

ASPECTS OF SOCIAL ORGANIZATION IN ANURAN CHORUSES

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ABSTRACT

This work examines aspects of chorus organization in six species of anurans. By utilizing acoustic playback experiments the exact nature of call timing in five species was determined. Four species each exhibited one of three distinct types of chorus organization, while in one species it was not possible to demonstrate any chorus organization. The distinct type of chorus organization that a species exhibits was shown to be a function of call duration and behavioural refractory period.

The significance of call intensity in male-male interactions and female mate choice was determined in further acoustic playback experiments. Males exhibited a graded type of response, with the percentage of aggressive calls increasing with increasing intensity of the playback. Although females were unable to compute absolute intensity, they were preferentially attracted to the louder of two calls in simple two-choice situations, but their discriminatory ability was impaired in more complex situations. Males of *H. marmoratus* were found to call at consistently different repetition rates and females preferentially selected faster rates in simple two-choice experiments as well as in the field.

This study provides valuable insight into the chorus dynamics of several species, enabling a better understanding of the function and significance of the ubiquitous phenomenon of chorus organization.

I declare that this thesis is my own, unaided work unless specifically acknowledged in the text. It has not been submitted before for any degree or examination in any other university.

Phillip

Phillip John Bishop

Signed on the 1st day of JULY 1994

The approach to the problem is more important than the problem itself..... for your prejudices, your fears, and your hopes will colour it. The correct relation results from a lucid approach without selection.

KRISHNAMURTI

In memory of Gertrude (*Bufo bufo*)
my familiar and companion during many
lonely months in the field
(1974 - 1985)

In memory of Gertrude (*Bufo bufo*)
my familiar and companion during many
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PREFACE

"These foul and loathsome animals are abhorrent because of their cold body, pale colour, cartilaginous skeleton, filthy skin, fierce aspect, calculating eye, offensive smell, harsh voice, squalid habitation, and terrible venom: and so their Creator has not exerted his powers to make many of them."

Carolus Linnaeus (1758)

"Frogs have comical expressions that never fail to fascinate young and old people alike. They are amusing in actions and entirely harmless, having no teeth nor claws."

Robert Broel (1937)

(The American Frog Canning Company)

From the above quotes it can be seen that it took nearly 200 years for frogs to evolve from despicable creatures to lovable animals that no home should be without.

Over the past 15 to 20 years there has been considerable interest in the communication and social behaviour of anurans. Despite this interest there are many aspects of their life histories that still need to be investigated. With the recent observations that many species of anurans are disappearing, it has become of utmost importance that future studies are planned and executed before too many of the species disappear forever. Frogs are ideal animals to use as models for various theories as they are relatively easy to study, they do not move vast distances in short spaces of time, parentage is usually unambiguous, and they are extremely tolerant of the human observer.

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Animal ethics clearance.

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Publications

Various papers reporting the findings detailed in this thesis have been published, or are being reviewed and the help received from the collaborative authors is greatly appreciated and hereby acknowledged.

"Calling behaviour influences mating success in male painted reed frogs, *Hyperolius marmoratus*" by Passmore, N. I., Bishop, P. J., and Calithness, N. (1992) *Ethology* 92, 227-241.

"Effects of increased sound level of advertisement calls on calling male frogs, *Eleutherodactylus coqui*" by Stewart, M. M. and Bishop, P. J. (1994) *Journal of Herpetology* 28(1), 46-53.

"Call rate variability and female mate choice in the African frog, *Hyperolius marmoratus*" by Jennions, M. D., Bishop, P. J., Backwell, P. R. Y., and Passmore, N. I. (submitted to *Animal Behaviour*, 1994)

ABBREVIATIONS USED IN THE TEXT

°	degrees Centigrade
cm	centimetre
dB	decibel
df	degrees of freedom
E	east
Fig.	figure
h	hour
Hz	Hertz (cycles per second)
ICI	intercall interval
ISI	inter-signal interval
kHz	kilohertz
km	kilometre
m	metre
min	minute
mm	millimetre
ms	millisecond
n	sample size
no.	number
NS	non-significant ($P > 0.05$)
P	probability
s	second
S	south
SD	standard deviation
SE	standard error
SPL	sound pressure level
SVL	snout-vent length
vs	versus
$\bar{x}$	mean

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 Preamble

The cacophony of sound produced by large breeding assemblages of frogs is well known to most people. Few people stop to wonder why these small animals expend so much time and energy in producing this very noisy dusk chorus. Sound production in most animals is primarily the means by which members of the same species advertise their presence to one another.

Most species of anurans have well developed vocal structures and are capable of producing very loud sounds that serve to advertise species type, attract mates, defend territories, repel intruders and express distress (Littlejohn and Michaud, 1959; Bogert, 1960; Snyder and Jameson, 1965; Allan, 1973; Rosen and Lemon, 1974; Fellers, 1975; Garton and Brandon, 1975; Wells, 1977a, b).

As anurans are biparental animals a fundamental prerequisite of reproduction is the bringing together of conspecific mates. In order for an individual to obtain a conspecific mate, it needs to effectively communicate its physical position to females. Due to constraints exerted by the environment, anurans have evolved a communication system which relies on the production and reception of auditory signals. There are many advantages in utilizing an auditory communication system, for example, acoustic signals can be used at night, they can be transmitted

around barriers such as vegetation in structurally complex environments, they can be turned off rapidly and can be transmitted over long distances. However, acoustic signals also have disadvantages such as increased conspicuousness to predators (Ryan and Tuttle, 1983), the repeated production of signals is energetically expensive (Wells and Taigen, 1989), and acoustic signals can easily be interfered with or obscured in a highly noisy environment.

Most vertebrates possess behavioural repertoires which enable information to be conveyed to other animals. These take the form of "displays", and although there are many different types of displays, only a limited number of messages are being conveyed (Smith, 1969). Anurans transmit information as a set of distinct messages in the form of vocalizations. In general, the message enables the behaviour of the communicator to be more predictable by the recipient of the message, and the information conveyed by the message permits the recipient to take appropriate action.

Most anuran vocalizations are associated with reproduction and the following classification of calls and their messages, as proposed by Brad (1988), is used throughout this thesis:-

A. Advertisement calls.

Advertisement calls are the primary calls of anurans and are the ones most commonly heard by human observers. They are emitted by sexually reproductive males, often in conjunction with other calling males. These calls are usually repeated at regular intervals and most species continuously produce advertisement calls for several hours at a time (e.g. *Eleutherodactylus coqui*, Narins, 1982a; *Hyperolius marmoratus*, Passmore et al., 1992). They serve to attract gravid females to the calling male and advertise his position to other competing males. These calls are either followed by successful mating, aggression

or more advertisement calls. Other males in close proximity are often stimulated to produce advertisement or aggressive calls in response to a calling male. The main message encoded in the advertisement call is that of species identity.

B. Courtship calls.

The male changes from advertisement calls to courtship calls on perception of an approaching female. Often males reduce the interval between calls (*Colostethus collaris*, Dole and Durant, 1974; *Hyperolius marmoratus*, Telford and Dyson, 1988) or increase the number of notes per call group (*Colostethus trinitatis*, Wells, 1980; *Hyla faber*, Martins, 1993). These calls are usually followed by amplexus.

C. Aggressive calls.

These calls are usually given when a male is interacting aggressively with competing conspecific males (and, to a lesser degree, heterospecific males e.g. *Hyla ebraccata* and *H. microcephala*, Schwartz and Wells, 1984a). The calls are sometimes emitted by males defending nest sites (Townsend et al., 1984). Aggressive calls are usually followed by pursuit, combat or silence.

D. Release calls.

These calls are given by a clasped individual either a male or an unreceptive female during an amplexus attempt. Release calls are often accompanied by distinct vibrations of the body wall and may also be produced by frogs which lack an advertisement call (e.g. *Bufo spinulosus*, Penna and Veloso, 1981). They are usually followed by the initiator releasing the calling individual and moving away.

E. Distress calls.

Distress calls are emitted by both sexes when seized by, or escaping from, a predator. These calls are usually emitted with the mouth open and it is unknown whether these

calls convey information to other conspecifics.

The vocal repertoire may vary between species from no calls at all (e.g. *Rana blythi*, Emerson and Inger, 1992) to an extensive series of vocal signals, as in *Eleutherodactylus coqui* (see Appendix A).

1.1.1 Chorusing behaviour

In most cases, large numbers of anurans congregate at the breeding site and vocalise together in unison. Earlier workers on animal vocalizations termed these aggregations of calling males a "chorus" (e.g. Goin, 1949; Alexander and Moore, 1958). By definition a chorus is "any simultaneous utterance" (The Concise Oxford Dictionary, Sixth edition, 1976). On first impression this appears to be a particularly apt description of the cacophony emanating from an aggregation of breeding anurans. Choruses formed by vocalizing male anurans may appear to consist of randomly produced calls but, upon closer inspection, these calls have been shown to be broadcast in a very systematic and organized sequence. The precise temporal chorus organization of several species is examined in detail in Chapter two and the following chapters investigate various issues which arise from the findings of Chapter two.

1.2 Study species

The following six species of anurans were studied in this thesis:-

1. *Afrixalus fornasinii*
2. *Eleutherodactylus coqui*
3. *Hyperolius marmoratus*
4. *Kassina maculata*

5. *Kassina senegalensis*

6. *Semnodactylus wealii*

1.2.1. Species description, breeding behaviour and advertisement call description

The research in this thesis centres around chorusing behaviour and, as this is an essential and integral part of anuran breeding behaviour, it is necessary to outline this activity and describe the advertisement call for each of the species studied. Only a brief description is given, but further detail may be obtained from the literature cited and Appendix B.

1.2.1.1 *Afrixalus fornasinii* (Bianconi, 1849)

Species description: A large *Afrixalus*, with a body length up to 41 mm (Poynton and Broadley, 1987). The ground colour varies with the incident light from a cream colour to a dark grey-brown at which point the median dorsal band becomes difficult to distinguish (Fig. 1.1).

Breeding behaviour: This species is fairly common, producing large choruses in December and January. The males call from elevated positions, often more than 1 m from the water's surface, on broad-leaved vegetation such as saw-grass (*Cyperus immensus*), reeds (*Phragmites* sp.) and bulrushes (*Typha latifolia*). Males begin calling shortly after sunset and continue until approximately 23.00 h, with a peak around 21.30 h. Once a male has attracted a female, oviposition takes place out of the water with the eggs being deposited in folded leaves above the water level.

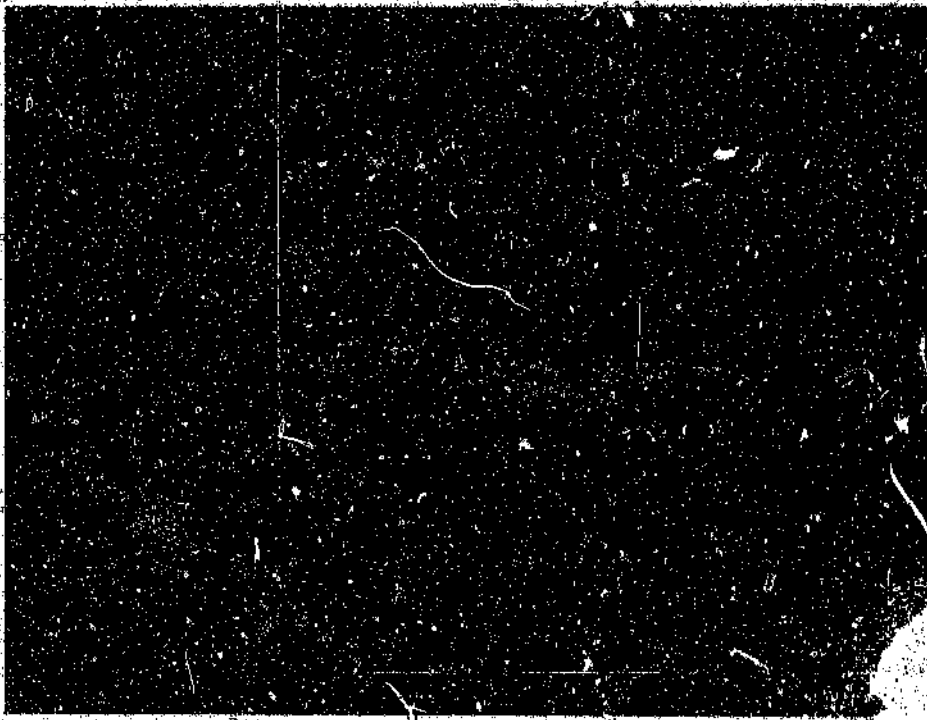


Fig. 1.1 Male *Afrixalus fornasinii*

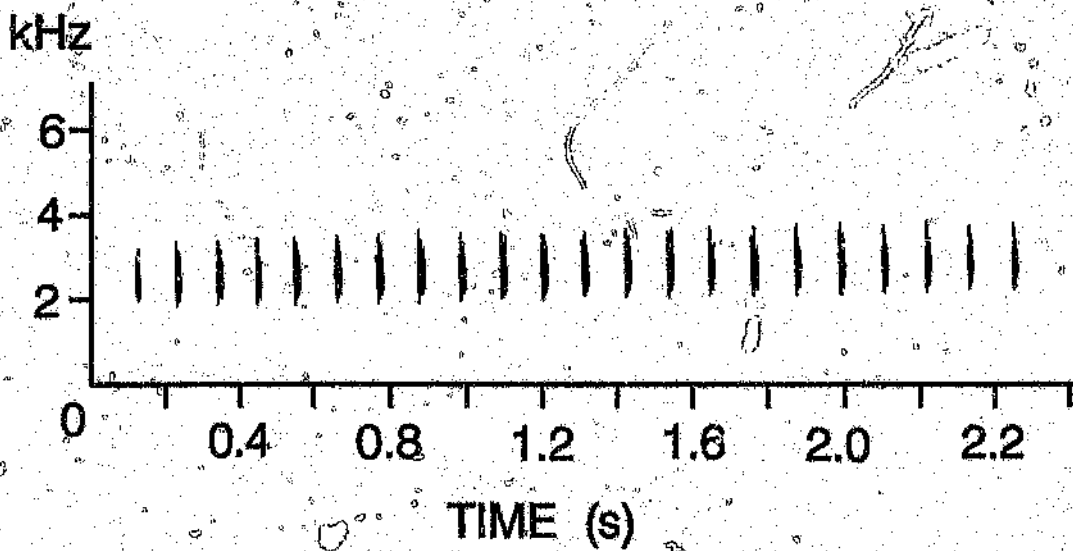


Fig. 1.2 Sonagram of the advertisement call of *A. fornasinii*

Advertisement call: The call has a mean duration of 2.17 s (range 1.5 - 2.9 s, $n = 53$) and is described as "a rapid series of loud and repetitive percussive notes. About twelve notes per second" (Passmore and Carruthers, 1979). On average the call is repeated 4.3 times per minute (range 1.4 - 6.1). The centre frequency of the call is about 2.5 kHz (Fig. 1.2) and it exhibits a constant degree of amplitude modulation throughout the call. The mean peak sound pressure level (SPL) at a distance of 50 cm, is 106 dB (range 103.5 - 109 dB) (Passmore, 1981). Detailed parameters of the call are given in Table 1.1.

1.2.1.2 Eleutherodactylus coqui Thomas, 1966

Species description: A medium-sized *Eleutherodactylus* reaching a maximum length of 62 mm (Lopez and Narins, 1991). The dorsal surface is grey to grey-brown with scattered dark mottling (Fig. 1.3).

Breeding behaviour: Male frogs call from exposed sites within 3 m of the ground. Calling males do not form dense aggregations, but are widely dispersed throughout the forest. Males vocalise from sunset to around midnight, throughout most of the year. The favoured calling, foraging, retreat and nest sites occur in areas in which *Prestoea montana* (sierra palm) predominates. When a male attracts a female he leads her to his nest site and after a period of pre-oviposition, amplexus, the pair adopt a reverse hind leg clasp (Townsend and Stewart, 1986). Internal fertilization occurs and the eggs are laid in the male's nest. The male remains with the clutch and protects them from conspecific egg cannibalism and desiccation. There is direct development and small froglets hatch within 17-26 days.

TABLE 1.1 Call parameters for 5 species ($\pm$ standard deviation)

SPECIES	CALL DURATION (ms)	UPPER FREQUENCY (kHz)	LOWER FREQUENCY (kHz)	REP RATE (CALLS/MIN)
<i>A. fornasinii</i> (n = 11)	2173 $\pm$ 312 R = 1500-2906	3.11 $\pm$ 0.13 R = 2.88-3.5	1.89 $\pm$ 0.2 R = 1.6-2.3	4.3 $\pm$ 1.6 R = 1.44-6.
<i>H. marmoratus</i> (n = 10)	111.3 $\pm$ 14 R = 81-150	3.4 $\pm$ 0.2 R = 2.92-3.76	2.73 $\pm$ 0.2 R = 2.24-3.12	49.3 $\pm$ 12.3 R = 35.1-72
<i>K. maculata</i> (n = 10)	66.7 $\pm$ 9 R = 56-93	2.83 $\pm$ 0.11 R = 2.64-3.24	0.71 $\pm$ 0.05 R = 0.64-0.84	17.5 $\pm$ 8.5 R = 4.6-35.1
<i>K. senegalensis</i> (n = 6)	146.7 $\pm$ 23.4 R = 112-193	2.1 $\pm$ 0.2 R = 1.8-2.32	0.67 $\pm$ 0.08 R = 0.5-0.8	16.7 $\pm$ 12.9 R = 2.4-39.1
<i>S. wealii</i> (n = 11)	341 $\pm$ 116 R = 131-562	2.82 $\pm$ 0.12 R = 2.6-3.0	1.97 $\pm$ 0.15 R = 1.68-2.24	9.8 $\pm$ 4.6 R = 3.1-19.1

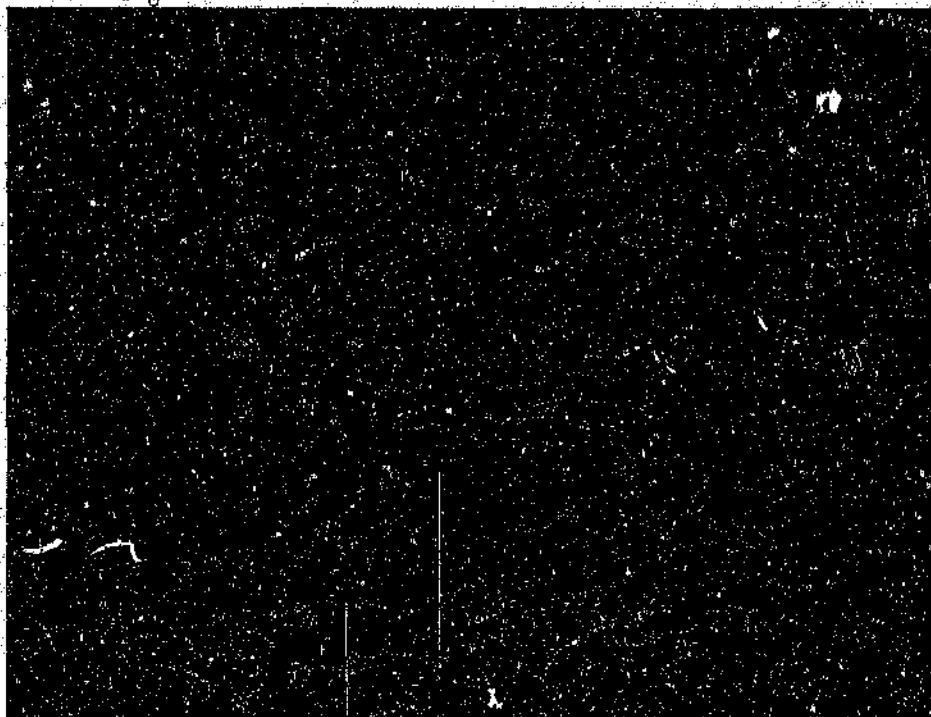


Fig. 1.3 Male *Eleutherodactylus coqui*
(photograph taken by M. M. Stewart)

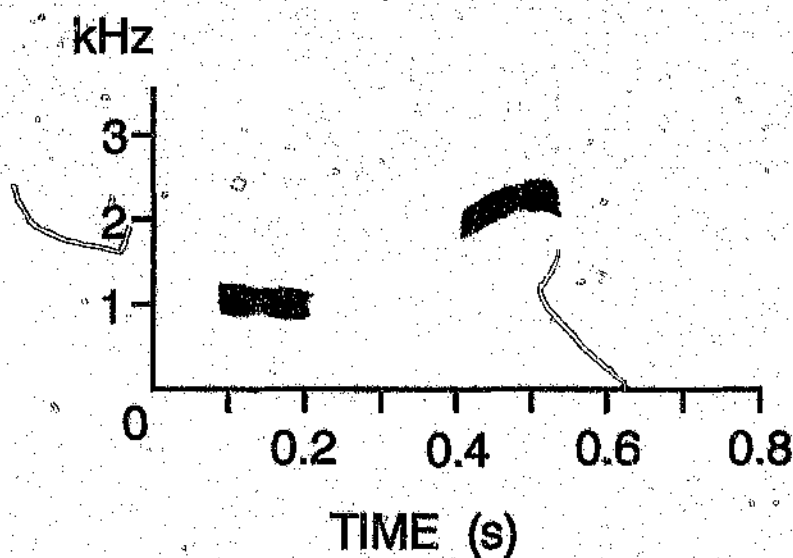


Fig. 1.4 Sonagram of the advertisement
call of *E. coqui*

Advertisement call: Males produce a two-note call ("co-qui"). The "co" note duration is approximately 100 ms and is a constant tone with a centre frequency of 1.15 kHz. The "qui" note has a duration of approximately 170 ms and is frequency modulated from about 1.8 to 2.1 kHz (Narins and Capranica, 1977) (Fig. 1.4). The two-note call is repeated 15 - 20 times a minute. At the site where these frogs were studied, the mean SPL of the "co" note was 84 dB, and the "qui" note 97 dB at a distance of 50 cm (Narins and Hurley, 1982).

1.2.1.3 Hyperolius marmoratus Rapp, 1842

Species description: A medium-sized *Hyperolius* with a mean body length of 28.5 mm (Dyson et al., 1992). The adult colour pattern is extremely variable and, at the breeding sites used in this study, the adults were usually patterned with yellow and dark brown irregular stripes which are sometimes broken up into spots of colour (Fig. 1.5).

Breeding behaviour: This species was the most common frog at the breeding sites, with very large dense choruses forming after the first good rains and continuing until the end of the rainy season. Males usually call from elevated positions (mean elevation = 68 cm, Telford, 1982) on emergent vegetation. Preferred elevated call sites were on sedges (*Eleocharis limosa* and *Cyperus papyrus*) and bulrushes (*Typha latifolia*) although they were often seen calling nearer the water's surface on *Polygonum pulchrum* and *Ludwigia stolonifera* and sometimes on waterlilies (*Nymphaea capensis* and *Nymphoides indica*). Males call from just after dusk until around midnight and then usually return to their daytime refuge in the canopy of the surrounding trees. Once a female has been attracted to a male, she normally initiates amplexus, and the pair descend to the water to lay eggs.



Fig. 1.5 Male *Hyperolius marmoratus*

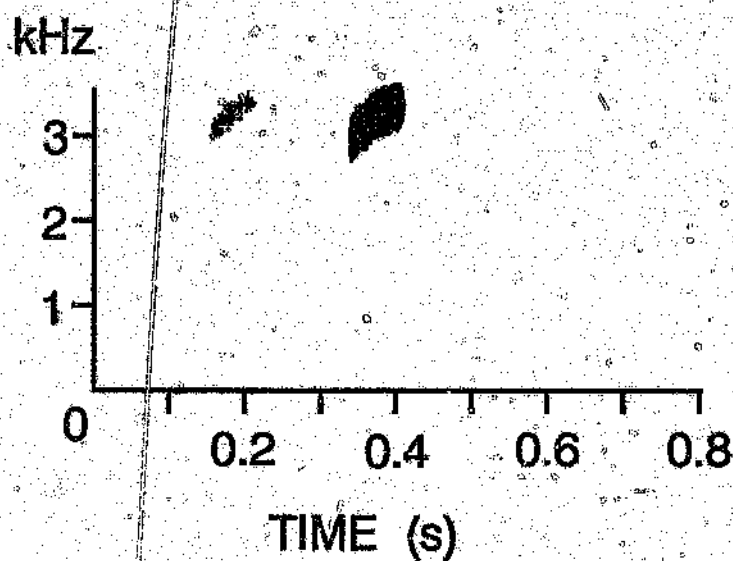


Fig. 1.6 Sonagram of the advertisement call of *H. marmoratus*

Advertisement call: The males produce a frequently modulated call approximately 110 ms long (range 81 - 110 ms). The call sweeps from about 2.7 to 3.4 kHz (Fig. 1.1) and can be described as a very loud, piercing whistle (Passmore and Carruthers, 1979). The call is normally repeated about 50 - 60 times a minute. The mean peak SPL at a distance of 50 cm, is 103.5 dB (range 102.0 - 104.0 dB) (Passmore, 1981). Detailed parameters of the call are given in Table 1.1.

1.2.1.4 *Kassina maculata* (Duméril, 1853)

Species description: A large, robust *Kassina* reaching maximum size of 68 mm (Poynton, 1964). The silvery-brown ground colour is replaced by a brilliant scarlet in the axilla, waist, and inner thigh regions (Fig. 1.7).

Breeding behaviour: This species forms fairly small choruses during the rainy season (November to February) with two distinct peaks in calling behaviour. The males are vocally active from about 16.30 h onwards, forming one chorus peak at about 18.00 h and another between 02.00 and 03.00 h. Males called from very concealed positions in vegetation which had collapsed into the water, usually hidden underneath overhanging reeds and saw-grass (*Eleocharis limosa* and *Cyperus immensus*). Occasionally males were found calling in the middle of clumps of saw-grass about 50 cm from the water's surface. Once a female has located a male, amplexus is initiated and the female deposits her eggs in the water.

Advertisement call: The call has a very short duration of approximately 67 ms (range 56 - 93 ms) and is repeated on average, 17 times per minute. It is frequently modulated from about 0.7 to 2.8 kHz (Fig. 1.8), and is best described as a very loud, explosive, incessant quacking.

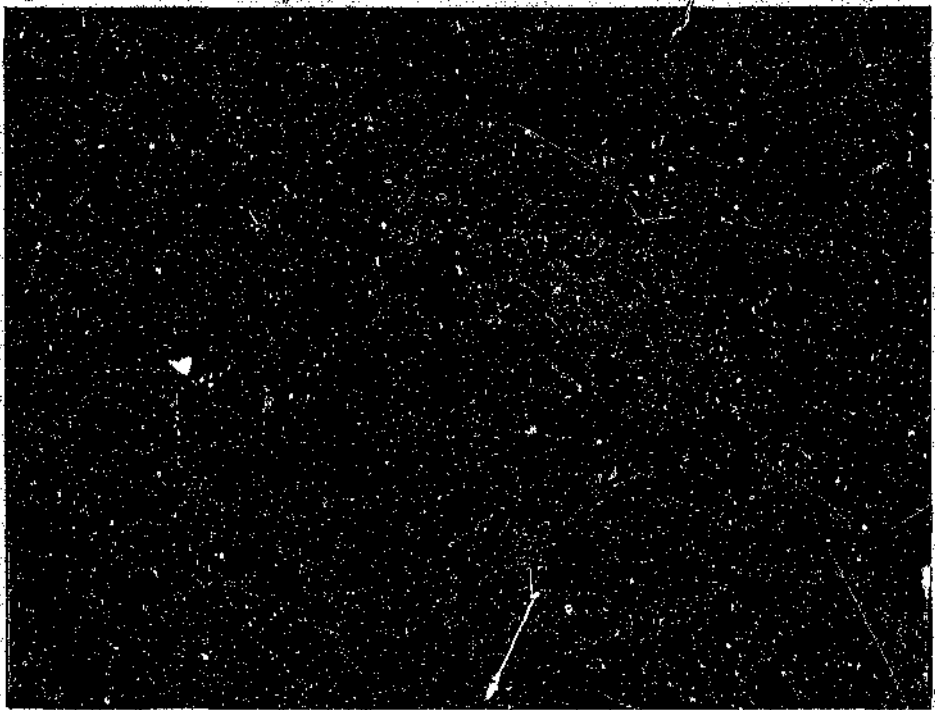


Fig. 1.7 Male *Kassina maculata*

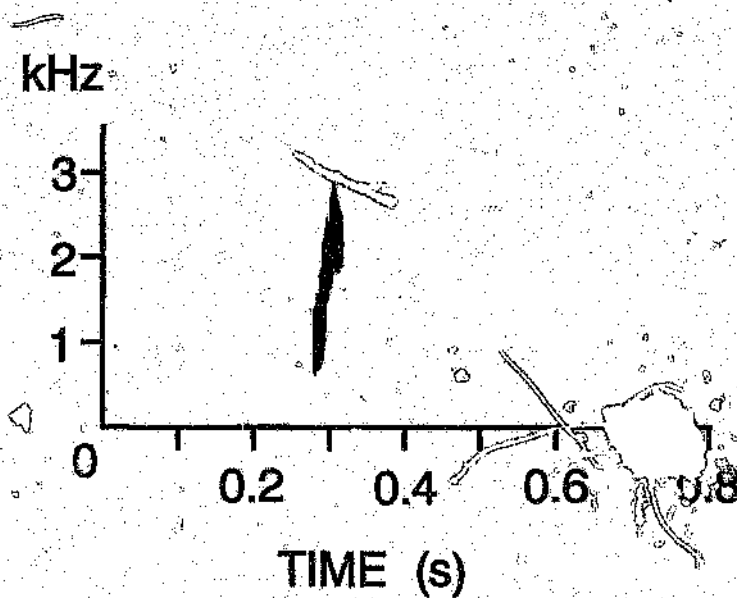


Fig. 1.8 Sonagram of the advertisement call of *K. maculata*

(Passmore and Carruthers, 1979). The mean peak SPL, at a distance of 50 cm, is 114 dB (range 112.0 - 116.0 dB) (Passmore, 1981). Detailed parameters of the call are given in Table 1.1.

1.2.1.5 Kassina senegalensis (Dumeril and Bibron, 1841)

Species description: A medium sized *Kassina* reaching a maximum size of 52 mm (Poynton, 1964). The ground colour varies from yellow through olive to dark brown (Fig. 1.9).

Breeding behaviour: This species forms dense clusters of calling males during the rainy season (November to February). The males begin calling from concealed call sites away from the water's edge before dusk. Around dusk the males move nearer the water's edge and begin chorusing from fairly exposed call sites in grass tussocks. Most males stop calling by midnight, although sporadic calling is heard throughout the night. Once a female has located a male the pair enter into amplexus and walk to the water where the eggs are deposited.

Advertisement call: The call is fairly short with an average duration of 147 ms (range 112 - 193 ms) and is best described as a loud, clear 'quoip' (Passmore and Carruthers, 1979). It is frequency modulated from about 0.7 to 2.1 kHz (Fig. 1.10) and repeated about 17 times per minute. Detailed parameters of the call are given in Table 1.1.

1.2.1.6 Semnodactylus wealii (Boulenger, 1882)

Species description: A small to medium sized member of the *Kassininae* reaching a maximum size of 44 mm (Poynton, 1964). The ground colour is usually a silvery-beige colour and the hands and feet are yellow (Fig. 1.11).

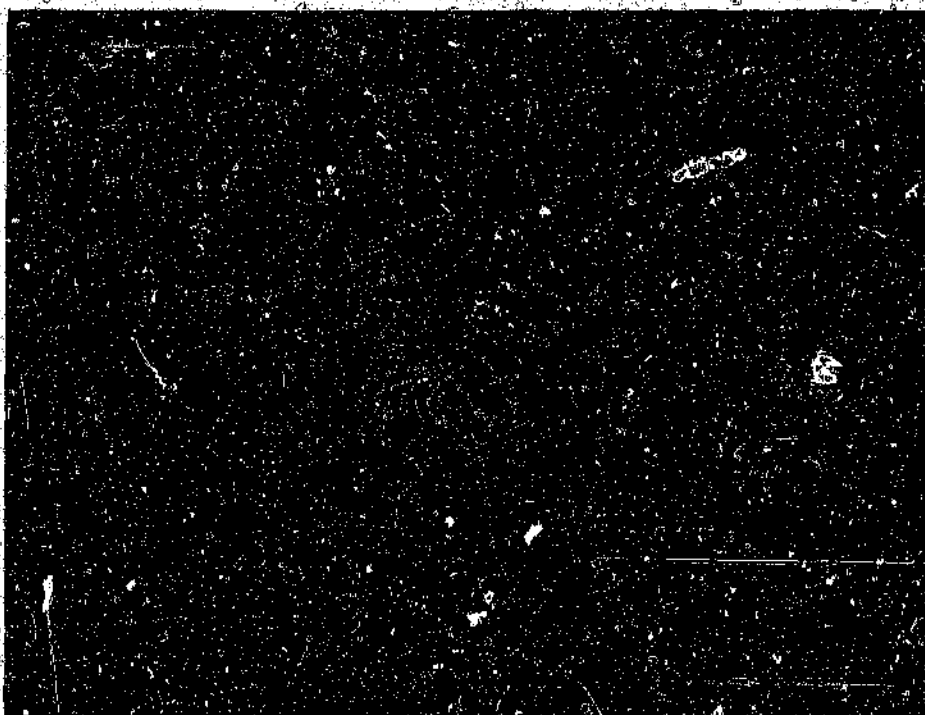


Fig. 1.9 Male *Kassina senegalensis*

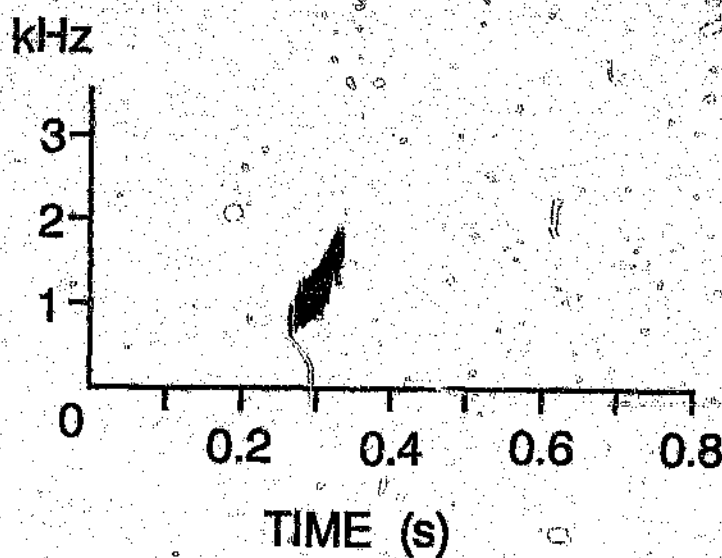


Fig. 1.10 Sonagram of the advertisement call of *K. senegalensis*

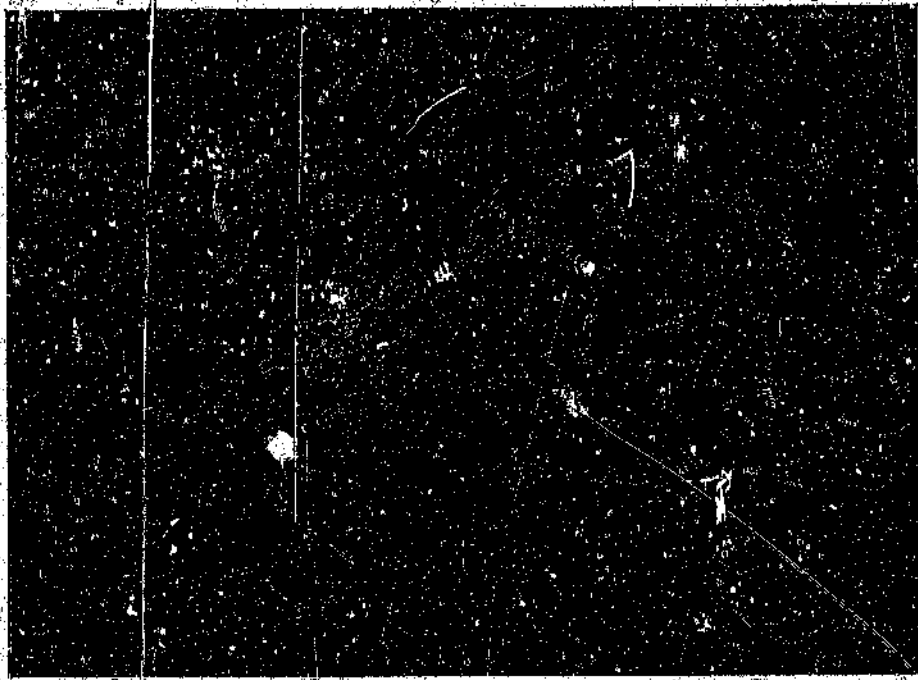


Fig. 1.11 Male *Semnodactylus wealii*
(photograph taken by V.C. Garruthers)

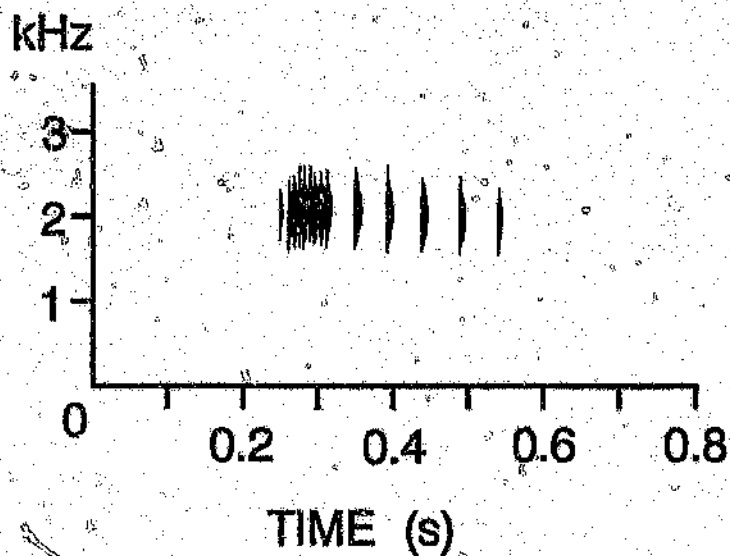


Fig. 1.12 Sonagram of the advertisement
call of *S. wealii*

Breeding behaviour: Males form moderately dense choruses from November to February. As with the other members of the Kassiniinae studied here, the males of this species also began calling, from concealed positions, before dusk. About an hour after dusk the males had taken up their call sites for the evening in the vegetation surrounding the dam. These call sites varied from concealed positions in the middle of grass tussocks to exposed positions, sometimes climbing up grass tussocks to a height of about 40 mm. Males were sometimes found calling from sites located at least 300 m from the water's edge. Once a female had located a male, amplexus was initiated and the pair walked to the water to deposit the eggs.

