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VOCAL COMMUNICATION IN THE REPTILIA - FACTS AND QUESTIONS

ELIEZER FRANKENBERG AND YEHUDAH L. WERNER*

INTRODUCTION

Communication:

Communication involves that *X* emits a signal and *Y*, perceiving the signal, noticeably changes its own behavior. In animals, communication occurs both intraspecifically (mainly to attract mates and deter rivals) and interspecifically (mainly to deter enemies). Both affect survival.

Communication employs signals of various modes, separately or in combinations: acoustical, chemical, tactile and visual. Each of these has different propagation properties, serving the animal accordingly, and needs to be studied separately with adequate techniques (Sebeok, 1968; 1977; Wallace, 1979).

Vocal Communication:

Acoustical communication employs signals of sound. In the vertebrates these are mostly emitted by the vocal organs (unlike the rattling of a rattlesnake or even its hissing), producing vocal communication. Vocal signals can give information about the sender, both information he wants to give and information he could prefer not to give. They bridge long distances but, unlike visual signals, they travel in darkness as well and are only partly obstructed by intervening objects. They also may inform about the location (distance and direction) of the sender relative to the receiver. Thus vocal signals have many advantages and could be expected to be widely employed. But they require suitable organs for sending and receiving and they may broadcast information to receivers whose presence is unknown to the sender and against his interest.

The research of vocal signals has progressed in recent decades thanks to equipment developed during the second world

* Department of Zoology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel.

war. The tape recorder preserves the signal and enables its repeated physical analysis, in terms of (1) time (duration, repetition rate, etc.), (2) intensity, (3) frequency (reciprocal of sound wave length) composition and (4) timbre (whether "tonal", pure frequency, possibly with harmonics, or "noisy", broad band noise). The oscilloscope displays mainly the distribution of acoustical energy over time. The sonograph serves mainly to display the frequency composition of the signal, over time, revealing also timbre. Lately these are augmented by real time analyzers and computarization (Lanyon and Tavolga, 1960; Busnel, 1963).

Vocal Communication in Reptiles: History of Study.

The investigation of vocal communication in reptiles has always lagged behind that in other vertebrates and in insects. Already Aristotele (4th century B.C.), who knew that "...the croaking... is made by the male frog, and is their call to the females at breeding time: all animals have special cries for this purpose...". said of reptile voices only, "...the oviparous quadrupeds produce a voice, but a feeble one; in some cases, a shrill piping sound, like the serpent; in others, a thin faint cry, in others, a low hiss, like the tortoise..." Even today, much less is known about vocalization in reptiles than in frogs or even fishes, not to mention mammals, birds or insects.

Nevertheless, Mertens (1964) already amassed anecdotal information on reptile vocalizations, obtained before the application of acoustic equipment. With the employement of such equipment much more has been learned in the following decades. The groups of reptiles which employ voices in the most conspicuous manner, and have therefore been the best studied, are gekkonid lizards and crocodiles. The latest review of reptilian vocalizations are those of Gans and Maderson (1973), Carpenter and Ferguson (1977), Kiester (1977) and Marcellini (1978), and of reptile hearing, those of Wever (1978) and Manley (1981).

Our aims in this report are to briefly review current knowledge of vocal communication in reptiles, with emphasis on (1) progress in the last decade or so, (2) gekkonid lizards and (3) our own efforts since 1967 (Werner, 1968) and 1969 (Frankenberg, 1973); and to point out some open questions. We shall minimize reference to the literature by limiting quotation where possible to the earlier reviews and other papers containing ample references. As will be seen, knowledge has advanced considerably concerning reptile vocalization on the one hand and their auditory capacity on the other hand, but only little concerning the communicatory function of the voice.

METHODS

Voice Analysis:

The technology, and problematics of the basic equipment --microphone, tape recorder, oscilloscope and sonograph-- as well as the terminology of acoustic and bioacoustica have been amply reviewed in the books edited by Lanyon and Tavolga (1960) and Busnel (1963) Suffice it to explain here that the sonograph, in its commonest mode, showing sound frequency versus time (fig. 1), operates through repeatedly examining a magnetic loop with recorded sound: with succesive revolutions, succesive acoustic filters for increasing frequencies operate; energy passing each filter is represented in the sonogram paper as a horizontal black line for the relevant duration; succesive lines representing rising frequencies are piled over each other to produce a sound-spectral representation as it changes over time. Although the sonograph produces the familiar pictures of bird songs and frog calls, it may produce arficial harmonic-like patterns (Watkins, 1967).

Auditory Analysis:

It is relatively difficult to examine the auditory capacity of reptiles by behavioral methods, and little has been achieved in this direction (Wever, 1978: 984-4). Instead, various physiological methods are employed. The most fruitful method has been that developed and employed by E. G. Weber and his associates: deriving audiograms as isopotential functions of the alternating potentials of the cochlea (= "CM"), in response to series of pure tones of known frequency and intensity. Wever (1978) details his methods and describes auditory function and structure for nearly 250 species of reptiles. Other physiological methods have been reviewed by Johnstone and Sellick (1972) and

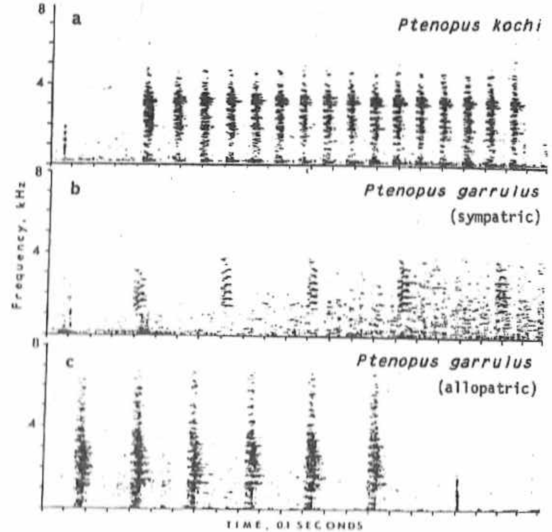

Fig. 1. Multiple-click advertisement calls of male *Ptenopus* spp. in the Namib Desert, demonstrating regular spacing of click rate (data from Haacke, 1969, 1974). Further explained in the text.

