

AN ABSTRACT OF THE THESIS OF

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Title: Sound Production in the Small-mouthed Salamander (*Ambystoma texanum*)

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Auditory signals are commonly used by vertebrates to communicate with one another. While not all vertebrates communicate in this way, vocal communication is an essential part of defense, courtship, and social cohesion in several taxa. Among the amphibians, frogs are well known for their vocalizations, some of which are used by males to attract females at breeding pools. The other extant amphibians (salamanders and caecilians) are generally regarded as mute. Despite this widespread assumption, there are numerous anecdotal reports of both aquatic and terrestrial salamanders that vocalize. Very few studies have attempted to put these sounds into any sort of behavioral context, despite the potential utility (e.g., mate attraction) such sounds may have. While salamanders are extremely limited in their ability to detect sounds transmitted through air, they are able to detect water-borne sounds. I placed Smallmouth Salamanders (*Ambystoma texanum*) into 19L plastic tanks containing aged tap water, and used hydrophones in an attempt to document underwater sound production in this species. Each tank contained one of the following combinations of salamanders: Isolate male, Isolate female, Male/Female pair, and Female/Female pair. I investigated a possible social context for the production of sounds by comparing the number of sounds produced in each tank. Although sound

production was rare, it was recorded at least once in 86% of tanks. No social grouping tested promoted sound production significantly differently from any other, but verifying that sound production occurs in this species at all is an important step in studying the behavior of Small-mouthed Salamanders and non-anuran amphibians.

Keywords: behavior, courtship, salamander, sound production

SOUND PRODUCTION IN THE SMALL-MOUTHED SALAMANDER

(AMBYSTOMA TEXANUM)

A Thesis

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PREFACE

This thesis was prepared following the publication style of the *Journal of Herpetology*. All organisms were collected under a Kansas Department of Wildlife, Parks and Tourism Collectors Permit (SC-029-2013). All research was conducted in accordance with the American Society of Ichthyologists and Herpetologists, Society for the Study of Amphibians and Reptiles, and Herpetologist's League guidelines for use of reptiles and amphibians in field and laboratory research (HACC, 2004), and all lab work was approved by Emporia State University's Animal Care and Use Committee (ESU-ACUC-13-002).

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INTRODUCTION

Auditory signals are commonly used by vertebrates to communicate. Among the most vocal vertebrates are the birds and amphibians (e.g., Rand and Ryan 1981, Ballentine et al. 2004), but members of most vertebrate classes are known to generate sound signals (examples: Colson et al. 1998 [bony fish]; Gans and Maderson 1973 [non-avian reptiles]; Palacios et al. 2007 [mammals]). These signals serve a variety of social functions, including group cohesion, aggression/conflict, alarms, and courtship displays (Bradbury and Vehrencamp 2011). Knowledge of an organism's sound-signal repertoire is therefore essential in understanding its natural history (Kroodsma 1983), recognizing threats which may interfere with effective communication (e.g., Bee and Swanson 2007; Crovo et al. 2015), as well as increasing our knowledge of the diversity of communication systems in different taxa (Bradbury and Vehrencamp 2011).

Among amphibians, frogs produce the most easily observed vocalizations. Not surprisingly, frogs are common test subjects in studies of vocalization (Gerhardt and Huber 2002). Their calling behavior is typically observed in breeding aggregations, and the most commonly heard vocalizations are "advertisement" calls, which are used by males to attract females and warn away competitors (Pough et al. 2004). In addition to general advertisement, specific information on individual identity (e.g., body size) is often conveyed (Bee and Gerhardt 2001). Many other vocalizations are used in situations involving conspecifics or potential predators (Cardoso and Heyer 1995; Emerson and Boyd 1999; Cooper 2011).

In contrast to frogs, the vocalizations of other amphibian groups have received very little study (Vitt and Caldwell 2009). Salamanders and caecilians, as well as some

frogs, lack external ears (Wever 1985), and therefore it is commonly assumed that they cannot hear with sufficient sensitivity to make auditory communication feasible. Many amphibians and reptiles that lack external ears are, nonetheless, able to transmit sounds through alternative pathways to the inner ear (Narins et al. 1988; Hetherington 2001). Earless frogs of the genus *Atelopus* have low and high frequency hearing comparable to that of eared frogs, which is presumably accomplished by transmitting vibrations along the opercularis muscle (Jaslow and Lombard 1988), although the exact coupling mechanism is unknown. The inner ear of salamanders (Wever 1985) and caecilians (Wever and Gans 1976) is also able to detect external sounds.

Wever (1985) documented the inner ear sensitivities to aerial sounds in a wide variety of amphibians. Salamanders are well represented in this account, and most show optimal hearing sensitivities between 200 and 1000 Hz. Specific examples include: *Ambystoma maculatum* (optimal hearing range from 400-600 Hz), *A. texanum* (200-500 Hz), and *Taricha torosa* (500-1000 Hz). Wever admits, in the same study, that his measured sensitivity ranges may not precisely match the sounds that salamanders are able to respond to behaviorally. More recent research indicates that airborne sounds are largely detected via the vibrations they induce to the substrate and the body of the animal, which is a relatively insensitive mechanism for audition (Christensen et al 2015).