Advertisement call: The call is long with an average duration of 341 ms (range 131 - 562 ms) and can best be described as a coarse, loud rattle (Passmore and Carruthers, 1979). The call can be divided into two distinct parts each with different degrees of amplitude modulation. The first part consists of about 8 pulses which have been compressed together and the second part usually has 5 pulses which are widely spaced (Fig. 1.12). The centre frequency of the call is 2.4 kHz and it is repeated at a rate of about 10 calls per minute. Detailed parameters of the call are given in Table 1.1.

1.3 Study areas

1.3.1 Twinstreams Farm, Zululand

This study site is located at the southern extremity of the Mozambique coastal plain, near the town of Mtunzini, on the north coast of Natal, South Africa. Two ponds on this farm (Matatiele and Mavungweni) were used to carry out experiments on *A. fornasinii*, *H. marmoratus*, and *K.*

maculata. The phonotaxis experiments with *H. marmoratus* were performed at a site situated about 3 km equidistant from the ponds (Mick's park conservation area - 28° 58' 52" S 31° 44' 13" E). The mean annual rainfall for this area was 1215 mm.

a) Matatiele pond (29° 00' 05" S 31° 43' 02" E). This pond is a natural coastal "pan" (a natural shallow depression which had filled up with water), situated in the coastal dune forest. It is a semi-permanent body of water approximately 100 m long, 30 m wide with a maximum depth of 1 m. The predominant vegetation of the pan is *C. immensus*, *L. stolonifera* and *P. pulchrum*, with dense clumps of *Phragmites* reeds at the southern end. Often during the winter, and particularly in dry years, the pan dries up completely.

b) Mavungweni pond (28° 58' 04" S 31° 45' 06" E). This pond was constructed in 1982 and lies between the coastal dune forest and a sugar cane field. The predominant vegetation is *L. stolonifera*, *P. pulchrum* and *T. latifolia*. The pond covers an area of approximately 150 square metres and extends at the southern end into a natural wetland swamp overgrown with *Phragmites*.

1.3.2 Pineta Saw Mill dam.

Ixopo (30° 04' 42" S 30° 02' 00" E)

This study site consists of a well established dam in the Natal highlands, near the town of Ixopo (South Africa). The dam wall runs due north and the stream enters the dam at the west end. During wet seasons the area covered by the dam was approximately 1000 square metres. The predominant vegetation around the perimeter of the dam was *E. ilmosa*, and the north and south banks of the dam bordered onto grass pastures. The banks of the stream before it entered the dam were covered with black wattle trees and arum lilies. Playback studies on *K. senegalensis* and *S. wealii* were carried out at this site.

1.3.3 Caribbean National Forest

This study site was situated in a subtropical wet forest surrounding the El Verde Field Station of the Center for Energy and Environment Research (18° 19' 33" N 65° 49' 19" W) at an altitude of 350-450 m in the Luquillo Mountains of northeastern Puerto Rico. The prominent trees in the forest were *Cecropia peltata*, *Sacryodes excelsa* (tabonuco), and *Prestoea montana* (sierra palm). The forest floor was littered with fallen leaves and covered with a typical herbaceous or shrub under story vegetation which varied from 0.02 - 2.5 m. The canopy of the forest varied from 7 - 20 m (Stewart, 1985) and the mean annual rainfall was 3456 mm (Lopez and Narins, 1991).

Playback experiments were conducted on *E. coqui* in the secondary growth rain forest adjacent to the El Verde field station.

1.4 Scope and objectives

This thesis is principally concerned with the extent of chorus organization occurring in aggregations of calling male frogs and determining its significance in mate attraction, mate selection and social behaviour.

Chapter two examines the existence and extent of temporal chorus organization in five species, utilizing call playback experiments. The results of this chapter clearly show that most species exhibit precise temporal chorus organization. The functional significance of this type of organization and how it relates to spatial organization is addressed in Chapter three.

In Chapter two the importance of call intensity is highlighted and the role this plays in spatial organization of the chorus is examined in Chapter four. Its importance in female discrimination within a chorus is examined in

Chapter five. A detailed study of the natural calling behaviour of one species of frog with particular reference to the importance of call rate and female choice is presented in Chapter six.

The final chapter re-evaluates chorus organization in the light of the data presented in the previous chapters.

CHAPTER TWO

CHORUS ORGANIZATION

2.1 Introduction

2.1.1 General

It was highlighted in Chapter one that the most characteristic feature of anurans is the production of sound. These vocalizations play an extremely important role in their reproduction by maintaining territories and attracting conspecifics as well as being used in many social interactions. The most well known vocalization, and the most commonly heard, has been termed the advertisement call (Wells, 1977a). By using this term, instead of the term "mating call", the assumption that the intended recipient of the call is known can be avoided. Bogert (1960) provided a "tentative classification of anuran sounds" which served as the basic classification for further studies. In more recent years the names of several other categories have also been changed e.g. territorial call changed to encounter call (McDiarmid and Adler, 1974; Wells, 1977a) and later to aggressive call (Rand, 1988), (for reviews see Littlejohn, 1977; Wells, 1977a; Rand, 1988). The classification of calls used throughout this thesis has already been discussed in Chapter one. Advertisement calls range widely in structure from almost pure single tones, e.g. *H. marmoratus* (see Fig. 1.6), to

very complex calls, e.g. *Hyla ebraccata*, (Wells and Schwartz, 1984a); *E. coqui* (see Appendix A); and *Physalaemus pustulosus*, Drewry et al., 1982.

These highly stereotyped signals are usually repeated at regular intervals and Loftus Hills (1974) proposed that a central pacemaker exists in anurans which initiates the beginning of each call. A similar central pacemaker has been suggested for acoustic or photic signalling in insects (Huber, 1962; Jones, 1966; Shaw, 1968; Walker, 1969; Hanson et al., 1971). This leads to a fairly constant repetition rate which can be modified by internal or external cues. Schmidt (1971) identified areas in the frog's brain which were involved in calling and were affected by hormonal inputs. Furthermore, the repetition rate and pulse rate of certain species has been shown to be positively correlated with ambient temperature (e.g. *Bombina variegata*, Zweifel, 1959; *Bufo americanus*, *Bufo wc dhousii*, Zweifel, 1968 and *H. marmoratus*, see Appendix C).

Frogs vocalize in breeding aggregations and the spatial distribution of males around the area available for breeding is seldom random (Salthe and Mecham, 1974). Although this may be thought of as a response to available calling sites or localized areas of suitable vegetation, it has been shown that even in apparently homogeneous areas, there is still a non-random distribution of calling males (e.g. Passmore and Carruthers, 1975; Whitney and Krebs, 1975b).

2.1.2 Definition of chorusing behaviour

A true chorus exists when many individuals aggregate at a breeding site and produce vocalizations. Greenfield and Shaw (1983) defined chorusing as "the singing of two or more conspecific males for relatively long periods of time during which there are statistically significant temporal

interactions involving the acoustic signals of neighbours". As anurans usually vocalize in mixed species assemblages and there have been reports of species which call without any statistically significant temporal interactions, this very specific definition may only be relevant to the Orthoptera. In this study, the term chorusing is used in a much more flexible sense referring to two or more calling individuals, in fairly close proximity, without inferring any specific temporal relationship between their calls.

2.1.3 Functional significance of chorusing

Chorusing is a fairly well known phenomenon and there have been many hypotheses erected to explain why males should come together to produce choruses. In an early study of frog vocalizations, Emlen (1968) found that female *Rana catesbeiana* were more attracted to a chorus of breeding conspecific males than the calls of a solitary male. Choruses have also been suggested to attract males as well as females (Oldham, 1966; Blair, 1968; Salthe and Mecham, 1974; Whitney and Krebs, 1975b; Green, 1990) and there may also be a reduction of predation risk (Ryan et al., 1981). Large choruses are thought to attract more females from a wider area (Wells, 1977a) and perhaps large choruses provide females with a better range of potential mates from which to choose (Alexander, 1975; Emlen and Oring, 1977; Bradbury, 1981). Experimental testing of these ideas is needed before any conclusion can be drawn concerning the functional significance of chorusing behaviour.

2.1.4 Chorus organization

Aggregation of vociferous males into choruses would be expected to produce substantial call overlap and acoustic interference. Several authors have suggested that this would be detrimental to the localization of a caller by an approaching female (e.g. Littlejohn and Martin, 1969;

Whitney and Krebs, 1975a, b; Wells, 1977a, b; Schwartz, 1987). One method of avoiding the problems of acoustic interference is to temporally space the calls with those of a neighbour, in the form of call alternation. Lemon (1971) proposed that call alternation could occur by chance alone if the intervals between the calls were equal to, or longer than, the calls themselves and if the frogs were calling at slightly different repetition rates.

Consequently, in very small choruses, call alternation (and therefore a considerable reduction in acoustic interference) may be a chance occurrence, although periods of overlapping calls would still exist. However, anurans do not usually call in very small choruses, and some form of precise organization is necessary to facilitate temporally separated calls. Obviously if call alternation is occurring by chance then as the number of participants in the chorus increases, so will the number of overlapping calls.

Goin (1949) was perhaps the first person to describe a specific type of chorus organization occurring in anurans. He recognised that the overall chorus consisted of various subgroups of three interacting individuals. He suggested that each of these subgroups always began in the same manner. Even when the chorus was dense, it could still be broken down into subgroups of three individuals. His work suggested that this kind of organization was not simply a chance occurrence but a specific social interaction between calling males.

Chorus organization was first categorized by Duellman in 1967. He divided chorus organization into two groups: spatial organization and temporal organization. These groups were further subdivided into three categories each, as shown below:-

Spatial organization.

A. Individual - no aggregation of calling males and no temporal organization.

B. Non-aggregate - no aggregation of calling individuals, although some form of duets or trios are present.

C. Aggregate - individuals congregate at the breeding site, and the calls may or may not be temporally organized.

Temporal organization.

A. Completely organized - individuals call in a set pattern throughout the chorus.

B. Initially organized - the chorus begins in a set pattern but as more individuals join, organization is lost.

C. Unorganized - no organization at all.

As Duellman's classification was based purely on observations, it is possible that the organization present in "initially organized choruses" was lost to the observer when more individuals joined, rather than the chorus losing organization per se. The work of Goin (1949) and Foster (1967) suggest that organization may still exist in small subgroups within the large chorus but is obscured by the complexity generated by many individuals calling in close proximity. Salthe and Mecham (1974) also suggested that Duellman's division into "completely organized" and "initially organized" was artificial as it would seem that these two categories depend upon the number of individuals participating in the chorus. Prior to Lemon's detailed description in 1971 of call alternation in *Eleutherodactylus martinicensis*, there were many published observations of temporal chorus organization which lacked experimental confirmation (Goin, 1949; Eibl-Eibesfeldt, 1952; Anderson, 1954; Jameson, 1954; Martof and Thompson, 1958; Hardy, 1959; Bogert, 1960; Brattstrom, 1962; Schmidt, 1964; Capranica, 1965; Snyder and Jameson, 1965; Brown and Pierce, 1967; Duellman, 1967; Foster, 1967; Schneider, 1967, 1968; Stewart, 1967; Brattstrom and Yarnell, 1968; Heinzmann, 1970).

By presenting frogs with broadcast calls of different repetition rates, Lemon (1971) demonstrated that male *E.*

martinicensis can precisely alternate their calls with the broadcast calls indicating this to be a true social interaction and not a chance occurrence. He suggested that this alternation is achieved by a short term inhibition of the production of calls so that each call fits into the periods of silence between the calls of the broadcast (or neighbouring frog). His work stimulated other authors to examine the precise nature of temporal organization and propose mechanisms for its occurrence.

Loftus Hills (1974) presented a variety of acoustic stimuli to calling male *Pseudacris streckeri* in the laboratory. He concluded that a central pacemaker existed with a cycle length equivalent to the spontaneous call period. The call period could be divided into three phases: a refractory phase, an excitatory phase and an activation phase. He found that only when an acoustic stimulus was presented during the excitatory phase did it evoke a response. As several of his subjects seemed to be triggered by the end of the acoustic stimulus and one individual was consistently triggered by the onset of the stimulus, he suggested that there might be a complex interaction between the onset and the termination of the stimulus in evoking the response.

Rosen and Lemon (1974) complemented acoustic broadcast experiments with recordings of two individuals naturally alternating their calls. They concluded that the alternation of calls in *Hyla crucifer* also fits into the excitation-inhibition model proposed by Lemon (1971) and Loftus Hills (1971, 1974) for frogs and by Shaw (1968) for katydids.

Utilizing precise call timing, frogs may exhibit two types of social interaction (Awbrey, 1978). Either they can adjust their calls so that overlap is kept to a minimum (minimum interference hypothesis) (Littlejohn and Martin, 1969; Whitney and Krebs, 1975a; Narins and Capranza, 1978;

Narins, 1982a, Zelick and Narins, 1982) or they may actively try to overlap and interfere with their neighbour's calls (Whitney and Krebs, 1975a). Awbrey (1978) tested both these ideas by presenting *Hyla regilla* males with different repetition rate broadcasts. The results were consistent with the minimum interference hypothesis and the acoustic pacemaker hypothesis of Loftus Hills (1974), as *H. regilla* males actively shifted their calls to avoid simultaneous calling with the broadcast calls. Lemon and Struger (1980) suggested that broadcasting a regular repetition rate of stimuli to a frog was inadequate for an accurate assessment of the whole call period. They presented *H. crucifer* males with randomly positioned calls, enabling them to assess directly the effect of a single stimulus on the placement of the following call. From their results they suggested that three oscillator models of signal interaction may occur. Firstly, individual frogs may only be sensitive to stimuli when their motor refractory period is over (this model is similar to that suggested by Loftus Hills, 1974). Secondly, they proposed that frogs may be sensitive to stimuli throughout the call period and the response is delayed until the motor refractory period is over (this model is supported by the results they presented), and thirdly, a similar model to the second but without the decay of the excitatory effects during the refractory period. This last model was considered unlikely as there was a conflict between producing equal spacing between the calls of individuals and producing the more characteristic leader-follower arrangement. They concluded that their first and second models may both be in operation during call alternation, at different times, within the same species. An important finding of Lemon and Struger (1980) was that (unlike *P. streckeri*, Loftus Hills, 1974) males of this species were sensitive to stimuli presented, not only during their refractory period, but also during the production of a call.

In order to test the hypothesis that the ability of a frog to precisely position its call with respect to a stimulus, is a function of the timing of the stimulus relative to the call period, Narins (1982a) studied the responses of *E. coqui* and *H. ebraccata* to broadcast synthetic acoustic stimuli. His results suggested that there was a common mechanism underlying the production of time-locked responses for both species. As the delay between the onset of the call and the initiation of the stimulus was increased then the probability of achieving a time-locked response also increased. Narins (1982a) suggested that the production of time-locked responses could be thought of as a two-stage process. Firstly, a delay following the acoustic stimulus, and secondly, a triggerable call generator with memory. The two species he studied differed in the length of the delay following the acoustic stimulus. This delay was 1133 ms in *E. coqui* and 210 ms in *H. ebraccata* and Narins (1982a) correlates this difference with discrepancies in nearest-neighbour distances of the two species, suggesting that it is adaptive in minimizing acoustic overlap. Wells and Schwartz (1984a) found a similar delay (140 - 200 ms) in their studies of vocal communication of *H. ebraccata*.

Besides shifting the timing of their calls relative to stimuli or other calling frogs, there are several other ways in which frogs have been reported to change their calling behaviour in response to broadcast stimuli. Males of *Bufo woodhousei* (Sullivan and Leek, 1986), *Geocrinia victoriana* (Littlejohn and Harrison, 1985), *Hyla versicolor* (Wells and Taigen, 1986), and *Rana clamitans* (Ramer et al., 1983) actually decrease their call repetition rate in response to broadcast stimuli. *G. victoriana* and *H. versicolor* also increase the duration of their introductory notes (Littlejohn and Harrison, 1985; Wells and Taigen, 1986 respectively). However, *Bufo americanus* (Rose and Capranica, 1984; but see Sullivan and Leek, 1986),

Hyla ebraccata (Wells and Greer, 1981; Wells and Schwartz, 1984a) and *H. phlebodes* (Schwartz and Wells, 1984b) have been shown to increase their call repetition rate in response to broadcast stimuli. Several species of frogs respond to broadcast stimuli by increasing the complexity of their call (*Crinia georgiana*, Lyre et al., 1984; *Hyla ebraccata*, Wells and Greer, 1981; Wells and Schwartz, 1984a; *H. microcephala*, Schwartz, 1986; *H. phlebodes*, Schwartz and Wells, 1984b; *Hyperolius tuberilinguis*, Pallett and Fassmore, 1988; *Philautus leucorhinus*, Arak, 1983b; *Physalaemus pustulosus*, Rand and Ryan, 1981; Drewry et al., 1982; *Rana clamitans*, Ramer et al., 1983).

2.1.5 Summary

Many workers have presented purely observational data concerning chorus organization and there have been relatively few detailed experimental studies. Most of these studies report a change in the timing of the frog's response to an acoustic stimulus but some species have also been noted to increase the complexity of their call and/or alter their call repetition rate. Several ideas have been proposed to explain the function of choruses but experimental confirmation is still lacking.

2.1.6 Aims

Utilizing acoustic playback experiments, this chapter examines temporal chorus organization in five species of anurans. The extent and form of chorus organization is compared among the species studied and a proposed reclassification of chorus organization, which encompasses all previously studied species, is put forward.

2.2 Methods

2.2.1 Study sites and species

Broadcast experiments on *Afraxalus fornasinii*, *Hyperolius marmoratus*, and *Kassina maculata* were carried out between the months of September and March at two shallow coastal ponds (Matatiele and Mavungweni) on Twinstreams Farm, Mtunzini. These species vocalized between the hours of 18.30 h and 23.30 h. Broadcast experiments on *K. senegalensis* and *Semnodactylus wealii* were carried out at Pineta sawmill dam between the months of November to January. These two species vocalized between 16.30 h and 03.00 h. For detailed descriptions of the species and study sites see Chapter one and Appendix B.

2.2.2 Preparation of stimulus broadcast tapes

Individual calling males of the five species studied were recorded under natural conditions in the field using an AKG D900E directional microphone and either a Nagra IVS or Nagra III tape recorder. The tape speed was 38 cm/s and speed fluctuation was negligible. High quality magnetic tape was used and recordings on the Nagra IVS were made on one track only. Additional data pertaining to air temperature, water temperature, subjects' rectal temperature and snout-vent length were collected. One call for each species was selected to be used in the preparation of the stimulus tapes. The criteria used for the selection of this call were call duration, upper and lower limits of emphasised frequency and, in the case of *A. fornasinii*, pulses per call. The call chosen for the stimulus was a normal call with parameters close to the mean determined by the analyses of approximately 10 individuals for each species (minimum 30 calls) (Table 1.1).

Once an appropriate call had been selected it was located by hand on a Studer-Revox B77 tape recorder and the beginning and the end of the call were marked with a wax pencil.

To prepare a stimulus tape with a specific repetition rate, the call was cut out and spliced into a loop of high quality magnetic tape of an appropriate length. For stimulus tapes which required more than one call per loop, (e.g. the double and triple broadcast tapes used in the *K. senegalensis* experiment), the same call was re-recorded several times and spliced into the loops at precise intervals. For the random stimulus tape for *H. marmoratus*, the selected call was recorded onto a tape with intercall intervals provided by a table of random numbers.

The tape loop was then analysed on a Uniscan II spectrum analyser (Multigon Industries, Inc., New York) to ensure that the correct intercall interval had been achieved. If any of the splices produced an audible click or hiss then the loop was discarded, and the above process repeated. In this way the resultant loop was a period of silence with one or several calls, with the required interval. This loop was then played on the Studer-Revox B77 or Uher Report Monitor Stereo tape recorder and recorded for 15 minutes with a Nagra III or Uher Report Monitor Stereo tape recorder onto high quality magnetic tape.

2.2.4 Acoustic broadcast experiments

At least three different stimulus tapes, all with different intercall intervals (ICI), were broadcast to each species. The stimulus tapes were broadcast to calling males using either a Nagra III or Nagra IVS tape recorder and a Nagra DH speaker-amplifier or a Portamon speaker-amplifier and a Peerless G50-MRC 3.2 ohm speaker (10 cm diameter, with a flat frequency response within the range of 1 - 7 kHz). The order of presentation of the stimulus tapes was random.

The stimuli were broadcast from a distance of approximately 50 cm from the subject at the mean SPL for that particular species (see Passmore, 1981). Peak SPLs were measured using a Brüel and Kjaer (B & K) 2209 precision sound level meter used in conjunction with a B & K 4165 microphone, a flexible microphone extension rod (B & K UA0196) and a microphone dehumidifier (B & K UA0308). The microphone was always protected from the wind by a B & K UA0237 foam windshield. Intervening vegetation between the broadcast speaker and the subject was pruned away and any conspecific individuals within 1 m of the subject were removed. The speaker was placed at the same height above the water level as the subject.

The broadcast was recorded on the left channel of a second tape recorder (Uher Report Monitor 4200), and the response of the subject was recorded using an AKG D900E unidirectional microphone on the right channel of the second tape recorder for later analysis. Additional data, including water and air temperature and the subject's rectal temperature were recorded using a Bailey's Instruments BAT-12 digital thermometer equipped with a PT-6 thermocouple. The subject's snout-vent length was measured using vernier callipers.

2.2.5 Analysis of data tapes

The data tapes from the broadcast experiments were analysed using a four-channel Harvard Universal Oscillograph. For most analyses, the chart paper was set at a speed of 10 cm/s and the Uher Report Monitor 4200 tape recorder was played at half the recording speed (i.e. 9.5 cm/s). The right and left channels of the tape recorder were fed to two adjacent channels of the oscillograph which enabled the relationship between the stimulus and the subject's response to be determined. The following parameters were

measured: stimulus-response interval, intercall interval, stimulus intercall interval and repetition rates (see Fig. 2.1 for an explanation of these terms). For more accurate measurements such as call duration and pulses per call, a Uniscan II spectrum analyser (Multigon Industries, Inc., New York) or a Kay model 7029A spectrum analyser (Kay Electric Company, New York) were used.

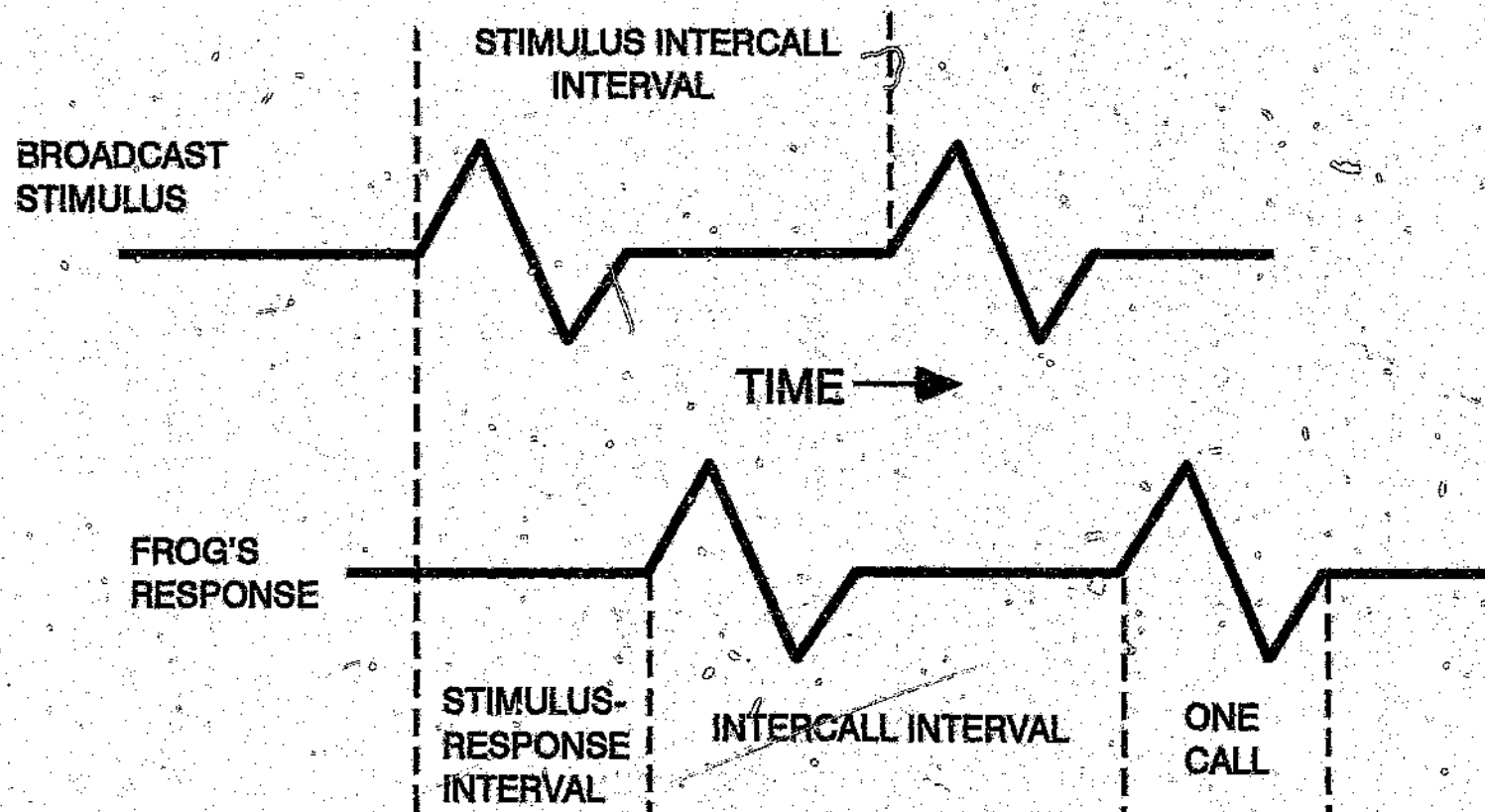


Fig. 2.1 Diagrammatic explanation of the terms used in the text

2.3 Results

2.3.1 Afruxalus fornasinii

Ten *A. fornasinii* were presented with three different broadcast stimuli. These stimuli were normal advertisement calls at different repetition rates (10, 15 and 20 stimuli/min). With the presentation of all these broadcasts a general trend can be seen. The majority (74.3%, $n = 278$) of calls produced during the broadcast ($n = 374$) overlapped with a stimulus (for example see Fig. 2.2), and more than half of the subjects' calls were initiated less than 800 ms from the onset of a stimulus. Most subjects' calls were therefore still "on air" after the stimulus had ended.

Furthermore, there were significantly more calls (Chi-square test $\chi^2 = 73.94$, $P < 0.001$, $df = 1$) in the first second than in the last second of the call period (i.e. the second immediately prior to the next stimulus, see Table 2.1). As the broadcast stimulus was 2.5 s in duration, most of the subjects' calls overlapped substantially with the stimulus (Fig. 2.2). As the distribution of the S-R intervals was skewed, the median S-R interval (0.7 s for all broadcast experiments) was more representative of the data than the mean. With the broadcast of 10 stimuli/min, although the first second of a stimulus only accounted for 17% of the stimulus call period, 57.5% ($n = 77$) of all the calls ($n = 134$) were produced during this time (median = 0.65 s, Chi-square test, $\chi^2 = 44.81$, $P < 0.001$, $df = 1$) (Fig. 2.3). Similarly, with the 15 stimuli/min broadcast, the first second of a stimulus accounted for 25% of the stimulus call period and 65.4% ($n = 87$) of the frog's calls ($n = 133$) were initiated in this portion of the stimulus call period (median = 0.6 s, Chi-square test, $\chi^2 = 42.65$, $P < 0.001$, $df = 1$) (Fig. 2.4).

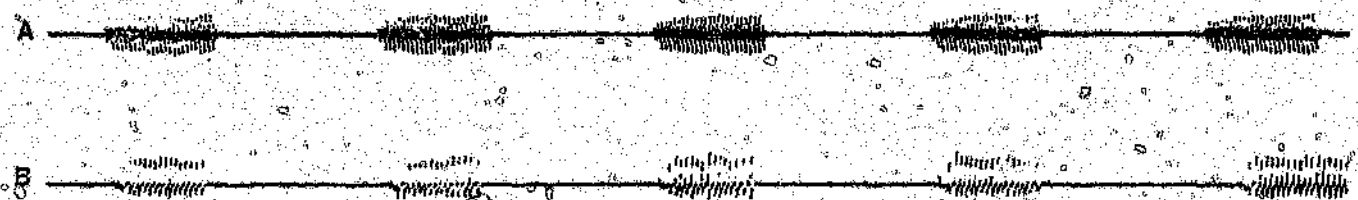


Fig. 2.2 *A. fornasinii* - Oscillograph tracing of responses to conspecific broadcasts.
(A- broadcast calls, B - subject's response)

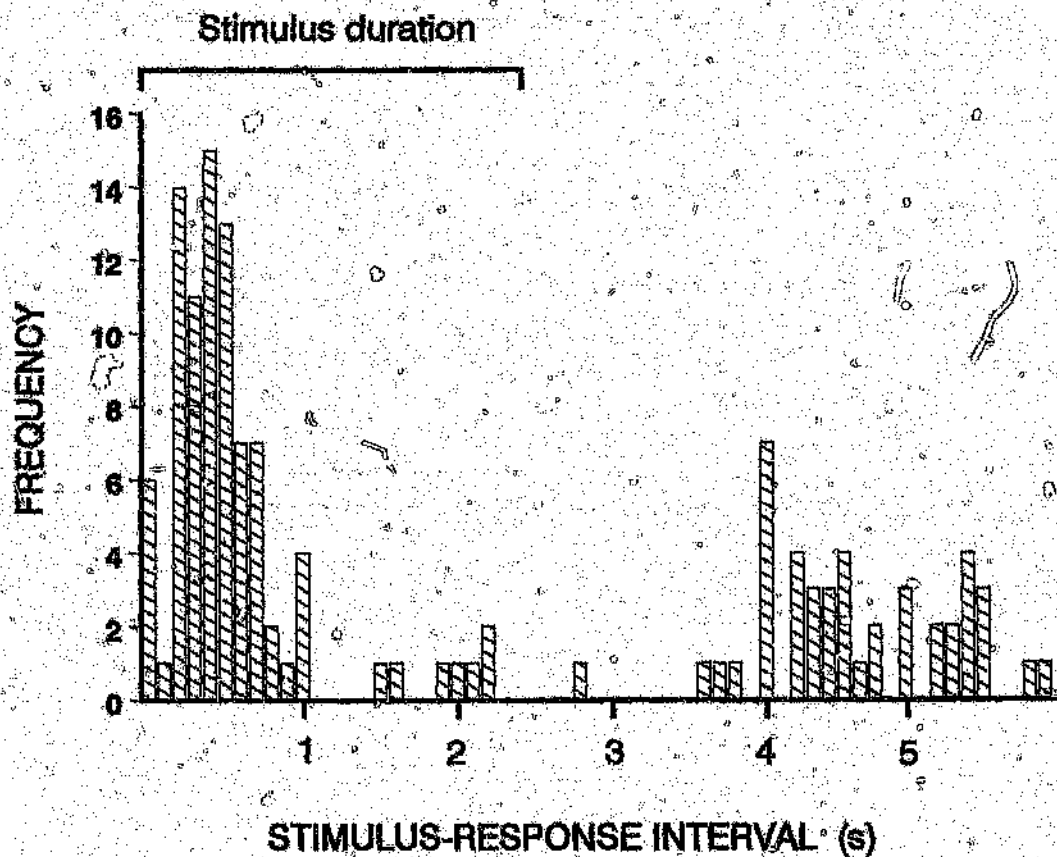


Fig. 2.3 Stimulus-Response intervals ($n = 134$) during a broadcast of 10 stimuli/min to 10 *A. fornasinii* males. Mean $\pm$ SD = 1.94 ± 2.01 s