Manley (1981). Regulation of the experimental temperature has been reviewed by Werner (1983). Following Wever (1978) we express auditory sensitivity by the sound pressure, in decibels (db) relative to a sound pressure of 1 dyne cm^{-2}, required to elicit a standardized summated response from the hair cells (on this scale the auditory thresholds of man and cat approximate -80 db; Wever and Lawrence, 1954).

Behavioral Analysis:

Basically, the information contents of a signal can be deduced from the response of the receiver (Marler, 1961). The methodology of behavioral analysis of communication is further discussed in Busnel (1963) and Sebeok (1968). Two major alternative experimental approaches are (1) to test the response of separate animals to standardized signals (Marcellini, 1977), or to observe interactions in a group of animals and statistically establish the relation of categorized signals to categorized responses (Frankenberg, 1982b).

EXAMPLE: VOCAL COMMUNICATION IN GECKOS

VOICE:

Organ: How geckos produce their vocalizations has been a subject of speculation and controversy (Haacke, 1969), despite the work of Mahendra (1947), until Paulsen (1967) analized the function of the larynx in *Gekko gekko*. By high speed cinematography, he demonstrated how the vocal chords operate during air expulsion to produce the vocalizations, somewhat similarly to their operation in frogs.

Repertoire: The fame of geckos as vociferous animals derives from two classes of vocalizations: the "advertisement" multiple-click (MC) call of (mainly) the males of some species, which may be very loud; and the "distress" squeaks of nearly all species when seized. Sonographic analysis and observation of the situations in which the calls occur show that the males of some species have at least six different types of calls. In *Hemidactylus turcicus*, *Ptyodactylus hasselquistii guttatus* and *P. h. hasselquistii* the males call different series of clicks to females than to other males. In addition, most gecko species appear to emit four distinct types of distress calls when attacked, as discussed below. Even parthenogenetic geckos, *Hemidactylus garnotii* and *Lepidodactylus lugubris* have a social call differing from their distress call (Frankenberg, 1982a; Frankenberg and Marcellini, 1982; Werner, in MS 1).

Multiple Click Calls: In principle this call is a train of more or less evenly spaced, fairly similar, clicks. In some species it is apparently only produced by males [e.g., *Ptenopus* spp. (Haake, 1969; 1974); *Ptyodactylus* spp. (Frankenberg, 1974)]; in others, also by females: in *Hemidactylus frenatus* the male and female MC calls are similar (Marcellini, 1974) but in *Cyrtodactylus kotschyi* they differ in rate, [female, 2.5 clicks per second; male, 10 clicks per second (Frankenberg, 1978a)], and perhaps in duration.

Likewise, species differ in the type of difference there is between male calls to a male and male calls to a female in *Ptyodactylus h. guttatus* they differ in click number, call duration, and specially, click rate (Frankenberg, 1974), in *P. h. hasselquistii* on the contrary they seem to differ only in frequency range (Werner et al., 1978); and in *Hemidactylus turcicus* the difference lies in the degree of orderliness (evenness of click length) (Frankenberg, 1982b). In a Hawaiian population of *H. frenatus* the natural nocturnal MC calls comprised two distinct structural types, of unknown context (Frankenberg et al, in MS). A comparable situation occurs in *Ptenopus g. maculatus* north of Gorob mine (Haacke, 1969; 1974).

Presumably the MC calls most commonly heard in nature are the males' territorial calls (= to other males). These differ between species in duration, number of clicks, click rate, and emphasized frequency (Table 1); the frequency range and the loudness are more difficult to investigate, and the former may well increase with the latter. Their comparative study is complicated by temperature effects, the nature of which seems to vary between species (Haacke, 1969; Frankenberg, 1974; Marcellini, 1974). So do their ecological correlates: *Ptenopus* spp. call from inside the entrance of the burrow, which is believed to amplify the sound (Haake, 1969; 1974), but *Hemidactylus frenatus* call mainly when "active", out of cover (Marcellini, 1974).

Widely ranging species may show intraspecific geographical variation (Simkin and Il'ichev, 1965), potentially in the same ways in which species differ. In *Ptenopus garrulus maculatus* the average number of clicks varies between populations from 2.3 to 9.7 (Haacke, 1975). Click rate in this subspecies shows geographical character displacement, so as to increase the difference from *P. kochi*, where the two are sympatric in the southern Namib (Table 1, fig. 1).

Of evolutionary interest are the irregular MC calls. Presumably, and in general, the more monotonously repetitive calls are the more primitive ones, whereas diversification involves later calls, finally minimizing monotony (Leroy, 1977). Indeed the regular calls have the widest distribution among gecko taxa. But in some taxa there also occur irregular calls, diversifying the repertoire: thus the type "B" MC call of *Ptenopus g. maculatus* (Haacke, 1969; 1974) or the male-to-male call of *Hemidactylus turcicus* (Frankenberg, 1982b). Lastly, whereas the MC call of *Ptyodactylus h. guttatus* is regular, that of *P. h. puiseuxi* includes a prelude of minor clicks before the main ones, and that of *P. h. hasselquistii* comprises a melodious mixture of major and minor clicks (fig. 2), which even seems to vary between individuals (Werner, 1965; Frankenberg, 1974; Werner et al., 1978).

