THE CALL OF THE BARKING GECKOS (GEKKONIDAE: REPTILIA)

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(With 4 figures and 1 colour plate)

INTRODUCTION

The Gekkonidae are the only lizards with true vocal abilities and of this group the southern African genus *Ptenopus* is probably one of the most vociferous. The call consists of a series of clicks, ticks or chirps, which are uttered in quick succession. Calls are usually uttered in reply to others, for which reason the type species was called *Ptenopus garrulus*. When describing this species in 1849, Sir Andrew Smith wrote:

"In the localities in which it occurs, many individuals may be seen peeping from their hiding places, each uttering a sharp sound, somewhat like chick, chick; and the number thus occupied is at times so great and the noise so disagreeable, as to cause the traveller to change his quarters."

At present three species are known, of which two were described within the last seven years. Each species has a characteristic call. *Ptenopus* is a terrestrial genus and each specimen lives in a self-made burrow. The call is uttered by the male only and the functional significance is still uncertain but probably is associated with territoriality and the attraction of females. Vocal activity usually starts towards sunset, reaching its peak just after sunset before darkness falls. Silence usually follows, but loud choruses may continue right through the night and isolated calls may be heard during the day. No calls are heard during the winter months and even in summer there may be silence for weeks. The correlation between season, weather and vocal activity is still not clear.

Since the original description by Smith a number of authors have described the call and Loveridge (1947: 35) summarized the various onomatopoeic interpretations. Brain (1962), when revising the genus and describing *P. carpi,* repeated most of them, adding his own observations and mentioning a call heard by Dr. Koch at Gobabeb, which had more clicks and followed in quicker succession than is known for *garrulus*. It was then assumed to have been the call of *carpi,* but was later found by the author to be that of *kochi,* a species still undescribed in 1962. When describing *kochi* in 1964 the author first mentioned a different call for each of the three species. At that stage it had already been noticed that not only a remarkable interspecific but also intraspecific variation in the calls existed and that fluctuations in humidity and temperature affected the reaction of the geckos. Since then an attempt has been made to obtain more detailed information about the call of *Ptenopus,* especially *P. garrulus*. The above-mentioned onomatopoeic reproductions might, to some extent, reproduce the sound and give some impression of the call, but, unless actual recordings are available, do not supply any information regarding the duration, rhythm, pitch and other characteristics which are even more difficult to describe. Because of these shortcomings an attempt was made to produce better comparative material by means of tape recordings and subsequent analyses.

Each call consists of a series of clicks uttered in quick succession. Although Broughton (1963: 16) defines " the shortest unitary rhythm element of sound emission that can readily be distinguished as such by the unaided human ear" as a 'chirp', the author prefers the term 'click' for the individual sound pulses of which a call consists, as it is a better description of these staccato sounds. A considerable variation in the number of clicks per call

and the rate at which the clicks were uttered has been observed.

There has been some speculation in the past concerning the sound-producing mechanism involved, and Loveridge (1947: 14 quoted by Brain 1962) assumed that the sound was produced by "the sudden removal of the fleshy tongue from contact with the palate" while Goin and Goin (1962: 267) thought "that the sound is perhaps produced by clicking the broad tongue against the roof of the mouth." As the larynx of gekkonids has membraneous folds which can be considered to be vocal chords (Keleman 1963: 491 and Tembrock 1959: 37), this family is the only one amongst the lizards with true vocal abilities. The presence and structure of this organ has not yet been investigated in *Ptenopus,* but, as this genus is so exceptionally vocal, it is provisionally accepted that the larynx is well developed and that the sounds are produced by it.

The function of the call is still uncertain. Mertens (1946: 36) suggests that it is part of territorial behaviour, but may also serve to attract females. This is possible, as no two holes were observed to be closer together than about two feet, which may indicate that females also show some degree of territoriality, which is unusual. However, as only males have been observed calling, it is uncertain in what way females would define their territory. It has been observed that the female of the Tokeh *(Gekko gecko)* is attracted by the call of the male (Mertens *op. cit.*). During the middle of October 1965 on the farm De Waal, Gobabis district, South West Africa, just after dark, six specimens of *P. garrulus* were collected while running in the road in the lights of an oncoming truck. At the time other geckos were still calling. As all the specimens collected were females, it is possible that this was a case where the females were responding to the call of the males.

Hunsaker *et al.* (1968) found indications that certain geckos, for example *Hemidactylus,* may not be able to hear their own calls, as their auditory thresholds are not in a direct relationship to their vocal ability. Although electro-physiological experiments have not yet been carried out with *Ptenopus,* to check their hearing, behavioural observations certainly showed clear reactions to the calls of other individuals.