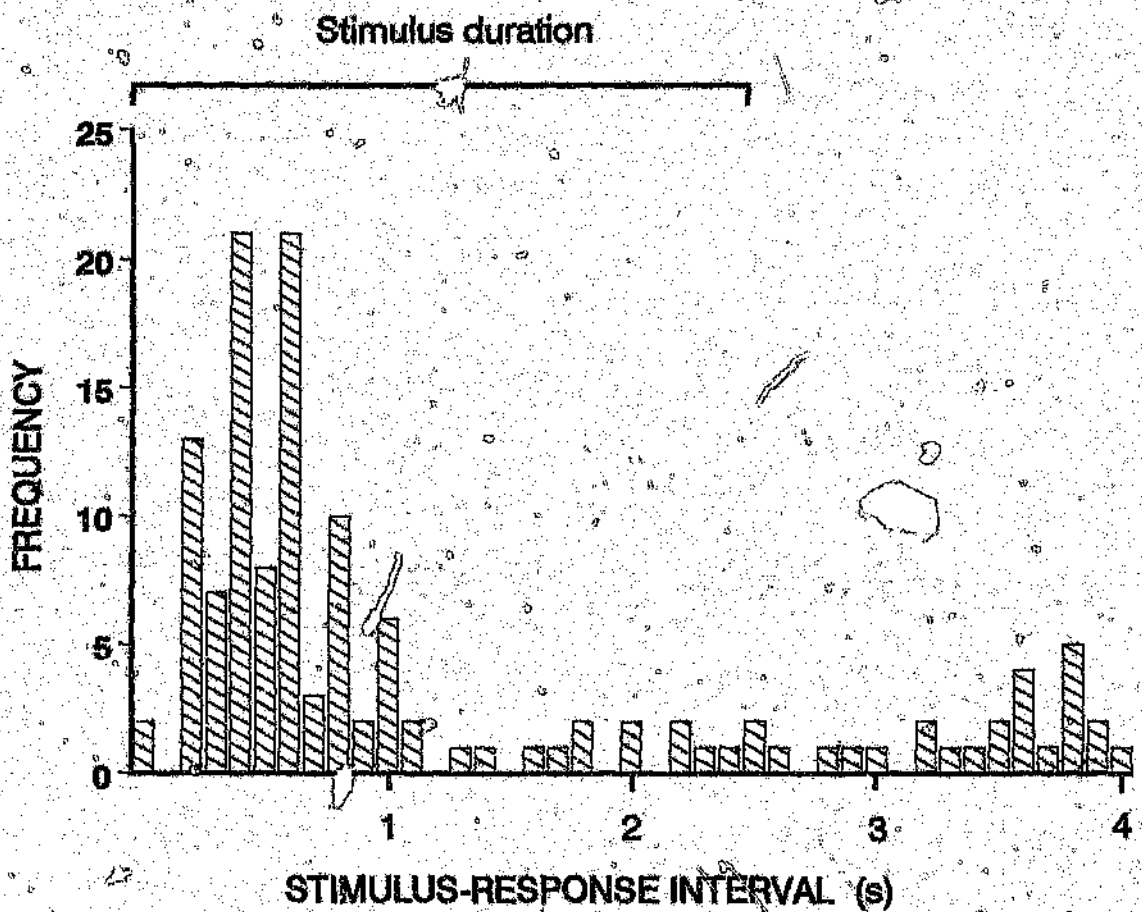


Fig. 2.4 Stimulus-Response intervals ($n = 132$) during a broadcast of 15 stimuli/min to 10 *A. fornasinii* males. Mean $\pm$ SD = 1.20 ± 1.20 s

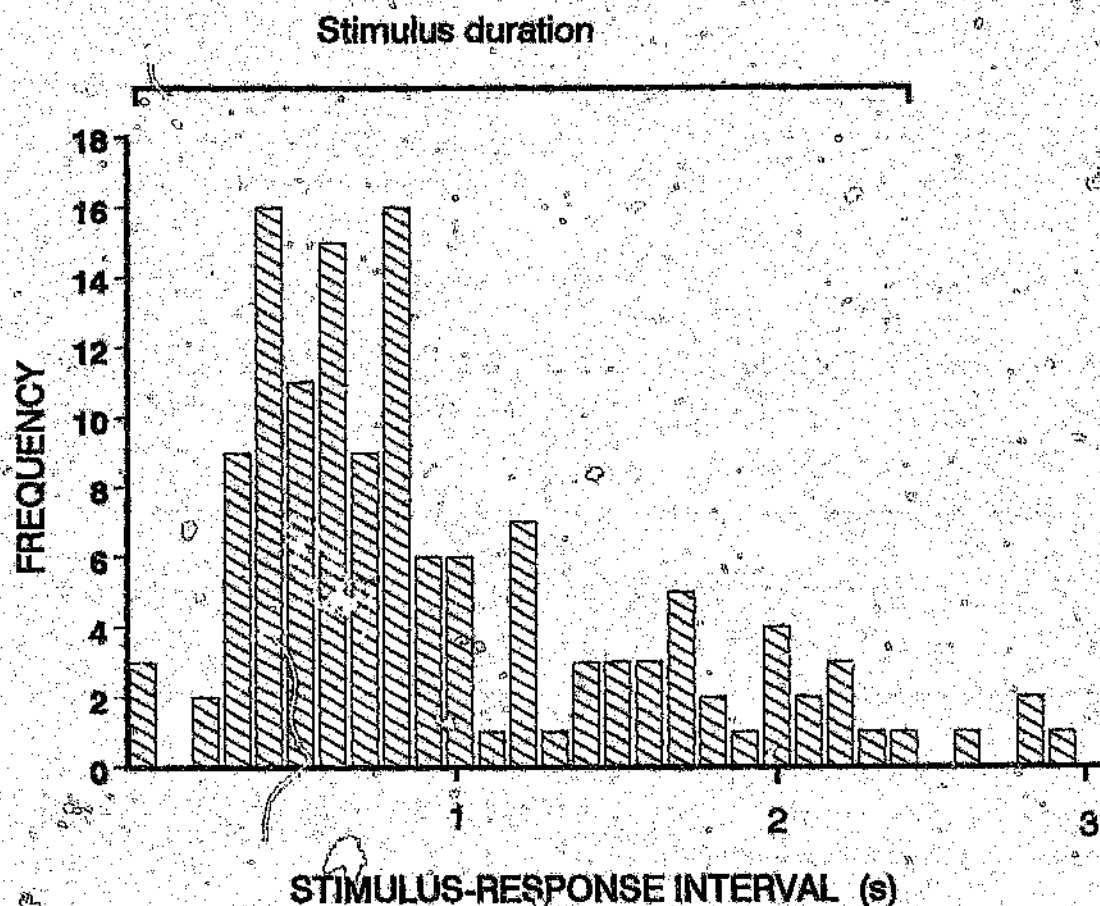


Fig. 2.5 Stimulus-Response intervals ($n = 134$) during a broadcast of 20 stimuli/min to 10 *A. fornasinii* males. Mean $\pm$ SD = 0.95 ± 0.64 s

At a repetition rate of 20 stimuli/min, the first second of a stimulus corresponds to 33.3% of the stimulus call period and 65% ($n = 87$) of the responses during this broadcast ($n = 134$) were initiated within this time period (median = 0.8 s, Chi-square test, $\chi^2 = 24.39$, $P < 0.001$, $df = 1$) (Fig. 2.5).

There was no significant difference in call repetition rate among broadcast sequences (Friedman ANOVA, $F = 5.91$, $P = 0.12$, $df = 3$).

TABLE 2.1

The distribution of S-R intervals with different rate broadcasts to 10 *A. fornasinii*

Stimulus rep. rate	S-R Intervals (s)					
	0-0.9	1-1.9	2-2.9	3-3.9	4-4.9	5-5.9
20/min	87	32	15	-	-	-
15/min	87	14	11	19	-	-
10/min	77	7	5	3	26	16

2.3.2 *Hyperolius marmoratus*

Hyperolius marmoratus males were presented with three different repetition rate broadcasts (40, 55 and 84 stimuli/min) and one broadcast with a random sequence of stimulus intercall intervals. The stimulus-response intervals, and the subject's intercall intervals, before and during the broadcasts, were recorded for 10 individuals.

The mean intercall interval before the broadcast was 1.27 ± 0.28 s and did not differ significantly from the mean intercall interval during the broadcast of 84, 55 and 40 stimuli/min (Friedman ANOVA, $F = 0.22$, $P = 0.88$, $df = 3$) (Figs. 2.6, 2.7, 2.8 and 2.9).

If call matching, or some other form of precise call timing had occurred one would expect a shift in the mean intercall interval (for example, see the distribution of intercall intervals of *S. wealii* during broadcasts, Figs. 2.28 - 2.30). The distribution of stimulus-response intervals during the three different repetition rate broadcasts are illustrated by Table 2.2 and Figures 2.10, 2.11 and 2.12.

TABLE 2.2

The distribution of S-R intervals with different repetition rate broadcasts to 10 *H. armatus*.

Stimulus rep. rate	S-R Intervals (s)						
	0-0.1	0.2-0.3	0.4-0.5	0.6-0.7	0.8-0.9	1.0-1.1	1.2-1.3
84/min	138	105	102	63	-	-	-
55/min	88	61	60	80	72	49	-
40/min	64	38	38	39	70	56	68

If a precise timing mechanism was in operation then one would expect to see a substantial increase in the occurrence of one or more stimulus-response intervals. However, it is very difficult to ascertain any regular pattern in the distribution of stimulus-response intervals and they do not differ significantly from a linear

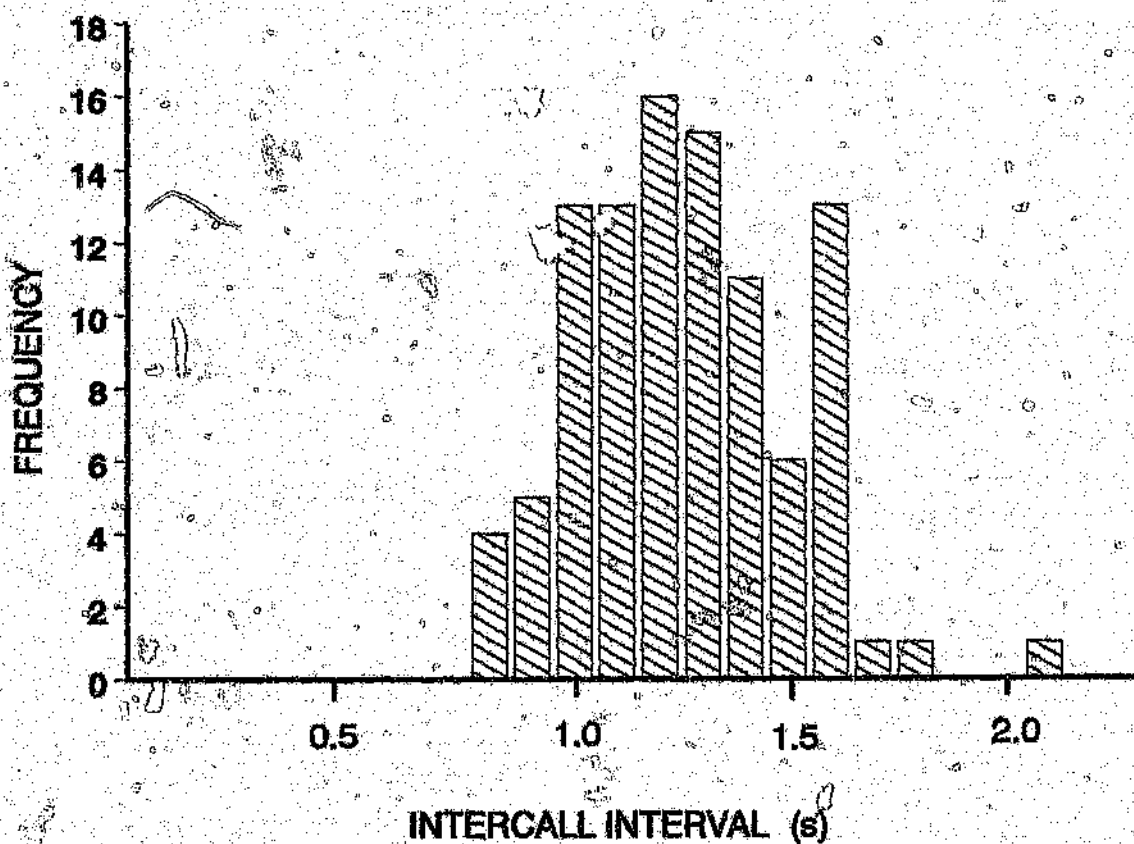


Fig. 2.6 *H. marmoratus* intercall intervals before the broadcast began ($n = 10$ males).

Mean $\pm$ SE = 1.27 ± 0.28 s

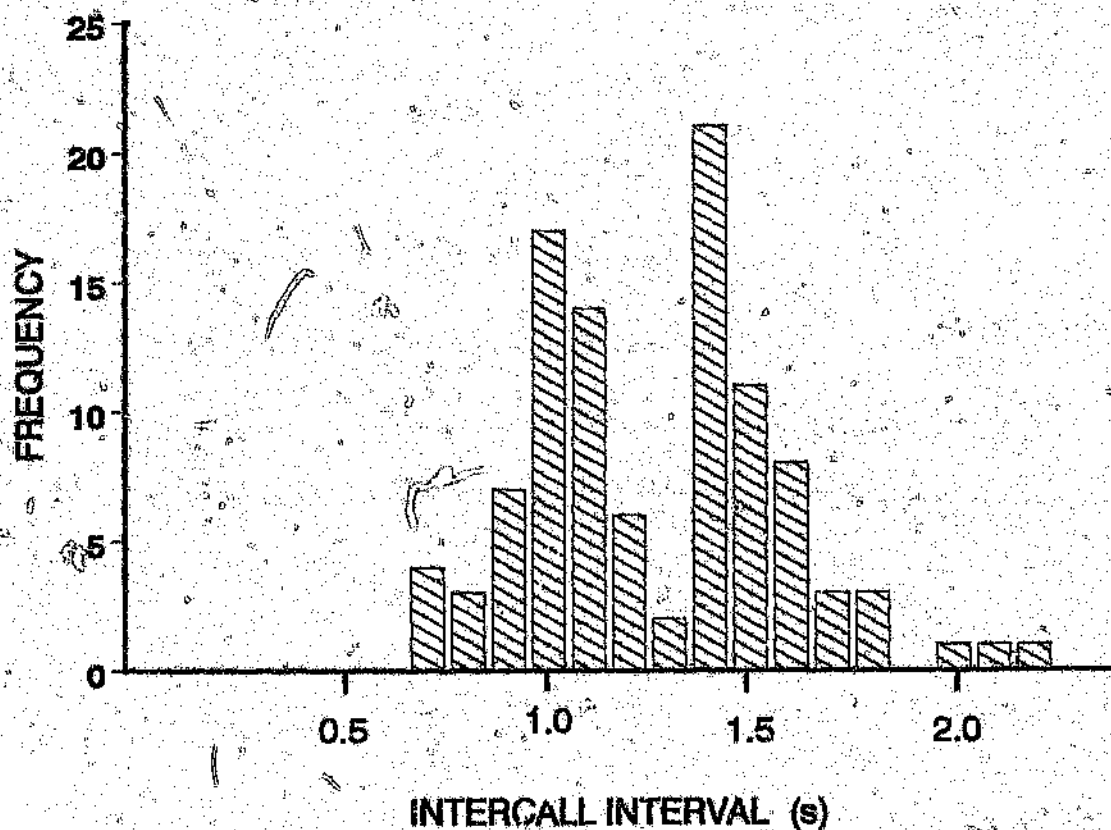


Fig. 2.7 *H. marmoratus* intercall intervals during the broadcast of 84 stimuli/min ($n = 10$ males).
Mean $\pm$ SE = 1.27 ± 0.31 s

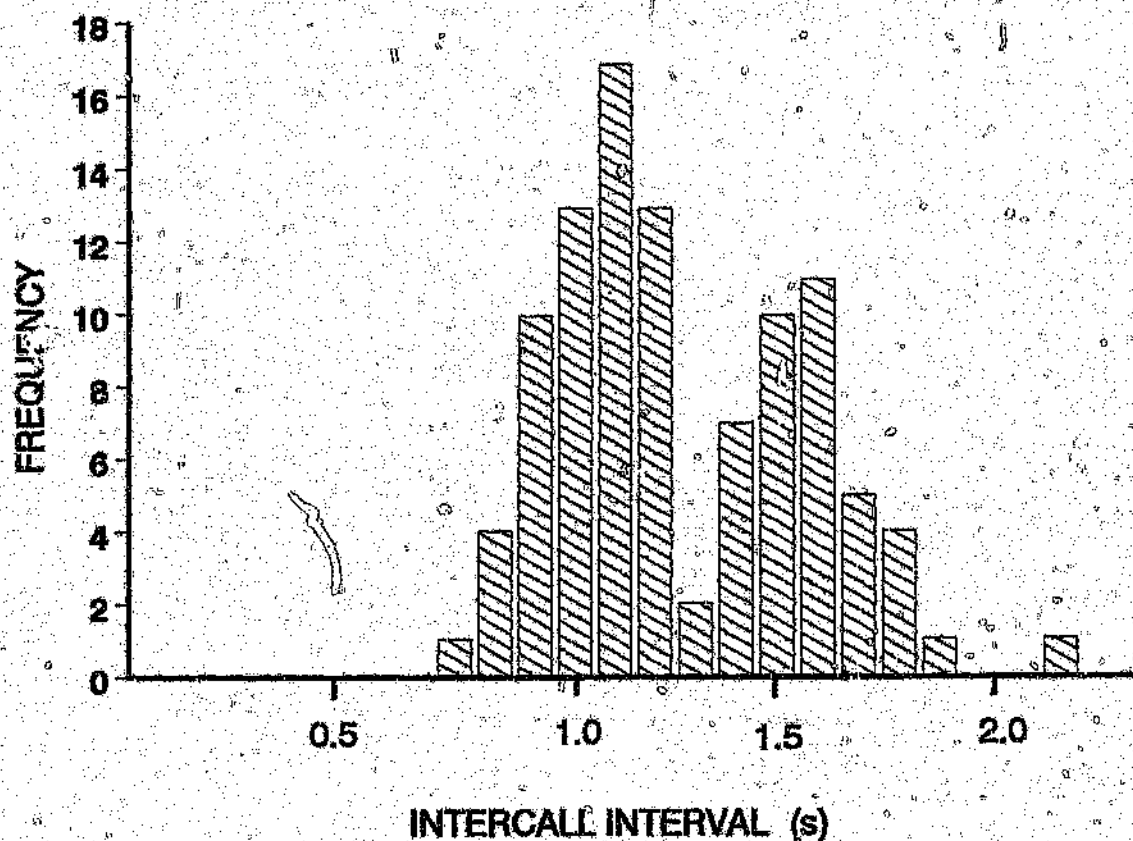


Fig. 2.8 *H. marmoratus* intercall intervals during the broadcast of 55 stimuli/min ($n = 10$ males).
Mean $\pm$ SE = 1.26 ± 0.31 s

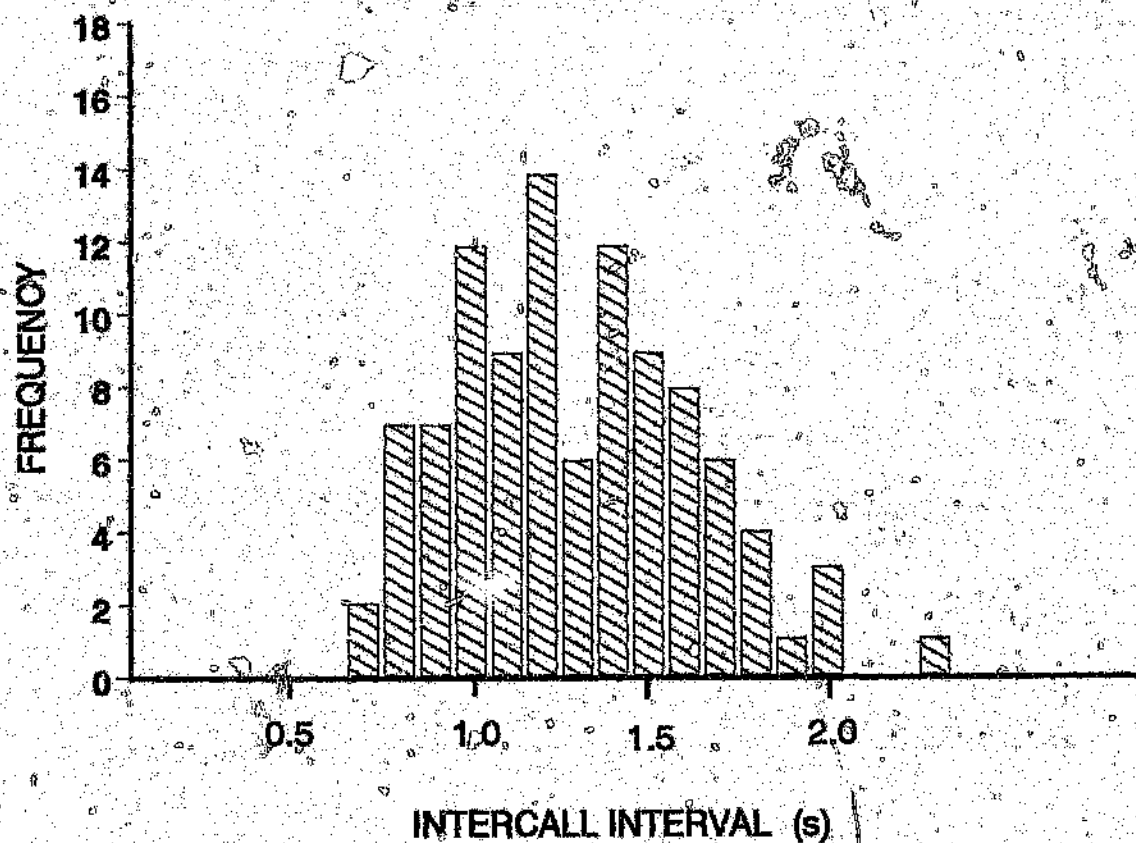


Fig. 2.9 *H. marmoratus* intercall intervals during the broadcast of 40 stimuli/min ($n = 10$ males).
Mean $\pm$ SE = 1.29 ± 0.33 s

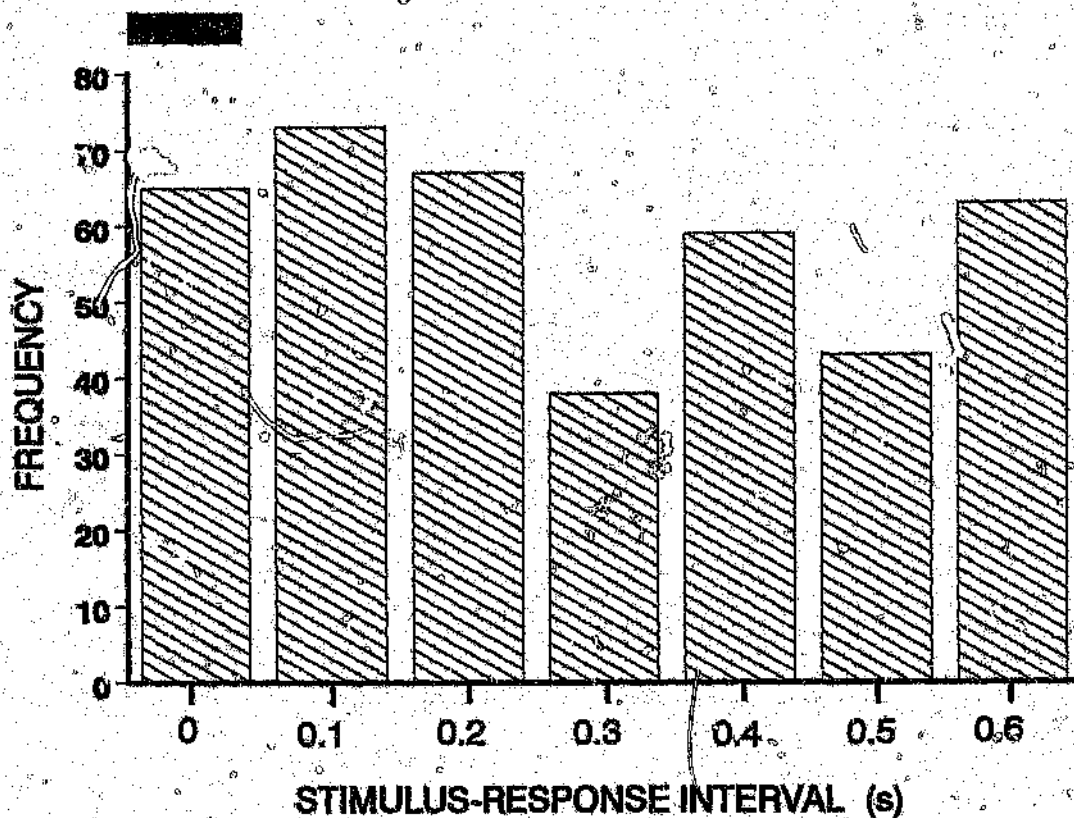


Fig. 2.10 *H. marmoratus* Stimulus-Response intervals (n = 408) during a broadcast of 84 stimuli/min (10 males). The solid black bar represents the duration and position of the stimulus.

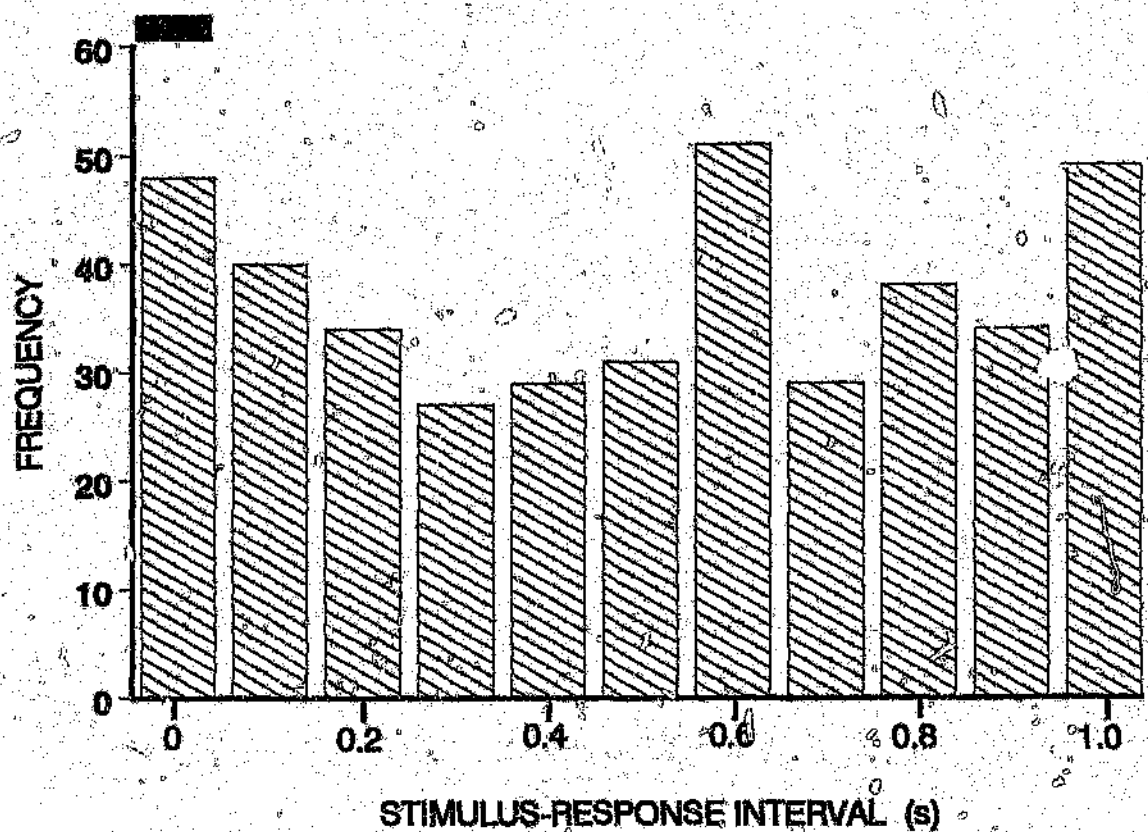


Fig. 2.11 *H. marmoratus* Stimulus-Response intervals ($n = 410$) during a broadcast of 55 stimuli/min (10 males). The solid black bar represents the duration and position of the stimulus.

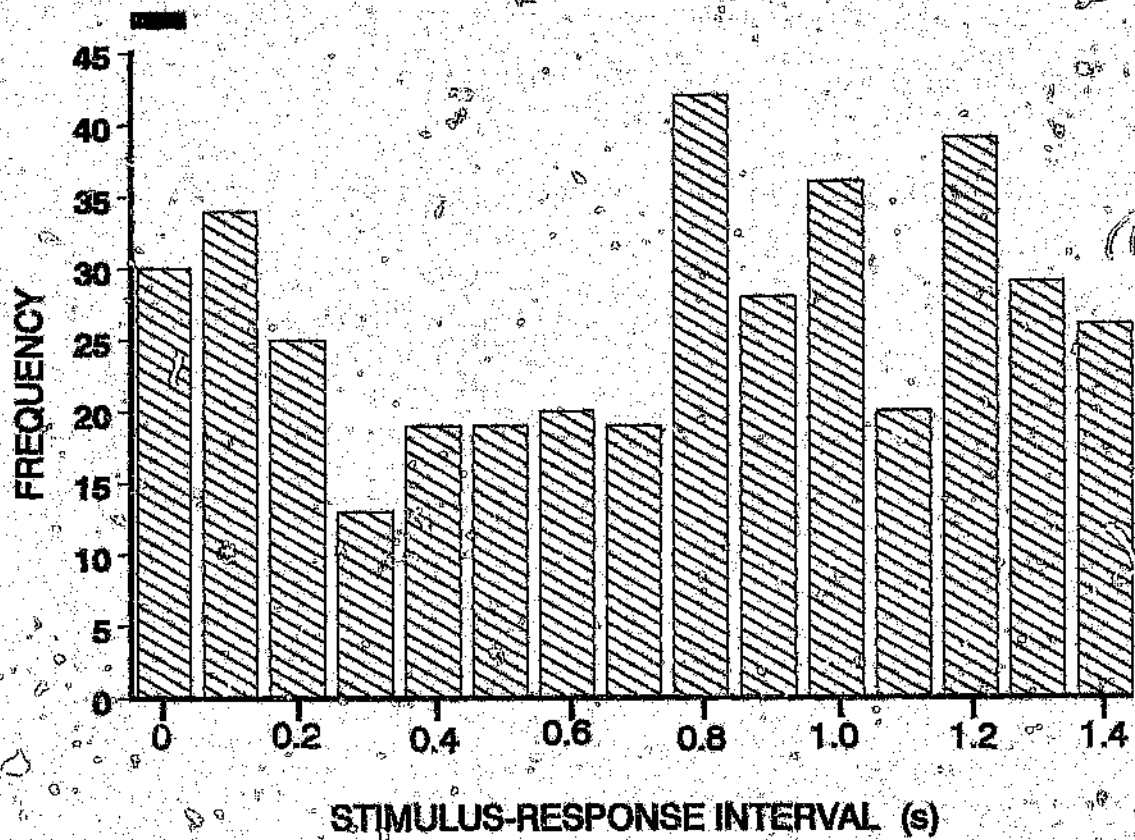


Fig. 2.12 *H. marmoratus* Stimulus-Response intervals ($n = 399$) during a broadcast of 40 stimuli/min (10 males). The solid black bar represents the duration and position of the stimulus.

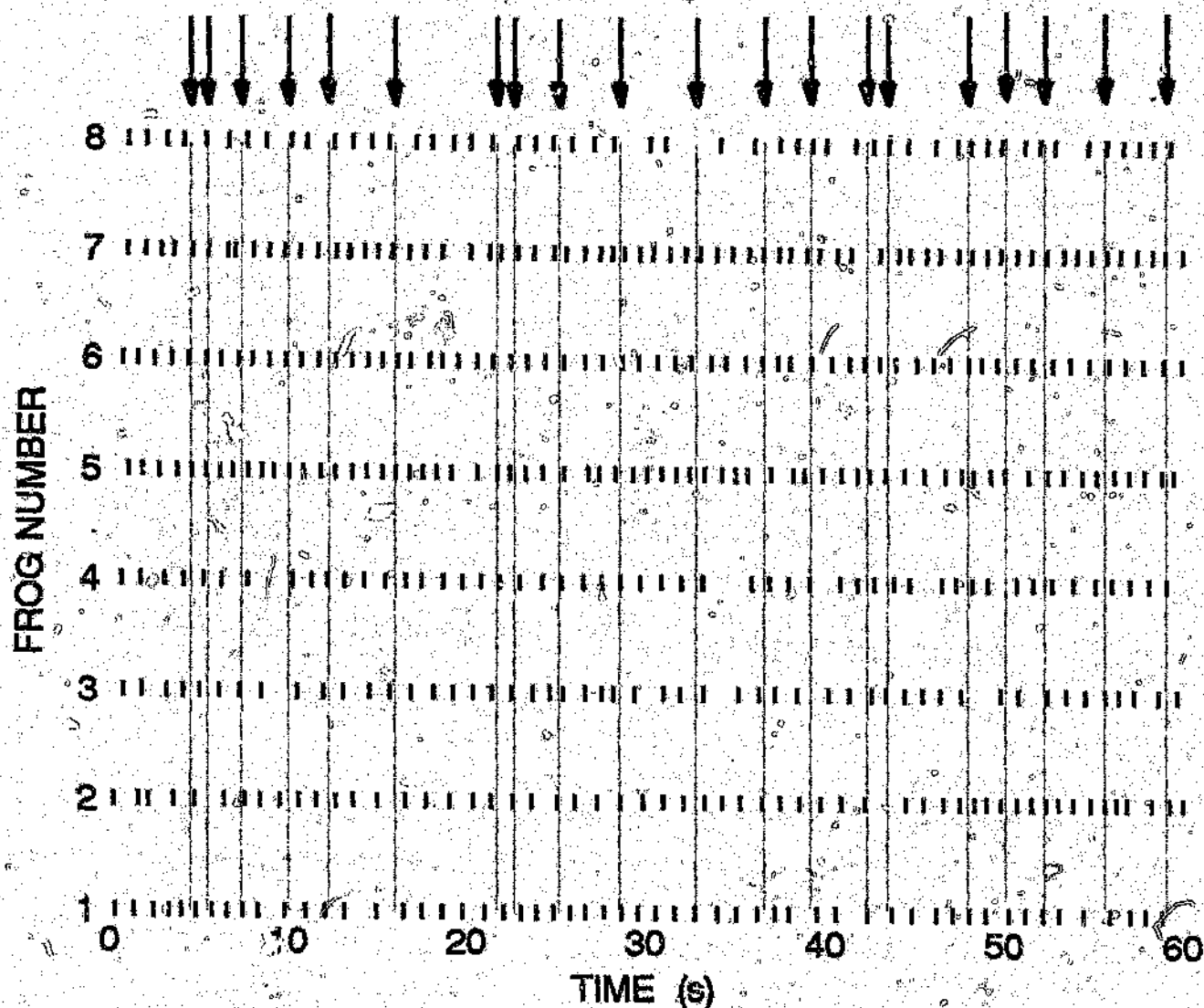


Fig. 2.13 The position of 8 *H. marmoratus* calls during a random broadcast ($n = 461$). The position of the random stimuli are indicated by arrows.

distribution (Spearman's correlation coefficient, stimuli @ 84/min, $r_s = 0.57$, $n = 7$, $P = 0.02$; stimuli @ 55/min, $r_s = 0.10$, $n = 11$, $P = 0.75$; stimuli @ 40/min, $r_s = 0.26$, $n = 15$, $P = 0.34$). In each case the mean intercall interval was very close to half the stimulus call period, indicating a similar number of responses on either side of the mean. Figure 2.13 shows the position of the calls of eight *H. marmoratus* in relation to the position of a broadcast sequence of random intercall intervals. Again, there is no alteration in call pattern or intercall interval. *H. marmoratus* continues calling at its own set pace irrespective of broadcast stimuli (Friedman ANOVA, $F = 0.18$, $P > 0.90$, $df = 2$). The call repetition rate of six *H. marmoratus* was not significantly altered by the different repetition rate broadcasts when compared with rates before and after the broadcast stimuli (Friedman ANOVA, $F = 4.44$, $P = 0.22$, $df = 3$).

2.3.3 Kassina maculata

Kassina maculata males were presented with three different repetition rate broadcasts (20, 30 and 40 stimuli/min). A common feature of all broadcast experiments was the delay of the response until at least 0.6 s after the onset of a stimulus (Fig. 2.14). The distribution of S-R intervals was also skewed with only three calls (0.3%) produced in less than 0.6 s from the beginning of a stimulus (apart from simultaneous calls). Sixty-one percent ($n = 559$) of the total number of evoked responses ($n = 909$) in all the broadcast experiments occurred between 1.0 and 2.0 s after the onset of a stimulus (see Table 2.3) (median S-R interval = 1.4 s). The distribution of S-R intervals during all broadcast experiments was highly significantly different from a uniform distribution (Chi-square test, stimuli @ 20/min, $\chi^2 = 291.85$, $P < 0.001$, $df = 30$; stimuli @ 30/min, $\chi^2 = 344.41$, $P < 0.001$, $df = 20$; stimuli @ 40/min, $\chi^2 = 304.62$, $P < 0.001$, $df = 13$).