Distress Calls: Geckos also produce a variety of non-MC calls. Previously we recorded the calls produced by four species when threatened by the hand or seized. The resulting repertoire was classified into four call types, all of which were produced by three of the species (*Cyrtodactylus kotschyi, Gehyra variegata* and *Stenodactylus sthenodactylus*): Type I, more or less resembling a single click of a MC call; type II, noisy, of long duration, amplitude-modulated

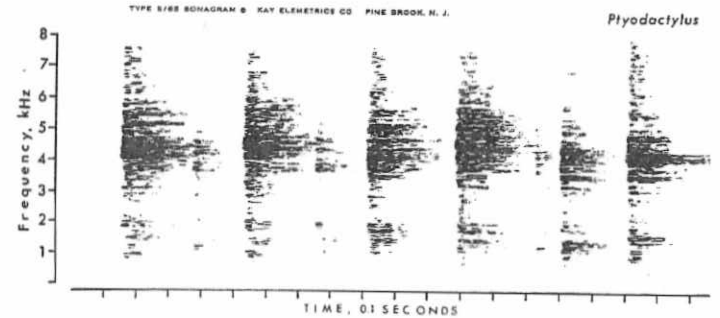

Fig. 2. Multiple-click advertisement call of male *Ptyodactylus h. hasselquistii*, demonstrating an irregular mixture of major and minor clicks (data from Frankenberg, 1974).

or segmented; type III, noisy, long, uninterrupted; type IV, tonal (with harmonics), long, frequency-modulated (Frankenberg and Werner, 1984). We suggested that because ten factors of variation were involved, this repertoire provided an unpredictable, hence effective, response to attack. But these call types have also been described (under a variety of names) as being employed in various social situations, in various species, and may be situation-specific, to varying extent. Some comparative data and terminologies are given in Table 2. Nearly all calls reported from geckos can be assigned to one of these categories of MC calls or distress calls defined here (figs. 3, 4). One must take into account some degree of intra-category variation; not only in variable parameters but also qualitative variation between species. Thus the type I distress call is noisy in *Ptyodactylus* (Frankenberg, 1975) but tonal and even modulated in *Hemidactylus frenatus* (Marcellini, 1974); however, in each case it appears derivable from a single click of the specific MC call. The type I calls of both species may probably be regarded as homologous, just like the MC calls of the two, despite the different internal structure. The "hissing bark" of *Teratoscincus* when counterattacking differs from these types, resembling type III but emphasizing certain frequencies; interestingly this gecko adds a broad band, high frequency "white" sound from its stridulating tail (Gans and Maderson, 1973; Hiller, 1974; Werner, pers. obs.).

Ultrasound Components: Many distress call contain (on the sonogram) energy up to above 8 or 10 (Marcellini, 1974; Frankenberg, 1975), apparently well above the useful hearing range of the same species (next chapter). Recently, by the ingenious application of a "bat detector" (Sales and Pye, 1974), Ann Brown (1985) demonstrated the presence of even higher frequencies in some distress calls of several Israeli and other geckos. The champions were *Gekko gekko* whose barks (type I ?) contained energy up to 60 kHz, and *Ptyodactylus h. hasselquistii* whose type IV call contained energy up to 50 kHz (no MC calls were available). It remains unclear whether the high frequency components of distress call represents a "wasted by-product" or function in deterring small mammalian and perhaps avian predators.

HEARING:

Low-frequency and high-frequency ears: Ear structure, and hearing as assesed by inner-ear function (CM), have been examined in 48 species and subspecies of Gekkonidae (*sensu lato*) (Wever, 1974; 1978; Werner, 1976). The level of sensibility varies between species; the champions are the larger eublepahrines,

Table I

SPECIES	SEX	REF	R/A	N OF CLICKS mean (range)	CALL DURATION sec:mean(range)	CLICK RATE clicks/sec	FREQUENCY OF CLICK (kHz) emphasized	FREQUENCY OF CLICK (kHz) Range (max)	SENSITIVE RANGE (CM audiogram, kHz)
Cyrtodactylus kotschyi orientalis	m	2	34			10			
Same	f	2	42	(14-23)	(1.1-3.1)	(7.4-12.7)			
Gekko gecko	m	7	?150	(59)	(23.2)	2.5	4-5	3.5-6.5	0.67-6.1
Hemidactylus frenatus		6	60	(9-10)		0.5	4-5.5	3-7.5	-
				8.78	1.97	4.5	0.5-2		0.18-1.0
Hemidactylus turcicus	m	3	51-56	(5-15)	(1.05-3.73)	(3.12-5.82)	1.3-2.4	<1-14<	(1.2-1.9)
				22.8	6.19	3.7			(0.4-7.5)
Phyllodactylus tuberculosus		7	<65	(5-55)			?1-3.5	0.5-5.5	(0.4-7.5)
				7	2	3.5			
Ptenopus carpi	m	5	<59	(5-9)			2-2.5	0.5-7	(0.18-6.1)
				?11.5					
Ptenopus g. garrulus	m	4	<52	(2-20)			?2-2.5&4-5	?0-6	
Ptenopus garrulus maculatus	m	4,5	<60	6	0.74-1.51		?1-3.5	0-7	
				5.3	1.23-1.75				
Ptenopus kochi	m	4	<65	(2-12)			?1.5-3.5	0-7	
Ptyodactylus guttatus	m->f	1		11-12	1.28	9	1.3-2.2 &		0.45-2
				7		1.29	3-5.6		
Same	m->m	1	<80	(5-8)		(1.18-1.54)	1.2-2 &		
				12		1	2.8-5.2		
Ptyodactylus hasselquistii		1,8	80-85	(11-14)		(0.87-1.09)	1.3-2.5 &	0.5-8<	
						5.55	3.8-5.5		
Ptyodactylus puiseuxi	m	1	<70			(3.57-12.5)	2.5-3 &		0.5-3.8
				7 + 4		4 + 1.4	4.8-6		
				(2-9)+(3-6)		(1.9-10+0.9-2.6)			

Table II

SPECIES	REF	TYPE I	TYPE II	TYPE III	TYPE IV	OTHER
Gekko gecko	1,5	"Bark" when approached		Distress hiss when handled		
Hemidactylus frenatus	4	"Single chirp" of m&f (not y) when grasped by hand or bitten by aggressor 2 (0-8) kHz	"Churr" of m resident antagonist before attacking 2 (1-5) kHz			
Hemidactylus garnotii	2		Squeak of f resident antagonist with counter-attack 1.3-6 kHz			
Hemidactylus turcicus	3	"Short noisy squeak" of f ("I") and m ("II") during a m MC call	"Long noisy AM squeak" of M ("III") attacked escaping or fighting	"Long noisy squeak" of m ("IV") in aggressive interaction or of f("II") when attacked	Harmonious "FM squeak" of f ("IV")or m("V") when chasing or threatening	f ("III"):"Long moderately FM & harmonious" when m calls or holds