METHODS AND MATERIAL

As *Ptenopus* rarely calls in captivity, all the recordings and behavioural observations had to be made in the field. Distress and agressive calls as defined by Hunsaker *et al.* (1968) are ignored in this paper. Tape-recordings were only made at the Nossob Camp in the Kalahari Gemsbok National Park and in the central Namib Desert in the vicinity of the Research Station at Gobabeb, while other observations were made during various trips to the northern Transvaal, Botswana, the northern Cape Province and South West Africa. In a number of places the frequency distribution of the number of clicks per call was established by writing down the number of clicks for a long series of calls at a given locality. This was done for *P. garrulus* only, as in the call of *kochi* the repetition rate of the clicks is so high that it is impossible to make accurate counts, while on the few occasions that the call which is assumed to be that of *carpi* was heard, no recording material was available.

The recordings were all made on a NAGRA III portable tape-recorder and a Beyer M88 microphone was used. The recordings in the central Namib Desert were made by placing the microphone on the ground about 12 inches away from the hole of the gecko, while in the Gemsbok Park the microphone was used in connection with a 36 inch parabolic reflector. The recordings were analysed on a Kay Electronic "Sona-Graph" 6061A while using a narrow band selector. A frequency spectrum of a signal is thus obtained. Signals or parts of signals lasting not more than 2.4 seconds and a frequency range between 85 cycles and 8 kilocycles are recorded on a strip of special paper. This recording is known as a "sonagram" (Andrieu 1963: 42) and by using the scale marked on the recording drum of the "Sona-Graph" the various time factors involved can be measured. The total time for various calls and their "pulse repetition rate" (Broughton 1963: 6) was thus established. The first measurement was obtained by measuring the distance between the beginning of the first and the end of the last click, while the second was established by measuring the time-lapse between the beginning of each pair of consecutive clicks in a call. For lack of a more accurate term one of the latter measurements is hereafter referred to as an "interval". No attempt was made at this stage to evaluate the frequencies of each click.

According to the Davis (1948) system the loci of the localities where these observations were made are as follows: Annisfontein 1628 Bd, Daberas 1628 Dc, De Waal 1823 Bd, Gobabeb 1523 Ca, Gorob Mine 1523 Cb, Hotsas 1522 Ca, Nossob Camp 2025 Bc, Sendelingsdrif 1628 Bb, Swartpoort 1628 Bb.

DISCUSSION AND RESULTS

Ptenopus garrulus (Smith)

Under normal conditions *garrulus* calls in the late afternoon towards sunset, with greatest activity just after sunset, quietening down rather abruptly as soon as darkness falls. However, especially during rainy weather, loud concerts may continue through the night, only stopping after sunrise. Odd individ-

PLATE I

a *P.g. maculatus.* Male in characteristic position at entrance of burrow, displaying yellow throat. Hotsas, central Namib Desert.

b *P.g. maculatus.* Male calling from entrance of burrow. Hotsas, central Namib Desert.

c *P. kochi.* Male emerging from burrow, displaying yellow throat. Gobabeb, S of Kuiseb River.

d *P. kochi.* Male calling from crater-like entrance of burrow, Gobabeb, S of Kuiseb River.