In water, salamander ears should behave similarly to fish ears. In both groups there is no specialized tympanum present or necessary, since sound is able to propagate easily from water into living tissue (Bradbury and Vehrencamp 2011). The inner ears of fish contain three or more otoliths, dense masses that respond to sound vibrations more slowly than the surrounding tissues do, and thus allow detection of the resulting

difference in motion between otolith and sensory cells. In amphibian ears the tectorial masses within the amphibian and basilar papilla serve an analogous function (Wever 1975). This method functions best when sound sources are nearby and of high amplitude relative to background noise (Schellart and Wubbels 1998). To detect sound vibrations from far-field sources, most fish make use of the secondary vibrations of their swim bladder or similar air-filled sacs reacting to the sound vibrations (Schellart and Wubbels 1998). With the exception of Plethodontids, similar air-filled sacs are available to salamanders in the form of lungs. Fish without swim bladders are still able to hear, however, although their sensory bandwidth and sensitivity is greatly reduced (Fay and Popper 1974), so it is possible that even lungless salamanders can perceive underwater sounds.

The majority of behavioral research that has been conducted on auditory communication in salamanders has been conducted on aquatic species. Evans and Ding (2005) detected a variety of vocalizations in the Chinese Giant Salamander (*Andrias davidianus*). The specific sounds the authors examined were used during territorial behavior and agonistic interactions between males, although they suggested that the salamanders also emitted other sounds outside of the formal trials. Davis and Brattstrom (1975) documented three distinct sounds produced repeatedly by California Newts (*Taricha torosa*). These sounds seemed to be used primarily in conspecific recognition and exploration of the salamanders' immediate surroundings, and all three were performed by both sexes. Large, aquatic salamanders such as mudpuppies (*Necturus* spp.) and amphiumas (*Amphiuma* spp.) produce "barking" noises when handled (Conant and Collins 1998), although these vocalizations have not been the subject of any particular

study. Terrestrial Marbled Newts (*Triturus marmoratus*) use the breeding choruses of Natterjack Toads (*Bufo calamita*) to locate pools suitable for their own breeding activities (Diego-Rasilla and Luengo 2002). It is worth mentioning that this level of terrestrial hearing is well beyond what Wever (1985) predicted to be within the capabilities of any salamander ear. Lesser Sirens (*Siren intermedia*) respond to playbacks of sounds produced by conspecifics by orienting and swimming toward the source (Gehlbach and Walker 1970). A commonality of all of these studies is that they were conducted using almost entirely aquatic salamander species.

In contrast to aquatic salamanders, terrestrial salamanders have been the focus of very little behavioral research regarding sound production. There have, however, been numerous observations of sounds produced by either fully or mostly terrestrial species. Such incidental observations are surprisingly common, considering how little study has been done on the functions of these behaviors. Members of the families Plethodontidae and Ambystomatidae are both well represented in these accounts (Maslin 1950; Neill 1952; Marshall 1997; Smith and Barichivich 2001; Hossack 2002; Milanovich and Trauth 2005). However, while a variety of clicking and squealing noises have been observed, their potential behavioral significance (e.g., mate attraction, predator deterrent) has usually been dismissed out-of-hand as being minimal or nonexistent (e.g., Hossack 2002; Gehlbach and Walker 1970), or otherwise not elaborated upon.

Wyman and Thrall (1972) reported the only documented aquatic sound production in a mostly terrestrial salamander. The salamander they examined was the Spotted Salamander (*Ambystoma maculatum*), a species that only enters water briefly in the early spring to breed. While sound production was rare, they detected two distinct

types of sound, one of which was only made during the breeding season immediately preceding and following mating. Although both sexes vocalized, they did so more frequently when in groups with other members of their sex (e.g., females vocalized more often in groups of other females). Furthermore, the recorded sounds were all of relatively low frequency (500-1500 Hz), which are more readily transmitted underwater (Hetherington 2008). Wyman and Thrall (1972) is the only published study on Ambystomatid sound production, and it hints at the potential for these largely terrestrial salamanders to utilize sound as a part of their aquatic courtship and mating behaviors. Christensen et al. (2015) provided further support for this by showing that larval and adult *A. mexicanum* are capable of detecting sounds underwater at biologically relevant levels.

I have personally observed Small-mouthed Salamanders (*Ambystoma texanum*) produce sounds above water. When held in hand, individuals periodically inflate their buccal cavity with air and then quickly expel it, producing a “clicking” noise. Handling seemed to be the primary motivator for producing this noise. I conducted a study (AWC, unpubl. data) to detect any effect social context might have on the number of sounds a salamander produced when an attack was simulated via handling (i.e., whether salamanders were more likely to vocalize when a group was “attacked,” as opposed to an individual). I hypothesized that the sound could function as an anti-predator mechanism, either by startling the predator or alerting conspecifics in a densely packed breeding aggregation, and was thus elicited in response to an apparent attack. No difference in the number of vocalizations was detected, but sample size was low ($n=9$), and the possibility remained that the salamanders were also vocalizing underwater or in untested social

contexts. My present study was designed to address this possibility and gain further insight into what prompts the behavior.

The objectives of my study were to: 1) determine whether or not Smallmouth Salamanders (*Ambystoma texanum*) produce sounds underwater, 2) examine the influence of conspecifics on the number of sounds produced by recording salamanders in isolation and the presence of another individual, 3) examine the influence of gender on the number of sounds produced by varying the gender of both isolated and paired individuals, and 4) determine whether perceived predation threat will elicit underwater sound production. I hypothesized that sound production does occur while these salamanders are underwater, and that these sounds are used as a part of courtship and predator avoidance. Certain sounds should, therefore, be elicited more often in the presence of a member of the opposite sex than in other social situations, while others increase in the presence of a predator.