Table I: Multiple-click calls of geckos. References (REF)= (1) Frankenberg, 1974; (2) Frankenberg, 1978; (3) Frankenberg, 1982; (4) Haacke, 1969; (5) Haacke, 1975; (6) Marcellini, 1974; (7) Marcellini, 1978; (8) Werner et al., 1978. R/A= Rostrum-Anus length in mm;

Table II: Homologies of distress calls of some geckos described by various authors as occurring in social contexts or when handled. Call Types I - IV & Other according Frankenberg and Werner, 1984. References (REF)= (1) Brown, 1985; (2) Frankenberg, 1982a; (3) Frankenberg, 1982b; (4) Marcellini, 1974; (5) Werner, unpublished.

Eublepharis maculatus and *Hemitheconyx caudicinctus*, some of which responded to sounds 20 db below the human threshold! Several other species, however, are less sensitive than various lizards of other families. For accurate results, such comparative studies need to be made at the ecologically optimal body temperature of each species (Werner 1976; 1983; 1985).

The range of frequencies at which geckos are sensitive varies between species. The audiograms of *Gekko gekko* shows two regions of best sensitivity: one at 400 - 600 Hz, another at 2000 - 4000 Hz. Although these numerical values vary interspecifically, such duality appears to be the rule, and presumably reflects two populations of hair cells (next paragraph). Usually but not exclusively, it is in the larger geckos that the lower range is the sensitive one (*Coleonyx, Eublepharis; Gekko, Ptyodactylus, Teratoscincus*), whereas, usually but not exclusively, in the small species the best sensitivity is in the thousand of Hz (*Cyrtodactylus kotschyi, Hemidactylus mabouia; Diplodactylus, Lucasium; Gonatodes, Sphaerodactylus*) (fig. 5). A few species appear similarly sensitive in both ranges (*Oedura ocellata*) (Wever, 1974; 1978; Werner, 1976). At least, this is the picture by the CM method. In some species the CM-audiogram shows a third peak of sensitivity around 12 - 15 kHz but this could be an artifact (Werner, 1976). Normally sensitivity rolls off rapidly above 5 kHz.

CM audiographs, similar to those obtained in response to series of pure tones, were also obtained in *Ptyodactylus* stimulated with a combination -tone derived from homospecific MC calls (Fray et al., in MS). Unlike in frogs, where audiograms based on hair cell potentials equal those derived from brain responses (Werner, 1979), in lizards a methodological bias needs to be considered: Audiograms based on evoked responses from the auditory nerve or brain (gross or compiled from single units) show poorer sensitivity of the lower frequencies and better sensitivity of the higher frequencies, compared to CM audiograms (fig. 6). The discrepancy may be due to the fact that the magnitude of the cochlear potential is frequency-dependent, or to the spatial-electrical relationships of the sources of potentials and of electrodes, or to both (Manley, 1972a; 1981; Werner, in MS 2).

Sensitivity as related to ear structure: The audiogram may owe its shape and sensitivity to the inner ear, the middle ear or both. This question can be analysed experimentally in a number of ways. When the ear drum and most of the ossicular chain is extirpated, and sound is applied directly to the oval window (still plugged by the stapedial footplate), the shape of the audiogram remains similar to that of the normal ear before the surgery. However, sensitivity is reduced, by about 35 db in *Gekko* and 53 db in *Eublepharis* (Fig. 7). By replacing the aerial sounds by vibratory stimulation which can be directed at selected points, one can usually show in lizards that this amplification, or impedance matching, of the middle ear results from two components: the hydraulic lever due to the ratio tympanic-membrane-area / stapedial-footplate-area, and the mechanical lever due to the excentric position of the columella relative to the drum. This is true, for example, in the iguanid *Crotaphytus*. But in the geckos *Gekko gekko* and *Eublepharis* the results indicated that the hydraulic lever alone was responsible for all of the magnification (Werner and Wever, 1972; Wever, 1978). Nevertheless, when the Mossbauer technique was applied to the ears of the geckos *Gekko gekko, Gehyra variegata* and *Phyllurus (= Underwoodisaurus) milii*, a significant mechanical lever was demonstrated (Manley, 1972b, c; Saunders and Johnstone, 1972; Johnstone and Werner, in preparation).

When closely related species are

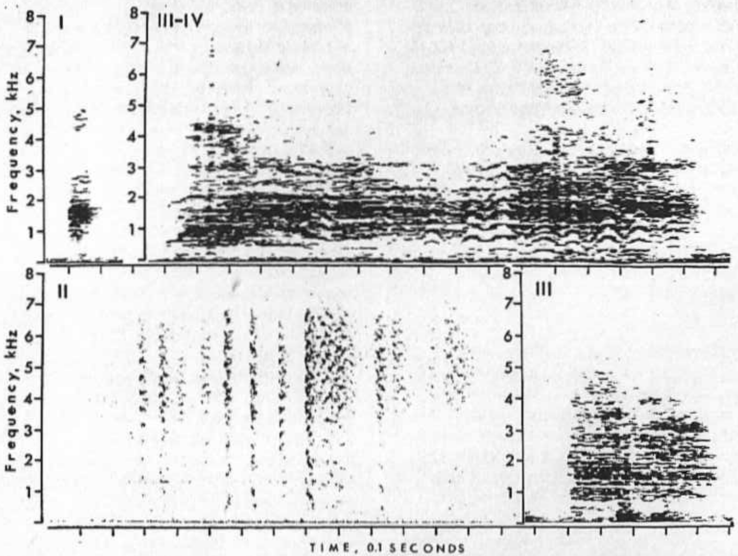

Fig. 3. Types of distress calls of geckos, according to the classification in Frankenberg and Werner (1984): I. click-like, from a female *Phyllurus platurus*; II, amplitude modulated, from a male *TropiocoloTes*; III, protracted noisy, from a juvenile *Underwoodisaurus milli* when approached (energy up to at least 25 kHz); III-IV (intermediate type), protracted, partly tonal and modulated, from a male *Phyllurus platurus* when approached (energy up to at least 40 kHz). (I, III and III-IV, sonograms courtesy Dr. Ann Brown; II, data from Frankenberg, 1975).

compared, e.g. among Eublepharinae, the degree of sensitivity is correlated to the size of the tympanum and to the value of the hydraulic ratio (which varies among eublepharine species from 21.9 to 32,1); and through these, to specific body size (Werner, in MS 3).