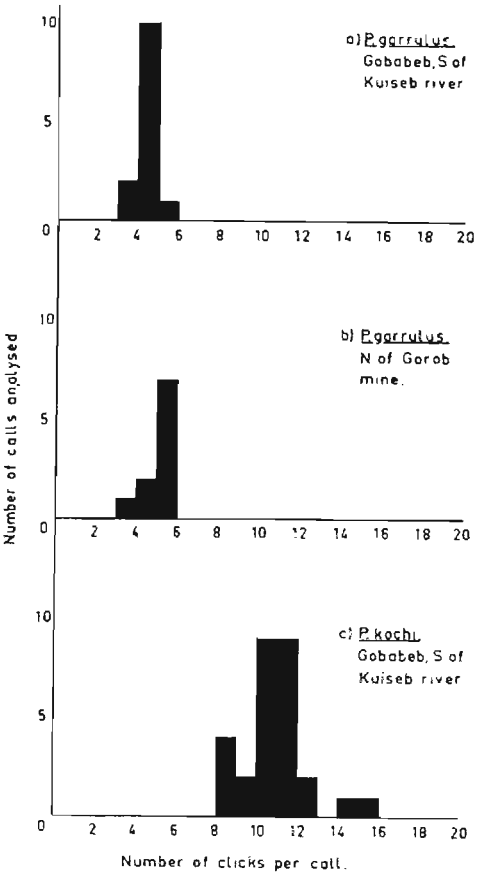
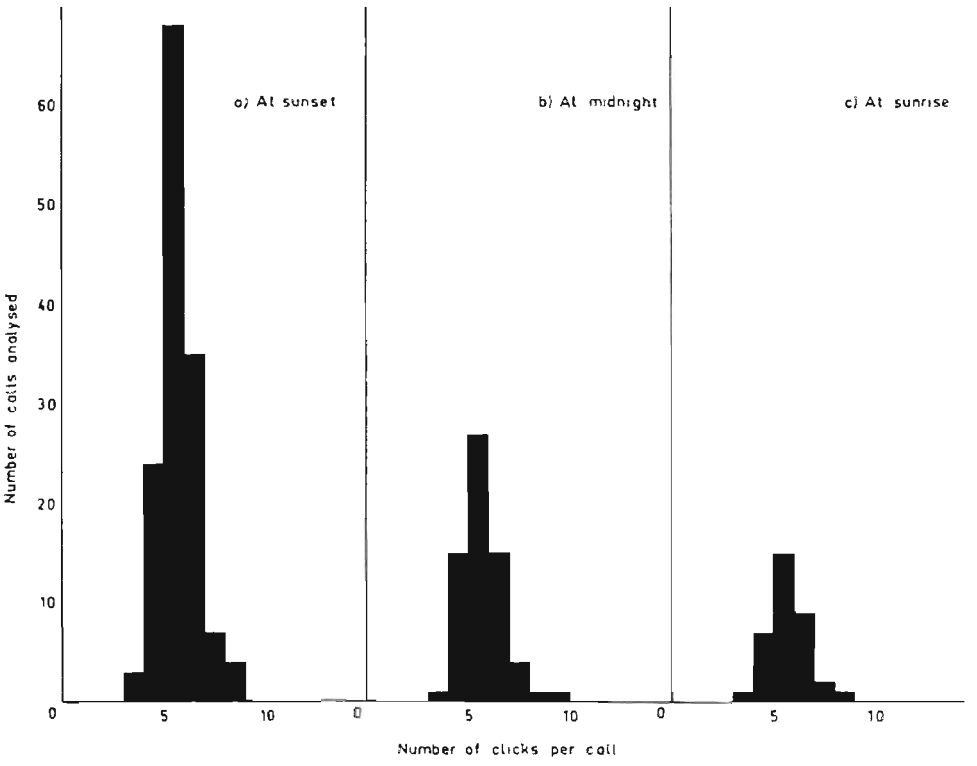


Figure 1: Histograms showing variation in number of clicks per call according to tape recordings.

Top: Central Namib Desert.

Bottom: Nossob Camp, Kalahari Gemsbok National Park.



uals may be heard calling right through the day, but this is definitely a rarity. Only a single case of a day concert, as described by Smith (*op. cit.*), has been reported to the author. This took place during dull overcast weather (*pers. com.*, Dr. C. Koch). No calls are heard during the winter months and even during summer the geckos may be quiet for weeks on end (personal communications with rangers of the Kalahari Gemsbok National Park). Wrong conclusions regarding their occurrence may thus be reached, as for instance Mertens (1955: 51) did not hear calls at Swakopmund, Hentiesbaai and at the Waterberg, thereby assuming their absence. In April 1963 the author heard *garrulus* call at Swakopmund, and specimens in the State Museum, Windhoek, prove their presence at the Waterberg.

The behaviour while calling has been observed and photographed on various occasions at localities in Botswana, South West Africa and the northern Transvaal and the same pattern was noted in all cases. Towards dusk the gecko emerges, takes up a position at the mouth of its burrow and surveys the surrounding area with about half of the body exposed. In this pose the yellow throat of the male is well displayed (Plate I a- b). Usually in response to other calls, it will suddenly start inflating and deflating its throat in quick succession, slip back into the opening of the burrow until only the head remains visible and call rhythmically, opening and closing the mouth for each individual click, accompanied by little jerks of the head (Plate I b). This action is reminiscent of a barking dog and as the sound produced is certainly not a whistling one, the name Barking Gecko appears to be more appropriate than Whistling Gecko (FitzSimons 1943).

In relation to the small size of this reptile the call is surprisingly loud and under ideal conditions can be heard for several hundred yards.

It appears that the volume is achieved by the amplifying effect of the funnel-shaped entrance of the burrow, into which the gecko withdraws to call. It is also quite difficult to locate the caller by homing in on the source of the sound, as the voice appears to have ventriloquistic properties. By calling upwards at an angle (Plate I b) the sound is scattered over a wide area, which makes its place of origin difficult to locate. These acoustic effects were first pointed out by Prof. P. de V. Pienaar of the Department of Speech Therapy at the University of Pretoria, when discussing sound analysis with him.