MATERIALS AND METHODS

Collection and Maintenance. – *Ambystoma texanum* were collected in eastern Kansas, USA, on rainy nights (~2100-0100 hrs) from mid-February through late March of 2013 when salamanders were migrating to breeding pools. Most salamanders were collected in or near a known breeding pool near the town of Neosho Rapids, KS (38.372658°N, 95.982703°W; WGS 84). Additional specimens were collected at a known migration site near the city of Emporia (38.404845°N, 96.135200°W; WGS 84), approximately 14 km from the Neosho Rapids pool. Breeding pools at both sites were flooded ditches alongside rural roads. In total, 56 *A. texanum* were captured for use in this project, of which 48 were used in data analysis (the remaining 8 were males which did not fit into one of my four social contexts). Individuals were sexed and separated into same-sex tanks containing only moist paper towels until they could be placed into their trial tanks.

Trial tanks were 19L Sterilite® containers, filled with aged tap water (1+ days) to an approximate depth of 15cm. Rocks, bricks, dead leaves and sticks were added to approximate a natural breeding environment. In each tank, one of the rocks or bricks was not completely submerged, providing the salamanders a place to leave the water. During an exploratory study in 2012, these mesocosms were sufficient to induce the deposition of spermatophores and viable eggs (many of which eventually hatched). While breeding activity within tanks did not approach the levels observed in 2012, two instances of spermatophore and egg deposition occurred, indicating that these tanks were acceptable for breeding behavior. I changed water and cleaned all tank materials once per week for the duration of the study (March-July). A single earthworm was provided for each

salamander once per week. All salamanders remained in these tanks for at least 24 hrs before testing commenced.

Salamanders were rotated between trial and holding tanks as needed to accommodate treatments for all experiments. After a trial was completed, the residents of that tank were placed in temporary holding containers. Holding containers were circular plastic crispers 18.5 cm in diameter and 8 cm deep. Each container had a thin layer of water as well as three wadded paper towels to allow salamanders to avoid sitting directly in the water. All salamanders rotated between the trial tanks and holding containers twice over the course of the study.

Experimental Design. – Salamanders were assigned into four treatment groups: Isolate Male, Isolate Female, Male/Female Pair, and Female/Female Pair. Each treatment group contained eight replications, and each individual or pair was kept separate from other salamanders for the duration of the study. This was done to allow for detection of any possible social (e.g., courtship) function of sounds produced, should they be detected. The number of males collected was insufficient to allow for a Male/Male Pair treatment containing the full eight replicates, so that treatment was omitted from analysis.

All salamanders went through four recording sessions (spring trial, summer trial, predation trial, and no-predation trial). Each recording was accomplished using an H1 Zoom digital recorder (Zoom Corporation, Tokyo, Japan) was connected to a SS03-10 model hydrophone (Cetacean Research Technologies, Seattle, WA) placed within a trial tank approximately 10cm below the waterline, resting flat on the bottom of the tank. A Nikon P90 digital camera (Nikon Corporation, Japan) placed above the tank recorded movements of the salamanders during each recording. A single recording session

consisted of two hydrophones placed in two different trial tanks (chosen randomly among replicates), and one placed in an empty control tank. Rocks/bricks were removed immediately before each recording so that salamanders were confined to the water. Recordings were conducted no earlier than 1 hr after sundown, and new recording sessions were conducted until I had worked through all trial tanks (typically after approximately 4 hrs). All recorders were switched on within 5 sec of each other, as was the camera suspended over the two tanks with salamanders present. Tanks were illuminated with a single red incandescent light suspended directly above the tanks to provide illumination for the video recording. This design did not allow sounds produced by different individuals in the same tank to be traced to their source, so pairs of salamanders were treated as one sound-producing “unit” in these sessions. Once I left the room, all equipment was allowed to run for 30 min. After all recording sessions were completed in an evening, I rotated new salamanders into the trial tanks and moved the old ones into holding containers. Trial tanks were washed with bleach between occupants.

Spring trials were conducted from late March to early May. This time frame encompasses the late stages of the breeding season as well as the time immediately after it. I hoped to capture any sounds produced in relation to courtship and egg deposition (if present). Summer trials were conducted in July, well after the end of the breeding season, when *A. texanum* is not normally aquatic, but were otherwise identical to Spring trials. By comparing these recordings to the Spring trials, I hoped to detect an effect of season on sound production.

Predation trials were completed immediately (<24 hrs) after the Summer trials, and salamanders were placed into tanks in the same way. Two tanks containing the same

social groups were tested at the same time (e.g., Female-Female and another Female-Female tank). One of the tanks was randomly designated the “predation” tank, and the other the “no predation” tank. As before, an empty tank served as a control for external noise during these trials. The salamanders in the predation tank were handled roughly (e.g., flipped over, held by the tail, chased) for approximately 20 sec before any recording commenced. Salamanders in the no predation tank were left unmolested. Recordings lasted for 15 minutes but otherwise were identical to the spring and summer trials. All treatments and replicates were tested in this way.

All recordings were examined using Raven Pro 1.4 sound analysis software (Cornell Lab of Ornithology, Ithaca, NY). Recordings were run in Raven, and all sounds that could not be ascribed to random noise were noted. Each recording was then compared to its associated empty-tank recording. Any sounds from the trial tanks recorded within 5 seconds of a sound from the empty tank were disregarded as external noise. This wide buffer was created to be certain that I did not count any stray echoes as sounds originated from the salamander(s). Also disregarded were any sounds produced when a salamander was seen on video brushing against the hydrophone or nearby objects. Such sounds were fairly distinct in the Raven Pro window (Fig 1) and were generally discarded on sight. Any sounds remaining were used for analysis. Sounds were characterized based primarily on dominant frequency and secondarily on amplitude (which could vary based on the position of the salamander relative to the recording).