On the other hand, the shape of the audiogram and its residual sensitivity after elimination of the ear are determined by the inner ear. The details are complicated, but as a general principle there is evidence that the sensitivity depends on the number of hair cells (Wever, 1974; 1978). Again, among closely related species, the number of hair cells correlates with body size.

EVIDENCE FOR COMMUNICATION

Circumstantial Evidence: Unfortunately we have almost only circumstantial evidence that the vocal communication indeed functions in geckos: (1) Advertisement calls (MC) are only known in nocturnal or crepuscular geckos, except for *Ptyodactylus hasselquistii puiseuxi* which, unlike its congeners, is diurnal in all seasons (Frankenberg, 1978b). It employs MC-calls (Frankenberg, 1974), the complexity of which, as explained above, indicates that this is a secondary situation. But the famous diurnal genera *Gonatodes, Sphaerodactylus, Lygodactylus* and *Phelsuma* are only known to produce distress vocalizations (Marcellini, 1974; Stamps, 1977; Werner, pers. obs.). These geckos

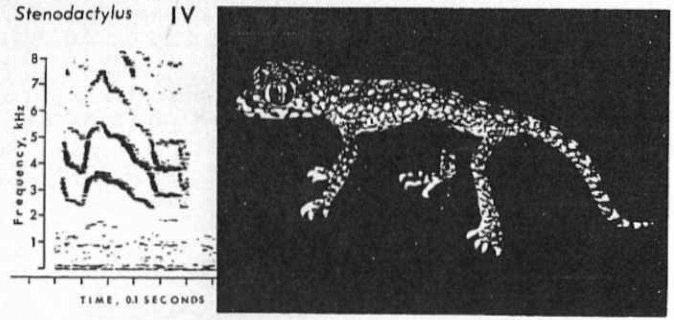

Fig. 4. Type IV distress call, protracted, tonal and modulated, from a female *Stenodactylus sthenodactylus* when approached (data from Frankenberg, 1975) and typical threat posture of this species while emitting such calls (from a juvenile while shrieking).

are coloured as if for visual identification and communication, and, excepting *Phelsuma*, show strong sexual dichromatism. Indeed, some of them have been shown to employ visual signals (Stamps, 1977). Some of the cryptically colored diurnal *Pristurus* spp. apparently signal with their barred tails (Arnold and Gallagher, 1977; Arnold, 1982). All these gekkos, except *Phelsuma*, are of small size and possess poor audition (when known) but they share these paired characters with many nocturnal forms. It is possible that in *Phelsuma*, auditory acuity varies strongly among individuals (Werner, 1976; Wever, 1978).

(2) There is a trend of agreement for the basic or emphasized frequencies of the MC calls, with the frequency ranges of the sensitivity peaks of the audiograms of the same species (Table 1). The agreement is closest with the upper-frequency peak of sensitivity, which in the larger geckos is minor in the CM-audiograms but prominent in the evoked-potential audiograms (fig. 6).

(3) Concerning the african burrowing *Ptenopus*, many observers have testified that the (usually unseen) animals seem to be calling in a coordinated chorus, each starting his call promptly after his neighbor concluded his own (Haacke, 1969; 1974; Werner, 1977).

(4) Lastly, in *Ptenopus*, Haacke (1969) demonstrated character displacement increasing the difference between the calls of *Ptenopus kochi* and *P. garrulus maculatus* who are sympatric.

Analytical Evidence: Some observations indicate that vocalizations occur, or occur more frequently, when the geckos are in the company of conspecifics: *Ptyodactylus* (Frankenberg, 1974; Werner et al., 1978); *Cyrtodactylus kotschyi* (Frankenberg, 1978a). Captive *Hemidactylus frenatus* "could occasionally be stimulated to call by the playing of a recorded MC call near their cage" (Marcellini, 1974).

Few investigators have observed groups of geckos, amassed ample direct observations, and undertaken statistical analysis of context: Dagmar Werner (1972) found in caged groupings of *Ptyodactylus h. guttatus* that the males' MC calls drove other males away but did not so affect the females (the calls were not analyzed acoustically). Marcellini (1974) found in a natural population of *Hemidactylus frenatus* that MC-calls occurred in aggression, courtship and feeding (the calls were not subclassified); that the "churr call" (Table 2) occurred only with aggression: and that the "single chirp call" (Table 2) occurred in various distress situations. Frankenberg (1982b) found in caged groupings of *H. turcicus* that the MC-calls differred when directed at males or at females, and that the various other calls of males, females and

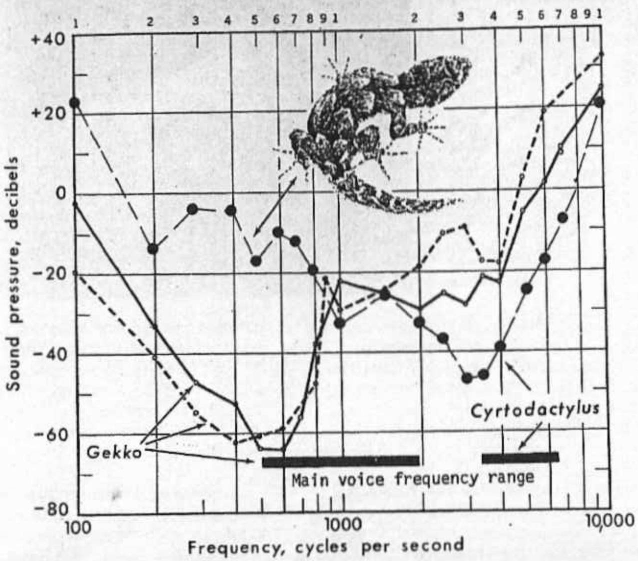

Fig. 5. Audiograms of two individuals of *Gekko gekko*, demonstrating a low-frequency ear, and of one *Cyrtodactylus kotschyi orientalis*, demonstrating a high-frequency ear (data from Wever, 1978); and main voice frequency ranges (sources as in Table I). (Methodology: CM, isopotential, audiograms).