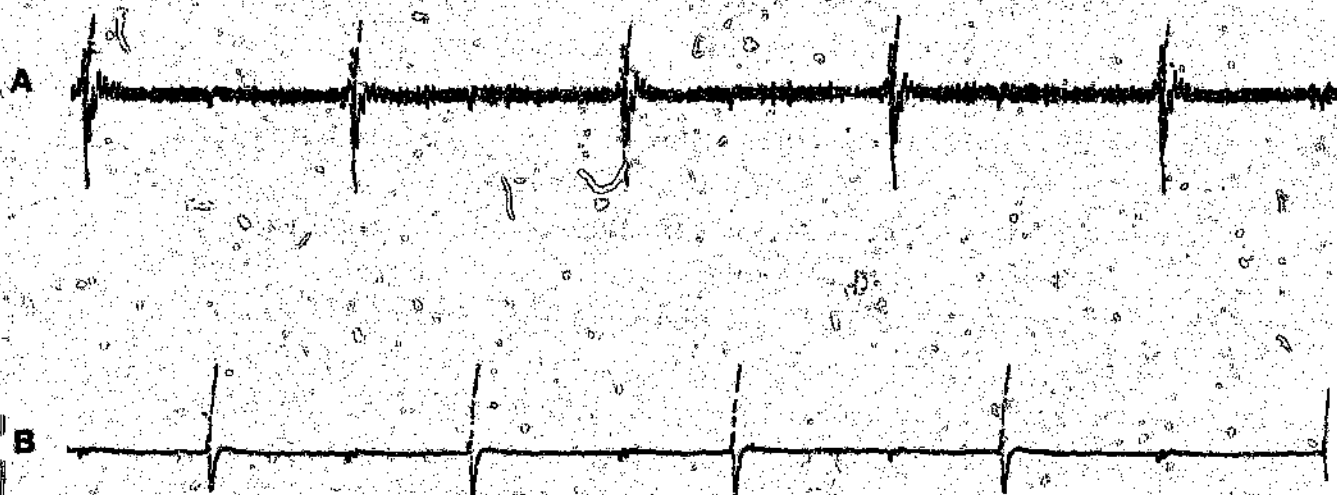


Fig. 2.14 *K. maculata* - Oscillograph tracing of responses to conspecific broadcasts.
(A- broadcast calls, B - subject's response)

An interesting result was that, as the repetition rate of the broadcast increased, the frogs decreased their median S-R interval. In the broadcast of 20 stimuli/min the median S-R interval was 1.8 s (Fig. 2.15) and this decreased to 1.5 s during the 30 stimuli/min broadcast (Fig. 2.16) and to 1.2 s with the 40 stimuli/min broadcast (Fig. 2.17). However, this apparent decrease was shown to be an artefact of the decreasing call period of the stimulus (i.e. the time between consecutive stimuli). When the mean S-R intervals are corrected for stimulus call period and compared they are not significantly different (Kruskal Wallis ANOVA, $KW = 3.63$, $P = 0.16$).

The call repetition rate of nine out of ten subjects increased during the broadcast (Binomial test, $P < 0.05$), (Table 2.4). However, repetition rate does not provide a good measure of interaction because, although the subject may be precisely positioning its calls with respect to the stimuli, it need not be producing the same number of calls per minute as the broadcast. The subject may match his calls to every second or third stimulus, thus resulting in a repetition rate one-half or one-third of the broadcast rate. The mean repetition rate of calls before the broadcast commenced was 15.6 calls/min and there was a slightly non-significant increase to 17, 20 and 18 calls/min during the broadcasts of 20, 30 and 40 stimuli/min respectively (Friedman ANOVA, $F = 7.11$, $P = 0.07$, $df = 2$) (Table 2.4).

TABLE 2.3

The distribution of S-R intervals with different repetition rate broadcasts to 10 *K. maculata*

Stimulus rep. rate	S-R Intervals (s)					
	0-0.5	0.6-1.0	1.1-1.5	1.6-2.0	2.1-2.5	2.6-3.0
40/min	8	86	181	-	-	-
30/min	13	43	154	170	-	-
20/min	1	22	65	88	39	39

TABLE 2.4

Kassina maculata repetition rates before and during broadcasts ($n = 9$)

Subject no.	Call Repetition Rates			
	Before	20/min	30/min	40/min
1	17.0	17.1	20.4	23.7
2	12.2	17.4	20.3	21.9
3	11.6	18.7	23.9	13.1
4	9.4	15.3	13.0	13.6
5	17.2	17.2	20.4	17.8
6	4.6	-	23.8	-
7	35.3	19.0	17.8	17.7
8	-	16.9	19.0	17.6
9	8.6	14.8	20.6	19.3
$\bar{x} =$	15.8	17.0	20.0	18.0
SD =	9.9	1.4	3.3	3.6

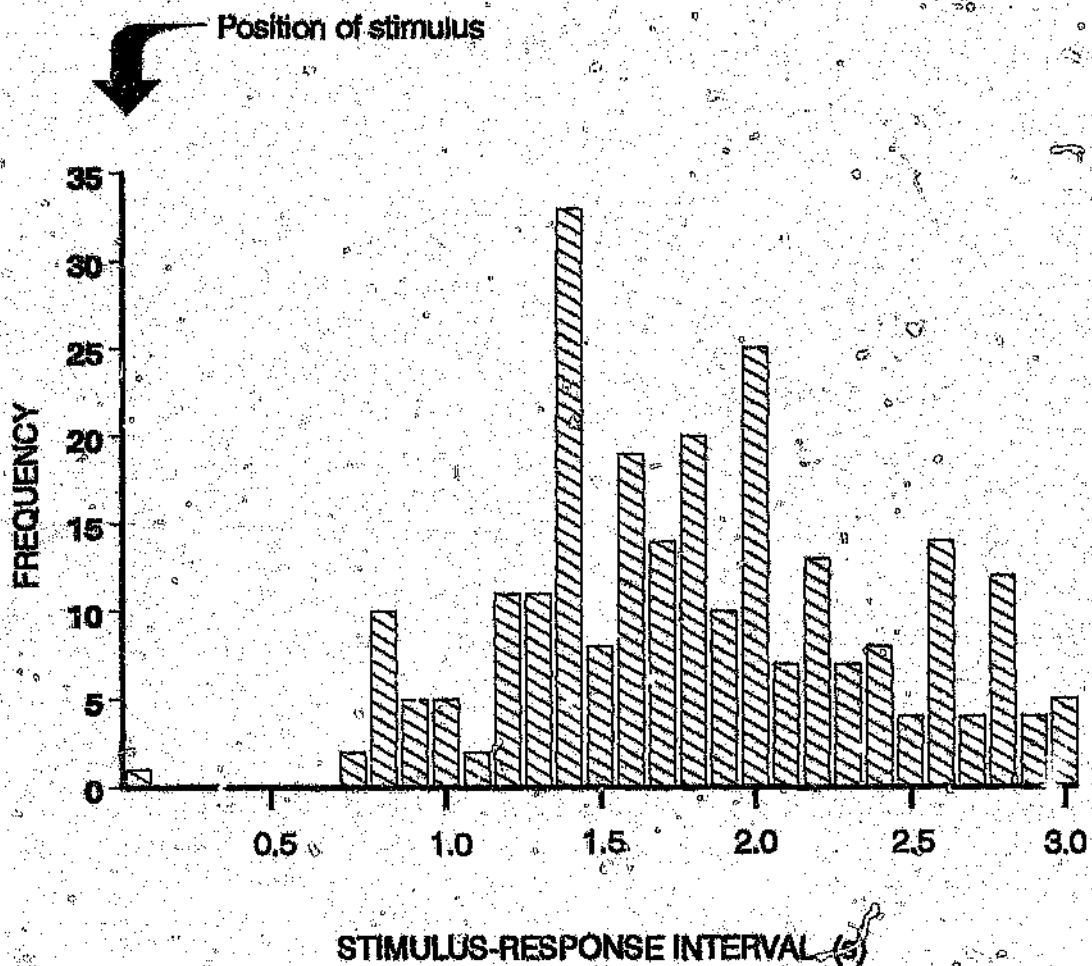


Fig. 2.15 *K. maculata* Stimulus-Response intervals (n = 254) during a broadcast of 20 stimuli/min (8 males). Mean $\pm$ SE = 1.81 $\pm$ 0.58 s.

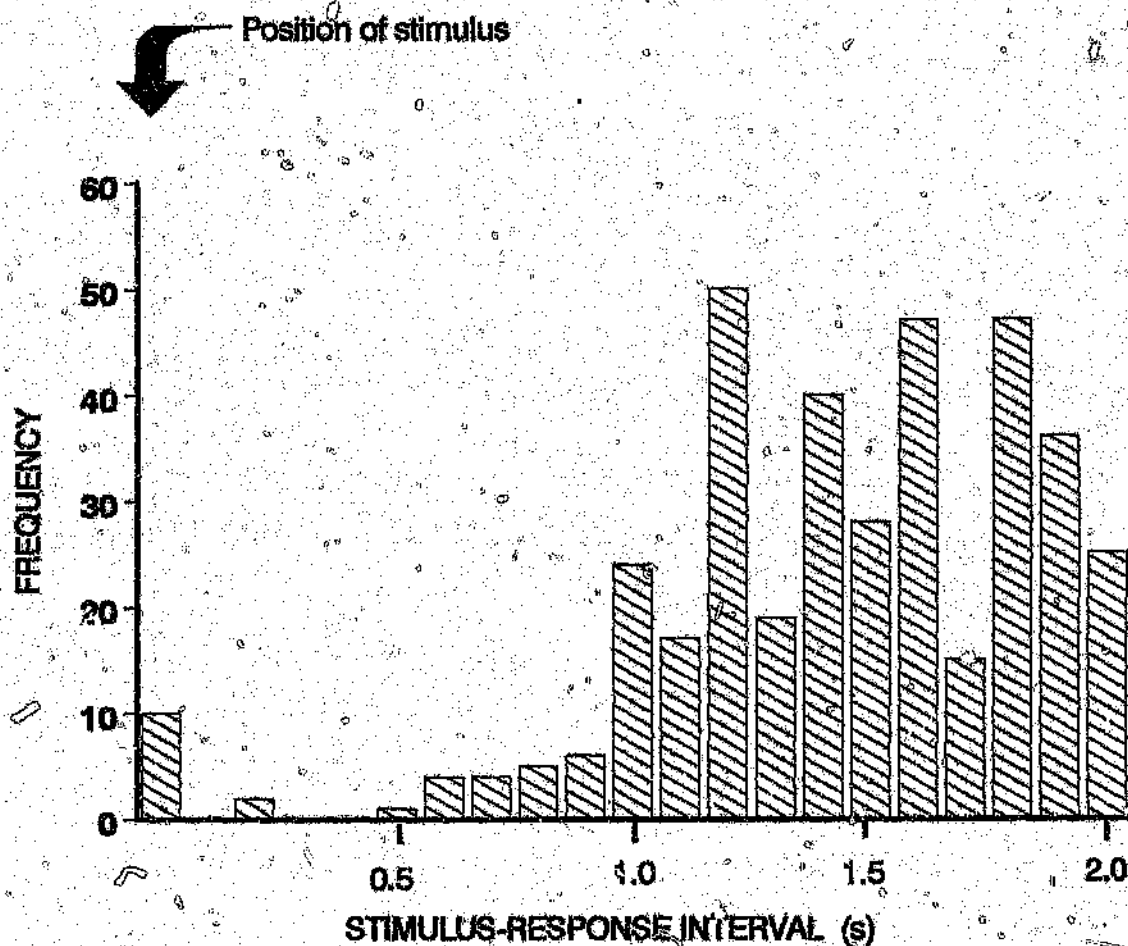


Fig. 2.16 *K. maculata* Stimulus-Response intervals ($n = 380$) during a broadcast of 30 stimuli/min (10 males). Mean $\pm$ SE = 1.43 ± 0.42 s.

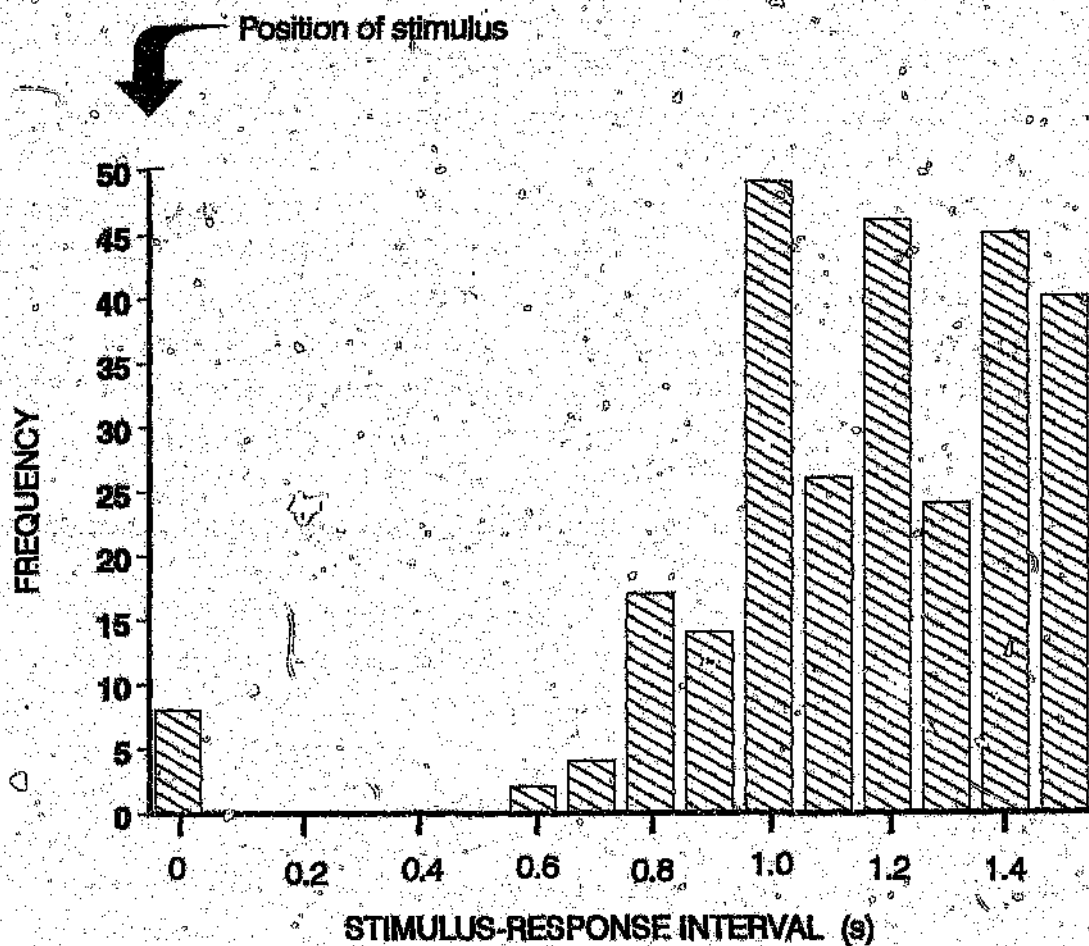


Fig. 2.17 *K. maculata* Stimulus-Response intervals ($n = 275$) during a broadcast of 40 stimuli/min (8 males). Mean $\pm$ SE = 1.15 ± 0.30 s.

2.3.4 Kassina senegalensis

Kassina senegalensis males were presented with four different repetition rate broadcasts of a single conspecific stimulus (12, 20, 40 and 60 stimuli/min). They were also presented with two multiple-stimulus broadcasts. The first multiple-stimulus broadcast consisted of two conspecific calls separated by an interval of 25 ms repeated 40 times a minute. The second consisted of three conspecific calls separated by intervals of 25 ms repeated 40 times a minute.

With the repetition rate broadcasts of single stimuli, *K. senegalensis* exhibited an extremely skewed distribution of S-R intervals and produced most of its calls within 0.2 s after a stimulus. There were significantly more responses produced within the 0.5 s period immediately after a stimulus than during the remainder of the stimulus call period (Chi-square test, stimuli @ 60/min, $\chi^2 = 134.19$; stimuli @ 40/min, $\chi^2 = 136.00$; stimuli @ 20/min, $\chi^2 = 133.33$; stimuli @ 12/min, $\chi^2 = 35.04$; for all broadcasts $P < 0.001$, $df = 1$, see Table 2.5). During the slow (12 stimuli/min) broadcast sequence, 93.6% of the responses occurred within this 0.2 s period (Fig. 2.18). Overall, of the 1281 responses which occurred during all the single stimuli repetition rate broadcasts 76.3% ($n = 977$) were produced within 0.2 s from the beginning of a stimulus (median S-R interval = 0.2 s) (Figs. 2.18, 2.19, 2.20, and 2.21). When the repetition rate of the broadcast stimuli was fairly slow e.g. 12 stimuli/min the call timing exhibited by *K. senegalensis* was extremely precise with all except 3 evoked responses ($n = 47$) falling within this 0.2 s period after a stimulus (median S-R interval = 0.2 s; Fig. 2.18). When the repetition rate of the broadcast was increased to 20, 40 and 60 stimuli/min, the call timing was still very precise with a mean of 75.6% of all calls falling within the 0.2 s period after a stimulus began. The trend with respect to call repetition rate was a

significant increase in the rate with increasing broadcast repetition rates (Friedman ANOVA, $F = 26.28$, $P < 0.0001$, $df = 3$), although matching of repetition rates was not very precise with the higher rate broadcasts. During the multiple stimuli broadcast there were significantly more responses in the 0.2 s period after the first stimulus of the multiple sequence than would be expected in a uniform distribution (Chi-square test, $\chi^2 = 46.09$ (double stimulus), 25.99 (triple stimulus), $P < 0.001$, $df = 1$). Although there were significantly less responses in the 0.2 s periods immediately after the second and third stimuli, than would be expected in a uniform distribution (Chi-square test, $\chi^2 = 22.56$, $P < 0.001$, $df = 1$), there were more responses during this period than in the remainder of the intercall interval (Figs. 2.22 and 2.23).

TABLE 2.5

The distribution of S-R intervals with different repetition rate broadcasts to 7 *K. senegalensis*

Stimulus rep. rate	S-R Intervals (s)					
	0-0.5	0.6-1.0	1.1-1.5	1.6-2.0	2.1-2.5	2.6-3.0
60/min	305	78	-	-	-	-
40/min	329	45	45	-	-	-
20/min	336	11	19	34	17	15
12/min	44	0	1	0	1	1

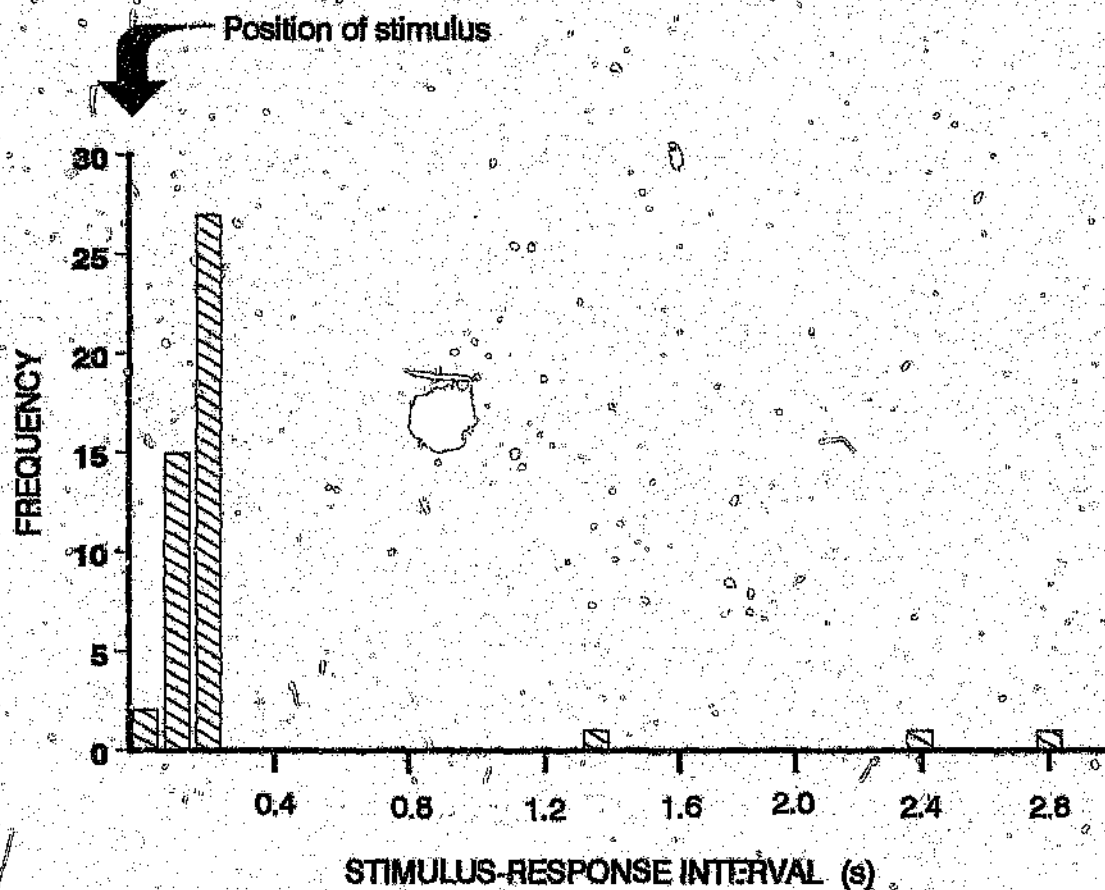


Fig. 2.18 *K. senegalensis* Stimulus-Response intervals ($n = 46$) during a broadcast of 12 stimuli/min (3 males).

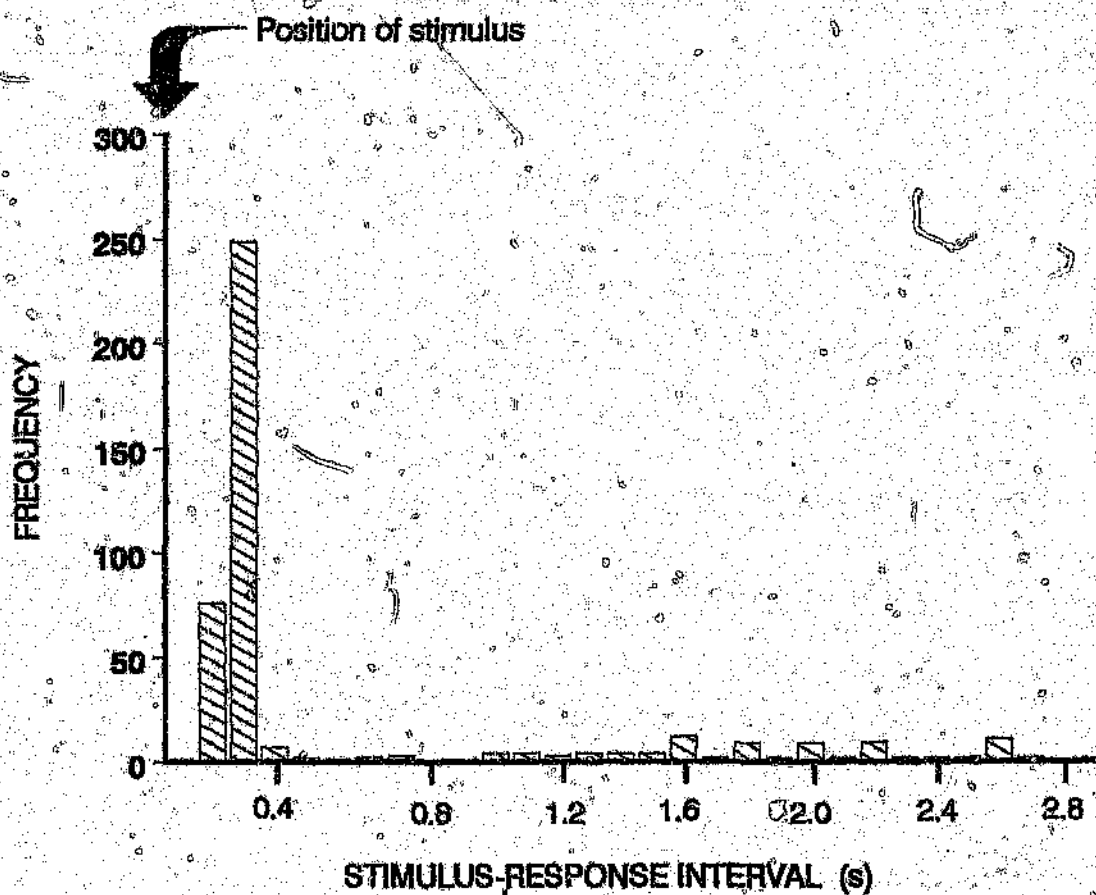


Fig. 2.19. *K. senegalensis* Stimulus-Response intervals ($n = 432$) during a broadcast of 20 stimuli/min (14 males).

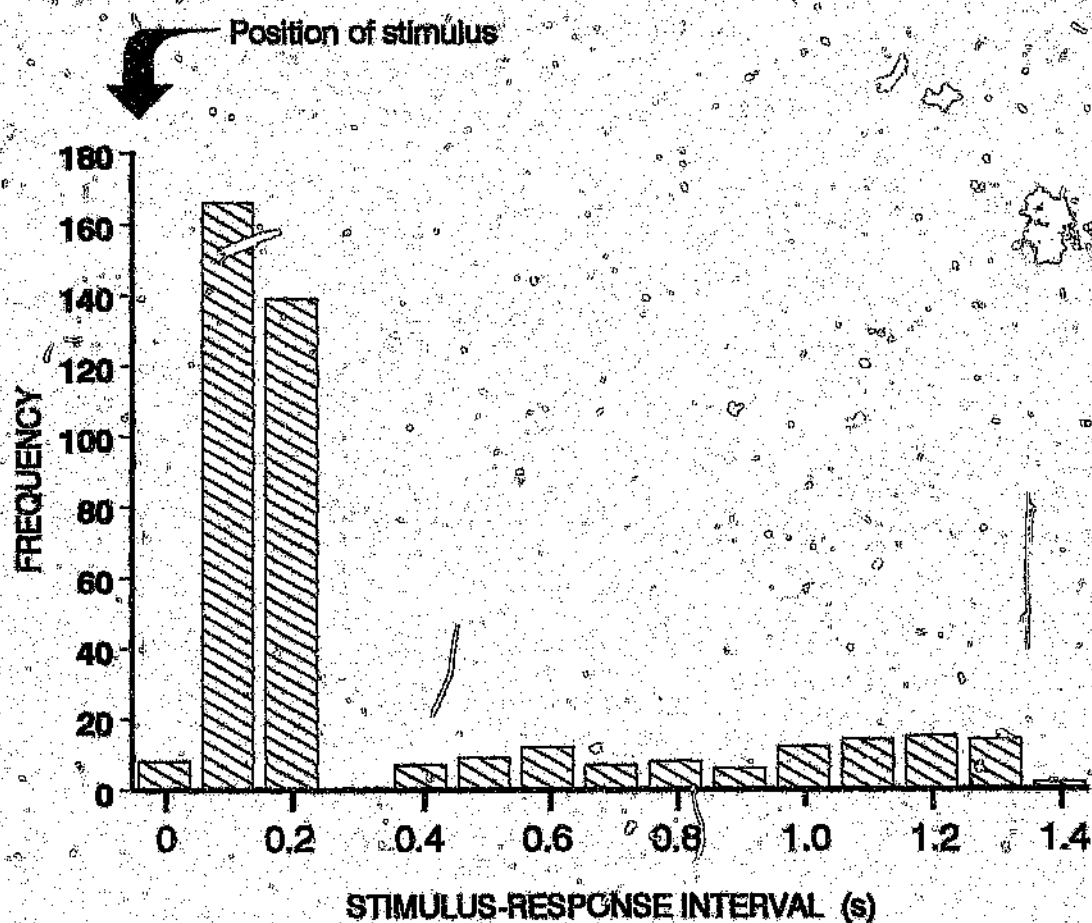


Fig. 2.20 *K. senegalensis* Stimulus-Response intervals ($n = 419$) during a broadcast of 40 stimuli/min (11 males).

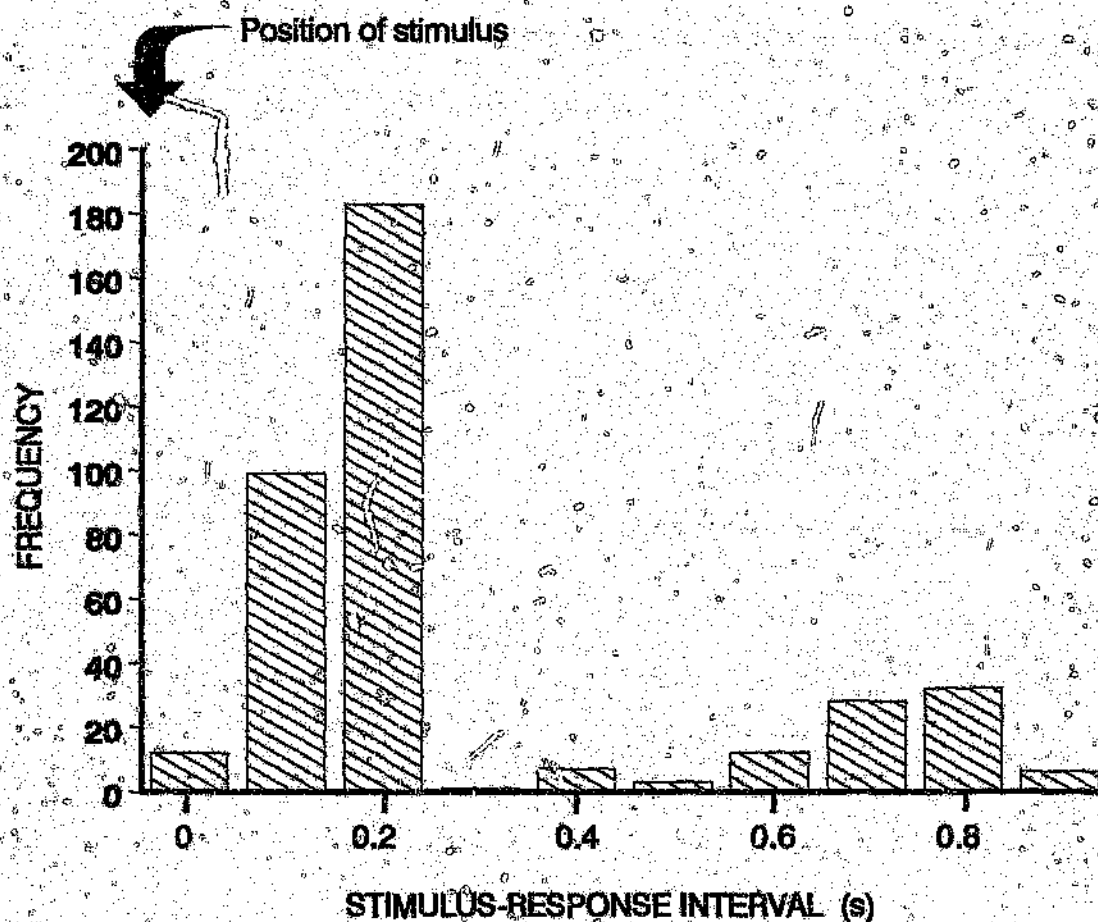


Fig. 2.21 *K. senegalensis* Stimulus-Response intervals ($n = 383$) during a broadcast of 60 stimuli/min (12 males).

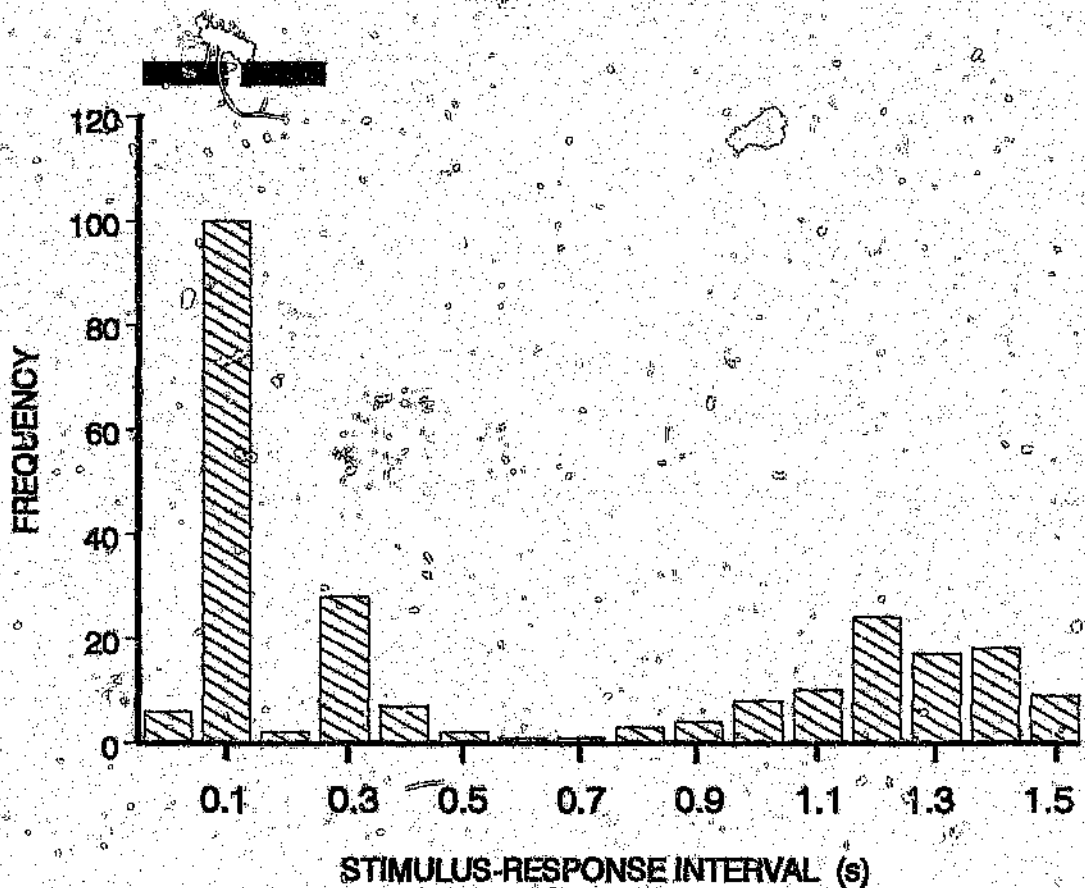


Fig. 2.22 *K. senegalensis* Stimulus-Response intervals ($n = 240$) during a broadcast of double stimuli (7 males). The solid black bars represent the duration and position of the stimuli.

