

## The call of the Aldabra tortoise (*Geochelone gigantea*) (Reptilia, Testudinidae)

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**Abstract.** Mating male Aldabra tortoises (*Geochelone gigantea*) emit loud, deep-pitched calls or “groans” while mounted. A bout of 34 groans was recorded and analyzed oscillographically and spectrographically. The sound energy occurs in periodic waves and there is no evidence of regularly pulsed energy. Calls are relatively stereotyped, with at least seven partial tones that range from 0.26 to 0.80 kHz. Only three tones occur throughout each call and in all calls, and these three have a harmonic relationship. More than half of the duration of the call, averaging 64%, consists of a steady decrease in frequency, which occurs at the end. The beginnings of calls have the most energy, especially in the deepest tone, but there is considerable variation in the pattern of amplitude modulation. Call length and duration of the pauses between calls are relatively stereotyped, averaging 0.47 and 3.86 seconds, respectively. Movements made during “groan-thrusting” may be related to sound production, but the structures involved in the production, modulation, and resonance of the call are unknown. As the majority of the groan is apparently within the frequency range of highest auditory sensitivity for tortoises, there is an excellent chance that the sounds are perceived by the female, possibly intimidating her and facilitating mounting. Sounds are made by mating tortoises of a variety of species, and it would be interesting to know how these behaviors evolved.

### Introduction

Giant tortoises have long been known to make deep-pitched calls, referred to as “groans,” “bellows,” “grunts,” or “roars” (e. g., DARWIN, 1845; GORDON, 1979). These calls are given by males during mating, and although commonly heard from both Galapagos tortoises, *Geochelone elephantopus* (HARLAN), and Aldabra tortoises, *G. gigantea* (SCHWEIGGER), there is only one study of giant tortoise calls. JACKSON and AWBREY (1978) were able to analyze two bouts of calling, involving two different mating male *G. elephantopus* in the San Diego Zoo. They reported that calls were low frequency with the energy below 0.8 kHz, and the intensity was high. Other research on smaller tortoises (e. g., *G. carbonaria* (SPIX) and *G. travancorica* (BOULENGER)) reported that calls are also given in mating situations, but they are higher in frequency (over 5 kHz in some cases) and apparently of lower intensity; however, there are relatively few studies of tortoise calls (CAMPBELL and EVANS, 1972).

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FRAZIER (1973) discussed the mating behaviors of tortoises on Aldabra. Calling, or "groaning," is done only by mounted males, and begins before insertion of the penis. It is relatively stereotyped, and occurs rhythmically with "groan-thrusting," a behavior in which: the male's hind legs and neck are extended so that his body is as far forward as possible on the partner, and his beak may almost touch the partner's head (which is usually withdrawn into its shell); the male occasionally nips at the partner's head. When fully forward, he flexes or lifts his hind legs so that the posterior and lower part of his body is unsupported, and he slides downward posteriorly, with his tail thrusting forward. At the same time, he emits a deep, resounding groan, which can be heard half a kilometer away. These behaviors are repeated cyclically at regular intervals.

On Aldabra, only large males mount and make rhythmic groan-thrusts, although small (young, inexperienced?) males may make clumsy attempts at mounting and irregular groan-thrusts. The partner may be of either sex and of any size smaller than that of the mounting male. Although precoital behaviors are similar with partners of both sexes, intromission has only been observed with females. After insertion, groaning may continue, but it is less frequent and less intense.

Details of just the mating calls of the Aldabra tortoise will be presented in this paper, which is the first study of the call of the Aldabra tortoise, or of any wild tortoise. The findings will be compared with those on other tortoises, especially giants. A general discussion on call production, causation, ontogeny, communication value, and evolution is also included in order to put the findings into a conceptual context. These points are rarely considered in relation to testudines, and it is necessary to raise them and develop a framework for future research.

## Methods

The present study involves the analysis of groans made by male 45, an adult that weighed about 60 kg and measured 78 cm in straight carapace length. At 1620 hrs on 30 March 1970, this animal interrupted his afternoon grazing to mount and groan-thrust a smaller male at Dune Jean Louis, South Island, Aldabra, male 45's usual location. Temperatures recorded at 1630 hrs in or near male 45 were: deep body = 32.5°C; air = 33.0°C; substrate = 36.5°C. The sky was fully overcast, and it began to rain after the mating attempt.

The calls were recorded on a Phillips (Norelco) cassette recorder, model EL 3301/220, with a Phillips C90 cassette, using its accompanying microphone between 1 and 2 m from the male. An entire bout of 34 groans was recorded over a period of 148 seconds. The first call recorded was the first in the bout and the last call was followed by a dismount.