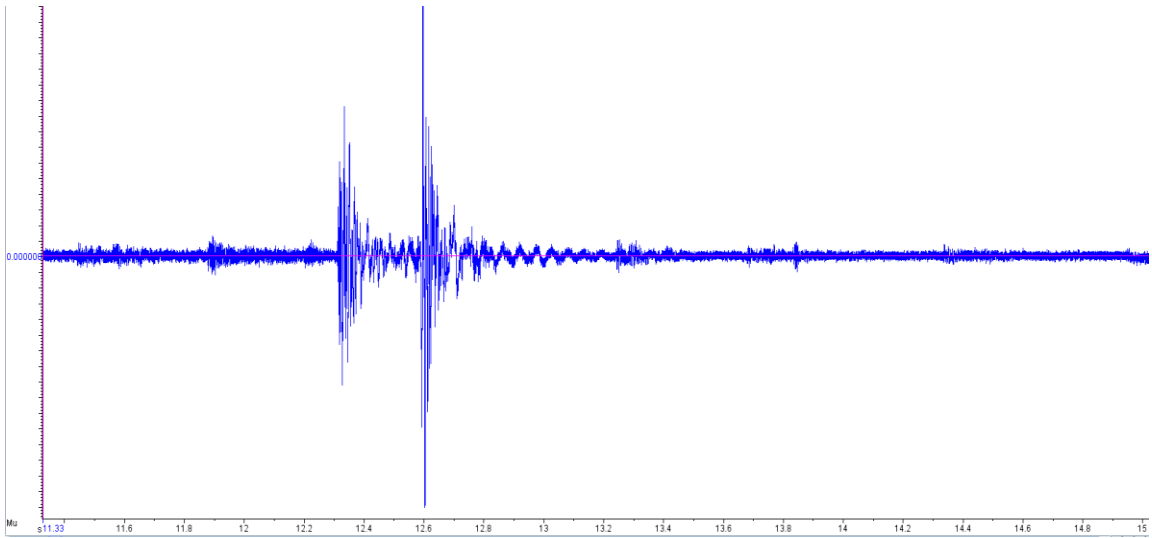


Figure 1. Waveform of external sounds recorded in an empty tank. Time is shown on the x-axis and sound pressure on the y-axis. Notice the extremely high sound pressure and very long, messy “tail”, neither of which were characteristic of sounds produced by salamanders. Waveforms with this appearance were discarded from consideration on sight.

Statistical Analysis. - All sounds recorded were isolated and characterized in Raven Pro 1.4 sound analysis software (Cornell Lab of Ornithology, Ithaca, NY). The number of sounds recorded was counted for each trial, and any tank which contained a pair of salamanders (MF and FF) had its total number of sounds recorded divided by two. This was done to allow comparison of the tanks with two salamanders to those that only had one. The mean rank number of sounds in these counts were compared between the four social groups using a Kruskal-Wallis test. This test was conducted once for the summer trial, once for the spring trial, and once each for the “predation” and “no-predation” groups. A non-parametric test was used in this case because count data were not normally distributed, and I sought to decrease the chances of a Type I error as much as possible. After the Kruskal-Wallis tests were performed on the spring and summer trials, the average number of sounds detected in each season was compared using a Two-way ANOVA (with “season” and “social group” as factors). The same test was applied to the predation trials (with “predation” and “social group” as factors). The use of a parametric test in this case is not ideal, but since no nonparametric equivalent to a Two-Way ANOVA exists, this was used as a low-power alternative. Finally a t-Test was conducted comparing the dominant frequency of the sounds produced by males and females. This test was conducted using only data obtained from isolated males and females, since I could not determine which salamander in a pair had produced a specific sound. For all tests significance was declared at $P < 0.05$.

RESULTS

Sounds were detected in 118 of the 137 recordings taken (86% of tanks). These sounds all take the same form, that of three to four initial peaks in pressure (μ) followed by a descending tail of lower peaks until fading into the background noise (Fig 2). These sounds are extremely short, typically lasting approximately 1 ms or less. The number of these sounds detected per tank ranged from 0-33 (mean 6.2 ± 0.608) across all tanks, trials and recordings which contained salamanders. All sounds had a wavelength of approximately 350 Hz, were sinusoidal, non-periodic and sounded like a sharp “click” of varying amplitude (64.6-71.6 dB). No differences were detected between the dominant frequency of sounds produced by individuals of different sex (t-Test: $T = 0.12$, $P = 0.9$).

The spring trial showed no significant difference in the mean rank number of sounds produced by different social groups (Kruskal-Wallis: $H = 2.96$, $P = 0.397$; Fig 3), nor did the summer trial (Kruskal-Wallis: $H = 4.37$, $P = 0.224$; Fig 4). The interaction term between social group and time of year, however, was marginally significant (Two-way ANOVA: $F_{\text{season}} = 1.478$, $P = 0.229$; $F_{\text{socialgroup}} = 0.878$, $P = 0.458$; $F_{\text{interaction}} = 2.703$, 0.054), suggesting some function of time of year on the number of sounds recorded. The likely candidate for this interaction was Isolate Males, which produced more clicks in the summer recordings than in the spring.

The predation trial tanks also showed no significant difference between social groups in “predation” and “non-predation” tanks (Respectively, Kruskal-Wallis: $H = 6.23$ & 2.95 , $P = 0.1$ & 0.40 ; Figs 5 & 6). No significance was suggested for the interaction term of predation on social group (Two-Way ANOVA: $F_{\text{interaction}} = 0.505$; $P = 0.681$).

