (and all crocodyilans') vulnerability and secretive nature during their post-hatchling, pre-sexual maturity stage (9-15 yrs in *A. mississipiensis*, Ferguson 1985; Somaweera et al. 2013), information regarding their ability to maintain group living and communication is vital to understanding their life history. Additionally, variability in individual crocodylian personality may provide valuable information for species behavior in captivity.

Similar previous studies have focused on the acoustic structure of juvenile crocodylian calls (Campbell 1973; Herzog & Berghardt 1977; Britton 2001), but otherwise were strictly observational in nature. Vergne et al. (2012) is perhaps the closest comparable study to this experiment, another controlled experiment testing whether one-month-old juveniles across several species responded to playback of not only conspecifics, but other crocodylian species. A notable element of this study is the aforementioned large sample size (*n* = 36) of a single species, in comparison to the smaller samples examined by Campbell (1973) (n = 6, four species), Herzog & Berghardt (1977) (n = 17, four species), Britton (2001) (*n* = 6, one species), and Vergne (2011) (*n* = 22, two species).

I observed a significant difference in response rates between recorded alligator contact calls and control sounds by way of movement toward the former. Though response to different call exemplars was also significant, this trend may be explained by the precision of those recordings (i.e. professional vs. amateur sound recordings), and it is notable that juveniles in both trials responded to all exemplars at least once. Conversely, not a single animal responded to a control source by way of movement.

There were no significant differences between movement responses across sex or size, however. It is possible there are no meaningful behavioral differences between males and females at this size or age range, and thus little inclination to respond to a greater or lesser degree between the sexes. While studying agonistic behavior in seven crocodylian species, Brien et al. (2013) never specified any differentiation in aggression by sex, and though Lance (2003) noted that there are distinct hormonal cycles in male juvenile alligators and no such comparable cycles in females of similar age, growth rate differences between sexes are not detectable until sexual maturity around 1.85 m in length.

I expected some variation in movement response between smaller and larger individuals, anticipating the former to respond more than the latter. Given that these individuals had acclimated to captive group-living for at least a few months, if not a few years, perhaps their immediate isolation during the experiment would make them equally likely to respond to contact calls regardless of size. Moreover, though juvenile crocodylian survival is highly dependent on size, perhaps the size range tested here (33 – 104 cm) was not large enough to detect a significant difference in responses. Given how rapid growth is during crocodylian adolescence (Lance 2003, Somaweera 2013), though, and how rapidly mortality in the wild declines as juveniles grow (Britton 2001; Somaweera 2013), this explanation seems unlikely.

The fact these juveniles as a group responded significantly to pre-recorded contact calls was anticipated given similar results in previous crocodylian bioacoustic studies (Campbell 1973; Vergne et al. 2012). Vergne et al. (2012) findings that multiple species can detect “crocodylian-specific” vocalization information through artificially altered signals, and American alligators’ general sociability and vocal nature (Vliet 1989; Wang et al. 2007) also predicted significant behavioral responses in similar experiments. These individuals would have much to gain and little to lose by seeking shelter among conspecifics of similar size, including safety from predators and greater ability to detect food. Moreover, juvenile crocodylians, including alligators, have been known to congregate even without the presence of a protective adult, and prefer to congregate with conspecifics, including non-related individuals, in captivity (Somaweera et al. 2013).

Juvenile alligators vocalized more in response to recorded contact calls than controls in both trials, but these differences were not significant. Indeed, although three individuals vocalized numerous times in Trial 1 and one individual (Female no. 18) vocalized in both trials, these totaled only five callback sessions (compared to one vocalization in response to a control, also by Female no. 18) out of a combined 144 sessions of either control or contact call stimuli. Why were there so few vocalizations despite significant responses through movement?

One possible hypothesis has to do with the juveniles' isolation, the experimental design of this study. Given smaller alligators' vulnerability to predation, perhaps responding through vocalizations of their own may disclose their position to predators. A juvenile conditioned to living in a pod may be apt to orient themselves toward contact calls if separated from their group, but may not be as likely to respond with their own vocalizations; if they can locate their pod without compromising their location, that may be the safest response strategy when separated. Future research could determine whether juvenile contact calls are related to isolation, crèche size, or proximity to adults.