Oscillographic study of all 34 groans was made at 1/64th of the original recording speed. Speed reduction, without undue distortion of waveforms, was accomplished in three steps: The original cassette recording was transcribed at speed to a Uher 4 000 Report IC tape recorder. This was recopied at speed to a Tandberg Model 10XD tape recorder and then recopied at 1/4th speed to a Hewlett Packard (HP) model 3960 FM tape recorder factory equipped for distortion-free reduction by a factor of 16. Oscillograms of each groan were made on a HP model 7402A strip chart recorder with a paper speed of

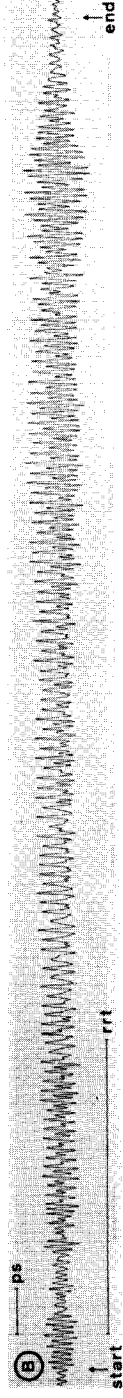
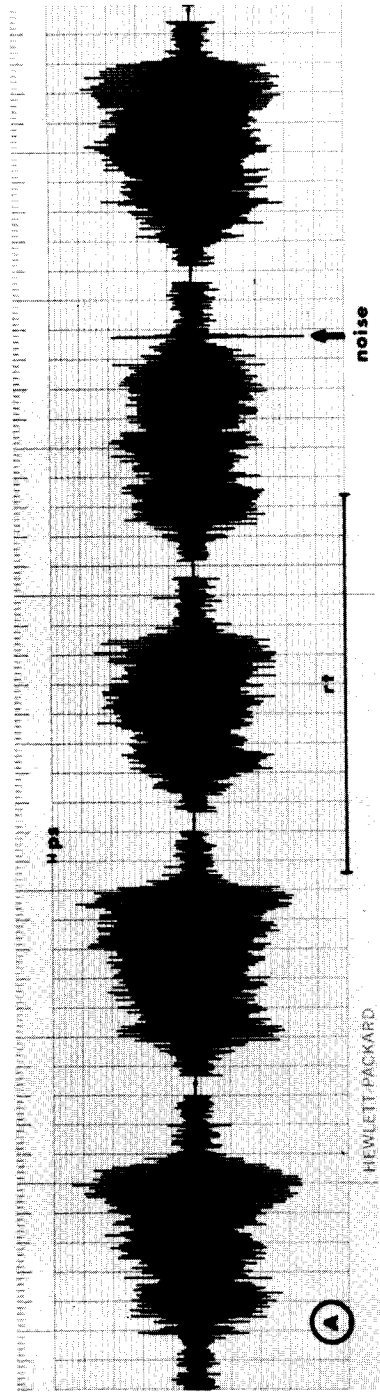


Fig. 1. Oscilloscopic strip chart recording of groans from male 45, an adult mating Aldabra tortoise. The inter-call pauses in the oscillogram do not represent their original durations. A) calls 5 to 9, paper speed 1 mm/s. B) one call, paper speed 25 mm/s. "ps" = 1 s paper speed; "rt" = 1 s real time; "rrt" = 0.1 s real time.

1 mm/s. Simultaneously, each call was monitored on a HP model 1211A Oscilloscope. Oscillograms of several representative calls were also made with paper speeds of 5 and 25 mm/s for more detailed analysis.

The Uher tape recording at original speed was analyzed using a Kay SonoGraph model 7029A, making a series of overlapping wide band audiospectrograms of each groan for measurement of temporal factors, and narrow band audiospectrograms for measuring parameters relating to frequency. The band widths for these two modes were 10 to 1,000 Hz and 20 to 2,000 Hz, respectively, but several calls were also checked with band width of 40 to 4,000 Hz. The time constant in the wide band mode is 0.027 s; the effective filter band width for narrow band mode is 11.2 Hz (BRADBURY and CAPRANICA, in press). Statistical analysis was done at the Office of Computer Services, Smithsonian Institution, using Statistical Package for the Social Sciences, version 6.02B-1 (NIE, et al., 1970).

No standards were included on the original recording, which was made opportunistically, without high quality equipment. However, in the following sections on structural and temporal analyses, it has been assumed that mechanical variables, such as tape speed, recording sensitivity, and the several steps of copying did not significantly modify temporal or structural characteristics of the calls recorded.

Innumerable other males were observed while mating, but in two the rate of groaning was timed with a stop watch. In all instances, the animal was clearly observable and behaved in a completely normal manner; there was no indication that the presence of the observer had any effect on the animals during the observation.