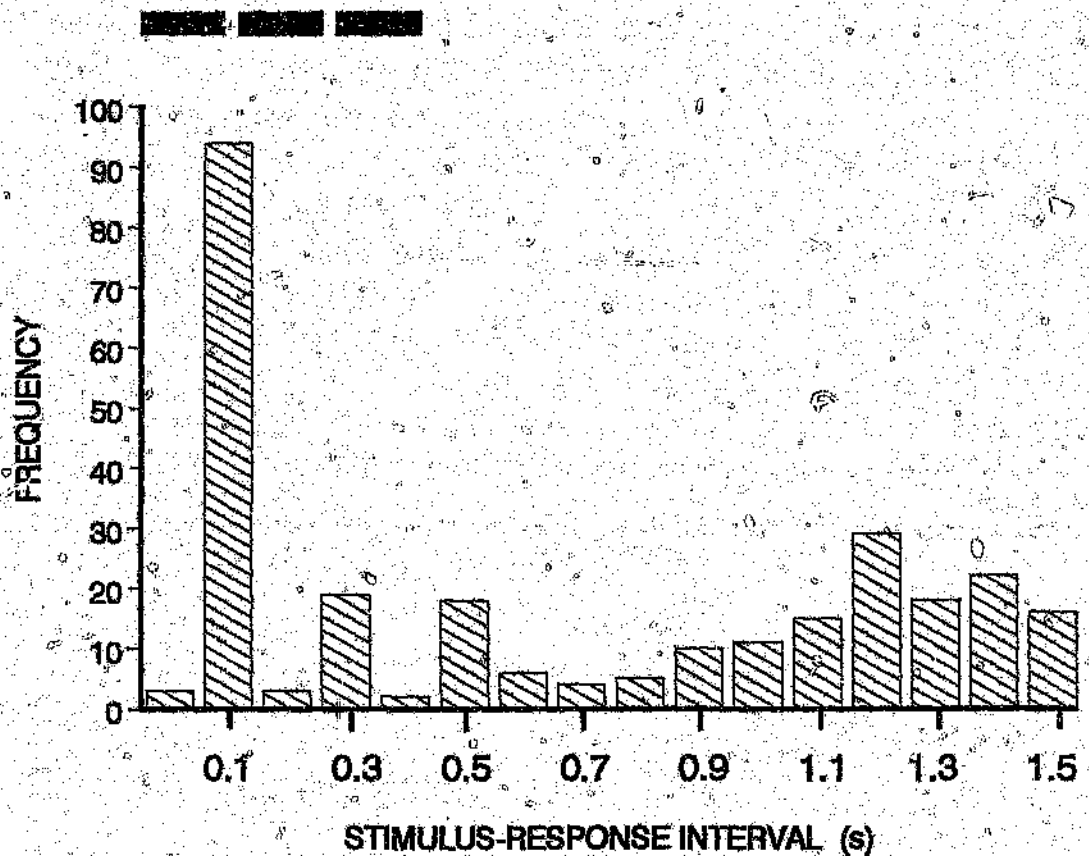


Fig. 2.23 *K. senegalensis* Stimulus-Response intervals ($n = 275$) during a broadcast of triple stimuli (7 males). The solid black bars represent the duration and position of the stimuli.

2.3.5 Semnodactylus wealii

Semnodactylus wealii males were presented with three different repetition rates broadcasts of a single conspecific stimulus (6, 12 and 20 stimuli/min). The overall trend was a skewed distribution of S-R intervals with a very high number of responses occurring within the 0.6 s period after the stimulus began. There was a highly significant number of responses produced within 0.5 s after the onset of the stimulus (Chi-square test, stimuli @ 20/min, $\chi^2 = 7.53$, $P < 0.01$, $df = 1$; stimuli @ 12/min, $\chi^2 = 12.63$, $P < 0.001$, $df = 1$; stimuli @ 6/min, $\chi^2 = 17.82$, $P < 0.001$, $df = 1$.) (Table 2.6).

TABLE 2.6

The distribution of S-R intervals with different repetition rate broadcasts to 9 *S. wealii*

Stimulus rep. rate	S-R Intervals (s)						
	0-0.5	0.6-1.0	1.1-1.5	1.6-2.0	2.1-2.5	2.6-3.0	Z
20/min	177	68	3	13	23	22	-
12/min	217	78	12	10	18	14	17
6/min	98	17	4	5	7	7	7

Z = mean for all S-R intervals longer than 3.0 s

With a broadcast repetition rate of 6 stimuli/min, the median S-R interval was 0.6 s and, of a total of 246 evoked responses, 46.5% ($n = 114$) fall within 0.5 s after the beginning of a stimulus (Fig. 2.24). A 0.5 s time interval only accounts for 5% of the stimulus call period. When the repetition rate of the broadcast was increased to 12 stimuli/min (Fig. 2.25 and Table 2.6) the median S-R interval was 0.5 s and the number of evoked responses which fell into this 0.5 s period immediately after a stimulus rose to 56.8% (262 responses, $n = 461$). When the repetition rate was further increased to 20 stimuli/min, the median S-R interval was 0.4 s with 70.6% ($n = 219$) of the total responses ($n = 310$) being produced within the 0.5 s period immediately after a stimulus (Fig. 2.26 and Table 2.6). In all broadcast experiments the number of responses which occurred between 0.40 and 0.49 s after the beginning of the stimulus were at least 3 fold greater than the number of responses occurring at any other 0.1 s interval after a stimulus (Figs. 2.24, 2.25, and 2.26).

Figs. 2.28 - 2.30 demonstrate how *S. wealii* attempted to match the stimulus intercall interval with their own intercall intervals. During a broadcast of 20 stimuli/min, the stimulus intercall interval is 3 s. From the histogram (Fig. 2.30) it can be seen that there was a large number of intercall intervals of 3 s duration (mean = 4.6 s). Also there was a small peak at 6 s illustrating that, if some males failed to respond to one stimulus, then the next stimulus produced a response, yielding an intercall interval of twice that of the broadcast (i.e. 6 s). With a repetition rate of 12 stimuli/min, the stimulus intercall interval is 5 s and again peaks occurred at 5 s and at twice the stimulus intercall interval (10 s) (Fig. 2.29). The mean intercall interval at this repetition rate was 4.5 s. When the repetition rate was as slow as 6 stimuli/min with a stimulus intercall interval of 10 s (Fig. 2.28), *S. wealii* matched this interval but, during this broadcast

sequence, no intercall intervals were longer than 16 s. In all the broadcast sequences, the longest intercall interval was 18 s (Fig. 2.29), which may account for the reason why there was no doubling of the stimulus inter-call interval (i.e. 20 s) during the slow repetition rate broadcast. The mean intercall interval of nine subjects before the broadcast commenced was 4.55 s and the longest interval measured from these 9 subjects was 14 s (Fig. 2.27).

The matching of the repetition rates of individuals to the different repetition rates of broadcasts was not very precise and showed only a slight significant increase with increasing repetition rate of the broadcast stimuli (Friedman ANOVA, $F = 9.4$, $P = 0.02$, $df = 3$)

The temporal relationships between the stimulus and the response are shown in Fig. 2.31.

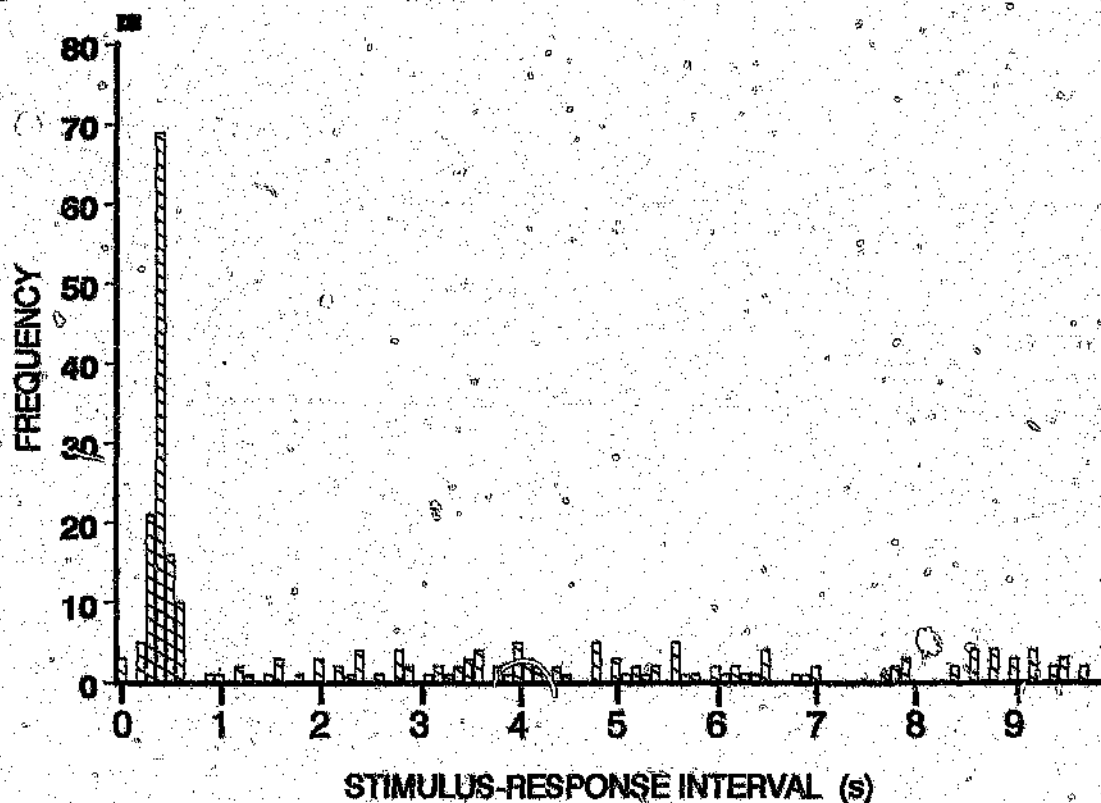


Fig. 2.24 *S. wealii* Stimulus-Response intervals ($n = 246$) during a broadcast of 6 stimuli/min (14 males). The solid black bar represents the duration and position of the stimulus.

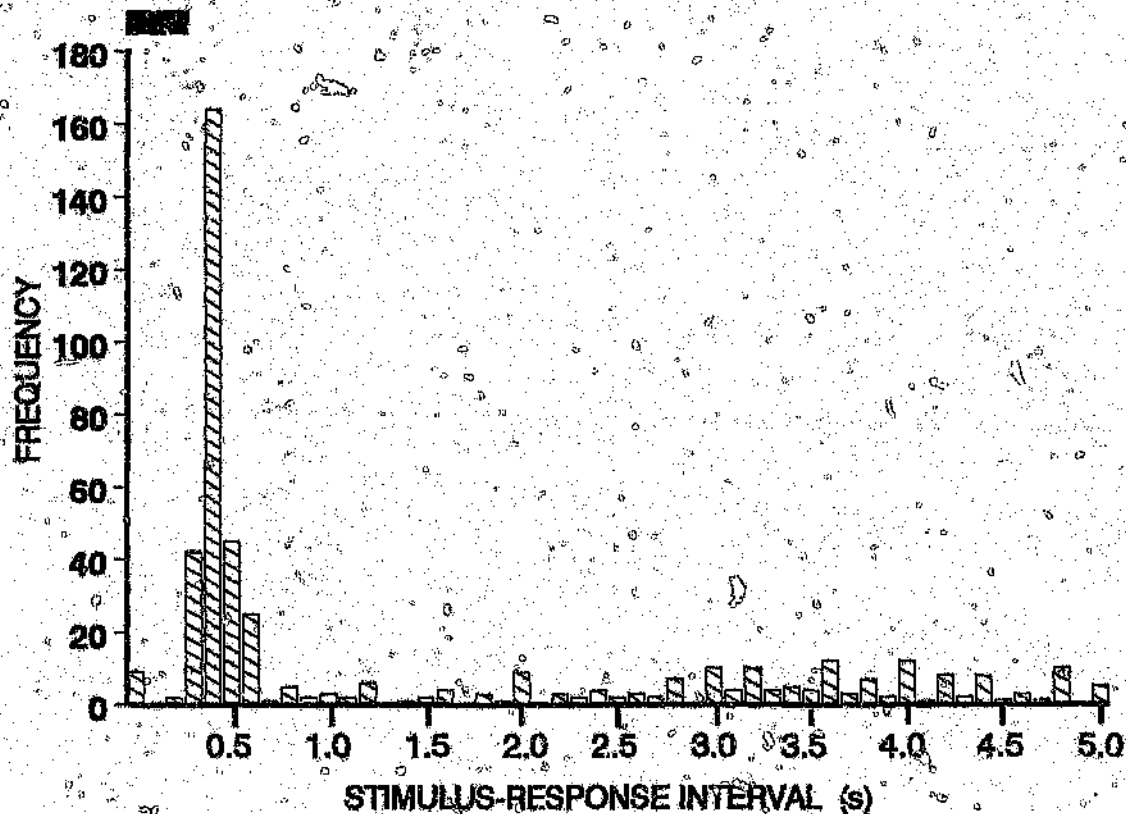


Fig. 2.25 *S. wealii* Stimulus-Response intervals ($n = 461$) during a broadcast of 12 stimuli/min (18 males). The solid black bar represents the duration and position of the stimulus.

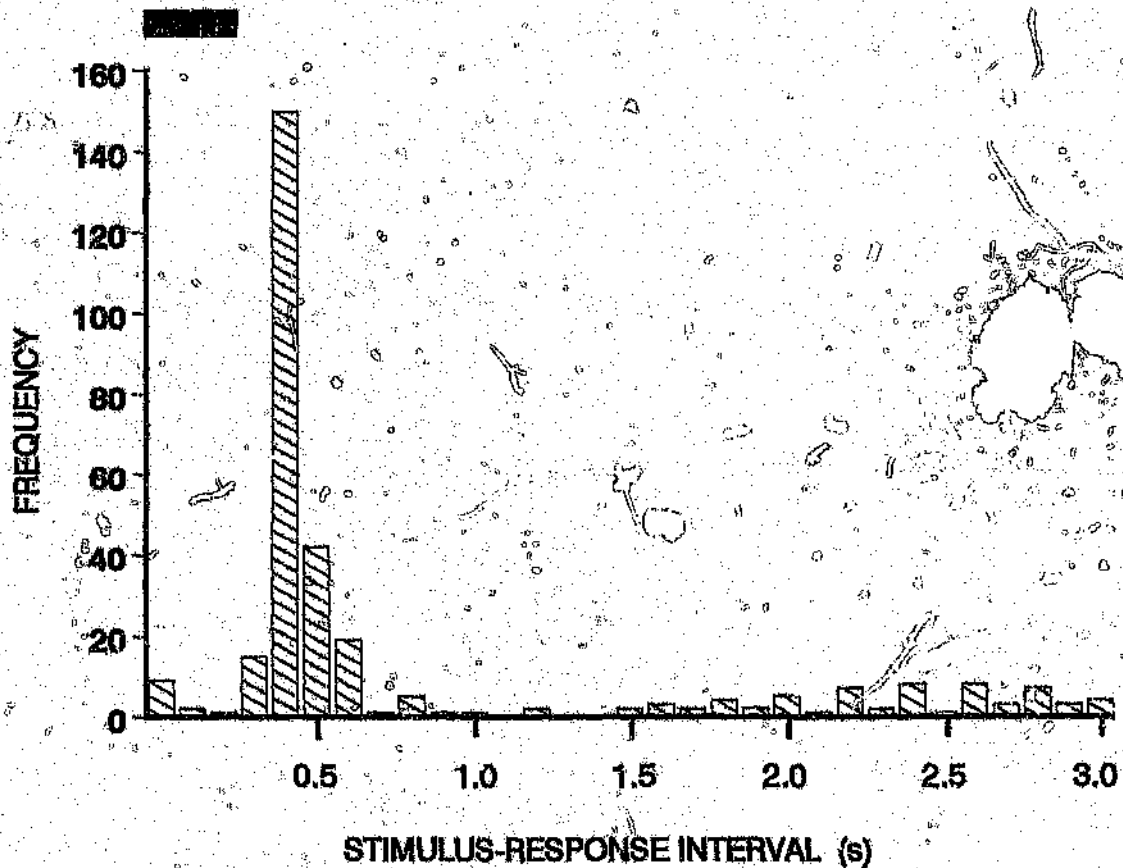


Fig. 2.26 *S. wealii* Stimulus-Response intervals ($n = 310$) during a broadcast of 20 stimuli/min (13 males). The solid black bar represents the duration and position of the stimulus.

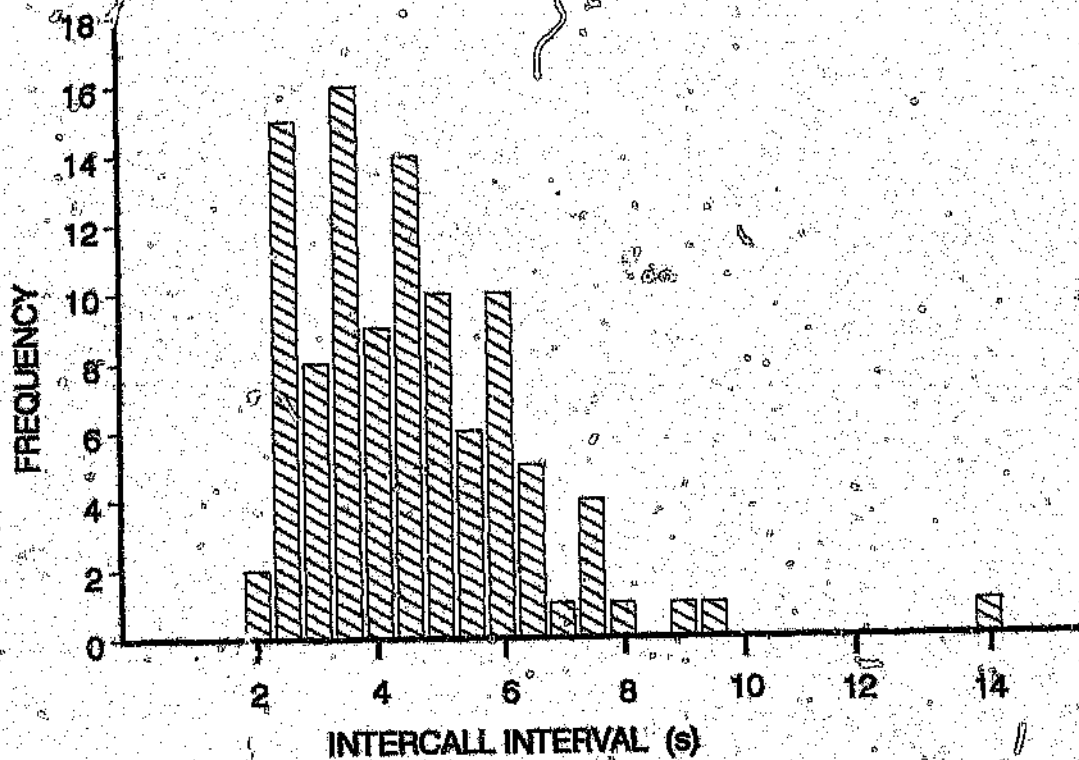


Fig. 2.27 *S. wealii* intercall intervals ($n = 104$) before the broadcast commenced (9 males).

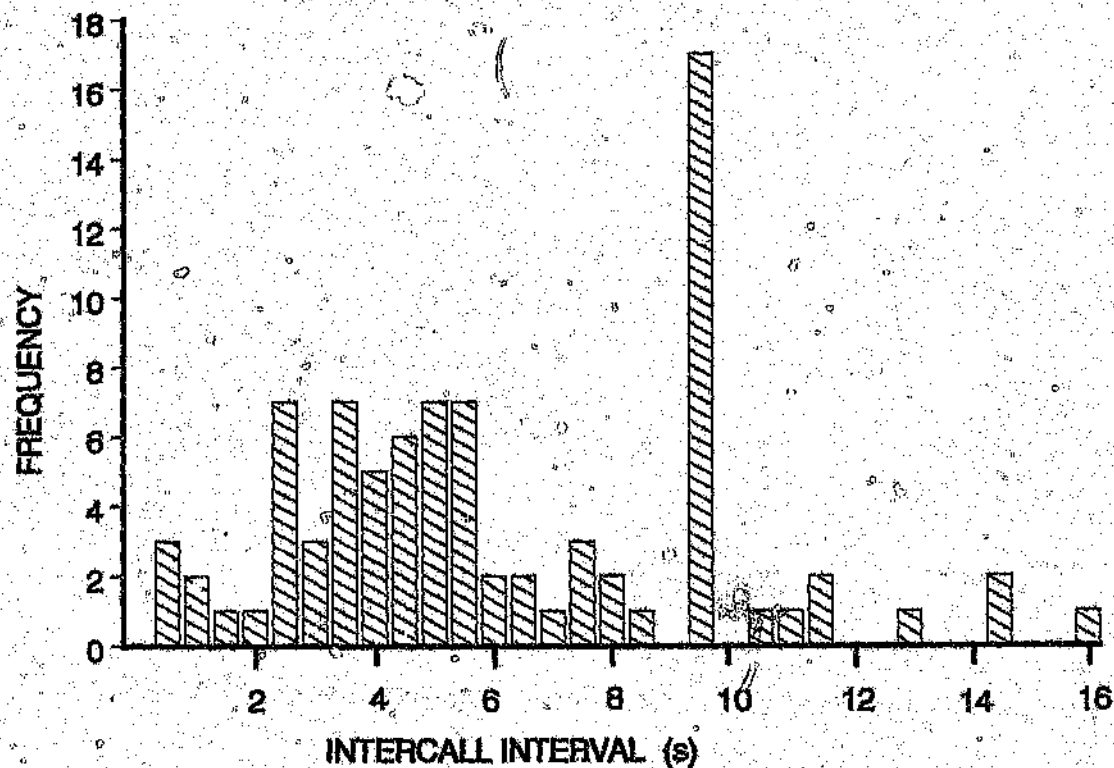


Fig. 2.28 *S. wealii* intercall intervals ($n = 85$) during a broadcast sequence of 6 stimuli/min (9 males).

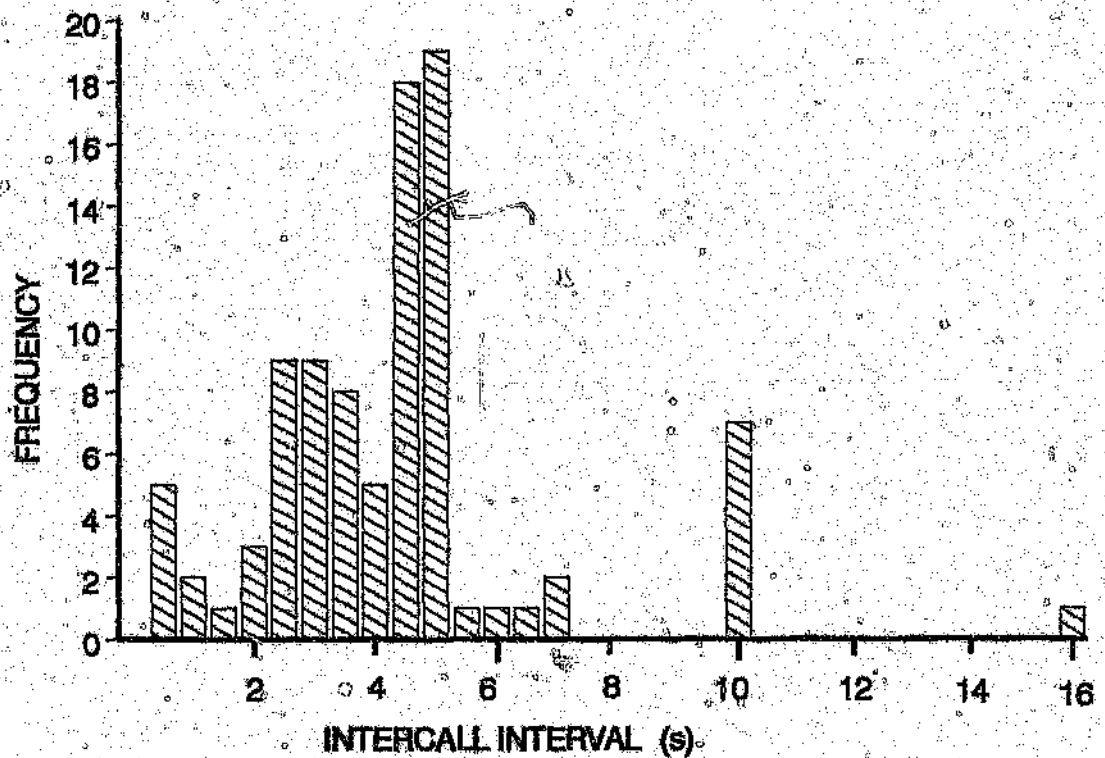


Fig. 2.29 *S. wealii* intercall intervals ($n = 92$) during a broadcast sequence of 12 stimuli/min (9 males).

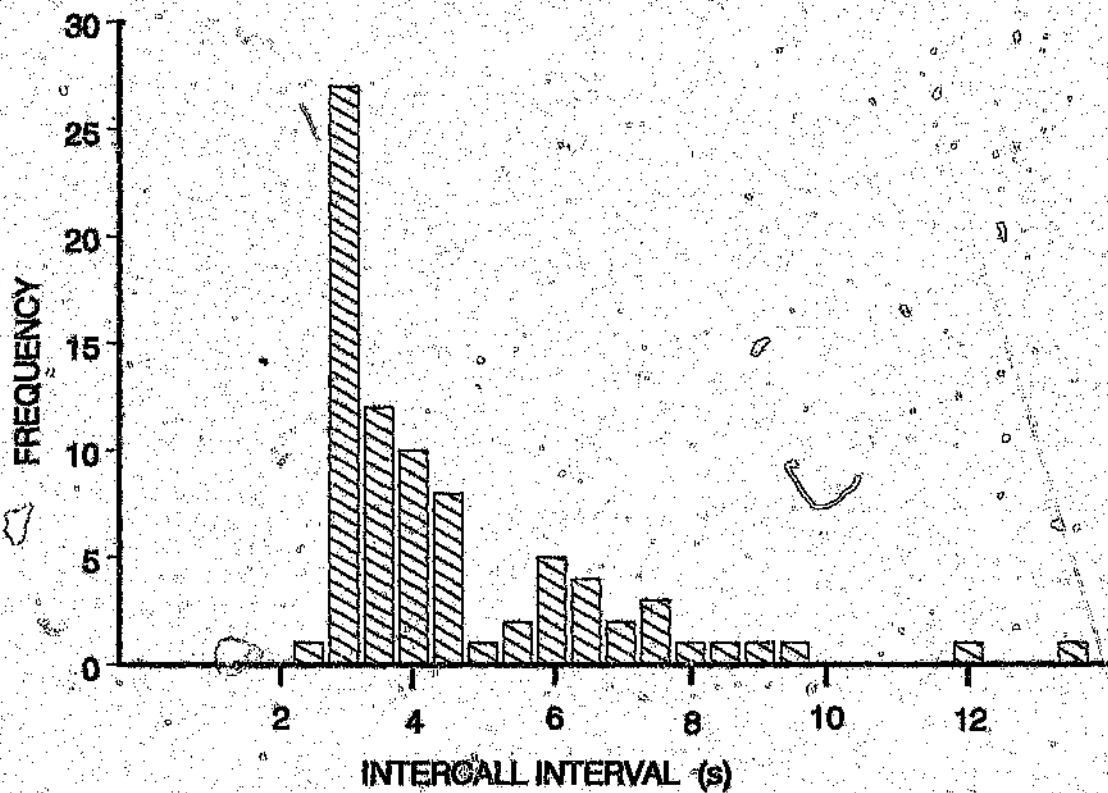


Fig. 2.30 *S. wealii* intercall intervals ($n = 81$) during a broadcast of 20 stimuli/min (9 males).

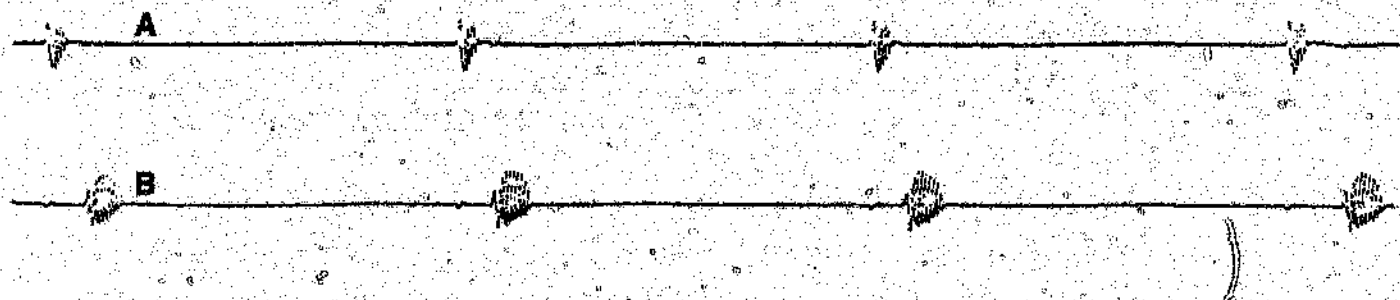


Fig. 2.31 *S. wealii* - Oscillograph tracing of responses to conspecific broadcasts.
(A- broadcast calls, B - subject's response)

2.4 Discussion

2.4.1 General

The species studied in this chapter showed four different types of responses to the broadcast stimuli. These ranged from no apparent form of organization, through simultaneous and antiphonal responses to very precise triggered responses. From the data presented here a new classification of temporal chorus organization is proposed and all other species previously studied by other authors are placed within this new framework.

2.4.2 Classification of temporal chorus organization

Category 1: Call triggered responses

During acoustic broadcast experiments two species exhibited a remarkably similar response. Both *K. senegalensis* and *S. wealii* responded to the broadcast stimuli by placing their calls almost immediately after the end of a stimulus. In natural choruses males are fairly widely distributed and, since this type of temporal organization leads to a triggering effect, the call of one individual sets off a chain reaction with other individuals and the calling appears to spread in a sequential fashion (see Figs. 2.32 and 2.33). This type of chorus organization is best described as a series of call triggered responses (see Fig. 2.34A). In the acoustic broadcast experiments a stimulus was usually followed immediately by an evoked response. This type of temporal organization, although involving an alternation of leader-follower calls, is not considered to be antiphony, as this term is generally used to describe a reciprocal alternation of calls. In antiphony, a frog (the initiator) produces a call and after an appropriate delay

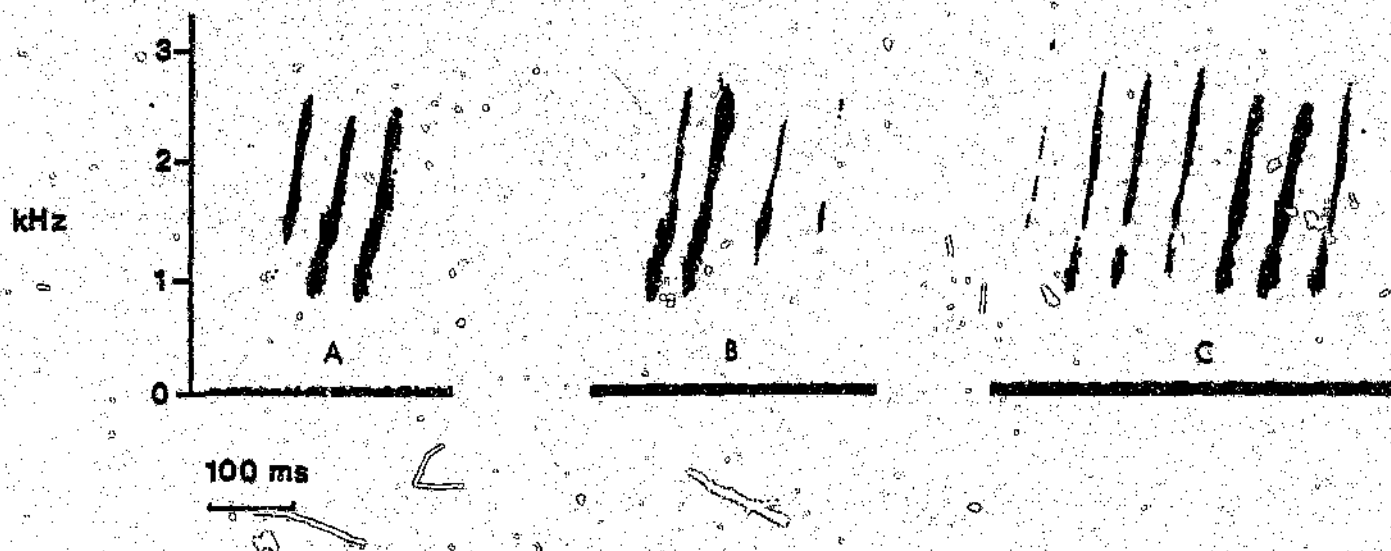


Fig. 2.32 Sonograms illustrating call frequency between 3, 4 and 7 male *K. senegalensis* (A - 3 males, B - 4 males, C - 7 males, analysis within the frequency range 40 - 4000 Hz, 300 Hz filter)

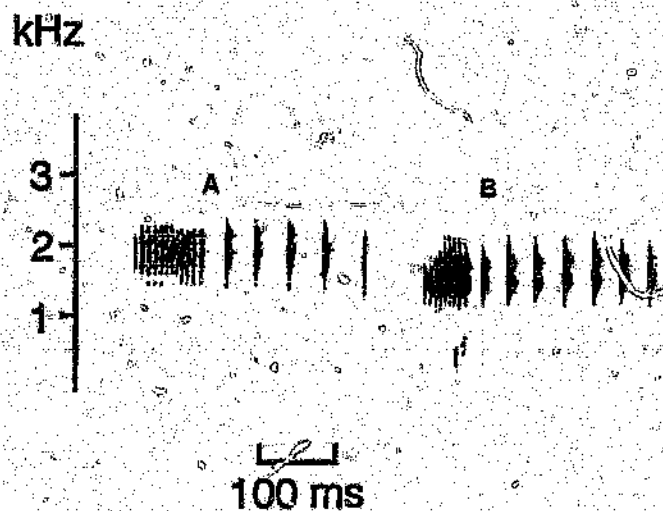


Fig. 2.33 Sonagram illustrating call triggering between two male *S. wealii* (A and B)

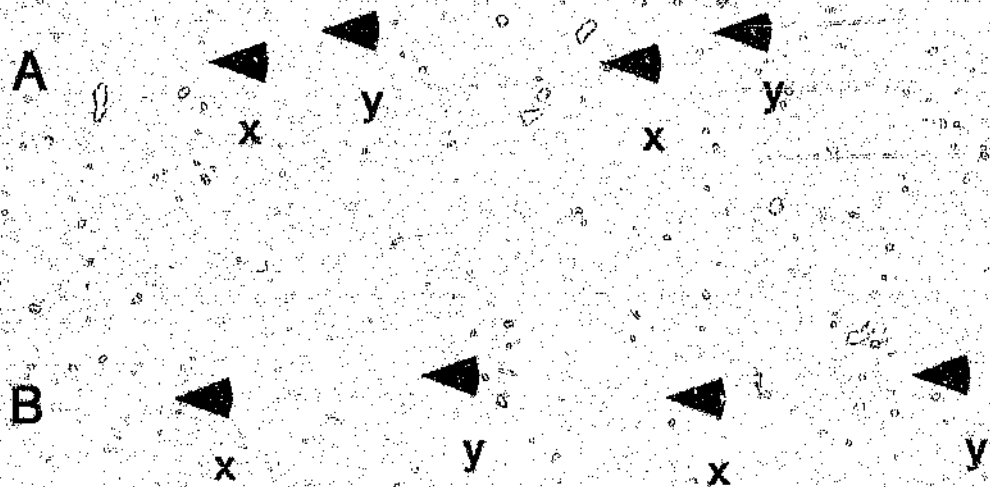


Fig. 2.34 A - Call triggered responses
B - Antiphonal responses

another frog responds. Following a similar delay the initiator will call again and there appears to be a reciprocal interaction between the two frogs, each of which waits for a similar time period to pass after the other's call, before producing its own call. With this type of interaction the time intervals between all calls in the sequence are similar. However, in call triggering, it is not necessary to have a reciprocal response. One frog calls immediately after another's call, irrespective of when the initiator produces its call (Foster, 1967; Rosen and Lemon, 1974). This type of organization results in one individual becoming a leader and the other a follower. It has not been demonstrated in this study that a leader consistently leads although, from personal observations, switching of leadership in *K. senegalensis* is a relatively common occurrence. This is very different to the arrangement found in antiphony where the calls of different individuals are separated by very similar time intervals. Consequently, with an antiphonal sequence it is impossible to decide which frog is leading or following (see Fig. 2.34B).

Category 2: Antiphonal responses

The results of the broadcast experiments with *K. maculata* show that this species responded to the broadcasts by alternating their calls with the stimuli. There was an inhibition of responses within 0.6 s from the onset of the stimulus, with most of the responses occurring halfway through the stimulus call period. This type of call alternation probably exists as true antiphony between two calling males under natural conditions.