Tape-recordings were made south of the Kuiseb River at Gobabeb, about 3 miles NNE of Gorob Mine in the central Namib Desert, and at the Nossob Camp in the Kalahari Gemsbok National Park. The populations of the two first-mentioned localities belong to the subspecies *g. maculatus* while that from the latter is of the typical *g. garrulus* form. While playing back the recordings at a slower speed than at which they were recorded, the individual clicks were counted and the resulting histograms (Fig. 1) show that most calls at Gobabeb consist of 5 clicks, while most of those from near Gorob Mine and the Nossob Camp consist of 6 clicks. This result gives the impression of a closer relationship between the last two populations although the first two are geographically much closer.

Of the 12 calls recorded at Gobabeb 3 were suitable for sonagram analysis, while 6 of the 9 calls from near Gorob Mine and 33 of the 239 distinguishable calls from the Nossob Camp were suitable for this purpose. The considerable inter- and intra-population differences existing in the rhythm only became apparent when studying these sonagrams.

The calls from Gobabeb were very monotonous, i.e. all the clicks of one call have a similar pitch and total amplitude and similar amplitudes at corresponding frequency levels (Fig. 2 b). The rhythm is fairly regular and the average length of the intervals for all the analysed calls is 0.39 seconds, from which the averages of the individual calls differ from 0.01 to 0.05 seconds. The longest total time for a 5 click call is 1.75 seconds. After a slow start the clicks follow in quicker succession, but towards the end the intervals become more extended again and the last is from 0.01 to 0.03 seconds longer than the previous one.

The population near Gorob Mine has two distinct calls, both of which consist of an average of 6 clicks (Fig. 1). The first type is regular and the clicks are of equal pitch, total amplitude and duration (Fig. 2 c and Fig. 3 b), and appear similar to those recorded at Gobabeb. However, the average length of the interval is 0.27 seconds, which is 0.11 seconds shorter than the average interval recorded for Gobabeb, and the total time of 1.45 seconds for a call of 6 clicks from Gorob is still much shorter than the 1.75 seconds for a call with only 5 clicks from Gobabeb. The first interval of a call is also 0.01 seconds shorter than the consecutive ones, in contrast to those from Gobabeb where they are up to 0.02 seconds longer. The median intervals are equal in length and towards the end the tempo slows down again, resulting in an increase of 0.01 seconds in the last or each of the two last intervals. The second type of call differs considerably from the first. This is without a doubt the type of call described by Bradfield (Loveridge 1947: 35) as "squee — chi — chi", as the first click is particularly emphasized. On the other hand, the first type of call discussed above conforms to the monotonous "gack — gack — gack" described by Brain (1962: 8) and accepted by Haacke (1964: 4). In the second type the initial click is louder (greater total amplitude) and more drawn out (about 0.05 secs. longer) than the subsequent ones. There is a slight rise followed by a sharp drop in the pitch at fairly