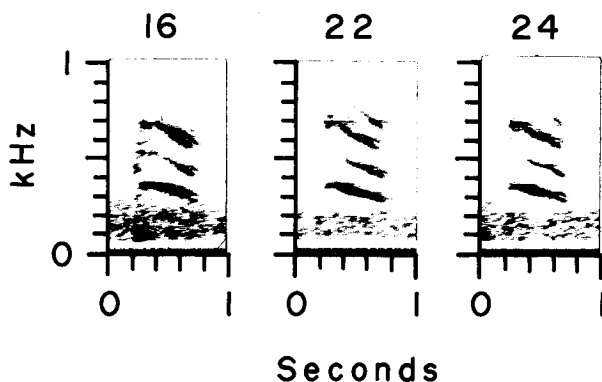


Fig. 2. Narrow band spectrograms of three groans from male 45, an adult mating Aldabra tortoise. All three calls show the lowest detectable tone and two other major tones,  $3/2$  and  $2$ ; in addition calls 16, 22 and 24 show various other partial tones. Note the dominant down-slope and bifurcate endings of the three major tones. Some faint components of some of the spectrograms have been lost in the several steps of photographic copying.

*Structural Analysis*

None of the oscillograms show any regular cyclic phenomenon in the envelopes of the amplitude peaks (Figure 1). Groans at the beginning of the bout have increasing amplitude (i.e., envelopes shaped like left-pointing arrows); groans at the end of the bout often decrease in amplitude (i.e., have envelopes shaped like right-pointing arrows), but there is considerable variation in the pattern of amplitude modulation after the sixth call.

A count of the individual amplitude peaks showed 576 to 640 per second (the actual count on paper, slowed by a factor of 64, was 9 to 10 per second). Throughout most of the call every other peak is considerably higher than its neighbor. This indicates two frequencies that confirm dominant sounds at 256 to 320 Hz and 576 to 640 Hz. There are no distinct pulses of energy and no other conspicuous periodicities.

In the spectrograms there is a continuous low frequency background noise throughout the entire recording, and no evidence of any call tones within this band, below 260 Hz (Figure 2). The deepest tone detectable ("dtd") rises above this frequency, and a total of six other partial tones appear during the bout, but not in all calls. The frequencies of each partial tone are related to the frequency of the dtd by each of the following ratios: 1 (the dtd),  $5/4$ ,  $3/2$ ,  $7/4$ , 2,  $9/4$ , and  $5/2$  (these numbers will be used in later discussions to identify the individual partial tones).

Only those tones at 1,  $3/2$  and 2 occur for the whole duration of the call, although the  $3/2$  tone may be interrupted just after the beginning. These three major tones are present in all calls and have a harmonic relationship. Two tones at  $5/4$  and  $7/4$  occur only at the beginnings of the calls; the second,  $7/4$ , is usually more intense and is conspicuous in all but nine calls. Slightly less frequent, the  $5/4$  tone is also less intense than the second, except toward the end of the bout. The  $9/4$  tone occurs in the beginning and middle of calls at the end of the bout, but it is not evident in the first half of the bout. Present in most calls is the  $5/2$  tone, but it only appears during the latter half of each call. The calls have an apparent harmonic structure, but it is also possible that there are harmonics together with side bands (see below).

The frequency range of the call is from 0.26 to 0.80 kHz, that of the dtd, from 0.26 to 0.36 kHz. In each call the major tones begin with a nearly constant frequency or "plateau". Although an increase in frequency may occur at the very beginning of some calls, resolution was inadequate to confirm the presence of a true "up-slope". The plateau is always followed by a continuous decrease in frequency, or "down-slope". Hence, frequencies of each of the three major tones are lower at the ends of the calls than at the beginnings. For example, starting frequency of the dtd averages 0.34 kHz and its ending frequency averages 0.28 kHz.

On average, the duration of the down-slope comprises 64% of the call length, although it may last from 56% to 75% of the call (Table 1). The duration of the down-slope is positively related to the length of the call (Table 2). The length of down-slope also shows a positive relationship with the starting frequency of the dtd: the higher the starting frequency, the longer the down-slope. However, ending frequency is also strongly related to starting frequency; the higher the starting, the higher the ending.

A bifurcate ending is characteristic of the three major tones, and is present in all calls. This may be the result of an echo (either natural or electronic) occurring where the call

**Table 1.** Descriptive statistics from spectrographic analysis of groans of a mating male aldbra tortoise (WB = wide band; NB = narrow band)

Parameter	Unit	Mean	Range		St. Dev.	N
			Minimum	Maximum		
Call length (WB)	s	0.47	0.38	0.53	0.036	34
Inter-call pause (WB)	s	3.86	3.55	5.09	0.324	33
Call period (WB)	s	4.33	4.00	5.60	0.339	33
Down slope length (NB)	s	0.34	0.256	0.416	0.033	34
% Call length in down slope (NB)		64.2	55.6	75.0	4.253	34
Start frequency (NB) of deepest tone detectable	Hz	340.	310.	360.	9.781	34
End frequency (NB) of deepest tone detectable	Hz	280.	260.	300.	11.106	34

is decreasing rapidly in frequency and is relatively intense in energy (FRANKENBERG, pers. comm.), although DREWRY (pers. comm.) questions this interpretation. Audible differences in the pitch between calls could be confirmed in the spectrograms as differences of the intensity relationships of the partial tones.