Category 3: Synchronous responses

Although *A. fornasinii* produced most of their evoked responses within 800 ms from the onset of a stimulus, their

calls were relatively long ($\bar{x} = 2.2$ s, ± 0.3 s), and there was considerable overlap between the stimulus and evoked responses. Nearly 80% of the calls produced during the broadcasts overlapped with a stimulus. This type of organization is termed synchronous calling. This should be differentiated from the use of the term synchronous in describing the responses given by some frogs such as *E. coqui* (Narins, 1982a), *H. ebraccata*, (Narins, 1982a; Wells and Schwartz, 1984a; Schwartz and Wells, 1984a), *H. phyllodes*, (Schwartz and Wells, 1984b) and *H. microcephala* (Schwartz and Wells, 1985) which, although "synchronized" to the stimulus (i.e. a precise temporal relationship exists between the stimulus and the response), are defined as responses which occur within 1 s of the stimulus onset (Wells and Schwartz, 1984a) and occasionally exhibit a small amount of overlap.

Category 4: Unorganized responses

Of the five species studied, only one failed to exhibit any form of temporal relationship with the stimuli. Simple acoustic broadcast experiments of different repetition rates to *Hyperolius marmoratus* failed to identify any response to the broadcasts. Temporal relationships between the stimulus and the subsequent call of the frog were analysed and displayed a fairly uniform distribution of stimulus-response intervals. Lemon (1971), pointed out that, if alternation were precise, there should be a mode in the distribution of stimulus-response intervals. This was not apparent in the broadcasts to *H. marmoratus*. Furthermore, when the intercall intervals recorded before the experiment, during the broadcast and after the experiment were compared, no significant differences were found. The frogs called at their initial rates, irrespective of the acoustic broadcast. The only response to regular repetition rate broadcasts was an aggressive interaction when the SPL of the broadcast surpassed a

certain threshold (see Chapters three and four). A random repetition rate broadcast was presented to *H. marmoratus* males in a further attempt to determine whether a temporal relationship existed between the stimulus and the frog's calls. Again the animals continued to produce calls at their initial rate, apparently unaffected by the randomly placed stimuli. The lack of temporal chorus organization may be attributed to the acoustic behaviour of *H. marmoratus* as well as the nature of their spatial distribution. These frogs call at very consistent repetition rates and, if undisturbed, call continuously, with very few pauses (see Chapter six for more details). Each frog calls at its own intrinsic rate, which is independent of snout-vent length, but positively correlated with ambient temperature (see Appendix C). This rate is probably set by a central pacemaker as suggested by Loftus Hills (1974), who presumed that the central pacemaker was influenced by external cues such as temperature. In order for considerable temporal overlap to occur between the calls of neighbouring frogs, they would have to call at exactly the same rate and start at the same time. Obviously, in natural populations, this is a very unlikely occurrence. Under natural conditions, *H. marmoratus* often appear to call in an antiphonal sequence but this would be due to chance alone. As pointed out by Awbrey (1978), call alternation can occur by chance if both frogs had similar call rates because of similar body temperature. Also Lemon (1971) proposed that alternation of calls can be expected to occur by chance alone when intercall intervals are equal to or longer than the calls themselves, even if the frogs are calling at slightly different rates. If this is the case, periods of alternation followed by periods of overlap, and then a return to alternation, would be heard. In *H. marmoratus* the call is about 10% of the average intercall interval and upon examining stimulus-response intervals it can be seen that the temporal relationship regularly drifts from a bout of alternation

through overlap back to alternation.

2.4.3 The central mechanism of chorus organization

Although there appear to be three distinct categories of chorus organization exhibited by these four species (call triggering, antiphonal calling and synchronous calling), these should be regarded as three arbitrary divisions within a continuum.

The common factor underlying these three types of chorus organization is the delay between a frog hearing another call at an appropriate SPL and responding with his own call. Depending upon the delay and the length of the call, various types of chorus organization can be achieved. For example, if the delay is fairly short (e.g. 300 ms) then this can give rise to either call triggering (in the case of species with short duration calls) (see Fig. 2.35A.i), or synchronous calling (in species with fairly long duration calls) (see Fig. 2.35A.ii). If the delay is equal to the sum of the call duration and half the intercall interval, then an antiphonal sequence will exist (see Fig. 2.35B.i). A species with a long call as well as a long delay will exhibit a type of organization which was not found in the species included in this study. If the delay and the intercall interval were both equal to one call duration then a type of antiphonal call triggering would exist where the leader - follower status was lost (see Fig. 2.35B.ii). This type of chorus organization may exist in some South African species of *Bufo* and *Phrynobatrachus* (personal observations) but further studies are needed to elucidate the actual form of chorus organization exhibited by these species. Based almost entirely on observation, Duellman (1967) offered a basic categorization of temporal and spatial chorus organization. This has been widely accepted by many authors although it has not been tested experimentally. This chapter is primarily concerned with the temporal

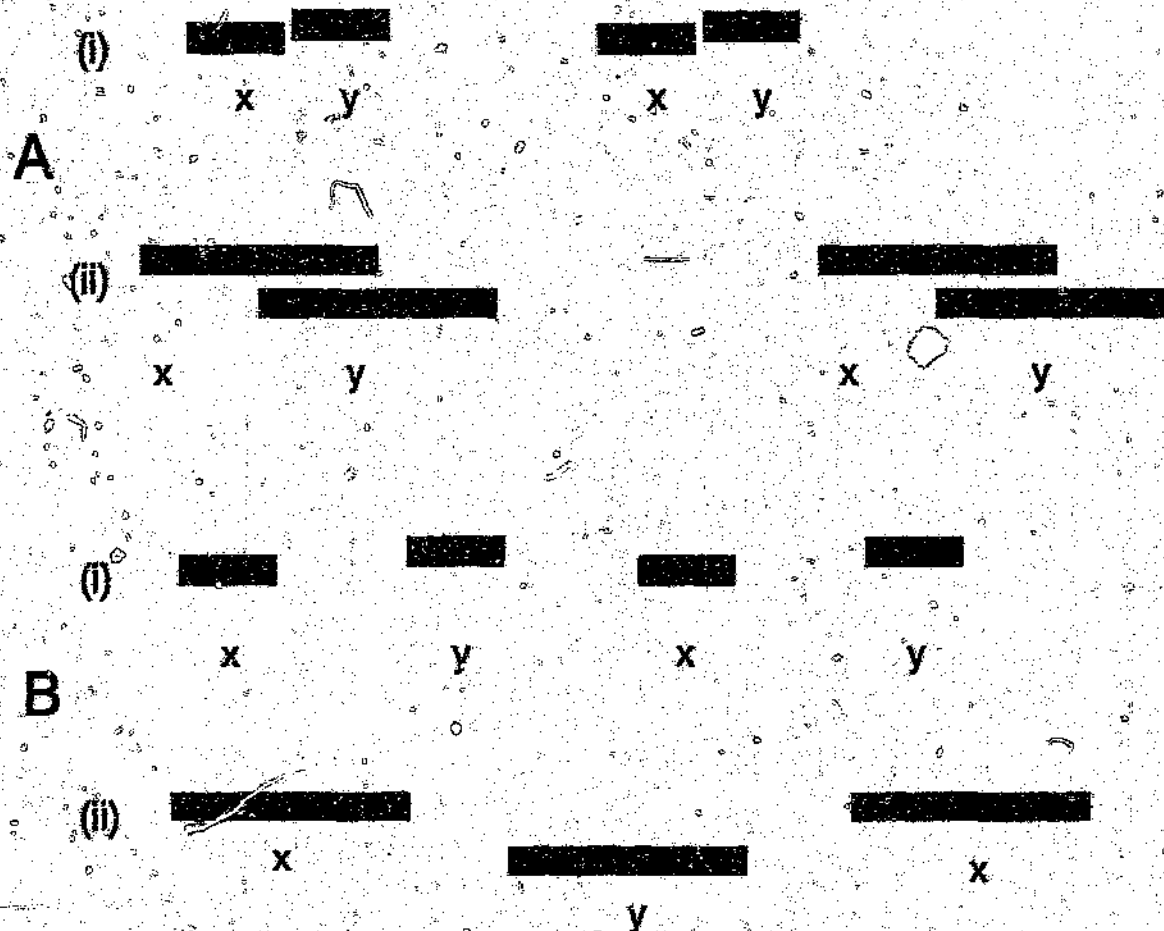


Fig. 2.35 A - Short Delay, (i) short duration call, (ii) long duration call
B - Long Delay, (i) short duration call, (ii) long duration call

organization of chorus structure and the spatial relationship between calling frogs is not addressed here. Duellman (1967) suggested that his categorization was sufficient until our knowledge of the calling behaviour of frogs had been extended. Since Duellman's study in 1967 there have been new reports on the temporal chorus organization of at least 45 species of anurans and it is now necessary to recategorize temporal chorus organization of anurans in the light of these findings. From the results presented in this chapter it is clear that firstly, choruses are either temporally organized or show no active form of temporal organization. Secondly, if choruses are temporally organized then the type of organization fits into three arbitrary categories depending upon the delay between the onset of the stimulating call and the initiation of the response.

There are published reports on the forms of chorus organization of at least 85 species of frogs, all of which fall into one of the categories proposed above (see Table 2.7).

Table 2.7

The different types of chorus organization exhibited by species previously studied by other authors.

No organization (13 species):

<i>Bufo</i> spp (various)	Duellman, 1967
<i>Colostethus trinitatis</i>	Wells, 1980
<i>Dendrobates histrionicus</i>	Silverstone, 1973
<i>Eleutherodactylus fitzingeri</i>	Duellman, 1967
<i>Gastrotheca ceratophrys</i>	Duellman, 1967
<i>Hyperolius marmoratus</i>	Bishop, this study
<i>Leptodactylus labialis</i>	Duellman, 1967

Table 2.7 (cont.)

<i>Leptodactylus melanonotus</i>	Duellman, 1967; Brattstrom and Yarnell, 1968
<i>Phyllomedusa</i> spp (various)	Duellman, 1967
<i>Pipa carvalhoi</i>	Weygoldt, 1976
<i>Rana esculenta</i>	Wahl, 1969
<i>Rana palmipes</i>	Duellman, 1967
<i>Rhinophrynus dorsalis</i>	Duellman, 1967
<u>Call triggering (29 species):</u>	
<i>Crinia georgiana</i>	Ayre et al., 1984
<i>Dendrobates pumilio</i>	Bunnell, 1973
<i>Eleutherodactylus coqui</i>	Narins and Capranica, 1978; Narins, 1982a; Zelick and Narins, 1982, 1983
<i>Eleutherodactylus diastema</i>	Duellman, 1967
<i>Eleutherodactylus artinicensis</i>	Lemon, 1971
<i>Eleutherodactylus portoricensis</i>	Zelick and Narins, 1983
<i>Engystomops pustulosus</i>	Brattstrom, 1962; Duellman, 1967; Brattstrom and Yarnell, 1968
<i>Hyla arborea</i>	Eibl-Eibesfeldt, 1952
<i>Hyla crucifer</i>	Goin, 1949; Rosen and Lemon, 1974; Fellers, 1979a; Lemon and Struger, 1980
<i>Hyla ebraccata</i>	Narins, 1982a; Wells and Schwartz, 1984a
<i>Hyla elaeochroa</i>	Duellman, 1967
<i>Hyla meridionalis</i>	Paillette, 1976
<i>Hyla microcephala</i>	Schwartz and Wells, 1985
<i>Hyla phlebodes</i>	Schwartz and Wells, 1984

Table 2.7 (cont.)

<i>Hyla regilla</i>	Snyder and Jameson, 1965; Foster, 1967; Whitney and Krebs, 1975a; Awbrey, 1978
<i>Hyla rosenbergi</i>	Duellman, 1967
<i>Hyla versicolor</i>	Wells and Taigan, 1985
<i>Kassina senegalensis</i>	Wickler and Seibt, 1974; Bishop, this study
<i>Limnodynastes dorsalis</i>	Loftus Hills, 1971
<i>Phrynobatrachus natalensis</i>	Stewart, 1967
<i>Phyllobates lugubris</i>	Duellman, 1967
<i>Phyllobates vittatus</i>	Duellman, 1967
<i>Pseudacris nigrita</i>	Martof and Thompson, 1958; Hardy, 1959
<i>Pseudacris streckeri</i>	Loftus Hills, 1974
<i>Pterohyla fodiens</i>	Bogert, 1960
<i>Rana catesbeiana</i>	Capranica, 1965
<i>Scaphiopus bombifrons</i>	Bogert, 1960
<i>Semnodactylus wealii</i>	Bishop, this study
<i>Smilisca sordida</i>	Duellman and Trueb, 1966
<u>Antiphonal calling (37 species):</u>	
<i>Alytes o. obstetricans</i>	Heinzmann, 1970
<i>Atelopus chiriquiensis</i>	Jaslow, 1979
<i>Bombina bombina</i>	Walkowiak, 1992
<i>Bombina orientalis</i>	Walkowiak, 1992
<i>Bufo regularis</i>	Wickler and Seibt, 1974
<i>Bufo woodhousei</i>	Sullivan, 1982a, 1985; Sullivan and Leek, 1986
<i>Bufo woodhousei fowleri</i>	Given, 1993
<i>Centrolenella fleischmanni</i>	Duellman, 1967
* <i>Eleutherodactylus</i>	
<i>augustii latrans</i>	Jameson, 1954

Table 2.7 (cont)

* <i>Eleutherodactylus</i>	
<i>ockendeni</i>	Duellman, 1967
<i>Epipedobates femoralis</i>	Roithmair, 1992
* <i>Gastrophryne (Microhyla)</i>	
<i>carolinensis</i>	Anderson, 1954
<i>Hyla a. arborea</i>	Schneider, 1967
* <i>Hyla a. meridionalis</i>	Schneider, 1968
<i>Hyla a. savignyi</i>	Brzoska, et al., 1982
<i>Hyperolius pictus</i>	Stewart, 1967
<i>Kassina maculata</i>	Bishop, this study
<i>Leptodactylus albilabris</i>	Moore et al., 1989
<i>Leptodactylus melanonotus</i>	Moore et al., 1989
* <i>Leptodactylus pentadactylus</i>	Duellman, 1967
<i>Philautus leucorhinus</i>	Arak, 1983b
<i>Polypedates maculatus</i>	Kanamadi et al., 1993
<i>Pseudacris t. triseriata</i>	Schmidt, 1964
<i>Ptychoadena anchietae</i>	Stewart, 1967; Passmore, 1978, 1981
<i>Ptychoadena mossambica</i>	Passmore, 1978
<i>Ptychoadena oxyrhynchus</i>	Stewart, 1967; Passmore, 1978, 1981
<i>Ptychoadena porosissima</i>	Passmore, 1978
<i>Ptychoadena taenioscelis</i>	Passmore, 1976, 1978
* <i>Rana clamitans</i>	Wells, 1978
* <i>Rana crassa</i>	Kanamadi et al., 1992
* <i>Rana limnocharis</i>	Arak, 1983b
* <i>Rana porosa brevipoda</i>	Shimoyama, 1993
* <i>Syrnophus marnocki</i>	Jameson, 1954
<i>Smilisca baudini</i>	Duellman and Trueb, 1966
<i>Smilisca phaeota</i>	Duellman and Trueb, 1966
<i>Smilisca puma</i>	Duellman and Trueb, 1966
<i>Uperoleia rugosa</i>	Robertson, 1984

Table 2.7 (cont)

Synchronous calling (8 species):

<i>Afrizalus fornasinii</i>	Bishop, this study
<i>Bufo americanus</i>	Wells, 1977a
<i>Bufo cognatus</i>	Brown and Pierce, 1967
<i>Bufo punctatus</i>	Sullivan, 1985
<i>Centrolenella granulosa</i>	Ibanez, 1993
<i>Hyperolius puncticulatus</i>	Stewart, 1967
<i>Phrynomerus annectens</i>	Channing, 1976
<i>Smilisca sila</i>	Tuttle and Ryan, 1982 (but see Duellman and Trueb, 1966)

Frogs marked with an asterisk are ones which have not been sufficiently studied to ascertain the actual call pattern in choruses, but have been stated to alternate their calls or exchange calls.

S.sila has been placed in the synchronous calling category although Duellman and Trueb (1966) claimed that "males often call in duets". The confusion surrounding this species again highlights the problems of purely observational data. Although it appears that *S. sila* call in duets, experimental investigation has shown that most of their calls actually overlap with a broadcast call (Tuttle and Ryan, 1982).

A common feature of frogs which lack temporal organization is the short call duration and a regular repetition rate e.g. *C. trinitatis* has calls which are 30 - 50 ms long with an intercall interval of 0.2 s (Wells, 1980); *R. esculenta* has a call duration of 40 - 60 ms repeated at regular intervals (Wahl, 1969); *D. histrionicus* produces

three calls per second (therefore, necessarily of a short duration) with a regular repetition rate (Silverstone, 1973); *H. marmoratus* has a call duration of 100 ms and a very regular repetition rate (this study).

It appears that, in species which produce very short duration sounds at regular intervals, there is little need for temporal organization as call overlap or interference is unlikely to occur to any great extent, even in unorganized choruses.

Frogs which exhibit the call triggering type of temporal organization have a very short delay from the beginning of the stimulus call to the initiation of their own call. With the six species that have been studied in detail, the delay between the termination of the stimulus call and the frog's response varies from 27 - 420 ms. (*L. dorsalis*, Loftus Hills, 1971; *H. crucifer*, Lemon and Struger, 1980; *H. regilla*, Ambrey, 1978; *H. crucifer*, Fellers, 1979a; *E. coqui*, *H. ebraccata*, Narins, 1982a; *C. georgiana*, Ayre et al., 1984). However, during the broadcast of fast repetition rate stimuli to *C. georgiana*, Ayre et al. (1984) found that, although the responses were still call triggered, they were also synchronous and overlapped with the stimuli. They concluded that this was probably "an artefact of the alternation process", noting that frogs would not normally encounter such fast repetition rates. Two species studied in this report produced call triggered responses. *Kassina senegalensis* produced its calls within 200 ms, and *S. wealii* within 500 ms, from the onset of the stimulus.

Even with the double and triple stimuli presented to *K. senegalensis*, most of the calls were produced within 200 ms from the onset of the first stimulus. These results suggest that in natural choruses one frog would call and others nearby would respond. Since all males responded after the same call-triggered delay, this resulted in a

considerable amount of overlap. From Fig. 2.32 it can be seen that the calls of individuals, in a natural chorus, actually spread in a sequential fashion with very little overlap. However, the broadcast of two or three stimuli at exactly the same sound intensity, simulates an unnatural situation where it appears that the calls are either produced by one super-individual or by two or three individuals exactly the same distance from the recipient. Normally the males of this species distribute themselves around the perimeter of a pond, and each individual would have a close neighbour on either side and all the other individuals would be further away. In this situation, when a frog hears a sequence of two or three calls, one call will be considerably louder than the others and it is this call that the frog responds to. There is also a slightly higher number of call triggered responses to the second and third stimuli than in the remainder of the stimulus call period (see Figs. 2.22 and 2.23). This probably indicates that the first stimulus was presented to a subject during its refractory period (Loftus Hills, 1974) and the subject was unable to call until after the second or third stimulus.

Very few detailed studies on antiphonal calling have been carried out. Most authors simply report perfect alternation or one frog calling in the periods of silence between another frog's calls. Arak (1983b), working on *B. leucorhinus*, found that the intervals between the ends of the calls of one individual and the onset of a follower's calls were fairly consistent and always over 1.5 s. This is similar to the situation found in *K. maculata* in this study where the majority of the responses occurred between 1 - 2 s after the stimulus began.

The term "synchronous" has been used to describe the kind of temporal interaction between the calls of several species of anurans (Wells, 1977a; Narins, 1982a; Wells and Schwartz, 1984a; Schwartz and Wells, 1984a; 1985). However, authors have used this term either to describe

animals which are acoustically active at the same time (Wells, 1977a) or animals which have a distinct time-locked relationship between their calls and the stimulus (i.e. their calls are synchronized to a certain stimulus although they do not occur simultaneously) (Narins, 1982a; Wells and Schwartz, 1984a; Schwartz and Wells, 1984a, b, 1985). The strict meaning of the term synchronous (i.e. occurring at the same time), has been widely applied to describe chorus activity of many insects (e.g. Walker, 1969; Otte, 1977; Greenfield and Shaw, 1983; Greenfield and Roizen, 1993). Walker (1969) reported the precise synchronous calling of the snowy tree cricket (*Oecanthus fultoni*), where during a sequence of 100 consecutive chirps between two males, all calls were synchronous with one call just following the other, with an average delay between the onset of the first and second calls being 27 ± 17 ms. He also noted that the leader changed 74 times with one individual leading 51 times and the other 49 times.

Otte (1977) proposed a classification of acoustic interactions between male Orthoptera. He divided interactions between calling males into two categories: (A) Random acoustic activity, where there was no temporal relationship between calls of individuals, and (B) non-random acoustic activity. This latter category has been further divided into unsynchronized calling, synchrony, alternation and spacing.

True synchrony, as described above, is rare among anurans (Tuttle and Ryan, 1982). Although synchronous calling has been reported in at least 8 species of anurans, in most cases the extent of synchrony was not studied and may be the result of individuals being active at the same time and/or the chorus being unorganised. However, Tuttle and Ryan (1982), discovered that when *Smilisca sila* is presented with a single call there is a tendency for males to produce synchronous rather than asynchronous responses. There may be a selective advantage in producing synchronous calls since bats (*Trachops cirrhosus*) which prey upon *S.*

silas, locate them via auditory cues, and are less likely to respond to synchronous calls than asynchronous calls. *Afraxalus fornasini* also produce synchronous calls but it is unlikely that this has any benefit with respect to predation as there are no known predators which locate them by acoustic cues alone. The significance of this type of organization is discussed in Chapter three.

2.4.4 Summary

Chorus organization exists in most species of anurans and should be viewed as a continuum embracing all categories of organization. The type of organization exhibited by a species, depends upon the duration of the call and the time delay between the onset of the stimulating call and the onset of the frog's response. The results of this chapter gave rise to various questions which are addressed in the remaining chapters of the thesis.

CHAPTER THREE

THE FUNCTION OF CHORUS ORGANIZATION

3.1 Introduction

3.1.1 General

It has been well documented that many species of animals form large breeding aggregations in which the males produce calls to attract females (e.g. Walker, 1969; Alexander, 1975; Wells 1977a, b; Otte and Loftus Hills, 1979; Cade and Otte, 1982; Greenfield, 1983; Pallett and Passmore, 1988). In choruses of anurans, males assemble at breeding sites using physiological and environmental cues. The advantages of participating in a chorus are: 1) a chorus can advertise itself more continuously, in both the short and long term (Robertson, 1984) than can an individual, and 2) a chorus can be perceived at a much greater distance than a single calling individual (Griffin and Hopkins, 1974). However, participating in a chorus has two main disadvantages: 1) Competition among males. In dense aggregations of calling males there is intense competition for both space and females. 2) Acoustic interference. The sonic environment of choruses is extremely complex and males have to communicate against very high levels of ambient noise and acoustic interference.

As anurans do not possess sharp spectral filters with which they can extract biologically relevant information from the background noise, it is necessary for them to utilize the time domain in order to communicate species-specific information (Narins and Capranica, 1980; Narins, 1982b). As discussed in Chapter two, an effective way of avoiding acoustic interference or jamming is for an individual to produce its call at a fixed time interval after a neighbour's call, thereby producing a distinct call with an increased chance of detection. By temporally organizing their calls males are able to minimize competition and acoustic interference.

The consequences of temporal call organization are: firstly, their calls may be more easily located by females i.e. their calls are more acoustically conspicuous, and secondly, their calls may be more conspicuous to other males. Males could then space themselves accordingly which may increase their spatial conspicuousness to females (Arak et al., 1990).

3.1.2 Acoustic conspicuousness

Although many authors have suggested that temporal organization of calls reduces acoustic interference and increases a male's locatability (e.g. Cody and Brown, 1969; Loftus Hills, 1974; Rosen and Lemon, 1974; Wells, 1977a, b; Awbrey, 1978; Narins, 1982a; Zelick and Narins, 1983; Schwartz and Wells 1983a, b, 1984a; Rose and Capranica, 1984), there is very little experimental evidence to support this idea. Passmore and Telford (1981) showed that female *Hyperolius marmoratus* located speakers broadcasting simultaneous calls as accurately as those broadcasting alternating calls. They demonstrated that temporal separation of calls does not increase the locatability of males in this species. Schwartz (1987) also found that, in three species of *Hyla*, temporal separation of signals did not increase the ease of localization of males by

females. In contrast, Ibáñez (1993) found that female *Centrolenella granulosa* actually prefer alternating calls to overlapping out-of-phase calls, but not to overlapping nearly in-phase calls.

3.1.3 Spatial conspicuousness (acoustically conspicuous to other males)

Lemon (1971) was perhaps first to suggest that male anurans alternate their calls in order to maintain certain spatial relationships with one another. Although Passmore and Telford (1981) suggested that call alternation may be related to male spacing it has only recently been demonstrated that male anurans avoid call overlap because it impairs their ability to assess the intensity of their neighbours calls and their ability to transmit information to potential mates (Schwartz, 1987).

In order to assess the function of the temporal separation of calls it was necessary to broadcast a conspecific call at exactly the same time as the call produced by the subject. However, this task was surrounded by technical problems. How does one predict when the frog was going to call and then initiate a broadcast so that it exactly coincided with the frog's call? Furthermore, if one is broadcasting to a frog and recording his response simultaneously, how is the problem of acoustic feedback avoided? These difficulties were overcome using a sophisticated experimental design (for details see Materials and Methods of this chapter) enabling the broadcast of the frog's own call at varying intensities, to be initiated at the instant of call production, without being obscured by acoustic feedback. Utilising this procedure, and another one involving delayed broadcasts, the answers to the following questions were sought:-

- 1) Does a frog behaviourally acknowledge a conspecific call broadcast at the exact time of its own call production?

2) If not, what delay is necessary, from the end of a male's call to the beginning of the broadcast call, to produce a behavioural response?

An investigation into the function of chorus organization was conducted by examining a) the response of males of three species to broadcasts of their own calls at the precise time of call production, and b) the response of males of one species to broadcasts of their own calls at varying delays after call production.

3.2 Methods

3.2.1 Species

The species used in these experiments were *Eleutherodactylus coqui*, *Hyperolius marmoratus*, and *Semnodactylus wealii*. For a detailed description of these species and the study sites see Chapter one and Appendix B.

3.2.2 Simultaneous broadcast experiments

A diagrammatic representation of the equipment used for simultaneous broadcasts is presented in Fig. 3.1. The experiments involving *E.coqui* were performed in Puerto Rico, necessitating the use of different equipment (the differences are presented in Table 3.1).

Once an isolated calling male had been visually located the response and relay microphones and loudspeaker (or speaker-amplifier in the case of *E.coqui*) were placed as close as possible without causing disturbance (10-100 cm). A natural calling sequence was recorded on the relay tape-recorder for 4 min, or for 1 min on a continuous tape loop for *E.coqui* and was later used as the unsynchronized broadcast sequence.

Simultaneous broadcasts were achieved by connecting the speaker-amplifier directly to the source monitor output of the relay tape-recorder. The relay tape-recorder was set to the record mode and in the pause position. In this way the signal received by the relay microphone is directly transmitted through the tape-recorder to the speaker-amplifier. A hypercardioid microphone was essential in the role of the relay microphone in order to avoid acoustic feedback. The directional nature of these microphones prevented the signal from the loudspeaker being received when the loudspeaker or speaker-amplifier was placed

directly behind the microphone (see Fig. 3.1). The time delay from the production of the signal to its subsequent arrival at the subject was 2 - 3 ms (Fig. 3.2) and was dependent upon the distance of the loudspeaker from the subject.

The SPL of the broadcast was increased in a step-wise fashion and, when there was no change in behaviour of the subject, the SPL was increased to the maximum permitted by the physical constraints of the equipment. All peak SPL measurements were made using a Brüel and Kjaer (B & K) 2209 sound level meter in conjunction with a B & K 4165 microphone, a microphone dehumidifier (B & K UA0308) and a foam windshield (B & K UA0237). The calls produced by the frog during this broadcast sequence were recorded on the response tape-recorder.

The broadcast was then stopped and the frog was allowed "settling" time (approximately 5 minutes) to resume its previous natural calling pattern. The unsynchronized broadcast sequence as described above was then presented to the frog via the relay tape-recorder and speaker-amplifier. The frog's calls during this broadcast were recorded via the response microphone and tape-recorder. The SPL of the broadcast sequence was again increased in a step-wise fashion until aggressive calls were evoked or a change in calling pattern observed.

Whenever there was a change in calling pattern the SPL of the broadcast was noted and this was later combined with the analysis of the response tapes on a Uniscan II spectrum analyser (Multigon Industries, Inc., New York).

3.2.3 Delayed broadcast experiments

The equipment was identical to that used in the previous experiments with *H. marmoratus* and *S. wealii* except that a Roland SDE 2000 digital delay line was placed between the relay tape-recorder and the Portamon speaker-amplifier (see Fig. 3.3). The broadcast signal was delayed by 70 - 210 ms

in 10 ms increments. After the equipment had been placed in position and the digital delay set, the signal intensity was gradually increased until either the maximum intensity permitted by the equipment was reached or the subject produced aggressive calls. The signal broadcast to the subject was its own previously produced call. The subjects' own calls were recorded with the response microphone and tape-recorder for later analysis of call duration on a Uniscan II spectrum analyser (Multigon Industries, Inc., New York). The species used in this experiment was *H. marmoratus*.

TABLE 3.1

Differences in equipment used for simultaneous broadcast experiments

Equipment	Species	
	<i>E. coqui</i>	<i>S. wealii/H. marmoratus</i>
Response microphone	Channel Master*	AKG-D900
Relay microphone	AKG-CES	Beyer Dynamic M66
Response tape-recorder	Channel Master	Uher Report Monitor 4200
Relay tape-recorder	Sony TC-D5M	Nagra III
Speaker-amplifier	Calrad 20-257	Portamon
Loudspeaker	-	Peerless G50-MRC

* The microphone used here was the built in condenser microphone of the Channel Master tape-recorder.

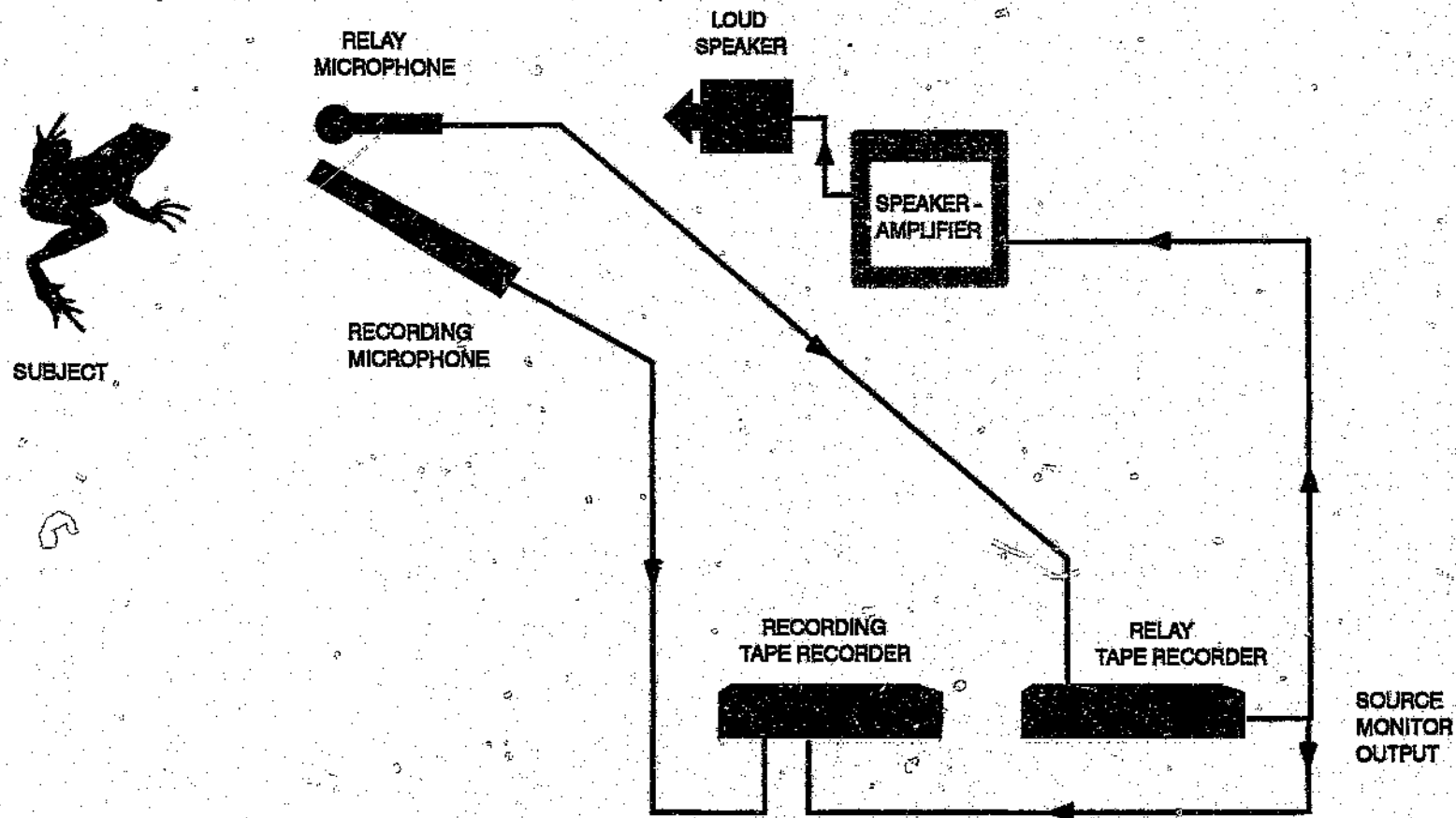


Fig. 3.1 Diagrammatic representation of the equipment used in the simultaneous broadcast experiment

SOURCE SIGNAL

DELAYED SIGNAL




5 ms

Fig. 3.2 Oscillogram to show the delay imposed upon the signal by the equipment during the simultaneous and delayed broadcast experiments

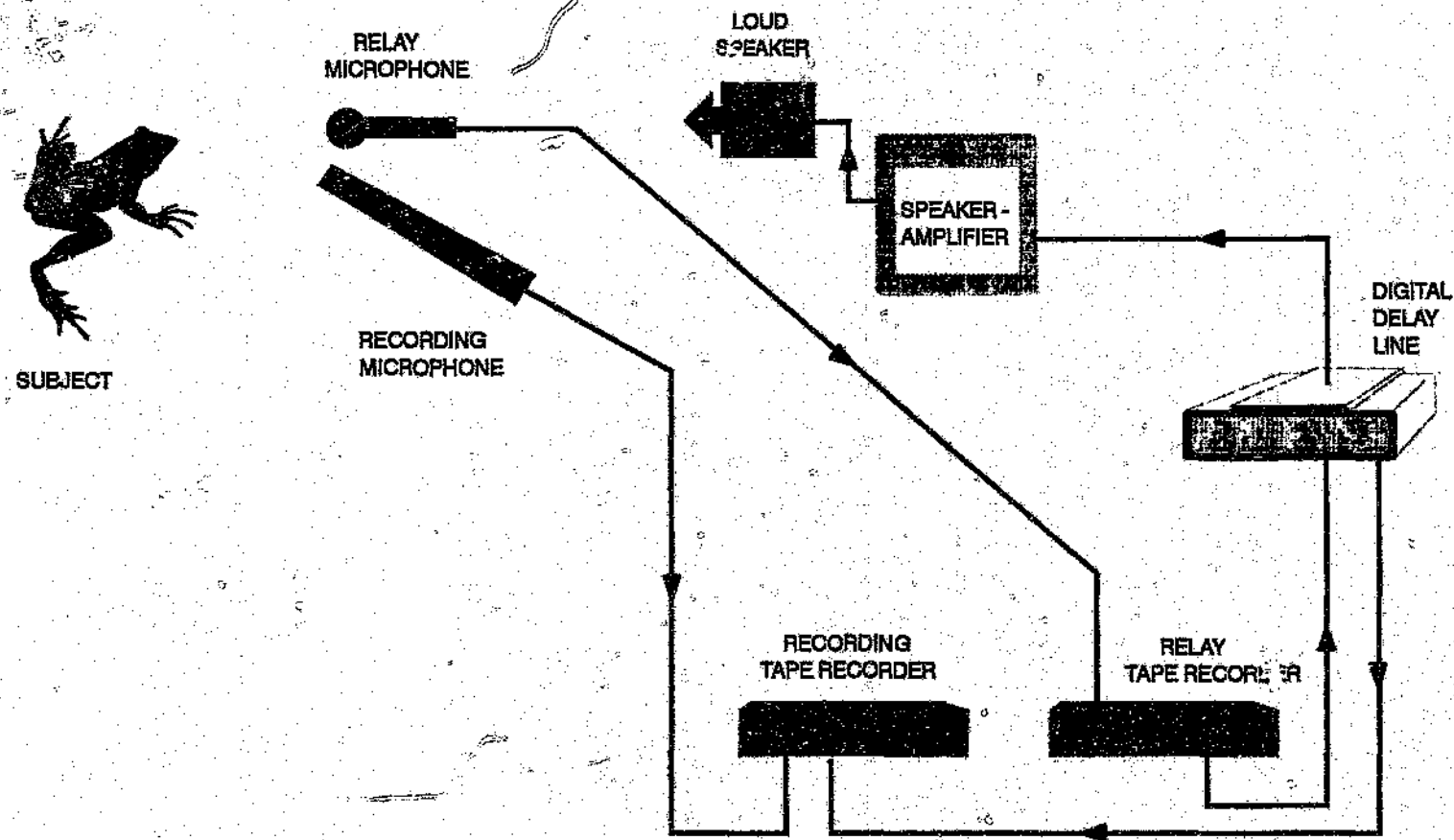


Fig. 3.3 Diagrammatic representation of the equipment used in the delayed broadcast experiment

3.3 Results

3.3.1 Simultaneous broadcasts

a). *Eleutherodactylus coqui*: When presented with a simultaneous broadcast (often at very high SPL) only one out of 44 frogs responded with an aggressive call. The other 43 frogs produced normal advertisement calls as they had done before the broadcast. Before the simultaneous broadcast *E. coqui* males ($n = 12$) only produced "coqui" and "co" notes and the mean call ratio, per 120 s, was 39 "coqui" notes to 3 "co" notes (Table 3.2). During the simultaneous broadcast the mean call ratio was unchanged (38 "coqui" to 3 "co" notes) (Wilcoxon test, $z = 0.46$, $P = 0.32$). When these frogs were presented with their own calls in a unsynchronized sequence there was a dramatic increase in the number of "co" notes and a decrease in the number of "coqui" notes produced. The change in "coqui" to "co" ratios during the unsynchronized broadcast was significantly different to the ratios before the broadcast and during the simultaneous broadcast (Friedman ANOVA, $F = 18.17$, $P < 0.001$, $df = 2$, post-hoc comparisons: before vs simultaneous $P > 0.05$; before vs unsynchronized, $P < 0.05$; unsynchronized vs simultaneous, $P < 0.05$). Furthermore, four of the 12 individuals produced "coqui +" notes, which were thought to represent highly aggressive calls (see Appendix A). The mean call ratio was 5 "coqui" notes to 16 "co" notes to one "coqui +" note (Table 3.2). When presented with the unsynchronized broadcast sequence, one individual stopped calling completely and six individuals moved towards the loudspeaker. However, when presented with the simultaneous broadcast all subjects remained where they were and continued calling with normal advertisement calls.