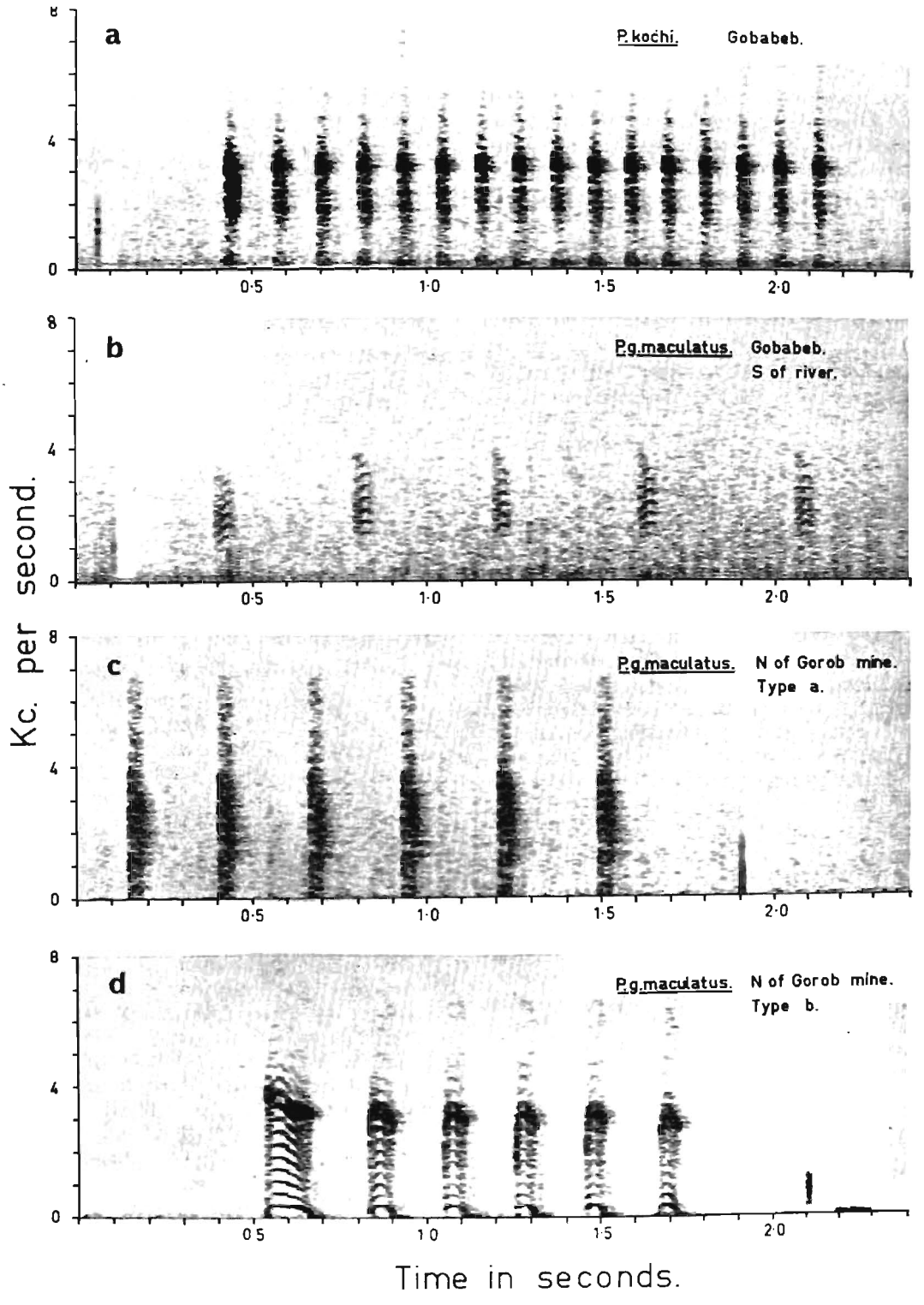


Figure 2: Sonagrams of calls recorded in the central Namib Desert.