The starts of most calls are "growly" (as described by JACKSON and AWBREY, 1978) and are marked by a burst of energy, which is most intense in the dtd, although the major tone at 2 has nearly as much energy. At the end of some calls, this tone has more energy than the dtd. The majority of energy is concentrated in the dtd and the partial tone at 2, between 0.26 to 0.72 kHz.

### *Temporal Analysis*

The duration of each of the 34 groans varies from 0.28 to 0.53 seconds, with an average of 0.47 s; most calls last from 0.45 to 0.51 s (Figure 3). Not only is there little variation in call length, but the rate of groaning is relatively constant (Figure 4). Inter-call pause, the interval from the end of one call to the beginning of the next, averages 3.86 seconds. Call period, the time between the beginning of one call and the beginning of the next, is derived by adding call length to inter-call pause; hence, call period averages 4.33 seconds (Table 1).

During the bout both call period and inter-call pause seem to vary almost sinusoidally, first increasing, then decreasing and then increasing again; at the end of the bout the increase is very marked (Figure 5). No other variables showed statistically significant trends with time, i.e., call number (Table 2).

Call length is strongly related to inter-call pause; hence, it is even more strongly related to call period. However, call length does not show any significant trend in time, although it is notable that the longest and shortest calls are given at the end of the bout (Figure 3).

The call periods for male 45 are comparable to those recorded for two other males on Aldabra. These range from 4.2 to 6.0 seconds (Table 3).

**Table 2.** Correlation matrix for parameters of spectrographic analysis of groans of a mating male Aldabra tortoise (WB = wide band; NB = narrow band)

PARAMETER	PARAMETER						
	Call length (WB)	Inter-call pause (WB)	Call period (WB)	Down slope length (NB)	% Call length in down slope	Start (NB) frequency	End (NB) frequency
Call number	.1151	.6333 ***	.6319 ***	-.0997	-.0548	-.0927	-.1974
Call length (WB)		.4133 *	.4925 **	.5868 ***	.1732	.2496	-.0362
Inter-call pause (WB)			.9960 ***	.2834	.1455	-.1406	-.1919
Call period (WB)				.3192	.1527	-.1293	-.1987
Down slope length (NB)					.6776 ***	.3890 *	-.0785
% Call length in down slope						.1835	-.2700
Start frequency (NB)							.4548 **

\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$

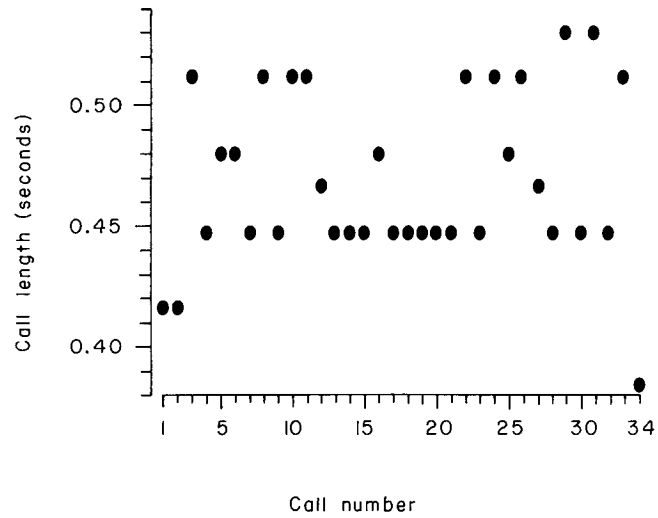


Fig. 3. Relationship between call length and call number, in a bout of 34 groans from male 45, an adult mating Aldabra tortoise