TABLE 3.2

E. coqui - results of simultaneous broadcast experiments

(Coqui:Co:Coqui+) Ratios

Subject no.	Before broadcast	During simultaneous broadcast	During unsynchronized broadcast
1	40:3:0	46:4:0	0:15:0
2	49:4:0	48:0:0	18:23:0
3	37:9:0	41:6:0	15:21:1
4	35:1:0	34:3:0	0:12:2
5	34:3:0	33:4:0	13:19:0
6	44:2:0	40:1:0	3:23:3
7	40:0:0	43:2:0	0:15:0
8	25:3:0	24:5:0	0:12:0
9	27:3:0	30:2:0	4:18:0
10	34:7:0	33:3:0	0:11:3
11	49:4:0	37:4:0	9:22:0
12	49:0:0	48:2:0	0:0:0
n = 12			
	$\bar{x} = 39:3:0$	$\bar{x} = 38:3:0$	$\bar{x} = 5:13:1$

(Ratios are for a two minute period. SPL of broadcasts were initially set at 95 dB at 50 cm from speaker-amplifier and increased up to a max. of 116 dB at 50 cm)

b) *Hyperolius marmoratus*: The mean SPL of the unsynchronized broadcast which evoked aggressive calls in 21 males was 109 dB at the subjects' call sites. When these frogs were presented with simultaneous broadcasts at the same or higher SPL (sometimes more than twice as loud, see subject no. 8, 12, 13, 15, 18, 19, and 21 in Table 3.3) they continued to produce normal advertisement calls (Table 3.3).

The mean SPL of the unsynchronized broadcast which evoked aggressive calls was significantly lower (Sign test, $n = 11$, $P < 0.001$) than the mean SPL of the simultaneous broadcast.

c) *Semnodactylus wealii*: Ten out of 11 males produced normal advertisement calls in response to the simultaneous broadcast at a mean SPL of 108 dB at the subject's call site (see Table 3.4). The one subject which produced an aggressive call during the simultaneous broadcast did so at the beginning of the broadcast sequence and then resumed with normal advertisement calls. It cannot be completely ruled out that this may have been a response to the broadcast, but considering the responses of all the other subjects it is more likely that this response was due to an extraneous factor. The mean SPL of the unsynchronized broadcast which evoked aggressive calls was significantly lower (Sign test, $n = 10$, $P = 0.001$) than the mean SPL of the simultaneous broadcast.

TABLE 3.3*H. marmoratus* - results of simultaneous broadcast experiment

Subject no.	SPL of unsynchronized broadcast which evoked aggressive calls (dB)	Max. SPL of simultaneous broadcast and type of call produced (dB)
1	108	113 adv
2	120	120 adv
4	116	116 adv
5	120	120 adv
7	120	120 adv
8	103	113 adv
10	120	120 adv
11	113	113 adv
12	103	113 adv
13	100	113 adv
14	120	120 adv
15	100	113 adv
16	120	100 adv
17	120	120 adv
18	100	108 adv
19	100	113 adv
20	100	105 adv
21	100	113 adv
22	105	108 adv
23	100	103 adv
24	100	100 adv
n = 21	$\bar{x} = 109$	$\bar{x} = 114$

(adv = normal advertisement calls, all SPL are those measured at the subjects' call site)

TABLE 3.4**S. wealii - results of simultaneous broadcast experiment**

Subject No.	SPL of unsynchronized broadcast which evoked aggressive calls (dB)	Max. SPL of simultaneous broadcast and type of call produced (dB)
2	108	110 adv
3	103	107 adv
4	101	107 adv
24	101	106 adv
25	100	106 adv/agg
26	104	107 adv
30	104	104 adv
31	104	109 adv
32	100	107 adv
34	103	115 adv
35	103	112 adv

 $n = 11$ $\bar{x} = 103$ $\bar{x} = 108$

(adv = normal advertisement call, agg = aggressive call, all SPL are those measured at the subjects' call site)

3.3.2 Delayed broadcasts

Delayed broadcasts were presented to 22 calling *H. marmoratus* males. The absolute delay (i.e. the time delay between the beginning of the subject's call and the beginning of the stimulus, see Fig. 3.4) was varied from 70 - 210 ms. The period of silence between the end of the subject's call and the beginning of the stimulus was calculated by deducting the subject's mean call duration from the absolute delay and adding the delay imposed upon the signal as it passes through the equipment (3 ms). The resultant time period is referred to as the inter-signal interval (ISI, see Fig. 3.4). When the subject changed from producing normal advertisement calls to aggressive calls, the absolute delay was noted. The mean call duration was determined and deducted from the absolute delay to yield the ISI. Results are summarized in Table 3.5. The mean call duration was 93 ms (± 22.7 ms, range 51-157 ms, $n = 22$). Three subjects had fairly long calls and the first absolute delay that they were presented with was shorter than their call duration (i.e. a negative ISI). Consequently the broadcast began whilst the subject was still calling and none of these subjects produced aggressive calls to this short delay.

When the ISI was low (0-15 ms) six out of twelve individuals produced aggressive calls and the minimum ISI which evoked aggressive calling was 5 ms. Generally, as the ISI increases more and more subjects produced aggressive calls. All the subjects responded with aggressive calls when the ISI was greater than 50 ms. The mean ISI which produced aggressive calls was 32 ms. There was a significant correlation between the ISI and the proportion of individuals to respond with aggressive calls (Kendal's correlation coefficient, $T = 0.73$, $P = 0.04$).

TABLE 3.5

Results of delayed broadcast to *H. marmoratus*

Inter-Signal Interval (ms)	No. of subjects	No. of subjects which responded with aggressive calls
-50 - 0	3	0
0 - 15	12	6
16 - 30	7	4
31 - 45	9	4
46 - 60	6	5
61 - 75	3	3

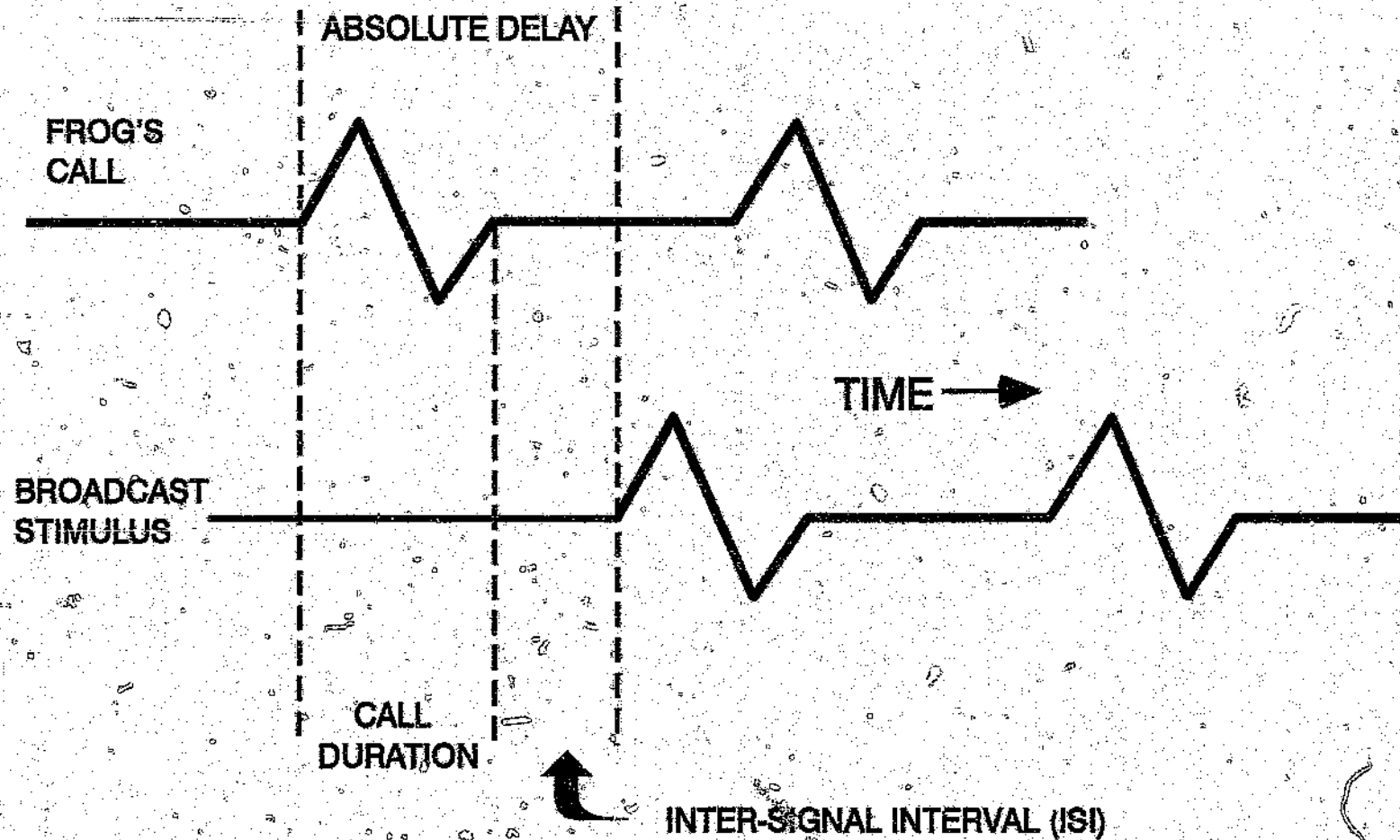


Fig. 3.4 Diagram to show the relationship between absolute delay, call duration, and inter-signal interval

3.4 Discussion

3.4.1 General

Temporal and spatial chorus organization in anurans has been fairly well documented (e.g. Duellman, 1967; Salthe and Mecham, 1974; Wells, 1977a; Awbrey, 1978; Narins, 1982a, b; Schwartz and Wells, 1984a, b; Wells and Schwartz, 1984a). In Chapter two it was demonstrated that males of several species actively organize their calls in such a way as to avoid acoustic overlap with one another. In this chapter the data show that male frogs do not respond behaviourally to a call which is produced at the same time as their own call. This has important repercussions with regard to the function and evolution of temporal organization, and raises questions regarding the damping mechanisms involved during call production.

3.4.2 Function and evolution of temporal organization

Passmore and Telford (1981), Schwartz (1987), Dyson and Passmore (1988a, b) and Ibáñez (1993,* see footnote) provide the only experimental proof that in phonotaxis experiments simultaneous stimuli are as easy to locate as alternating stimuli. Dyson and Passmore (1988a, b) have shown that female *H. marmoratus* prefer the leader of two calls placed very close together, irrespective of frequency and intensity differences, within the normal range. This is probably due to the relative effectiveness of the calls on the female's auditory system rather than a

*Ibáñez (1993) found that although females did not show a preference for alternating calls over overlapping nearly in-phase calls, they did show a preference for alternating calls over overlapping out-of-phase calls.

deliberate active choice by the female. The first call a female receives causes a neurophysiological response which probably masks any response elicited from another call received in quick succession.

The fact that females can just as easily locate speakers broadcasting simultaneous calls and alternating calls, together with the evidence that many anurans temporally organize their calls (see Chapter two for references), suggests that call alternation *per se* has not evolved as a result of selection pressure imposed by the constraints of the females' auditory system. However the fact remains that, in the species studied here, no males were able to behaviourally respond to a call presented at the exact time of call production, even in species which do not exhibit temporal call organization (*H. marmoratus* see Chapter two for details). Telford (1985) has shown that, in phonotaxis experiments, female *H. marmoratus* prefer calls that are spatially separated to those that are close together. Temporal call organization has probably evolved from selection pressures exerted by female preference for sound sources that are spatially separated. If males actively share time and avoid masking each other's calls, then they can assess the position of nearby neighbours and space themselves accordingly. It may also enable them to detect another male impinging upon their active space and interfering with their access to potential mates. Consequently, temporal call organization may be viewed as a mechanism used by male anurans to effect spatial organization which may, in turn, increase their reproductive success (see Arak et al., 1990).

The data in this chapter confirm the suggestion made by Passmore and Telford (1981) that the widespread occurrence of call alternation is related to the equally widespread phenomenon of non-random male spacing rather than the ability of females to locate males. Why then, do some species fail to exhibit any form of call organization? It

has been suggested that the rhythmic calling pattern of frogs is governed by some kind of internal oscillator (see Loftus Hills, 1974; Lemon and Struger, 1980; Zelik and Narins, 1985a). As pointed out by Klump and Gerhardt (1992) if the internal oscillators of two individuals are very similar in their frequency and constant in their relative phase then it would not be necessary to engage in direct interaction to produce constant intercall intervals in order to avoid overlap. *Hyperolius marmoratus* has a very regular call repetition rate, a relatively short call (approximately 100 ms) and a fairly long intercall interval (1000 ms). As a result, even if individuals do not interact, there would still be very few calls that overlap. In order to effectively space themselves from one another, males of this species must produce non-overlapping calls. Since this is achieved by chance alone (see Chapter two), it is not necessary for males to actively avoid call overlap.

3.4.3 Damping mechanisms during call production

In mammals it has been demonstrated that, during the self-production of sounds, there is an attenuation which takes place via two separate pathways (Henson, 1965; Borg and Zakrisson, 1975). Firstly, there is an acoustic reflex in response to high-level sounds which causes contraction of the muscles of the middle ear thus attenuating the sound reaching the inner ear. Secondly, there is a central activation of the middle ear muscles which contract immediately prior to vocalization (Henson 1965).

Wever (1979, 1985) suggested that, in amphibians, there is a "lock mechanism" that protects the ear against excessive sounds, particularly the frog's own call. In response to loud sounds the columella and opercular muscles work as an antagonistic pair, locking the pars interna and operculum together, thus restricting the movement of the

columella. He also suggested that this method of protection against excessive sounds is far more effective than that achieved by the contraction of the malleus and stapedius muscles of mammals. However, both the existence and the function of the columella muscle in most anurans is a contentious issue. Jaslow et al. (1988) have suggested that there may be a passive damping system in the anuran middle ear. They proposed that, during vocalization, the increased pressure in the buccal cavity exerts a concomitant increase in pressure on the middle ear via the open Eustachian tubes. Narins (1992) has discussed another possible method in which the inner ear may be protected from large displacements of the columella (caused by loud sounds). He pointed out that, as frog's ears act as pressure-gradient receivers (Rheinlaender et al., 1979; Pinder and Palmer, 1983; Palmer and Pinder, 1984) sounds produced by their own calls would arrive simultaneously and in phase on both sides of the tympanum. This alone would result in reduced tympanic movement. Using laser vibrometry Narins (1992) measured the tympanic membrane velocities of calling *E. coqui* males. He concluded that there was a strong mechanism operating in the frog ear that dampens the movement of the tympanic membrane during vocalization. He suggested that the increase in buccal cavity pressure during vocalization exerted a pressure on the tympanic membranes via the Eustachian tubes. The data presented in this chapter suggests that frogs have a damping system which reduces the damage to the inner ear and has the effect of rendering the frog unable to perceive sounds at the time of call production and shortly thereafter. In contrast, Lemon and Struger (1980) thought that, in some cases, *H. crucifer* appeared to be sensitive to random playback calls even while they were calling. As male *H. marmoratus* only responded to calls broadcast with an approximate delay of 132 ms from the beginning of their call (mean delay from end of call [32 ms] plus call duration [100 ms]), this delay represents the time taken

for the auditory system to return to normal and is analogous with the absolute behavioural refractory period (BRP) (Narins, 1982a). This is a very small absolute BRP, when compared to *E. coqui* and *H. ebraccata*, 1,133 ms and 210 ms respectively, (Narins, 1982a); *P. streckeri*, 107 ms, (Loftus Hills, 1974); *H. crucifer*, 329 - 950 ms, (Lemon and Struger, 1980). The result confirms Narins' (1982a) suggestion that a short absolute BRP is associated with a small mean distance between calling males (as found in *H. marmoratus*). The absolute BRP is usually considered to be the time period after a call in which a stimulus will not evoke a response. However, with the varying time delays utilized in the experiments presented here, it has been shown that the call duration should also be part of the absolute BRP. As the absolute BRP begins at the moment of call production, it is possible that this period represents the time that the damping system is in operation. It is only when the effect of the damping system has worn off that the frog can respond to another stimulus and the absolute BRP ends. The absolute BRP may in fact be the period of time required for the operation of the damping system.

CHAPTER FOUR

THE SIGNIFICANCE OF CALL INTENSITY

4.1 Introduction

4.1.1 General

Anurans produce surprisingly intense vocalizations and several authors have suggested that these play an important role in inter-male spacing (Brenowitz et al., 1984; Wilczynski and Brenowitz, 1988; Rose and Brenowitz, 1991). Loftus Hills and Littlejohn (1971) were probably the first to measure SPL of anuran calls. Due to the very slow response of sound pressure level meters available at that time, they utilized field recordings and an oscilloscope to calculate the intensities of anuran vocalizations. They discovered that larger species of Australian frogs produce louder vocalizations and the maximum reading obtained was from *Limnodynastes tasmaniensis* with a peak SPL of 103.1 dB at 50 cm. Other authors have also recorded very high levels from anurans (e.g. *Rana virgatipes* 113 dB peak at 50 cm, Gerhardt, 1975; *Tomopterna krugerensis* 120 dB peak at 50 cm, Passmore, 1981; *Hyla versicolor* 109.3 dB peak at 50 cm, Wells and Taigen, 1986) but have failed to find a relationship between species' body size and call intensity. However, many authors have shown that, within a species, larger individuals do produce slightly more intense signals (e.g. Gerhardt, 1975; Wilbur et al., 1978; Berven, 1981).

Although the energetic cost of producing very intense signals will be high, signal intensity plays a pivotal role in spatial distribution, and the maintenance of territory and active space. These factors associated with call intensity are outlined in the following sections.

4.1.2 Costs associated with the production of intense signals

The energetic cost of producing very high call intensities are likely to be considerable. MacNally (1984) suggests that there are two major costs to be considered when advertising by sound. Firstly, there are the metabolic and energetic costs of calling and secondly there is the increased risk of predation by predators who are locating their prey items by sound. Although Ryan et al. (1981) suggested that increase in predation risk was a major cost to *Physalaemus pustulosus*, it appears that with most species the major cost involved in communicating by sound is an energetic and metabolic one (MacNally, 1984; Taigen and Wells, 1985; Prestwich et al., 1989). This major cost can be seen to be acting upon breeding males as they often experience considerable weight loss during the breeding season (Wells, 1978a; MacNally, 1981; Arak 1983a; Robertson, 1986a), as well as reduction in body lipids and the mass of energy storing organs (Jenssen, 1972; MacNally, 1981).

Several authors have shown that the resting metabolic rate of frogs undergoes a five-fold elevation during periods of vocalization (Bucher et al., 1982; MacNally, 1984) and Taigen and Wells (1985) indicate that in *Hyla versicolor*, a frog with a particularly high intensity call (Gerhardt, 1975), acoustic advertisement is one of the most energetically expensive activities regularly undertaken by any anuran. Hence, most anurans produce particularly intense sounds for their size at an appreciable energetic cost.

4.1.3 Spatial distribution and signal intensity

Brown (1975) pointed out that the basis of all social behaviour of a species is dependent upon the spatial distribution of the individuals in their preferred habitat. Random distributions of animals in nature are rare, usually they are evenly distributed or clumped together in small groups.

Duellman (1967) reported that most pond breeding frogs formed aggregations of calling individuals, and many authors have shown that the spatial distribution of calling males within these aggregations is seldom random (Whitney and Krebs, 1975b; Wells, 1977a; Passmore, 1978; Brzoska, 1982 and others). At first this was thought to be the result of the heterogeneity of the vegetation causing small clusters of vocalizing animals around suitable call sites. However, upon closer inspection, the spatial distribution of calling frogs was found to be independent of vegetation with a relatively organized arrangement (Whitney and Krebs, 1975b; Wells, 1977a; Passmore, 1978; Brzoska, 1982 and others).

It has been well documented that most calling frogs maintain a fairly rigid inter-male spacing in breeding choruses and the role of vocalizations in maintaining these spatial patterns has been the subject of several studies (e.g. Allan, 1973; Rosen and Lemon, 1974; Fellers, 1975, 1979a; Whitney and Krebs, 1975b; Brzoska et al., 1982; Telford, 1982; Robertson, 1986a). It has also been suggested that the distance between calling frogs is related to the SPL of each individual's call (Fellers, 1979a; Brzoska et al., 1982; Wilczynski et al., 1982; Robertson, 1986a).

4.1.4 Territoriality

Although the conventional definition of territory as a "defended area" (Noble, 1939) was widely used, it was very simplistic as the meaning of the term "defended" was not specified. Hinde (1956) redefined territory as a topographically localized, defended area and this excluded regions defined by reference to a moving point. Brown and Orians (1970) suggested that there are three essential characteristics of a territory and if one of these was not satisfied then the area could not be classified as a territory. The characteristics are:

- (1) a fixed area, which may change slightly over a period of time,
- (2) acts of territorial defence by the possessor which evoke escape and avoidance in rivals, and
- (3) the area becomes an exclusive area with respect to rivals.

Territoriality has been reported in many species of frogs (Kartof, 1953; Sexton, 1960; Emlen, 1968, 1976; Wiewandt, 1969; Lemon, 1971; Allan, 1973; Bunnell, 1973; McDiarmid and Adler, 1974; Whitney and Krebs, 1975b; Wells, 1977a; Howard, 1978a; Fellers, 1979a, b; Ryan, 1980). Observations on the species studied in this thesis showed only one (*E. coqui*) to have a fixed site attachment. *Hyperolius marmoratus* and *S. wealii* tend to vocalize from elevated reeds and grass tussocks respectively and once mated move to the water to spawn. Therefore, the only species studied in this report which satisfies all three characteristics is *E. coqui*. These frogs defend an area in which they have a call site, a retreat site and an oviposition site and in some cases these sites are one and the same. *Hyperolius marmoratus* and *S. wealii* fall into the category first proposed by Conder (1949) of individual distance. In these cases, when another conspecific produces a vocalization closer than a certain threshold distance (individual distance) typically agonistic

behaviour will result. The fact that several authors have reported the occurrence of silent satellite males in close proximity to a vocalizing male is strong evidence that individual distance in anurans is vocally mediated.

In some species the advertisement call was thought to convey a male's spatial position to other males as well as attracting mates. Bogert (1960) used the term "territorial call" to describe a specialized call that appeared to function in the maintenance of spacing. This term was loosely applied to any agonistic call produced by males and has since been replaced by the term aggressive call (see Chapter one for the classification of calls used in this thesis).

Generally males produce aggressive calls during short range interactions usually when their individual distance has been violated by a vocalizing conspecific. If the aggressive call is ignored then physical combat will usually ensue. This graded escalation of social interaction has been reported for a number of anurans (Narins and Capranica, 1976; Whitney, 1980; Brzoska et al., 1982; Arak, 1983b; Robertson, 1984; Wells and Schwartz, 1984b; Littlejohn and Harrison, 1985; Telford, 1985). Although there has been considerable attention paid to the role of vocalizations in spatial organization of anuran choruses, not many authors have highlighted the importance of the intensity of these vocalizations and its effects on the spatial distribution of calling individuals. As inter-male spacing is vocally mediated it would be expected that individual distance is positively correlated with SPL of the advertisement call. Furthermore, as many authors have found that larger males produce more intense vocalizations than smaller males (Gerhardt, 1975; Wilbur et al., 1978; Berven, 1981; but see Robertson, 1986a), it would also be expected that larger males have larger individual distances. Arak (1988a) found that there was a significant relationship between a male's SVL and his distance from

other callers over the breeding season. He suggested that this might reflect that larger males were more successful in fights for calling sites. It could, however, equally reflect the importance of the higher SPL of larger males in maintaining greater individual distances.

4.1.5 Active space

The area in which individuals are intolerant of trespassers may be described by the term "active space". This term was first used by Marten and Marler (1977). They suggested that, in order to determine the active space of a vocal signal, the following parameters must be known:- a) the source intensity of the signal, b) the auditory threshold of the listener, and c) how the listener's ears are capable of hearing that signal above the background noise. They estimated that the maximum distance at which another canary (*Serinus canarius*) could hear the song of a male perched at 10 m was 416 m. This term was also used by Brenowitz (1982) with his studies on red-winged blackbirds (*Agelaius phoeniceus*) and Brenowitz et al. (1984) in their studies on spring peepers (*Hyla crucifer*). All these authors used this term to describe a linear distance from the signal source over which the intensity of the signal remains above the hearing threshold of potential receivers. Brenowitz (1982) pointed out that the term 'space' implies a three dimensional quality. As most anurans studied do not produce totally directional calls, active space in anurans should be used to describe a three dimensional area around the signaller. Active space of an anuran can be generally redefined as the area surrounding a calling individual which is delimited by the distance at which the signal intensity is above the auditory threshold i.e. the detection threshold, of the receiver.

4.1.6 Problems associated with SPL measurements

The previous sections in this chapter highlight the importance of accurate measurements of SPL of vocalizing animals which have been recorded in the animal's natural environment, at the time of day that the animal normally vocalizes, and under natural conditions of temperature, humidity and air movement. SPL measurements in the laboratory or anechoic chamber will reveal absolute levels but may not reflect the true propagation of these signals in the field.

One major problem surrounding the measurement of SPL is the accurate positioning of the microphone relative to the vocalizing animal. The microphone should be placed close enough to the animal in order to minimise the effects of excess attenuation, but not so close as to render measurements inaccurate due to near field effects. The microphone distance used by most workers in the field of anuran vocalization is 50 cm.

Another important problem involved with SPL measurements is the complexity of the acoustic environment. The propagation of an animal's signal is affected by the frequency and SPL of the signal, temperature gradients, humidity, air movement, density of vegetation and ground attenuation (Kurze and Beranek, 1971; Piercy et al., 1977; Michelsen, 1978; Zimmerman, 1983; Cosens and Falls, 1984; Waser and Brown, 1984; Nishimura et al., 1991; Arak and Eiriksson, 1992; Römer and Lewald, 1992).

4.1.7 Aims

I investigated the responses of three species of frogs to a broadcast of a normal conspecific call at gradually increasing intensities. The answer to the following question was sought:-

How do frogs respond to a conspecific call that gradually gets louder, simulating an approaching neighbour?

By presenting frogs with broadcasts of normal calls, at

gradually increasing intensities, this chapter shows that the escalating aggressive responses are a function of perceived SPL and relates this to territoriality and active space.

4.2 Methods

4.2.1 Study sites and species

Broadcast experiments were carried out on three species of anurans (*Eleutherodactylus coqui*, *Hyperolius marmoratus*, and *Semnodactylus wealii*).

Eleutherodactylus coqui was studied during July 1984 in Puerto Rico and was vocally active on most nights between the hours of 19.00 h and midnight, although some individuals call throughout the night (Drewry, 1970).

Hyperolius marmoratus was studied at two shallow coastal ponds (Matatiele and Mavungweni) near Mtunzini, S. Africa between the months of September to March in 1983 and 1984. This species was mainly vocally active between the hours of 19.30 h and 23.30 h.

Semnodactylus wealii was studied at an artificial dam between the months of November to January in 1983 and 1984, 15 km north of Ixopo in the Natal highlands, S. Africa. For a detailed description of these species and the study sites see Appendix B and Chapter one.

4.2.2 Preparation of the stimulus broadcast tapes

The stimulus tape used in the broadcast experiments with *E. coqui* was prepared by Dan Townsend at the Department of Biological Sciences, State University of New York at Albany. It consisted of 20 natural advertisement calls recorded onto a Realistic continuous tape loop of one minute duration (repetition rate 20/min).

The stimulus broadcast tape used in the experiments with *H. marmoratus* was a synthetic call with a repetition rate of 48 calls/min. This call was generated on a MINC computer

in the Section of Neurobiology and Behaviour, Cornell University, Ithaca, New York by Garry Harned. Its parameters were very similar to an average natural call and are as follows:-

Start frequency - 2850 Hz
Stop frequency - 3350 Hz
Total duration - 80 ms
Rise time - 10 ms
Fall time - 25 ms
Repetition rate - 48/min.

The preparation of the stimulus broadcast tape for *S. wealii* has already been described in Section 2.2.2 of Chapter two. The stimulus tape used for this experiment had a repetition rate of 12 stimuli per minute.

4.2.3 Increasing intensity broadcast experiments

In the case of *H. marmoratus* and *S. wealii* the stimulus tapes were broadcast to calling males using either a Nagra III or a Nagra IVS tape recorder, a Portamon speaker-amplifier and a Peerless G50-MRC 3.2 ohm speaker (10 cm diameter, with a flat frequency response within the range of 1 - 7 kHz). With *E. coqui* the stimulus tape was broadcast to the calling males with a Channel Master cassette tape recorder and a Calrad 20-257 portable speaker-amplifier. A calling male was selected for the experiment and all nearby males that might interfere were removed.

In all the experiments the speaker-amplifier was placed 70-200 cm from the frog and all intervening vegetation was pruned away to give a direct line of sight from the speaker to the frog. The stimulus was broadcast at a particular intensity for two minutes, then turned off and played at the next intensity level after a two minute pause. This

procedure was repeated until, either the subject stopped calling or, the maximum SPL of the equipment was reached.

Peak SPLs were measured using a Brüel and Kjær (B & K) 2209 precision sound level meter used in conjunction with a B & K 4165 microphone, a flexible microphone extension rod (B & K UA0196), and a microphone dehumidifier (B & K UA0308). The microphone was always protected from the wind by a B & K UA0237 foam windshield. When the experimental procedure had been completed for one individual, the peak SPL of the broadcast was measured at the subject's call site. Due to differing speaker-frog distances, there was considerable variation in the SPL at the subject's call site and this necessitated pooling the data for analysis into various SPL categories.

The broadcast stimulus was recorded (in-line) on the left channel of a second tape recorder (a Uher Report Monitor 4200 in the case of *H. marmoratus* and *S. wealii*, and a Sony TC-D5M stereo cassette recorder with *E. coqui*). The response of the subject was recorded on to the right channel of the second tape recorder using an AKG D-900 unidirectional microphone. By recording the stimulus and the subject's response on different channels of the same tape recorder, the temporal relationship between the stimulus and response was preserved for later analysis.

Temperature and humidity were also recorded using a Bailey Instruments BAT-12 digital thermometer equipped with a PT-6 thermocouple and a whirling hygrometer. The data was analysed on a Uniscan II spectrum analyser (Multigon Industries, Inc., New York) and the sonagrams were prepared using a Kay model 7029A spectrum analyser.

4.3 Results

4.3.1 Eleutherodactylus coqui

Broadcast stimuli of varying intensities between 76-107 dB, at the subject's call site, were presented to 31 *E. coqui*. There was a general trend for the subjects to decrease the number of "coqui" responses and to increase the number of "co" notes with increasing intensity of the broadcast stimuli (see Table 4.1 and Figure 4.1). Also, it was noted that subjects responded to stimuli of increasing intensity by increasing the proportion of multi-note calls. These are aggressive calls and are thought to play a role in the maintenance of spacing (Stewart and Rand, 1991, 1992; Stewart and Bishop, 1994) (for a detailed description of the vocal repertoire of *E. coqui* see Appendix A).

During the normal calling sequence of 23 males, before any broadcasts had been presented, the mean call types produced in a two minute period were 31 "coqui" notes, six "co" notes and 0.04 multi-note calls. A noticeable departure from this sequence was observed when the intensity of the broadcast signal was between 83-88 dB at the subject's call site. At this intensity there was an increase in the mean number of "co" notes produced and a slight decrease in the mean number of "coqui" notes produced i.e. 25 "coqui", 12 "co" and one multi-note. The "coqui" notes continued to decrease while the "co" notes increased with the increase in the intensity of the broadcast. At intensities between 95-100 dB there were almost the same mean number of "co" notes as "coqui" notes (i.e. 11 "coqui" and 10 "co" notes). In addition the mean number of multi-notes given during the two minutes of broadcast at this intensity increased to four (range 0-10).

TABLE 4.1

The change in response of male *E. coqui* to increasing intensity broadcasts (23 individuals, $n = 3881$).