juveniles could each be associated with threat, attack, defense, release, escape or even approval. In caged groupings of parthenogenetic *H. garnotti*, the sole type of vocalization (amplitude modulated) routinely accompanied the counterattacks of animals approached by others (Frankenberg, 1982a).

Experimental Evidence: To date the best evidence of functioning vocal communication in geckos come from an experiment of Marcellini (1977; 1978): single individuals of *Hemidactylus frenatus* were exposed to MC-calls. Females responded indifferently but males tended to turn away from the calls (statistically significant) although they did not avoid white noise (control). In this project no distinction was made between MC-calls directed to males and those directed at females. Still, the main result parallels the observations of Dagmar Werner (1972) on *Ptyodactylus*.

Because of the difficulties in conditioning gekkos to respond to sound, we monitored the effects of homospecific vocalizations on heart and respiration rates of *Ptyodactylus*. The responses demonstrated that "hearing" in the psychological sense indeed occurred (Werner et al., in MS).

VOCAL COMMUNICATION IN OTHER REPTILES

Testudines:

Testudines, especially Testudinidae, are well known to vocalize; Carpenter and Ferguson (1977) quote some sixty records. Most records

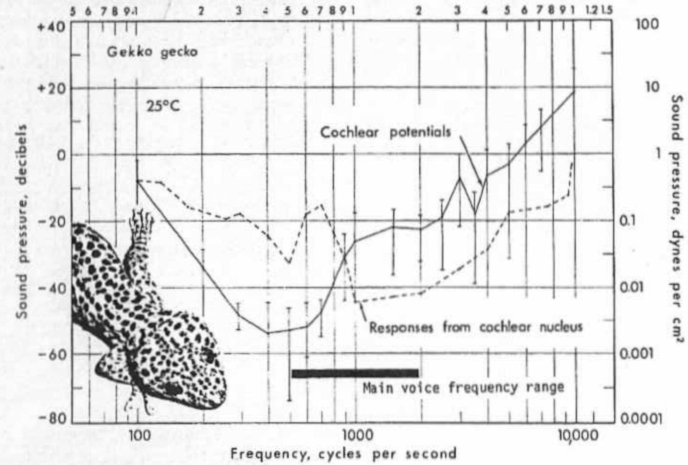

Fig. 6. Comparison of two methodologies for deriving audiograms: audiograms of *Gekko gekko*, one based on CM potentials (isopotential), the other on evoked neural responses (threshold) (data from Werner, in MS 2); and main voice frequency range (data from Marcellini, 1978).

concern the rythmic grunts or squeaks of the male while mounted on the female in copulation. Possibly for this reason, some reviewers have not attached much importance to turtle vocalizations: Harless (1979: 438) says, "It seems that most vocalizations... simply occur in stressful situations and may or may not be eliciting and discriminative stimuli for other turtles". Petzold (1982) summarizes (we translate), "in general today one considers the vocalizations only a by-product of the copulatory excitement".

But evidence is accumulating to the effects that more may be involved. In some species, males vocalize while chasing the female (De Sola, 1930; Snedigar and Rokosky, 1950). *Geochelone travancorica* in India call in chorus, especially at night; juvenile *Platysternon megacephalum* squeal when picked up or disturbed (Campbell and Evans, 1972). Gans and Maderson (1973), Auffenberg (1977) and Frazier and Peters (1981) bring additional examples, including cases of species known for more than one type of vocalization.

Most turtle vocalizations have been described verbally, without acoustic analysis. Together with the few available analyses, these descriptions indicate considerable acoustic variety. A rough correlation emerges between specific body size and the frequency range of the vocalizations from *Geochelone gigantea* (260 - 800 Hz) through *Geochelone carbonaria* and *G. travancorica* (up to ca. 2.5 kHz) to juvenile *Platysternon maegacephalum* (up to 4.5 kHz). Other interspecific differences also occur: the rhythmic copulation squeaks of *Testudo kleinmanni* sound very different from those of *Testudo graeca* (Hoofien, 1971). Incidentally, a large female of *T. graeca* which behaved homosexually sounded more low-pitched than the males (Werner, pers. obs.).

Audition has been tested electrophysiologically in 27 species and subspecies, and in *Pseudemys scripta* the results have been corroborated by behavioral

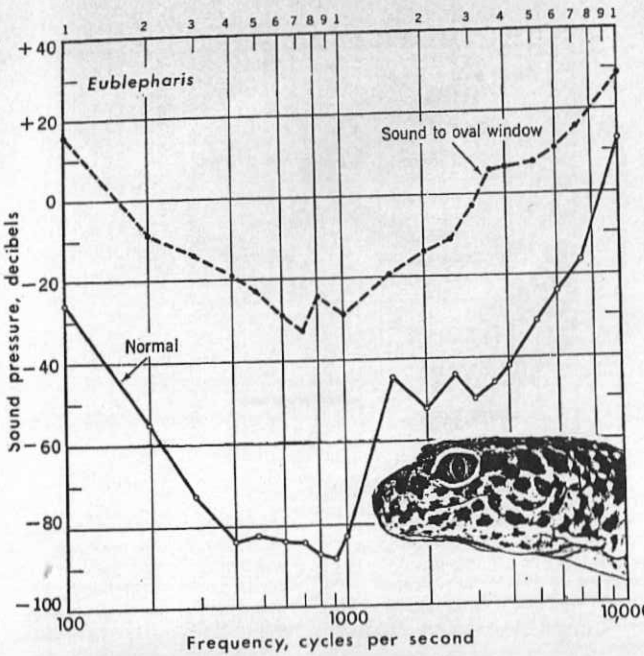

Fig. 7. The amplification effect of the middle ear demonstrated in *Eublepharis macularius* by the distance between the two audiograms: one in response to normal aerial stimulation of the intact ear, the other in response to direct aerial stimulation of the oval window, after middle ear extirpation (data from Werner and Wever, 1972; Wever, 1978).

tests. The ranges of specific sensitivity and frequence response resemble those of non-gekkonid lizards (Wever, 1978). There is every reason to believe that turtles can hear homospecific vocalizations, perhaps excepting the smallest species with the highest voices, as pointed out by Frazier and Peters (1981).