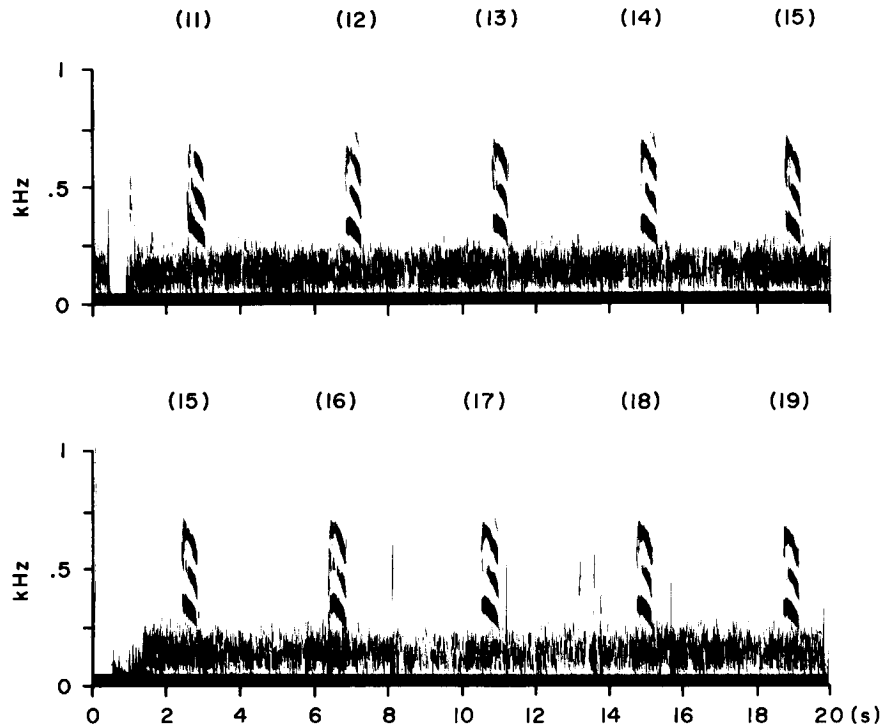


Fig. 4. Wide band spectrograms of a sequence of nine groans from male 45, a mating Aldabra tortoise; call numbers (11) to (19) are shown in parentheses



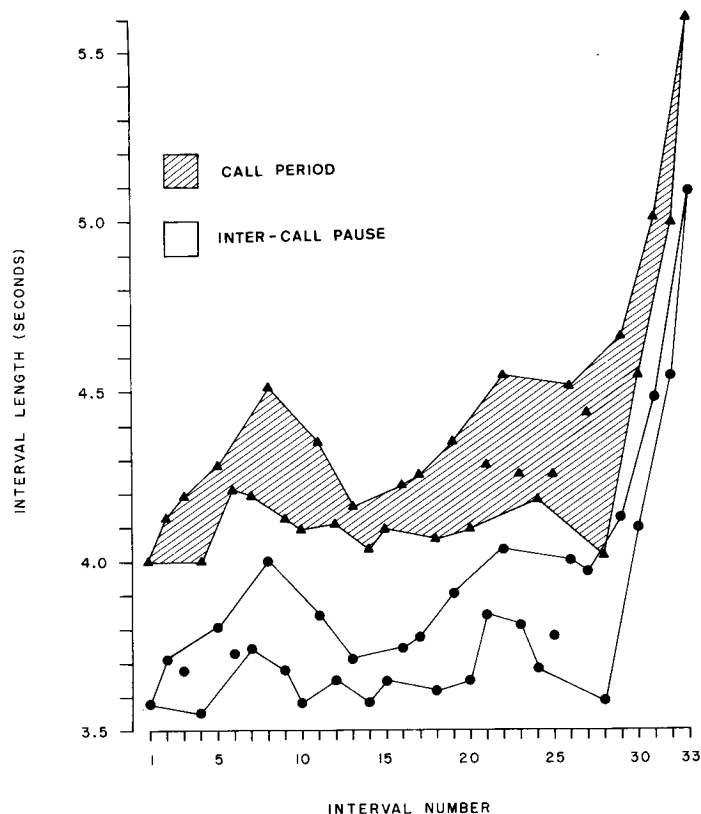


Fig. 5. Relationship between inter-call pause and interval number, and call period and interval number, in a bout of 34 groans from male 45, an adult mating Aldabra tortoise (lines are drawn by eye as upper and lower limits)

## Discussion

The bout recorded and analyzed was representative of innumerable bouts observed by JF during nearly two years of field work on Aldabra Atoll. The calls recorded sounded like other calls heard on the atoll, and call periods of male 45 are comparable with those of other mating males that were timed (FRAZIER, 1973). However, fine points of call and interval lengths, and frequencies probably vary between individuals and situations. Pitch of the groan is likely to relate to body size of the male; and rate of movement and activity, possibly also call rate, is related to his body temperature (FRAZIER, 1973). FRANKENBERG (1974) reported a temperature effect on the interval between vocalizations in geckos, and many important aspects of anuran calls are temperature-dependent (see FOUQUETTE, 1980). Behavior of the partner may also influence call parameters and temporal sequencing. Nonetheless, there is no question that groaning during mating is

relatively stereotyped in time and low pitched, with a characteristic decrease in frequency at the end of each call.

The cycles indicated by the oscillograms correspond to the two dominant frequency bands in the sonograms, centered around 300 and 600 Hz; actual tones, and not pulse trains, are responsible for these frequencies. The absence of any regular form or periodicity in the envelopes of the oscillograms indicates that the calls are not amplitude modulated in a constant manner.

#### *Comparison with G. elephantopus*

The calls of the Aldabra tortoise reported here are comparable to those reported from two Galapagos tortoises in the San Diego Zoo by JACKSON and AWBREY (1978). In both species of giant tortoise, calling occurs in bouts during mating, and calls are structurally complex, with several partial tones. There are also differences between the Aldabra and Galapagos tortoises, although comparisons between the two studies are limited by the small sample sizes available. The frequency ranges for both species are similar, but the Galapagos tortoises show lower partial tones in their calls. The deepest tone detectable on the spectrograms of the Aldabra animal is from 260 to 340 Hz. One Galapagos tortoise had four conspicuous tones below 300 Hz, one of which was below 100 Hz. The second animal from Galapagos had three tones below 300 Hz, one below 100 Hz. Most of the energy in the calls of the Galapagos tortoises was in tones between about 250 and 350 Hz. Hence, although tones below 100 Hz were produced, the efficient frequencies for broadcast were two or three tones higher. In some anuran amphibians the fundamental frequency produced at the site of sound production is not always broadcast (DREWRY, et al., in press), and evidently in the Aldabra tortoise the deepest tone detectable on the spectrograms is not the fundamental, but it was absorbed before broadcast or was so weak that it was masked by the background noise. If the tone at 3/2 is indeed a true harmonic, the frequency separation between the three major partial tones indicates a fundamental frequency at approximately 150 Hz. However, if all seven of the partial tones are true harmonics, the fundamental would be at 75 Hz.