A limitation of this study is variation in juvenile time in captivity. The animals in this study represented a diverse collection of alligator rescues from the previous summer, rescues from years past, and individuals that had been born and raised entirely in captivity. It was impossible to determine how long individuals had been in captivity because the animals were not marked prior to this study. This may have significant yet unknown implications for this study, given how Kerfoot et al. (2014) found that feedings mechanisms of juvenile *A. mississipienses* scale allometrically with age, that Erickson et al. (2004) found significant differences in biomechanical performance between captive and wild individuals, and that Dinets (2013) noted how adult vocalization behavior differs in captivity.

Another possible limitation of this study involves the acoustic similarities of different juvenile crocodylian calls and possible mislabeling of the recordings themselves. Campbell (1973) and Herzog & Burghardt (1977) noted the subtle gradation of juvenile crocodylian contact calls (labeled as "barks" or "grunts," respectively) into distress calls, which Britton (2001) and Vergne et. al (2009) pointed out are sometimes difficult for humans to discern while yielding opposite reactions among their pod recipients (i.e. one attracts siblings, the other repels them).

That being said, these authors acknowledged contextual and environmental factors involved in differentiating contact vs. distress calls (e.g. the presence or absence of an intruder, the presence or absence of food or other stimuli, etc.), and given the non-threatening situations of this experimental procedure (no individuals were harassed within the testing area; all individuals were allowed to acclimate to their surroundings), it is unlikely my test subjects were coaxed into producing unnatural reactions to distress or contact calls out of context. Individuals responded positively or neutrally to pre-recorded vocalizations, while none were repelled by them, implying these recordings functioned the way contact calls would in the wild.

One final notable observation of this experiment involves a possible personality profile on Female no. 18 ("Tiny"), who had been born and raised in captivity and used as a "show animal" for the past year. Tiny was well habituated to humans by the time of this experiment, and had been observed responding to conspecific calls in other enclosures prior to this experiment. Her distinct sociability may be noted in her increased tendency to vocalize. As previously noted, she vocalized almost as frequently as the rest of her cohorts combined (14 calls vs. 15 calls) and was the only individual who vocalized in both trials, including to different exemplars.

Animal personality is defined as a stable, consistent suite of behaviors across a variety of different environmental or social contexts, independent of (or in addition to) broader sexual and ontogenetic trends of a given species (Carere & Eens 2005;

Bergmuller & Taborsky 2010; Carere & Locurto 2011). Personality profiles have been identified in hundreds of species from insects to all major groups of tetrapods, but this experiment is the first, to my knowledge, which identifies a possible personality archetype in crocodylians.

Analysis of crocodylian behavior by way of exposure to human presence could have important implications for crocodylian management in the wild and behavioral diagnoses in captivity. Given American alligators' particularly sociable nature, testing how young individuals develop in relation to humans and in the presence (or absence) of conspecifics may lend insight into how individual behaviors (such as vocalizations) are shaped in relation to social hierarchies or through social niche specialization (Bergmuller & Taborsky 2010; Dingemanse et al. 2010). Possible variation in social behavior may be further juxtaposed to alligator foraging specialization (Rosenblatt et al. 2015) and habitat use patterns (Rosenblatt et al. 2013).

In conclusion, this study reaffirms juvenile alligators' ability to recognize and respond to conspecific contact calls in a laboratory setting, raises questions as to the influence of isolation on juvenile vocalization, and offers insights into crocodylian personality profiles. I did not find any relationship between juvenile sex or size and response rate, either in movement toward sound sources or vocalizations. Prior to sexual maturity, it may be in juvenile alligators' interest to stay in a crèche given its defensive benefits against predators and combined ability to detect food or shelter, and size differences under 1 m may not influence conspecific tolerance or influence benefits of their company. Finally, alligators raised in captivity may offer further insight into animal personality development, and further research may reveal additional nuances of crocodylian individuality and social plasticity.

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