Crocodylia:

Since the reviews of Gans and Maderson (1973), Carpenter and Ferguson (1977) and Kiester (1977), our understanding of the social and sexual roles of the roars and bellows of crocodiles has been expanded mainly by Garrick and associates (Garrick, 1975; Garrick and Lang, 1977; Garrick et al., 1978). A few species show complex signalling systems including vocal, other acoustic, visual and chemical signals. The vocal signals differ interspecifically in call structures, repertoire and vocal behavior and intraspecific (sexual and individual) variation may also occur. The vocal repertoire is more important in *Alligator mississippiensis*, possessing six distinct call types, than in *Crocodylus* spp. This may be an adaptation to a habitat with denser vegetation; *A. mississippiensis* seems to use visual signals mainly for short distances, and its vocal signals appear adapted for long range transmission. Vocalizations of adult crocodilians are mostly low-frequency, up to 500 Hz, rarely up to 1 kHz.

An analysis of distress calls in juvenile *Caiman crocodylus* showed that temperature affected several call parameters but hardly the frequence spectrum (Garrick and Garrick, 1978). These juvenile vocalizations contain energy, in modulated tonal harmonics, throughout the spectrum up to 3 - 4 kHz.

The direct observations quoted leave no doubt that vocal communication occurs [it is interesting that crocodiles employ additional non-vocal acoustic signals (water splashing, etc.)]. The CM audiograms of three species all reach sensitivity of -60 db and remain quite sensitive (-40 db) from 100 Hz to 3 or 4 kHz (Wever, 1978).

Of outmost interest is the partial evidence of vocalization of the babies within the eggs, to synchronize hatching and to signal to the mother to open the nest, and of parental responses to distress cries of juveniles (Kiester, 1977).

Rhynchocephalia:

It is difficult to interpret the many verbal descriptions of the vocalizations of *Sphenodon* and it is not clear whether both sexes vocalize. But *Sphenodon* produces at least two different sounds, under different circumstances (Carpenter an Ferguson, 1977). The sound described as a croak emitted when handled was analysed on oscilloscope by Wojtusiak and Majlert (1973) who concluded that its energy peaked in the range of 1 - 4 kHz. They heard but did not analize the weaker grunting sound which the animals produce of their own accord.

Gans and Wever (1976) analyzed *Sphenodon* calls on a wave analyzer and found energy peaks at 300 Hz and from 600 Hz to 2 kHz. They also electrophysiologically tested the animal's hearing and found that with aerial sound de audiogram peaked at 200 Hz, and with vibratory stimulation at 200 to 700 Hz. They concluded that vocalization and auditory sensivity coincided, despite the absence of a conventional tympanic membrane (Gans and Wever, 1976; Wever, 1978). Because the audiograms were insensitive above 1 kHz, Gans and Wever proposed that the technique of Wojtusiak and Majlert (1973) may have been faulty. Theoretically, these teams could have examined different call types, and the distress croak could be directed at predators. But one of us (YLW), has experienced the distress croak when catching a *Sphenodon* in the wild: the call is loud, startling, unpleasant to the ear, and indeed unlikely not to include low frequencies.

Sauria:

Other than the Gekkonidae, the only saurian family with widespread vocalization is Pygopodidae, Australian lizards resembling Scincidae but related to Gekkonidae (Weber and Werner, 1977). Most reports concern distress squeaks or barks aroused interspecifically but at least two *Delma* spp. squeak in intraspecific social situations (Weber and Werner, 1977; Annable, 1983). Distress squeaks of *Delma* and *Lialis* can be noisy or tony and modulated, with harmonics, and reach up to 12, sometimes 16 kHz, much above homospecific audition (up to 4 kHzin *Lialis*). Presumably they are directed at mammalian or avian predators (Weber and Werner, 1977).

Several species of certain genera of Iguanidae vocalize (Carpenter and Ferguson, 1977; MArcellini, 1978). The distress squeal of *Gambelia wislizenii* averages 2.5 seconds and has its main energy at 2 - 3 kHz; it accompanies the counterattack against aggressors, which the species displays at low temperatures, rather than flee, as it does in high temperatures (Crowley and Pietruszka, 1983). Several species of *Anolis* vocalize, sometimes in social contexts. Rothblum et al. (1979) succeeded in conditioning *A. grahami* to respond to sounds having the frequency of its own voice.

Some Scincidae (in Australia and New Zealand) consistently squeak in distress (Werner, 1973a) but of hundreds of Israeli *Chalcides ocellatus* handled, only one individual squeaked and only when freshly captured, never again in captivity (H. Almagor and Werner, pers. obs.). Two scincids click spontaneously (Werner, 1973a). In another scincid Johnstone and Johnstone (1969) demonstrated that cochlear and auditory nerve responses peaked in the mating season. Possibly in this species, perhaps also in other lizards, intraspecifical vocal communication arises seasonally.

Vocalization has been reported in occasional species of the Agamidae, Anguidae, Lacertidae, Teiidae and Varanidae (Gans and Maderson, 1973; Weber and Werner, 1977; Marcellini, 1978). Although some of these families contain species lacking a normal tympanic membrane, all the reports on vocalization concern taxa possessing normal middle ear (Mertens, 1971; Wever, 1978).