JACKSON and AWBREY (1978) felt that calls in the Galapagos tortoises had a "strong harmonic structure". The calls of the Aldabra tortoise also have a harmonic structure, but some of the less intense tones may be side bands (see WATKINS, 1967, for a detailed discussion of these problems). Another complication is in sounds produced by the creaking of the shell, as the male slides backwards on the partner. In the Galapagos tortoises this evidently produced high frequency components with considerable energy to at least 10 kHz (JACKSON and AWBREY, 1978). This problem was not evident in the male 45, and creaking was not commonly heard on Aldabra.

JACKSON and AWBREY (1978) were able to make some measurements of intensity, not possible in this study. Two peaks in energy over 40 and 50 dB were found, supporting the field observations that calls are loud. They reported partial amplitude modulation at 70 to 85 Hz, and that the call ends with a stronger exhalation, the increased sibilance giving it a more broad band ending. The increased pitch and intensity at the end of Galapagos tortoise calls is opposite to most calls of Aldabra tortoises, in which the beginnings are most intense, tending to be more broad banded, and followed by a decrease in pitch.

However, the concentration of energy is in about the same frequency range for both species.

Other differences are seen in temporal factors. The Galapagos tortoises' calls averaged two to three times as long as the calls of the Aldabra tortoise. The call periods of the Galapagos tortoises also averaged longer than the calls of male 45; in one case they were nearly three times as long. These differences may be species specific, but much larger samples are needed.

### *Production of the Call*

The testudine larynx is "poorly adapted for sound production", but "short, vocal cord-like structures" are suspected to occur (KELEMEN, 1963: 491). However, no indication of a complex vocal apparatus was found in general dissections of two adult Aldabran males, although the glottal valves are well developed (FRAZIER, 1973; see also SCHUMACHER, 1973). Groaning seems to be tied to exhalation, but the power for producing so loud a call is unknown. The length and diameter of the vibrating chamber — probably the pharyngeal cavity — will be of major importance in determining pitch of the call. Dimensions of the trachea may also be critical in formation of the deep pitched sound, as is thought to be the case in geese and swans (SUTHERLAND and MCCHESENEY, 1965) which, like giant tortoises, have long necks. The omnipresent and conspicuous down-slope, or decrease in frequency, is evidence, with so simple a sound producing system, for an increase in volume of the sound-producing and/or resonating cavity. Groan-thrusting Aldabra tortoises do open their mouths during the call.

### *Causation of Calling*

The physiological or behavioral state that leads to groaning is clearly related to mating, but groans are not unique to a mating situation. A large tortoise, of either sex, produces a groan-like gasp under conditions of physical stress, such as occurs while heaving its body over or down a difficult step. In the larger animals, notably males, the gasp is not only deep pitched, but of considerable intensity. However, such sounds are, to the ear, different from groans emitted during mating and they are unlikely to have the same structural characteristics. This indicates, however, that muscular contraction of some force may begin the groan. In the mating situation the flexation of hind legs, and evident loading of much of the body weight on the forelegs, may result in strong muscular contractions that lead to a powerful exhalation.

However, it is notable that a male that is interrupted from completing the body movements in a groan-thrust cycle, often emits a final groan in rhythm with previous calls. Hence, groaning does not seem to be merely an accident of the male's physical efforts. CAMPBELL and EVANS (1967) argued that sound production in two smaller species of tortoise is not accidental; JACKSON and AWBREY (1978) concluded the same with Galapagos tortoises. AUFFENBERG (1978) suggested that "mounting vocalizations" in *Geochelone radiata* (SHAW) may serve as important signals, thus implying that they are not simply accidental sounds. However, BURCHFIELD, et al. (1980) could not hear anything other than loud exhalations in mating tortoises of this species.

The increase in inter-call pause at the end of the bout could be related to several factors: the male may become fatigued during a bout of groan-thrusting. This fatigue could

occur in muscles responsible for producing the energy for the call, and possibly also used in body movements during the behavior, which would enhance the rate of fatigue. Continued calling could also result in fatigue or a change in the composition of the structure(s) responsible for the vibration (e.g., by drying the "vocal cords"). This might induce the animal to slow its rate of calling. Other explanations are less easily tested, but may be valid just the same: the male could become frustrated after a series of calls without achieving insertion, or his "drive" to groan-thrust may be reduced after a certain number of groan-thrusts.