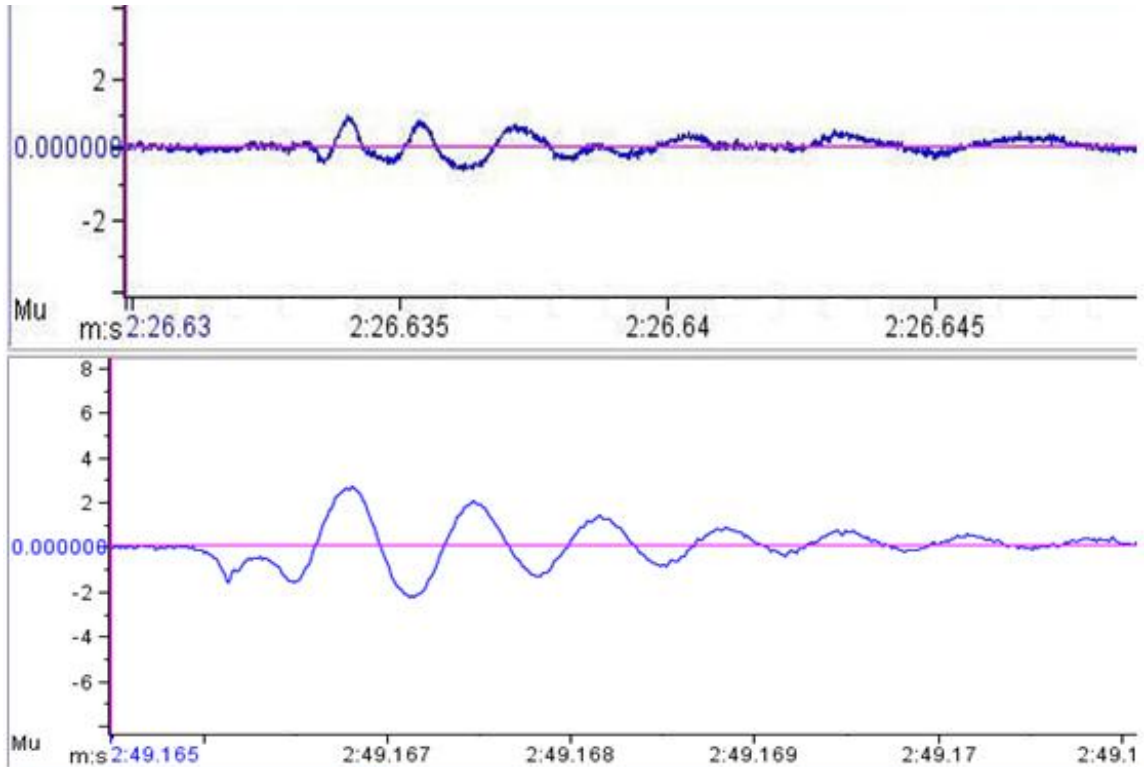


Figure 2. The waveforms of sounds produced by two female Smallmouth Salamanders (*Ambystoma texanum*) in separate trials. Wavelength and amplitude did not vary substantially between recordings. Time is shown on the x-axis, and sound pressure is shown on the y-axis. Note that amplitude is shown here in terms of absolute pressure (Mu), rather than decibels.