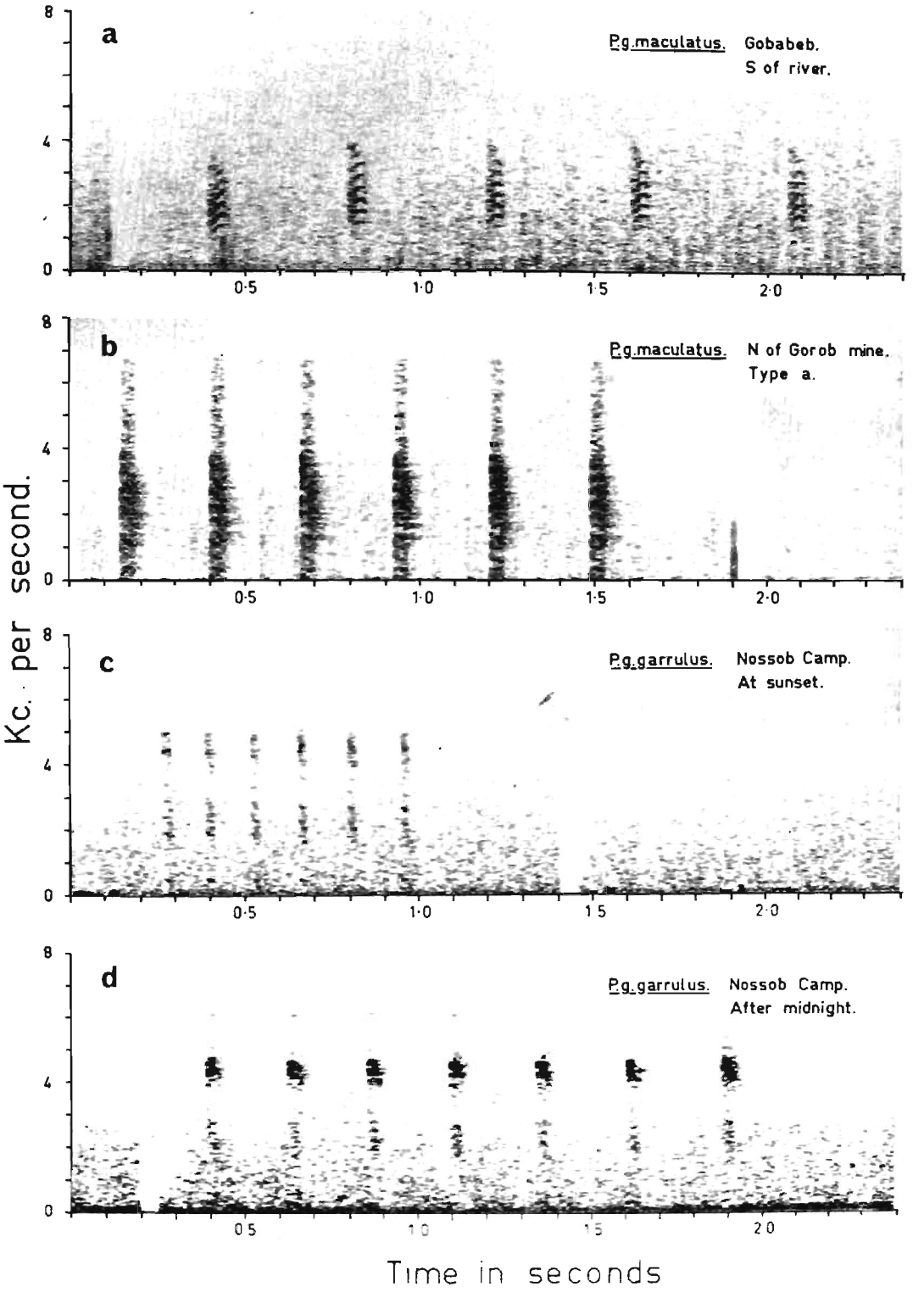


Figure 3: Sonagrams of regular calls of *P. garrulus*.

regular frequency levels over the whole range of this click. A similar picture, although to a lesser extent and over a shorter period, exists in the consecutive clicks (Fig. 2 d). On an average the interval between click 1 and 2 is 0.27 seconds long, which is 0.08 seconds longer than the 0.19 seconds of the following intervals. The slowest time for a call of the second type, with 6 clicks, is 1.23 seconds (average 1.11 secs., 3 calls), which is considerably shorter than the 1.45 seconds for the calls of the first type. In all the calls of the second type the last interval was again 0.01 seconds longer than the previous ones.

Both types of calls were heard at the same time of the day and in the same area. It was not ascertained whether one specimen could produce both types of calls and an attempt to dig up a specimen producing the second type was unsuccessful.

During March 1967 at the new Nossob Camp Mr. O. P. M. Prozesky recorded 239 distinguishable calls of *P. g. garrulus,* of which 141 were taken at and just after sunset, 63 between midnight and 1 a.m. and 35 just before sunrise at about 6 a.m. A light shower had fallen in the afternoon and the geckos were particularly vociferous, continuing to call right through the night, stopping only after sunrise the next morning. After a warm evening the temperature dropped noticeably and at midnight as well as in the morning the calls were slow and drawn out and sounded as if the geckos were cold and tired (*pers. com.* O.P.M. Prozesky). Although varying in rhythm, the average number of clicks per call remained six throughout the night (Fig. 1). Amongst the recordings made at sunset were those of six specimens, of which from two to four calls each were suitable for analysis. The average interval between the beginning of consecutive clicks for these calls is 0.14 seconds, which is 0.09 seconds shorter than that from near Gorob Mine and 0.16 seconds shorter than that of calls from Gobabeb and is very similar to the 0.13 seconds of the call of *P. kochi.* The averages for the six individuals vary from 0.13 to 0.15 seconds. In 9 calls the first interval was as long as the subsequent ones, while in the remaining 5 the first interval was from 0.005 to 0.01 seconds shorter than the consecutive ones. The median intervals of a call are of exactly the same length, with only occasional minute variations, while the final interval is usually 0.005 to 0.07 seconds longer than the preceding ones. In general, it can be said that the clicks in calls uttered during the evening are of similar pitch and follow one another at a quick, regular rate with only a slight delay between the two final clicks (Fig. 3 c).

A remarkable difference exists between the calls uttered during the evenings and those uttered at midnight (Fig. 3 c and d). The pulse repetition rate of the later recordings becomes much slower, with an average of 0.23 seconds per interval for 51 intervals from 10 analysed calls of 4 geckos in comparison with the 0.14 seconds of those recorded in the evening. Otherwise they are similar as far as regular repetition rate and the delay of 0.01 to 0.04 seconds of the last click are concerned. Although the average interval for all calls from the Gorob Mine area of 0.23 seconds is nearly identical to that of the midnight calls this gives a wrong impression. One can only compare the regular calls of the first type with those of the midnight recordings, but in those calls from Gorob the average interval lasts 0.27 seconds with a resulting duration of 1.45 seconds for the total of a 6 click call in contrast to the 0.12 seconds of those recorded at midnight.