There is evidence for a motivational change during groan-thrusting. As is typical of an unsuccessful mating, tortoise 45 made two chews after the last call. Conspicuous blinks also occur at the end of an unsuccessful mating and both blinking and chewing are characteristic of tortoises in conflict or ambivalent situations, and these behaviors fit the definition of "displacement activities" (FRAZIER, 1973).

As call length does not show any clear trend in time, it seems more stereotyped than call period, and unaffected by fatigue, satiation, or whatever factors are influencing the rate of calling.

#### *Ontogeny of the Call*

The mating behavior of adult males is different from that of animals judged to be immatures on the basis of size and growth marks. The latter are less forceful and employ more pre-mounting "courtship"; their groan thrusts, although rare, are arrhythmic. The mating groans are also dissimilar; the quiet, high-pitched cough of immatures is unlike the deep resonating groan of adults. Both the mating behavior and the call evidently develop as a male grows and matures. However, a simple increase in body size, with accompanying increase in the size of the pharynx, trachea, and associated structures of the respiratory system, does not seem sufficient to explain the increase in amplitude and decrease in frequency that distinguishes the calls of adults from those of immatures. Even large immatures make quiet, high-pitched coughs, while adults that are only slightly larger in body size make much louder, deeper calls (FRAZIER, 1973).

A similar phenomenon may also occur in *G. radiata*. Large (experienced) males have faster, and possibly louder, more structured calls than do small, young males (AUFFENBERG, 1978; see sonagram in Figure 4).

Experience and learning, so important in avian call development, might be involved, but the differences may be related to an allometric increase in secondary sexual characters related to call production. This problem has received little attention in herpetology.

#### *Communication Value*

It is unknown if and what value the groan has in communication between male and partner. FRAZIER (1973) hypothesized that a successful mating in *G. gigantea* necessarily involves dominance and subjugation of the female by the male, and that the male's behaviors while mounted seem to be aimed at frightening the female and causing her to withdraw into her shell and remain stationary. Nipping at the partner's head and bellowing into its face from a few centimeters away seem clearly to have an intimidating function (see also MERTENS, 1964; and JACKSON and AWBREY, 1978).

The mounted male is in a precarious position and, if the copulation is to be successful, it is imperative that the female remain still while he positions and groan-thrusts. However, intromission depends not only on the female's passive cooperation, but on her lifting her posterior and exposing her cloaca. Hence, the initial function of the male's mating behavior may be to intimidate, but this does not rule out the possibility that the call and/or associated behaviors also have a signal function which stimulates the female to actively cooperate.

The auditory abilities of testudines have long been debated, since physiologists have found the capacity for hearing in turtles, but behaviorists have observed little evidence of responsiveness to auditory stimuli. One of the problems seems to be in the experimental designs (PATTERSON and GULICK, 1966). Experiments with *Pseudemys scripta* (SCHOEPPFF) showed this terrapin to be most sensitive to airborne vibrations between 200 and 700 Hz, and physiological studies on a variety of testudines have found the greatest auditory sensitivity to be below 1,000 Hz and often in the region of 0.5 kHz (see CAMPBELL and EVANS, 1972, for a review).

This range of highest sensitivity coincides almost precisely with the frequency range of the Aldabra tortoise's call, suggesting that groaning is likely to be perceived by a conspecific, if we assume a similar optimum hearing range for *G. gigantea*. As the groan is emitted only centimeters from the partner's head, this further enhances the chances that it will be heard and that there will be communication.

Preliminary playback studies have been made with *Geochelone carbonaria* which did seem to respond (CAMPBELL and EVANS, 1972), but these experiments have yet to be run with giant tortoises.

### *Evolution of the Call*

Sound production in tortoises, Testudinidae, is common and documented in a dozen species from all continents (except Australia where they do not occur). During mating, species both large and small emit sounds, which differ in pitch, intensity and temporal patterning; but deep bellows are made only by the giant tortoises: *Geochelone gigantea* (this study); *G. elephantopus* (JACKSON and AWBREY, 1978); and *G. sulcata* (MILLER) (BÖHME, pers. comm.). The smaller species typically produce sounds that are over 2 kHz, much higher in pitch (see CAMPBELL and EVANS, 1967, 1972; FRAZIER, 1973; GANS and MADERSON, 1973, for reviews). An exception may be *G. emys* (SCHLEGEL and S. MÜLLER), a medium sized tortoise reported to make a sound like a roar (BURCHFIELD, et al., 1980). *G. radiata*, also medium sized, was reported to make mating calls in a frequency range from 0.3 to 1.2 kHz (*sic.*) (AUFFENBERG, 1978), but in fact there are regular components of the call, apparently with considerable energy, at about 3.5 kHz, which AUFFENBERG (in litt.) regarded as harmonics (see also AUFFENBERG, 1978: fig. 4).