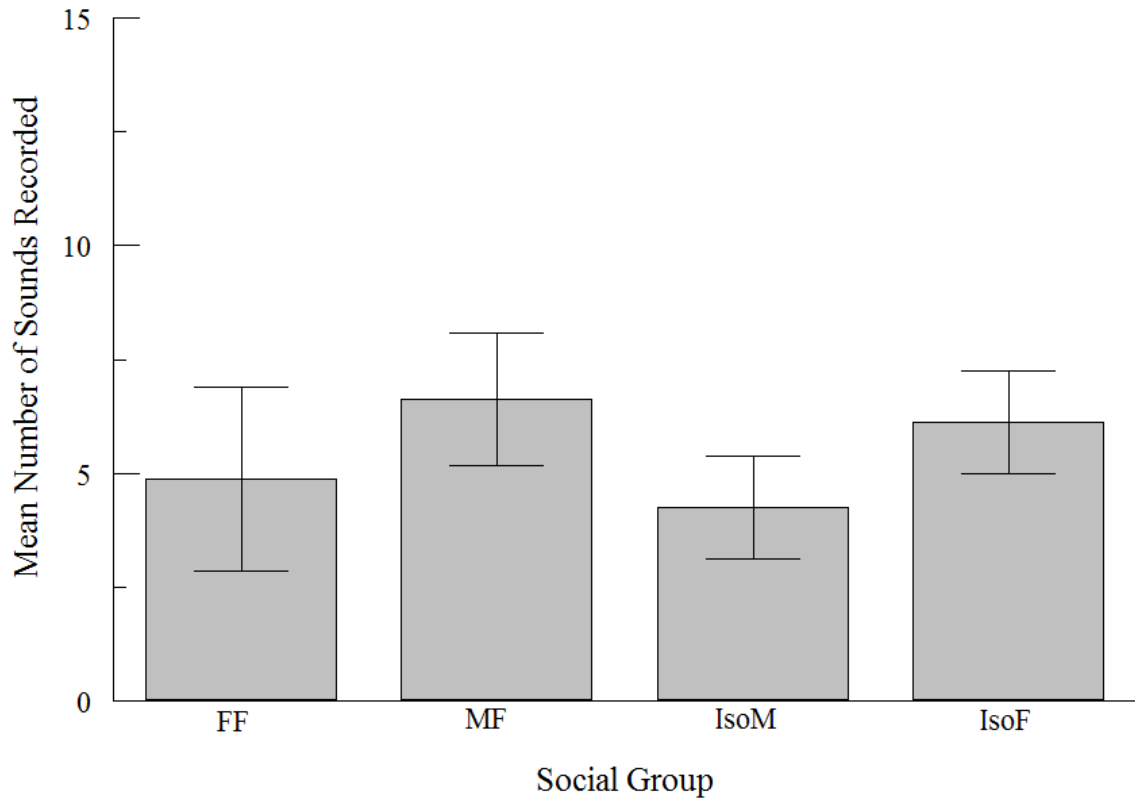


Figure 3. The mean number of clicks recorded are presented (\pm SE) for each of the 4 social groups tested in mid-late April, 2014. Abbreviations are as follows: FF = 2 Females, MF = 1 Male and 1 Female, IsoM = Isolate Male, and IsoF = Isolate Female ($n = 7$ FF, 8 MF, 8 IsoM, and 8 IsoF). All tanks that contained two individuals (i.e., FF and MF) had their number of recorded sounds divided by 2 before means were calculated.

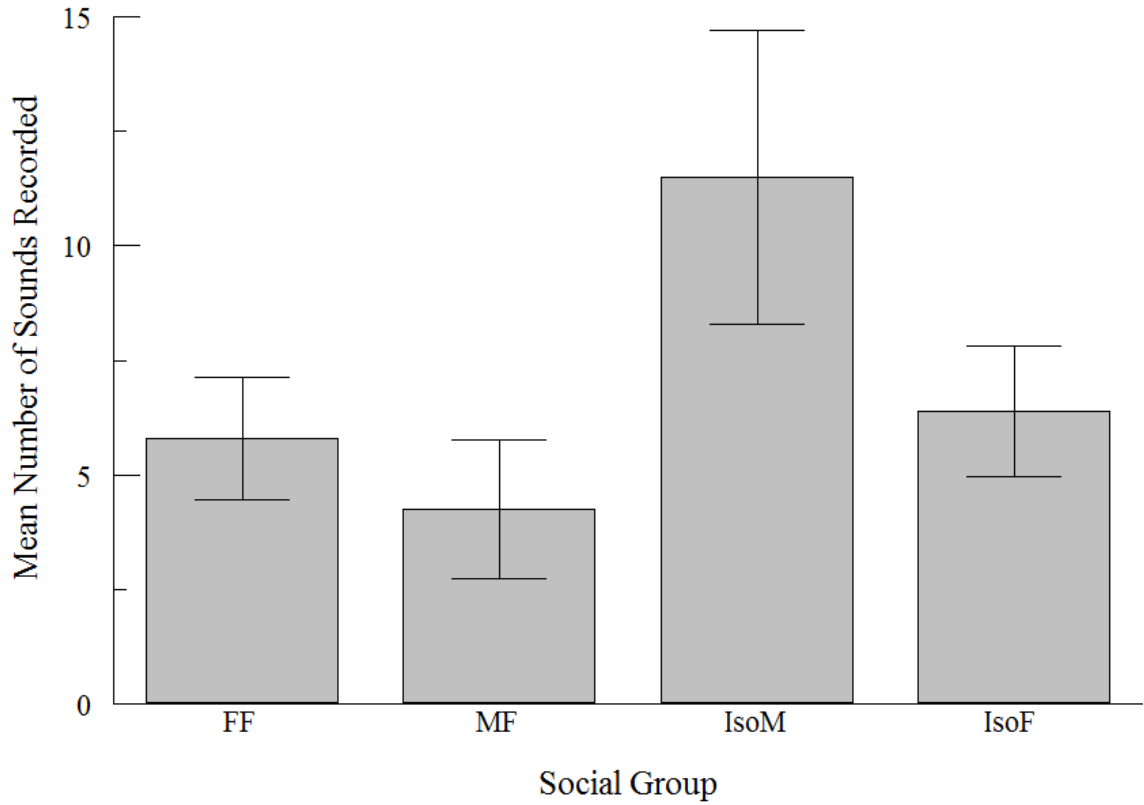


Figure 4. The mean number of clicks recorded are presented (\pm SE) for each of the 4 social groups tested in mid-July, 2014. Abbreviations are as follows: FF = 2 Females, MF = 1 Male and 1 Female, IsoM = Isolate Male, and IsoF = Isolate Female ($n = 7$ FF, 8 MF, 8 IsoM, and 8 IsoF). All tanks that contained two individuals (i.e., FF and MF) had their number of recorded sounds divided by 2 before means were calculated.