Of the calls recorded in the morning 7 were analysed and the average for the 35 intervals was 0.25 seconds, which is 0.03 seconds slower than that recorded at midnight and 0.12 seconds slower than that recorded during the previous evening. Although odd calls during the evening and night had intervals which became progressively longer towards the end of the call, usually about 0.01 second per interval, this is a fairly common occurrence amongst the morning calls while the regular rhythm is the exception and the sequence for one of the calls, which is 0.26, 0.27, 0.28, 0.29, and 0.34 seconds, although exceptionally regular, can serve as a good example.

The recordings made at the Nossob Camp give a good impression of the variation which can be encountered at a given locality under varying conditions. The indications are that high humidity after rain will cause prolonged vocal activity, while a drop in temperature slows down the pulse repetition rate. At present no exact correlation can be made due to insufficient observations. The recordings from near Gorob Mine show the variation of calls which can be uttered by specimens of the same population under identical conditions. A comparison of the recordings from the three different populations indicates to what extent various populations differ.

On two recent trips some additional observations were made, which indicated that inter-population variation is even greater than previously accepted. Unfortunately no tape-recorder was available so that only the number of clicks per call for a number of calls per locality was noted. In the Richtersveld of the north-western Cape Province calls were analysed at the following four localities: Annisfontein, Daberas, Sendelingsdrif and Swartpoort. As the populations in this relatively small area are all considered to be of the subspecies *P. g. maculatus,* the variation observed in their calls is quite considerable (cf. Fig. 4). Similarly, on farm De Waal in the Gobabis district, South West Africa, calls were heard which differed from those recorded at the Nossob Camp (cf. Figs. 1 and 4). These two

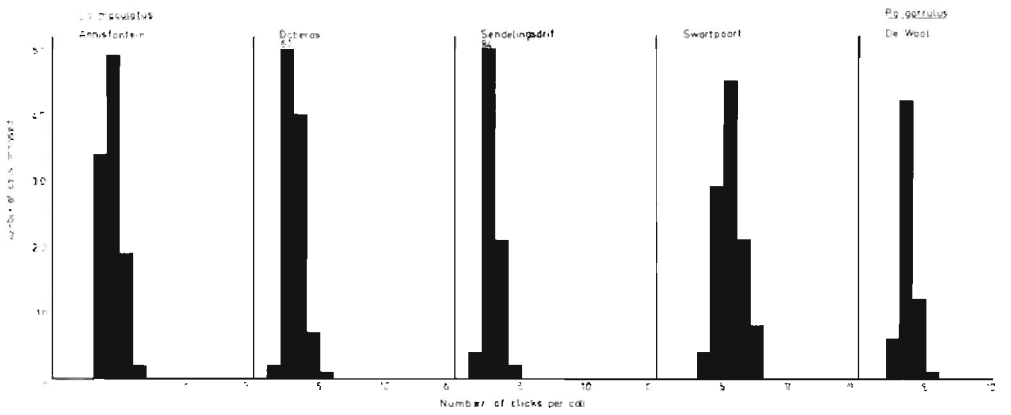


Figure 4: Histograms showing variation in number of clicks per call according to direct counts.

last-mentioned populations are of the typical subspecies *P. g. garrulus*. From the given histograms it is obvious that the number of clicks per call varies to such an extent that it is unsuitable to substantiate morphological subspecific differences.

Another impression gained on farm De Waal was that the most frequent number of clicks per call in a population on the one side of one of the long, consolidated dunes of Kalahari sand differed from that of the population occurring on the directly opposite side. As this gecko does not burrow in the softer sand of the dunes and probably rarely crosses this stretch of 150 to 200 yards, these dunes may be important barriers. As they may be several miles long they could even be as effective as river-beds, as was noticed in the central Namib at Gobabeb. Unfortunately only one evening could be spent at De Waal and the difference in the calls on the other side of the dune was only noticed very late, after the main period of vocal activity.

This observation suggests that the number of clicks is likely to be genetically fixed in a population. Where the distribution of this gecko is continuous gene flow can occur, resulting in gradual changes in the calls, while barriers, such as mountain ranges, dunes and river-beds, will cause a discontinuity resulting in noticeably different calls. On the other hand it is possible that the number of clicks per call in a population is imitated by and imprinted in juveniles, which would also result in a certain degree of homogeneity within a given area. This could be verified by transferring young specimens to other areas where they could grow up under observation in close contact with a different call.