Serpentes:

Hissing and some other variations of air expulsion are common in snakes (Gans and Maderson, 1973; Carpenter and Ferguson, 1978) but proper vocalization also occurs. Hoofien (1971) has referred to earlier reports and convincingly described vocal squealing in a captive female colubris, *Spalerosophis diadema cliffordi.*

Although intraspecific vocal communication has never been proposed for snakes (e.g., Carpenter, 1977), a word on hearing is warranted. Contrary to past belief based on anatomy, Wever and Vernon (1960) have conclusively proven the audition of airborne sound in snakes, and this has been amply confirmed by later work (Hartline and Campbell, 1969; Wever, 1978). The CM audiogram of several snakes reaches -40 db and below, and up to 400 or 600 Hz. Nevertheless, when an Indian snake charmer was tested by separating him and his flute from his performing cobras by a partition, it transpired that the cobras had been responding to the visual and tactile, not the acoustic, stimulation (Werner, 1973b).

DISCUSSION OF OPEN QUESTIONS

Except for the geckos so few reptile vocalizations have even been recorded, that little is known about vocal communication in reptiles, other than indications that it may be much more important than has usually been acknowledged (Busnel, 1963; Schwartzkopff, 1977). Thus in sauria the numerous scattered reports on vocalization, perhaps based on usually loud individuals, together with the finding (where tested) of seasonality in auditory physiology, raises a suspicion of widespread low-intensity vocal communication related to mating. Obviously many more species, including geckos, need to be studied, for us to understand the structure and communicative function of reptilian vocal repertoires. But we would like to emphasize here a group of questions with ecological aspects which have not yet been touched.

Signal production: The vocal mechanism of *Gekko* (Paulsen, 1967) may occur in all Gekkonidae but next to nothing is known for other vocalizing reptiles (Gans and Maderson, 1973). This ignorance prevents an evolutionary consideration of vocal communication of reptiles. Further, the absence of any measurements of voice intensity restricts all considerations involving relative loudness to an anecdotal level (see below).

Loudness relations: There is an incomplete dichotomy, with considerable overlap, between the majority of nocturnal or crepuscular geckos which employ acoustic signals, and the minority of diurnal geckos which employ visual signals (coloration and postures) (Stamps, 1977). What are the energetic and other ecological costs of the two modalities? And how expensive is it to have a louder voice? For example the late Hermann Zinner stated (pers. com.) that he had observed the barn owl, *Tyto alba*, direct itself to calling *Ptyodactylus.*

One may expect the larger species to be more widely spaced (Stamps, 1977) and thus to employ a louder voice. To some extent it seems to be the case, but the little *Ptenopus* is rather loud, so if there is a rule, what is it? There are anatomical foundations for larger species to have keener hearing, which could help bridge the distance expected between the large individuals. But how much correlation is there among loudness, sensitivity and spacing?

Adaptation to habitat: Adequate loudness and range are not necessarily the key characteristics for an acoustical signal. It may evolve so that its deterioration over distance, in itself, will inform about the distance. Certainly it would tend to be relatively deformation-proof in its relevant acoustic environment. Investigators have differed in their conclusions as to how various habitats of birds, especially forest versus open field, differ in their effects on signal transmission (Wiley and Richards, 1978). Beyond the suggestion that alligator vocalizations (unlike those of crocodiles) are adapted to vegetation-rich habitats (Garrick and Lang, 1977; Garrick et al., 1978), the application

of this approach to reptile vocalizations awaits the investigation of sound propagation in additional environments, notably rocks and crevices.

Echolocation?: The occurrence of high frequence components in many vocalizations of nocturnal, sometimes cavernicolous, Gekkonidae and Pygopodidae, even up to 60 kHz (Brown, 1985), intensifies the question of echolocation, already raised by Wojtusiak and Majlert (1973) concerning *Sphenodon.* The auditory physiology of reptiles, as well as the functional morphology of their middle ear, suggest that reptile ears are inefficient above 5 kHz or so (Johnstone and Sellick, 1972; Saunders and Johnstone, 1972; Schwartzkopff, 1977; Wever, 1977; Manley, 1981). But no actual tests of sound perception in the 20 - 60 kHz range have been reported. The audiograms of some geckos showed a third area of (relative) sensitivity at 10, 12 or 15 kHz but this was regarded an artifact and the testing was not continued to higher frequencies (Werner, 1976).

CONCLUSIONS

1 - Vocalization is widespread in the Reptilia, given the limitations that (a) it occurs mainly in nocturnal or crepuscular groups or species [most geckos, *Lialis, Sphenodon* and crocodiles have slit pupils; the snake *Spalerosophis* is seasonally nocturnal (Werner, 1970)]; and (b) it occurs only in species possesing a normal tympanic membrane (exceptions: *Sphenodon* and the vocalizing snakes).

2 - Some species have a repertoire of at least six distinct calls, classified as (a) advertisement calls and (b) distress calls.

3 - The advertisement, multiple-click, calls of geckos vary between sexes and between motivations, and the method of such variation differs among species.

4 - Circumstantial evidence points to an interspecific, predator deterring, employment of distress calls, which often contain energy at frequencies apparently above homospecific audition. In geckos some of the rich and variable distress repertoire also serves in intraspecific social situations.

5 - As far as known, in most vocalizing reptiles auditory sensitivity, as measured electrophysiologically, is keen and includes the frequency range of homospecific vocalizations. Behavioral evidence for the hearing of the latter exists for *Anolis* and *Ptyodactylus.*

6 - Evidence for intraspecific communication is mostly circumstantial (as above) or observational (interaction, chorusing) but some analytical and experimental evidence exists for geckos.

7 - Some reptile vocalizations include ultrasound. Given the known limitations of the ear, echolocation is unlikely, but has not been ruled out conclusively.

8 - Further research is needed on the behavioral aspects of vocal communication in reptiles, but also, and especially, on the ecological aspects: ecological cost of vocalization; relations among loudness, auditory sensitivity and spacing; effects of the environment's transmission properties on vocal signals and on their evolution.

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