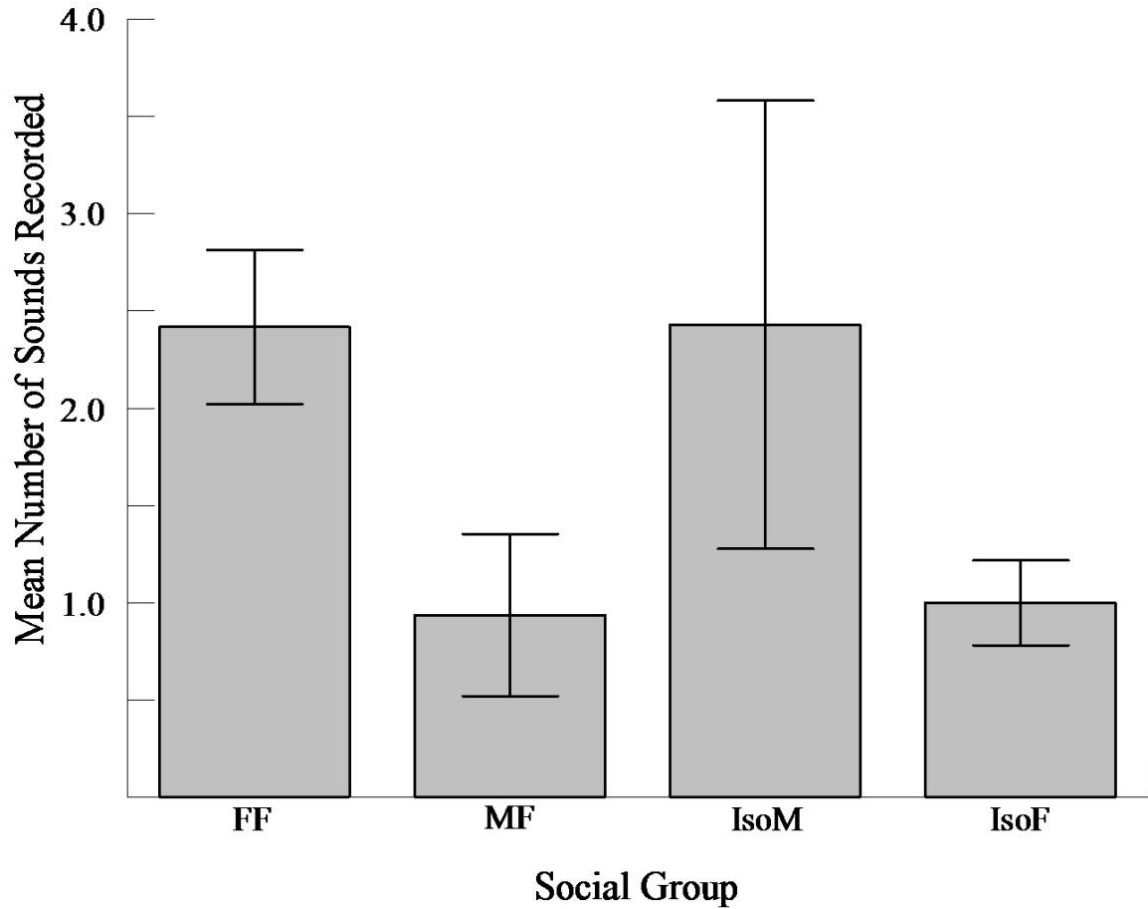


Figure 5. The mean number of clicks recorded are presented (\pm SE) for each of the 4 social groups tested following a mock predation event. Abbreviations are as follows: FF = 2 Females, MF = 1 Male and 1 Female, IsoM = Isolate Male, and IsoF = Isolate Female ($n = 7$ FF, 8 MF, 8 IsoM, and 8 IsoF). All tanks that contained two individuals (i.e., FF and MF) had their number of recorded sounds divided by 2 before means were calculated.