Ptenopus kochi Haacke

The call consists of a series of clicks of apparently identical pitch and loudness, uttered in extremely quick succession and sounding similar to the stridulation of the large pamphagid grasshoppers, such as *Lamarckiana*. The number of clicks per call of 27 calls recorded at Gobabeb varied from 9 to 16, with 11 and 12 the most frequent numbers (Fig. 1). The average time-lapse between the beginning of consecutive clicks in 8 calls was 0.134 seconds. There is an indication that the pulse repetition rate increases in proportion to the number of clicks per call, as in a call with 16 clicks the average interval lasts only 0.113 seconds, while in 3 calls with 11 clicks each it lasts 0.148 seconds. If this can be proved to be constant, it means that the number of clicks per call is predetermined by the gecko. Although the calls of this species have a great number of clicks, an analysed call of 16 clicks lasted only 1.775 seconds (Fig. 2 a), which is not much longer than the 1.75 seconds of a 5 click call of *garrulus* recorded at the same time and at the same locality. The pulse repetition rate is so high that it is practically impossible to recognise and count the individual clicks of a call in the field. This caused the erroneous statement by the author (1964: 4) that the call consists of 9 to 11 clicks. Only when studying the sonagrams and replaying the recordings at a slow speed was it realised that the actual numbers were usually higher than previously accepted. The pulse repetition rate usually starts off slowly, i.e. with a long interval between click 1 and 2, then picks up speed, i.e. the intervals become progressively shorter, and slows down towards the end. The following series of intervals from a 13 click call illustrates this clearly: 0.160, 0.155, 0.150, 0.150, 0.145, 0.140, 0.140, 0.140, 0.140, 0.135, 0.135, 0.140, 0.140 seconds.

The behaviour while calling is similar to that described for *garrulus* and its position in relation to its burrow, before and while calling, can be seen in Plate I c and d. The call is also loud and, under favourable conditions, can be heard for a few hundred yards. It is difficult to pinpoint the exact position of a gecko by listening to its call because

of the habit of calling upwards from inside a small crater, thereby scattering the sound. Only males have been observed calling. Although vocal activity usually commences just before sunset and reaches its greatest volume just after sunset, calling may continue right through the night and on rare occasions, especially on overcast days, individual calls may be heard during the day. According to Dr. C. Koch and Mr. J. du Preez *(pers. coms.)* no calls are heard during the winter months at Gobabeb.

The call of this species was first noticed at Gobabeb by Dr. C. Koch, whose observations were published by Brain (1962: 15). It was then tentatively attributed to *P. carpi.* At a later stage the author found that this was the call of *P. kochi,* a species still undescribed in 1962.

Ptenopus carpi Brain

No specimen of this species has yet been observed while calling. In October, 1963, on the gravel plains north of the Kuiseb River, calls were heard which were quite different from those of *garrulus* and *kochi.* They consisted of monotonous series of up to 16 clicks, which were uttered at a very slow but constant repetition rate and with a rather low pitch. It was already too dark to see geckos calling. A few moments later, with the aid of a flashlight, a specimen of *P. carpi* was found in the area from where these calls were heard, and the calls were attributed to it. At the same time the normal calls of *kochi* and *garrulus* could be heard at a distance along the river-bed. A similar observation was made near the Swartbank Weather Station. In its immediate surroundings this slow, monotonous call with up to 16 clicks was repeatedly heard, while from a distance, near the river, *kochi* called. Attempts to record this call, and to make observations of *carpi* while calling, have failed up to now.

SUMMARY

1) The call of *Ptenopus,* the most vociferous of the southern African geckos, is studied.

2) Each of the three species, *garrulus, carpi* and *kochi,* has a different call.

3) The males of *garrulus* and *kochi* have been observed and photographed while calling and their behaviour is essentially the same. *P. carpi* is rarer and no definite observations have been made yet.

4) Certain populations of *garrulus* have more than one type of call.

5) The call of *garrulus* shows extensive inter-population variation and cannot be correlated with morphological variation.

6) The pulse repetition rate of the call and the vocal activity within a population of *garrulus* varies according to season, time of day and prevailing weather conditions.

7) The pulse repetition rate and number of clicks per call of *kochi* is much higher than that of *garrulus* in the same area.

8) Locality	Av. number clicks/call	Av. length intervals	Duration of calls
P. g. garrulus			
Nossob Camp			
Evening	6	0.137 sec.	6 clicks 0.74 sec.
Midnight	6	0.225 sec.	6 clicks 1.26 sec.
Morning	6	0.254 sec.	6 clicks 1.51 sec.
De Waal	4	—	—
P. g. maculatus			
Gobabeb			
S. of river	4	0.390 sec.	5 clicks 1.75 sec.
Gorob Mine			
Type a)	6	0.270 sec.	6 clicks 1.45 sec.
Type b)	6	0.200 sec.	6 clicks 1.23 sec.
Annisfontein	4	—	—
Daberas	3	—	—
Sendelingsdrif	3	—	—
Swartpoort	6	—	—
P. carpi			
Gobabeb			
N. of river	Up to 16?	—	—
P. kochi			
Gobabeb	11—		
S. of river	12	0.134 sec.	16 clicks 1.78 sec.

ACKNOWLEDGEMENTS

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