In giant tortoises the call potentially has a communication value, but it is unclear how high-pitched calls of smaller species could be perceived, given the apparent auditory sensitivities for low-frequency sounds. This raises the question of what function these calls have and how they evolved. Are the low-pitched or the high-pitched calls more like the ancestral form? The need for comparative studies is obvious, and this topic will be addressed in a later paper.

**Table 3.** Rate of groan-thrusting in two male Aldabra tortoises recorded in 1969 on Aldabra; these were timed, by stop watch, from call start to call start

Male	Date	Time		Number of call periods timed/event time (s)	Mean length of call period (s)
T14	15 April	0610		1/4.5	4.5
T14	15 April	0650		1/5	5.0
T14	15 April	0740		5/30	6.0
T14	15 April	0740	and following	5/30	6.0
T14	15 April	0740	and following	5/30	6.0
T14	15 April	0740	and following	5/30	6.0
T14	15 April	0740	and following	5/30	6.0
T14	15 April	0740	and following	5/30	6.0
T14	27 April	1745		6/25	4.2
unmarked	1 May	1610		5/21.5	4.3
unmarked	1 May	1610	and following	5/22.5	4.5
unmarked	1 May	1610	and following	5/23.5	4.7

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### Literature cited

- AUFFENBERG, W. (1978): Courtship and breeding behavior in *Geochelone radiata* (Testudines: Testudini-  
dae). Herpetol. 34(3): 277-287.
- BRADBURY, J. W., CAPRANICA, R. R. (in press): The Handy Pocket Summary of Fourier Analysis and Sono-  
graphic Mystique.
- BURCHFIELD, P. M., DOUCETTE, C. S., BEIMLER, T. F. (1980): Captive management of the radiated tortoise  
(*Geochelone radiata*) at Gladys Porter Zoo, Brownsville. Int. Zoo Yb. 20:1-6.
- CAMPBELL, H. W., EVANS, W. E. (1967): Sound production in two species of tortoises. Herpetol.  
23(3):204-209.
- CAMPBELL, H. W., EVANS, W. E. (1972): Observations on the vocal behavior of chelonians. Herpetol.  
28(3):277-280.
- DARWIN, C. (1845): The Voyage of the Beagle, 2nd. ed. London, John Murray.
- DREWRY, G. E., HEYER, W. R., RAND, A. S. (in press): A functional analysis of the complex call of the frog,  
*Physalaemus pustulosus*. Copeia.
- FOUQUETTE, M. J. (1980): Effect of environmental temperatures on body temperature of aquatic-calling  
anurans. J. Herp. 14(4):347-352.
- FRANKENBERG, E. (1974): Vocalization of males of three geographic forms of *Ptyodactylus* from Israel  
(Reptilia: Sauria: Gekkoninae). J. Herp. 8(1):59-70.
- FRAZIER, J. (1973): Behavioural and ecological observations on giant tortoises on Aldabra Atoll. Unpub-  
lished D. Phil. Thesis, University of Oxford.

- GANS, C., MADERSON, P. F. A. (1973): Sound producing mechanisms in recent reptiles: Review and comment. *American Zoologist* 13:1195–1203.
- GORDON, C. (1979): Appendix I. Gigantic land tortoises of Seychelles. In: Historical records of Indian Ocean giant tortoise populations, STODDART, D. R. and PEAK, J. F., *Phil. Trans. R. Soc. Lond. B.* 286:147–161.
- JACKSON, C. G., AWBREY, F. T. (1978): Mating bellows of the Galapagos tortoise, *Geochelone elephantopus*. *Herpetol.* 32(2):134–136.
- KELEMEN, G. (1963): Comparative anatomy and performance of the vocal organ in vertebrates. In: *Acoustic Behavior of Animals*, p. 489–521. BUSNEL, R.-G., ed., New York, Elsevier Publishing Co.
- MERTENS, R. (1946): Die Warn- und Droh-Reaktionen der Reptilien. *Abh. Senckenberg. Naturforsch. Ges.* 471:1–108.
- NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K., BENT, D. H. (1970): *SPSS: Statistical Package for the Social Sciences* (2nd ed.), New York, McGraw Hill Book Co.
- PATTERSON, W. C., GULICK, W. L. (1966): A method for measuring auditory thresholds in the turtle. *J. Aud. Res.* 6:214–227.
- SCHUMACHER, G.-H. (1973): The head muscles and hyolaryngeal skeleton of turtles and crocodiles. In: *The Biology of the Reptilia*, Vol. 4, p. 101–199. GANS, C. and PARSONS, T. S., eds. New York, Academic Press.
- SUTHERLAND, C. A., MCCHESENEY, D. S. (1965): Sound production in two species of geese. *The Living Bird* 4:99–106.
- WATKINS, W. A. (1967): The harmonic interval: Fact or artifact in spectral analysis of pulse trains. In: *Marine Bioacoustics*, Vol. II, p. 15–43, TAVOLGA, W. M., ed., New York, Pergamon Press.

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