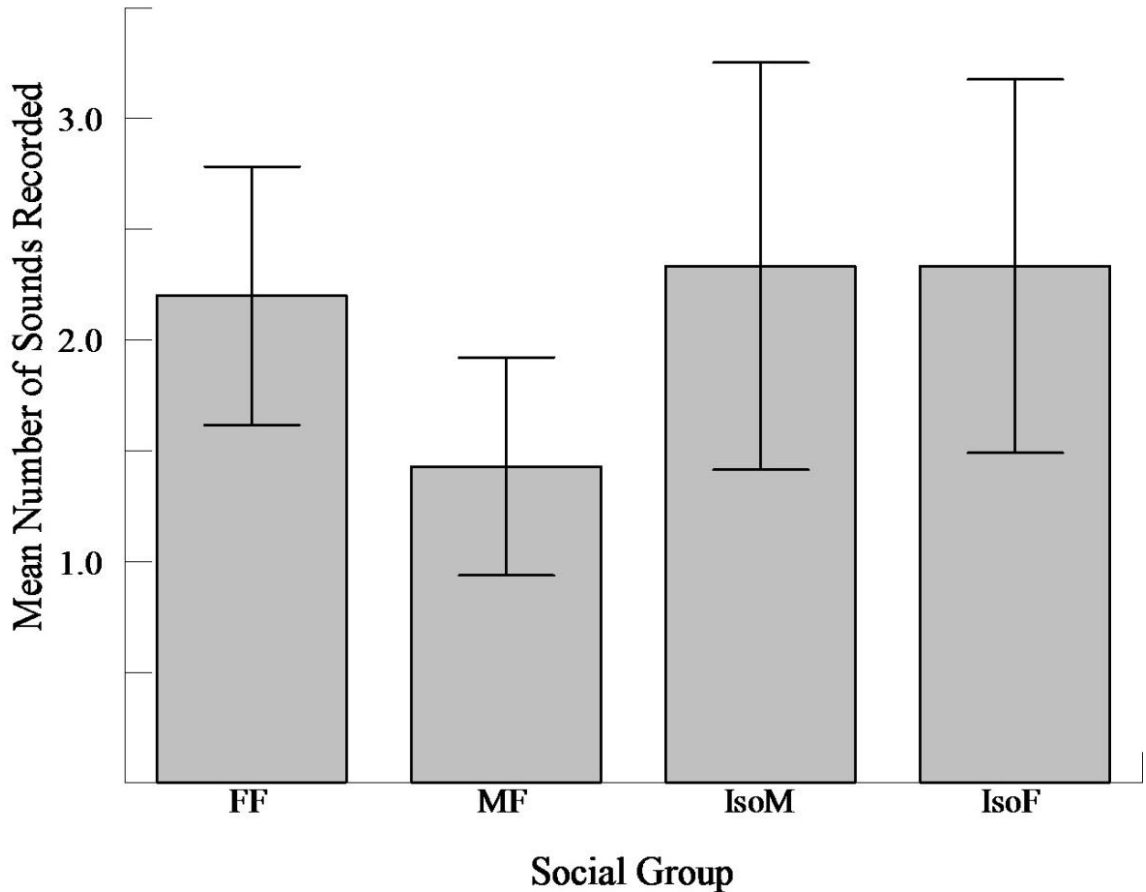


Figure 6. The mean numbers of clicks recorded are presented (\pm SE) for each of the 4 social groups not exposed to the mock predation event of Figure 4. Tests were conducted at the same time as those of Figure 4. Abbreviations are as follows: FF = 2 Females, MF = 1 Male and 1 Female, IsoM = Isolate Male, and IsoF = Isolate Female ($n = 7$ FF, 8 MF, 8 IsoM, 8 IsoF). All tanks that contained two individuals (i.e., FF and MF) had their number of recorded sounds divided by 2 before means were calculated.

DISCUSSION

I was unable to isolate any specific context for sound production in *A. texanum*. However, I did record relatively frequent sound production in a species that is typically thought of as being mute. Such recordings are extremely rare in the literature on terrestrial salamanders (and only slightly less so for aquatic species), the most recent being Wyman and Thrall (1972). Smallmouth Salamanders in my study produced far more sounds during my trials than did Wyman and Thrall's Spotted Salamanders (*Ambystoma maculatum*). Although possibly representing some courtship or physiological difference between the two species, it seems more likely that my hydrophones were more sensitive to the faint sounds produced by these salamanders than the microphone and tape recorder used by Wyman and Thrall. Unlike Wyman and Thrall, I only observed one type of sound, and it was not unique to, or used preferentially by, any sex or group, nor was it used more or less often in the context of predation.

Despite my inability to establish firm context for these sounds, the data are nonetheless valuable. With data on salamander sound production so scarce, and completely nonexistent for *A. texanum*, even the somewhat ambiguous results obtained here are valuable in directing future research. My results do highlight that these sounds, having a frequency of approximately 350 Hz, are in the range of maximum auditory sensitivity for *A. texanum* (Wever 1985). Although this does not necessarily mean that the sounds have behavioral significance, it is suggestive of it.

I observed that when held in hand, *A. texanum* will occasionally produce loud clicking sounds not unlike the ones detected in the present study. On visual inspection it became apparent that the sounds were always accompanied with a swelling of the buccal

cavity far beyond that which they normally employ for respiration. The floor of the buccal cavity was then rapidly brought back to normal size, at which point the “click” was heard. Presumably air is being forced back into their lungs rapidly to produce the sounds, and the same mechanism should be available to them underwater, via air stored in the lungs. Future studies should focus on isolating the sound producing mechanism, as this would provide clues to the environments where these sounds could be most easily transmitted and received. *Ambystoma texanum* has not been the subject of any research concerning alternative auditory pathways. To further our understanding of this phenomenon, we need to understand how exactly they perceive the sounds they are capable of hearing, especially in air. Studies modeled after Hetherington (2001) could be particularly useful, as the lungs and body wall seem to be the most likely candidate for an alternative auditory pathway, and one that would work very well underwater.

During my preliminary study I noticed that most salamanders would produce loud clicks outside of the water while held in hand (this was the way I originally noticed sound production occurring). It is worth mention that during the present study, sounds produced in air were quite rare, completely unlike the behavior of the salamanders from a year before. The experimental designs were very similar between studies, but in the earlier project I housed the salamanders in much larger groups. Whereas the most tank-mates any salamander had in this study was one, salamanders in the previous study could have up to four tank-mates at a time. The aquaria were the same size as those used in the present study. It is therefore possible that these sounds are in some ways prompted by audience or network effects.

Network effects are those that arise during communication involving multiple senders and/or receivers of information (Bradbury and Vehrencamp 2011). This can take the form of a large group of many receivers and senders (a true network) or a single individual observing the interactions of others (an audience or eavesdropper). In either case, emergent behaviors will often become apparent as the numbers of individuals involved increases, as has been shown by Plath et al. (2008) with Molly's (*Poecilia* spp.). Such an audience effect has even been observed in *A. texanum* during the mating process. McWilliams (1992) showed that the presence of another male during courtship will cause the courting male to alter the time he spends in different stages of courting. In particular, courting males spend less time in positions where they are more vulnerable to attack by an aggressive competitor. While more data are required to be certain, a similar effect could be on display with *A. texanum* sounds, where the above-water sounds I heard serve as indicators of some sort, but are only provoked in the presence of a group.

The communicative abilities of salamanders have been extremely understudied, and most of the research there is has focused on chemical communication (Duellman and Trueb 1986). Future research should strive to determine conclusively what functional significance the sounds produced by salamanders may have. In *A. texanum* sounds are readily emitted with little to no apparent human provocation, though it remains to be seen whether the above-water sounds are at all different from the underwater sounds I monitored in the present study, and the salamanders have shown themselves willing to engage in many behaviors in the lab that are otherwise difficult to detect in situ. Field work should also be undertaken to determine whether the same sounds are detectable in breeding pools. These behaviors have the potential to be enormously important to the

organisms using them, and our knowledge of their ecology and natural history will remain conspicuously incomplete until this hole in our understanding is filled.

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