SPL of broadcast (dB at subject's call site)	Ratios of		
	"coqui"	"co"	"coqui+"
Before broadcast	82.9%	17.0%	1.1%
< 77	72.7%	27.3%	0
77 - 82	75.3%	23.6%	1.1%
83 - 88	67.0%	30.5%	2.5%
89 - 94	55.7%	36.5%	7.8%
95 - 100	48.5%	40.6%	10.9%
> 100	43.2%	56.8%	0

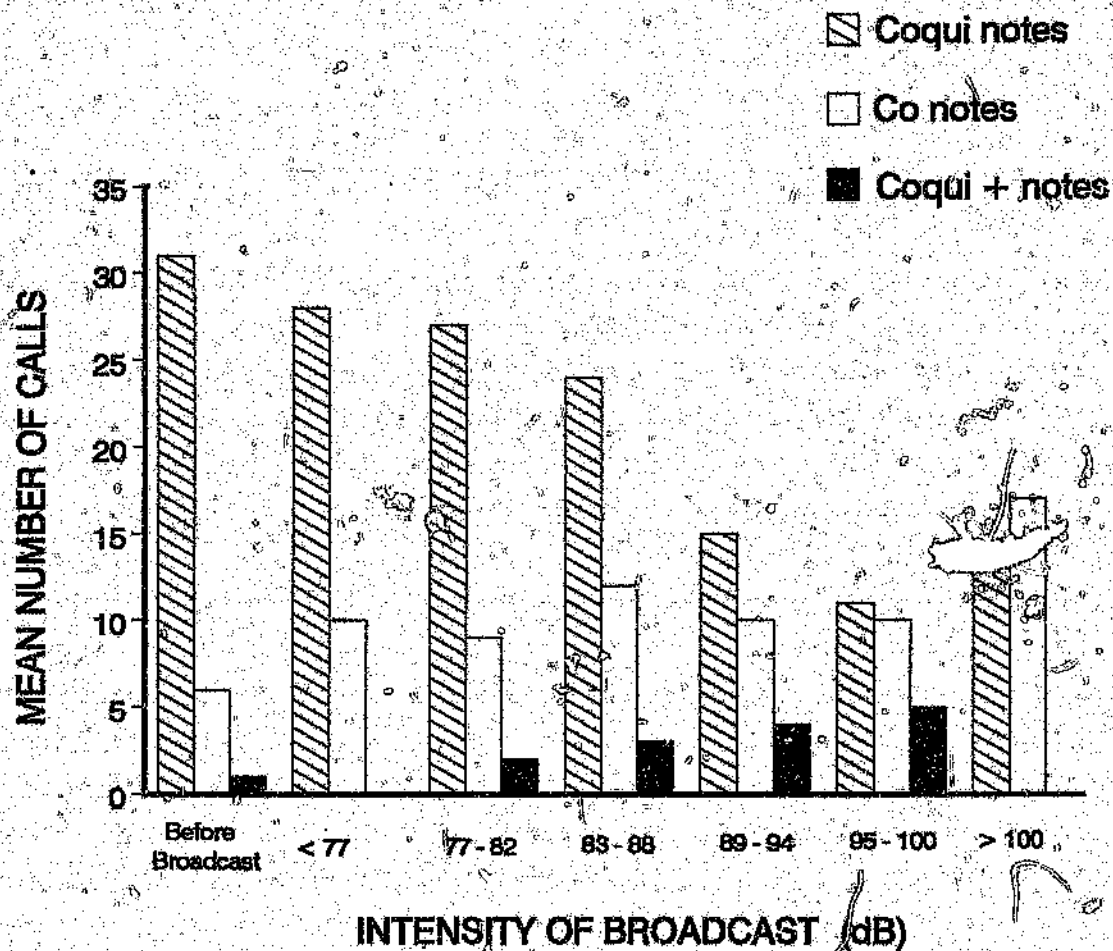


Fig. 4.1 Changes in the proportion of 'coqui', 'co', and 'coqui +' notes given in response to an increased intensity of the broadcast to 23 *E. coqui*.

As the intensity of the broadcast was increased the percentage of subjects which were inhibited from calling by the broadcast stimuli also increased. At intensities less than 83 dB no subjects were inhibited from calling, but at intensities between 83-88 dB 18% (4 out of 22) stopped calling. At higher intensities significantly more and more subjects were inhibited from calling i.e. at 89-94 dB 50% (6 out of 12), at 95-100 dB 66.7% (6 out of 9) and at 100 dB and above 75% (3 out of 4) (Spearman's correlation coefficient, $r_s = 1$, $P < 0.02$, $n = 6$, [2 tailed] see Table 4.3). The 19 frogs which were inhibited from calling either remained at the call site in a "low" position or moved away from their call site. Nearly all the frogs which moved away from their call site moved towards the loudspeaker (8 out of 9 individuals, Binomial test, $P = 0.04$, [2 tailed]) while one individual moved away from the loudspeaker.

Figures 4.2 - 4.7 show how the subjects change the temporal position of their calls with increasing intensity. At a low intensity of 76 - 80.5 dB, 12.5% of the responses occur within 500 ms from the onset of the stimulus (Fig. 4.2). When the intensity of the broadcast stimuli was increased up to 104 dB 62.5% of the responses occurred within 500 ms from the onset of the stimulus (Fig. 4.7). As the intensity of the stimulus increases there is a significant decrease in the mean stimulus-response (S-R) interval of "co" notes (Spearman's correlation coefficient, $r_s = -1$, $P < 0.005$, [2 tailed], $n = 6$), and a concomitant increase in the mean S-R interval of "coqui" notes (Spearman's correlation coefficient, $r_s = 0.829$, $P = 0.06$, [2 tailed], $n = 6$) (see Table 4.2). Associated with this increase in the number of responses occurring very shortly after the stimulus was a decrease in the percentage of "coqui" notes occurring in this period (see Table 4.1). At a broadcast intensity of 76 - 80.5 dB 10.5% of the calls produced 500 ms after the onset of the stimulus were "coqui" notes, the

remainder being "co" notes. When the broadcast intensity was increased to 101 - 104 dB only 3% of the calls produced in this period were "coqui" notes (Spearman's correlation coefficient, $r_s = -0.95$, $P = 0.02$, [2-tailed], $n = 6$, see Table 4.3).

TABLE 4.2

Mean S-R intervals ($\pm$ SE) for "co" and "coqui" notes during increasing intensity broadcasts to 10 E. coqui ($n = 704$).

SPL of broadcast (dB at subject's call site)	"co" S-R interval (ms)	"coqui" S-R interval (ms)
< 77	726.5 ($\pm$ 887.1)	1571.4 ($\pm$ 752.7)
77 - 82	538.2 ($\pm$ 780.5)	1801.9 ($\pm$ 731.1)
83 - 88	149.3 ($\pm$ 293.1)	2003.5 ($\pm$ 823.2)
89 - 94	105.5 ($\pm$ 19.7)	2093.0 ($\pm$ 732.3)
95 - 100	97.0 ($\pm$ 12.9)	1912.4 ($\pm$ 513.1)
> 100	94.5 ($\pm$ 23.8)	2128.3 ($\pm$ 765.0)

TABLE 4.3

Percentage of "coqui" notes occurring within 500 ms from the beginning of a stimulus and percentage of males inhibited from calling during increasing intensity broadcasts to 23 *E. coqui*.

SPL of broadcast (dB at subject's call site)	% coqui notes within 500 ms from stimulus onset	% silent males
< 77	10.5	0
77 - 82	7.3	0
83 - 88	7.3	18
89 - 94	3.6	50
95 - 100	4.3	67
> 100	3.0	75

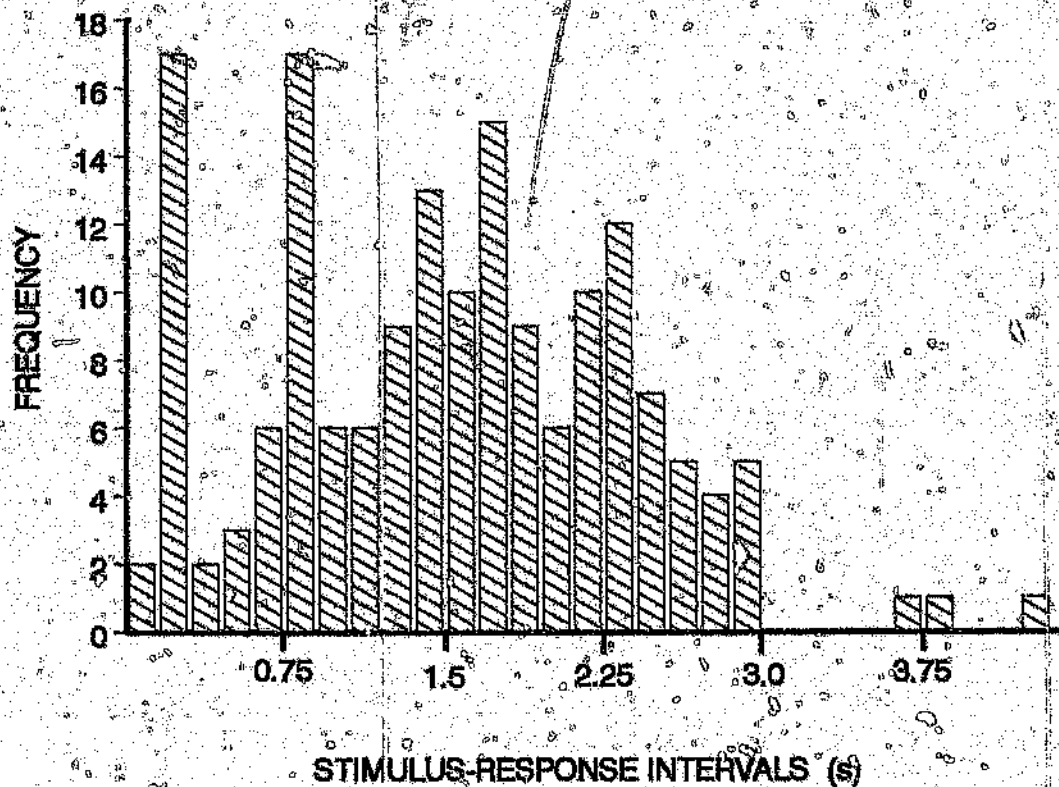


Fig. 4.2 *E. coqui* Stimulus-Response intervals ($n = 168$) during a broadcast at an intensity of 76 - 80.5 dB (9 males). The solid black bars represent the duration and position of the stimuli.

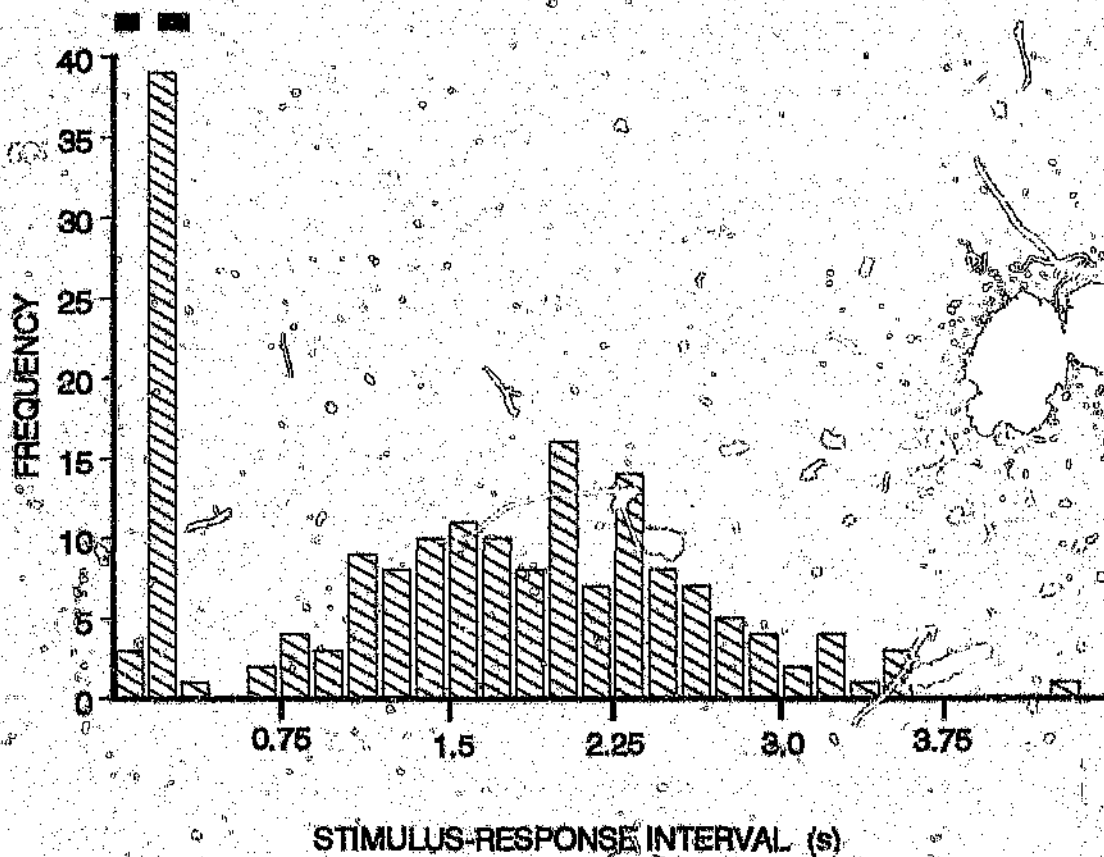


Fig. 4.3 *E. coqui* Stimulus-Response intervals ($n = 180$) during a broadcast at an intensity of 81 - 84 dB (10 males). The solid black bars represent the duration and position of the stimuli.

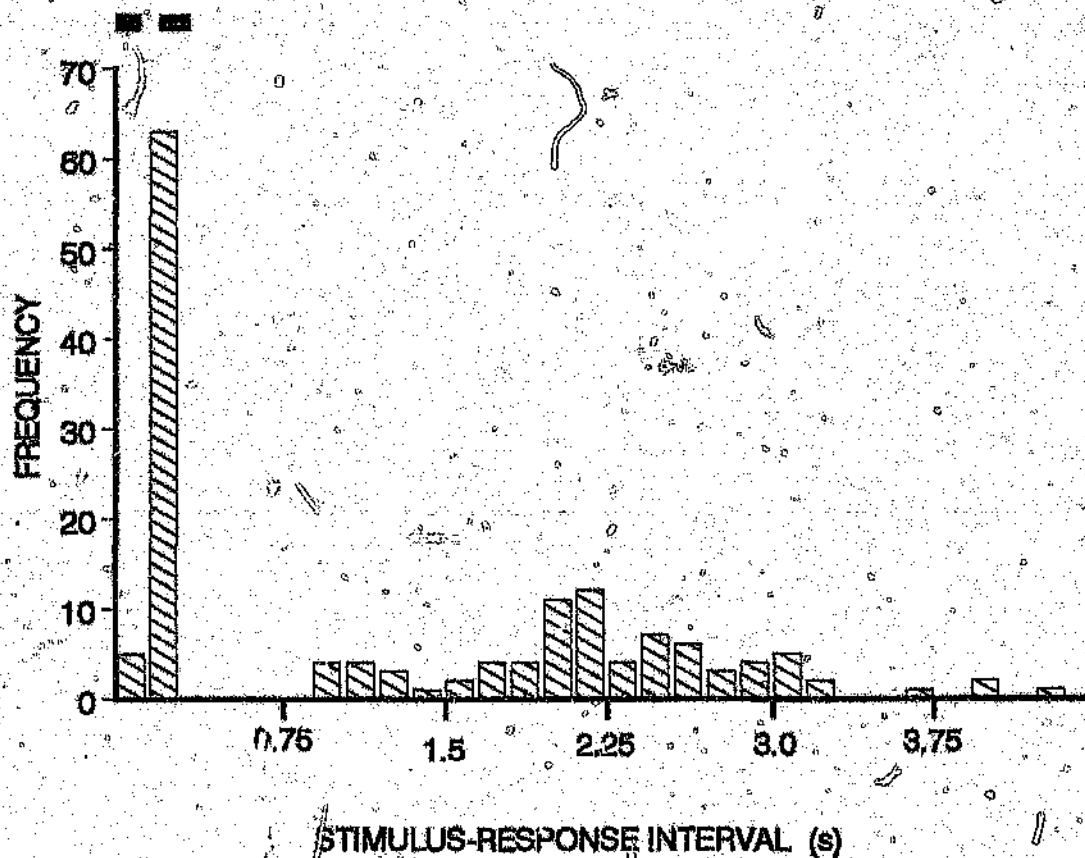


Fig. 4.4 *E. coqui* Stimulus-Response intervals ($n = 148$) during a broadcast at an intensity of 84.5 - 88 dB (8 males). The solid black bars represent the duration and position of the stimuli.

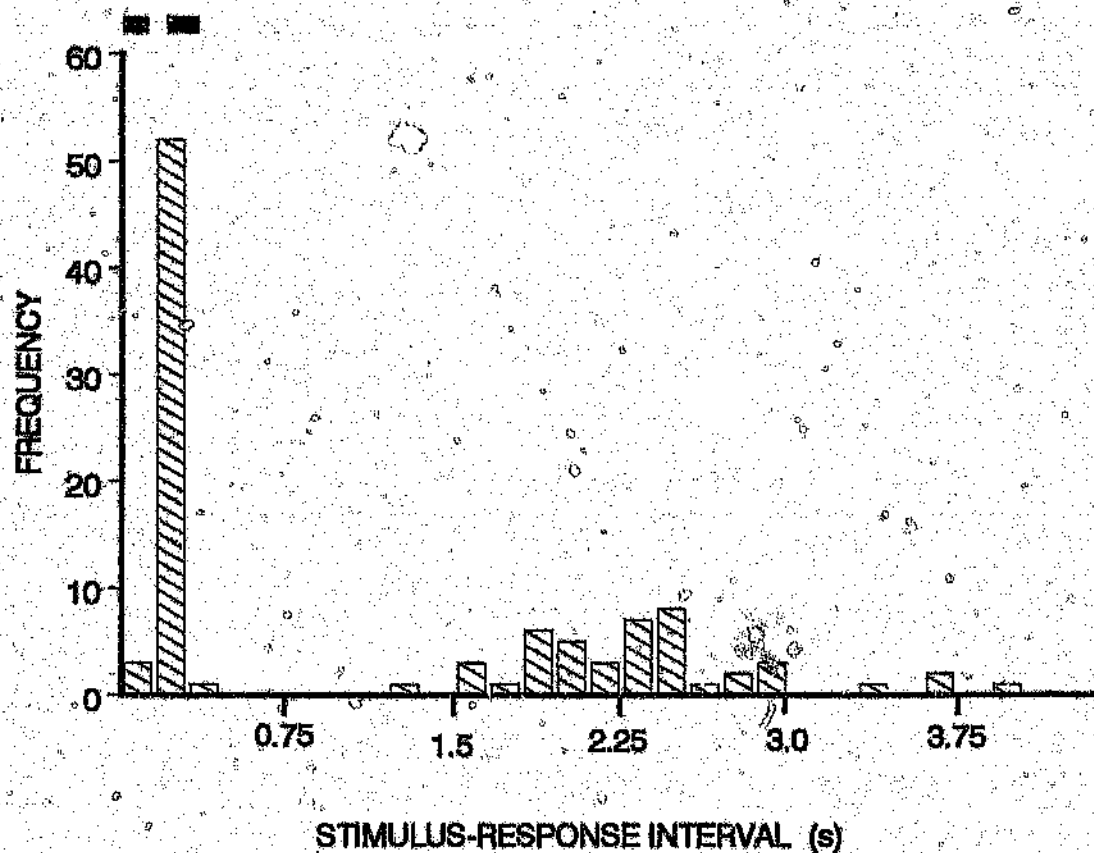


Fig. 4.5 *E. coqui* Stimulus-Response intervals ($n = 100$) during a broadcast at an intensity of 90.5 - 94.5 dB (6 males). The solid black bars represent the duration and position of the stimuli.

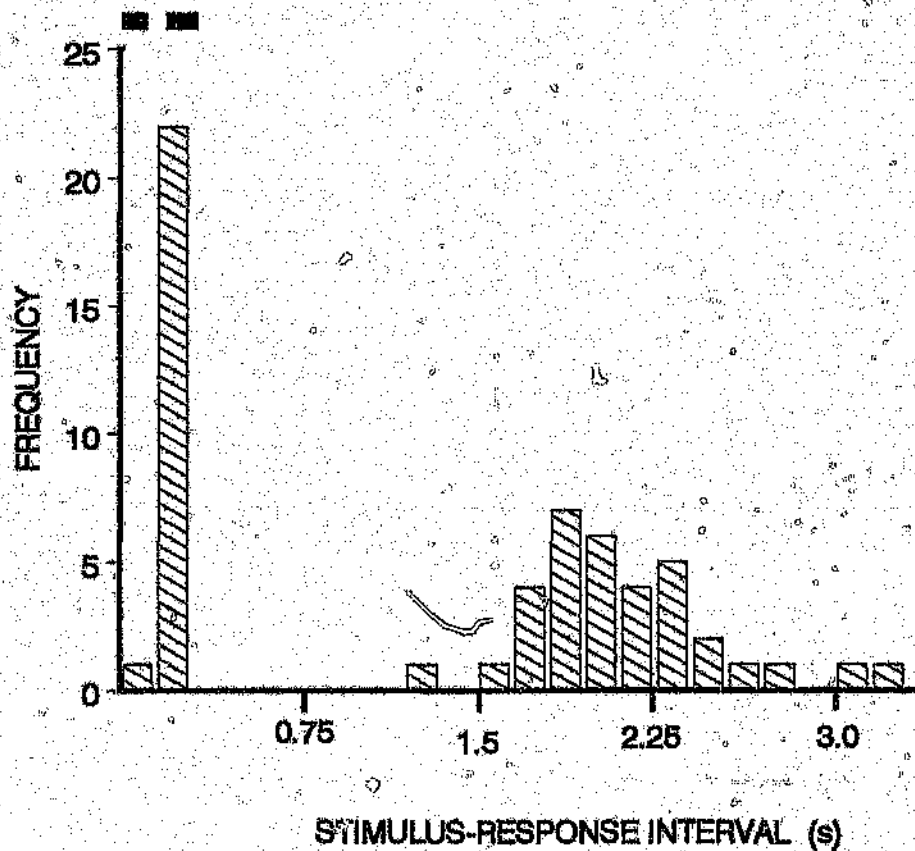


Fig. 4.6 *E. coqui* Stimulus-Response intervals ($n = 57$) during a broadcast at an intensity of 95.5 - 98 dB (3 males). The solid black bars represent the duration and position of the stimuli.

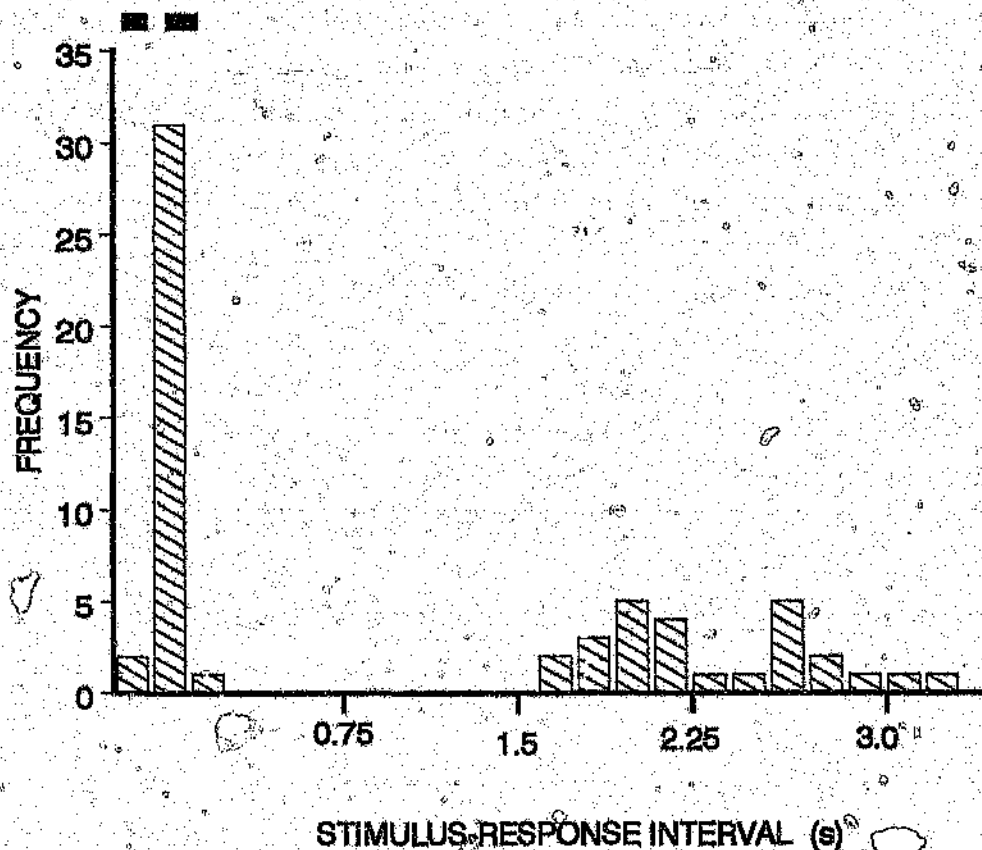


Fig. 4.7 *E. coqui* Stimulus-Response intervals ($n = 60$) during a broadcast at an intensity of 101 - 104 dB (3 males). The solid black bars represent the duration and position of the stimuli.

4.3.2 Hyperolius marmoratus

Ten individuals of *H. marmoratus* were presented with broadcast stimuli at varying intensities between 94 - 109 dB at the subject's call site. At low intensities of 94 - 97 dB the subjects displayed a slightly bimodal distribution in their stimulus-response intervals (Figure 4.8). The first peak is at 200 ms and the second peak is at about 1.1 s from the beginning of a stimulus. The latter peak corresponds to the natural inter-call interval and would occur in this position even if there was no broadcast as evidenced by the histogram of natural inter-call intervals before the broadcast began (see Fig. 2.6 in Chapter two).

As the intensity of the stimuli increases, slightly more responses are placed around this first peak and less around the second peak (see Figs. 4.9, 4.10, 4.11 and Table 4.4). However, these changes are not significant (Spearman's correlation coefficient, $r_s = -1$, $P > 0.1$, [2-tailed], $n = 4$, and Kruskal Wallis ANOVA, $KW = 6.59$, $P = 0.09$).

At the lower intensities (i.e. 94 - 101 dB at the subject's call site) 4.6% of the subject's responses overlap in some degree to a stimulus while at the higher intensity broadcasts (i.e. 102 - 109 dB) only 2.1% of the responses overlap with a stimulus.

There were no significant changes in the temporal or spectral properties of the subjects' calls until the intensity of the broadcast reached 103 dB and then one subject changed to aggressive calling (see Fig. 4.12). The number of subjects which produced aggressive calls during the broadcast increase with increasing stimulus intensity so that, at an intensity of 106 - 109 dB, 50% of the subjects had produced aggressive calls.

TABLE 4.4

Mean S-R intervals ($\pm$ SE) for 9 *H. marmoratus* ($n = 1485$).

SPL of broadcast (dB at subject's call site)	S-R interval (ms)

94 - 97	609.0 $\pm$ 14.5

98 - 101	574.8 $\pm$ 18.8

102 - 105	569.2 $\pm$ 21.7

106 - 109	547.4 $\pm$ 23.0

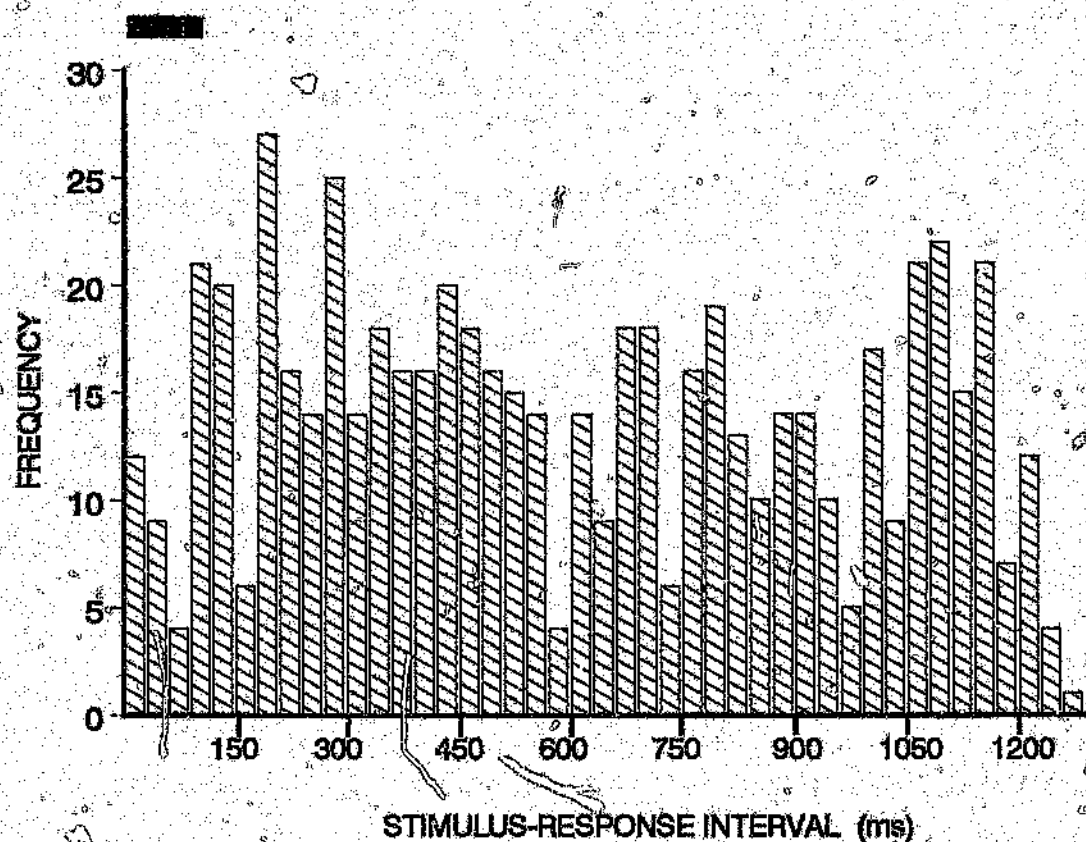


Fig. 4.8 *H. marmoratus* Stimulus-Response Intervals (n = 600) during a broadcast at an intensity of 94 - 97 dB (9 males). The solid black bar represents the duration and position of the stimulus.

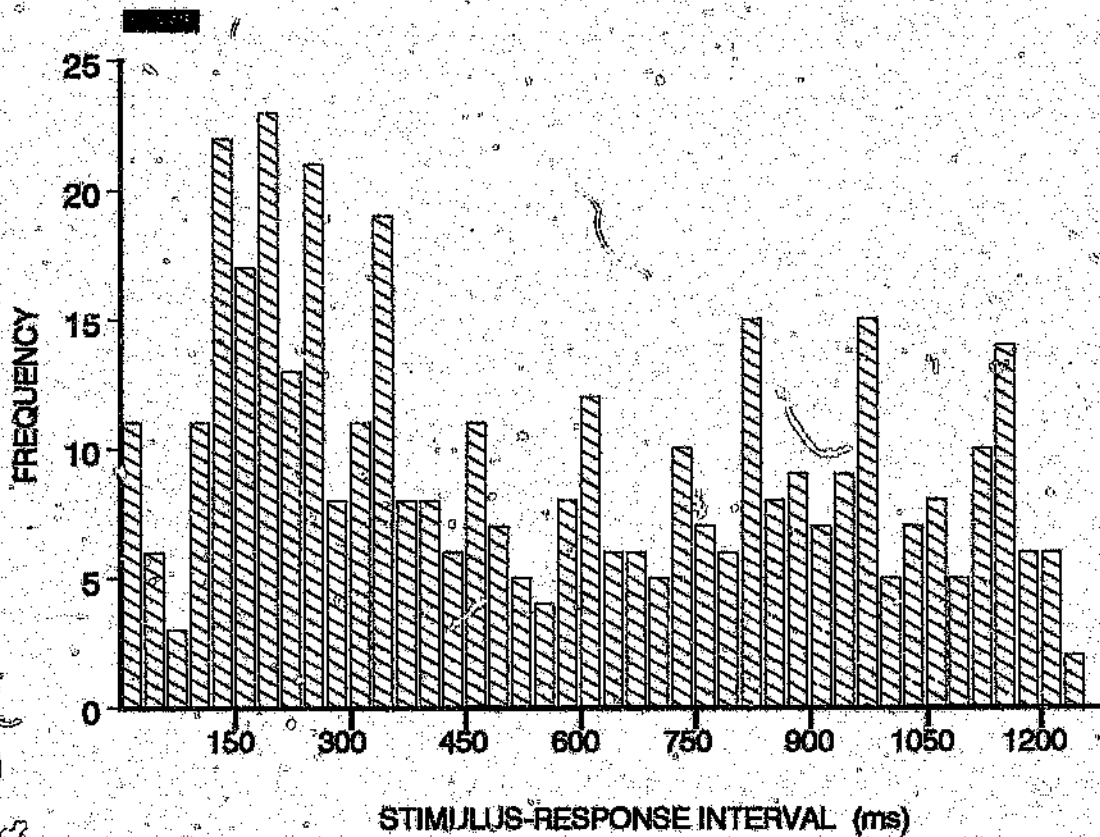


Fig. 4.9 *H. marmoratus* Stimulus-Response intervals ($n = 400$) during a broadcast at an intensity of 98 - 101 dB (9 males). The solid black bar represents the duration and position of the stimulus.

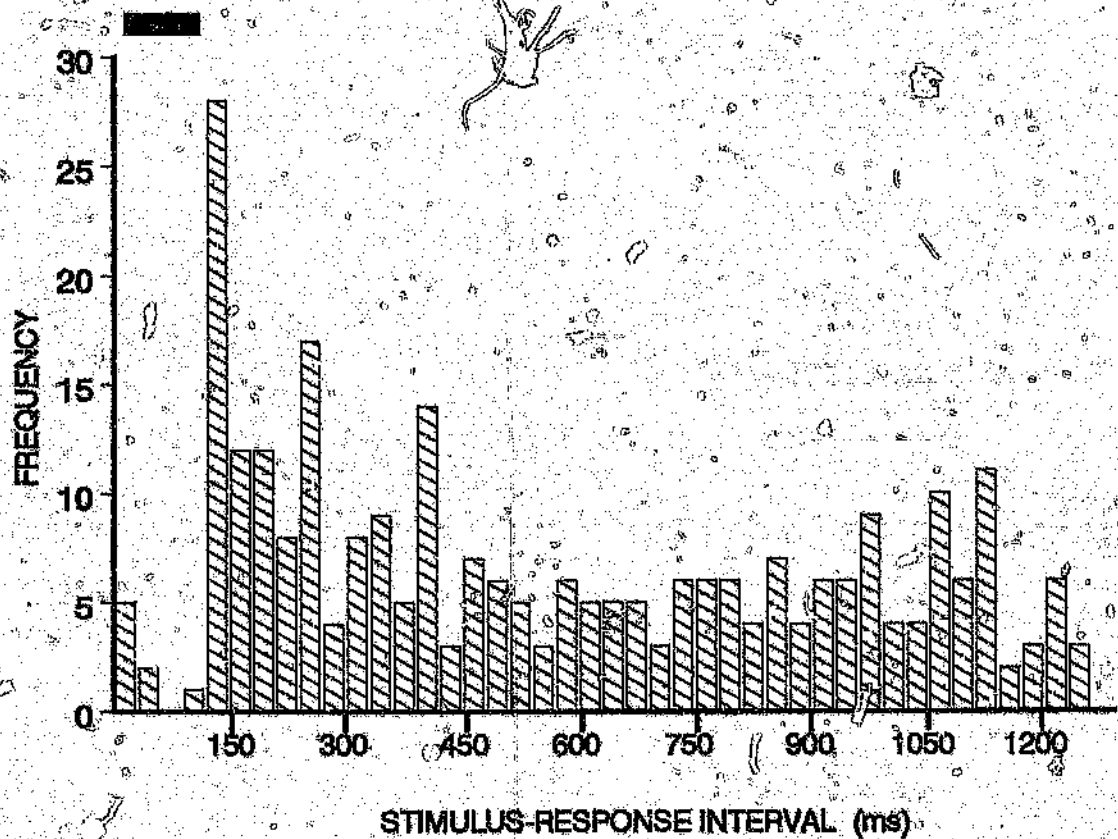


Fig. 4.10 *H. marmoratus* Stimulus-Response intervals ($n = 276$) during a broadcast at an intensity of 102 - 105 dB (6 males). The solid black bar represents the duration and position of the stimulus.

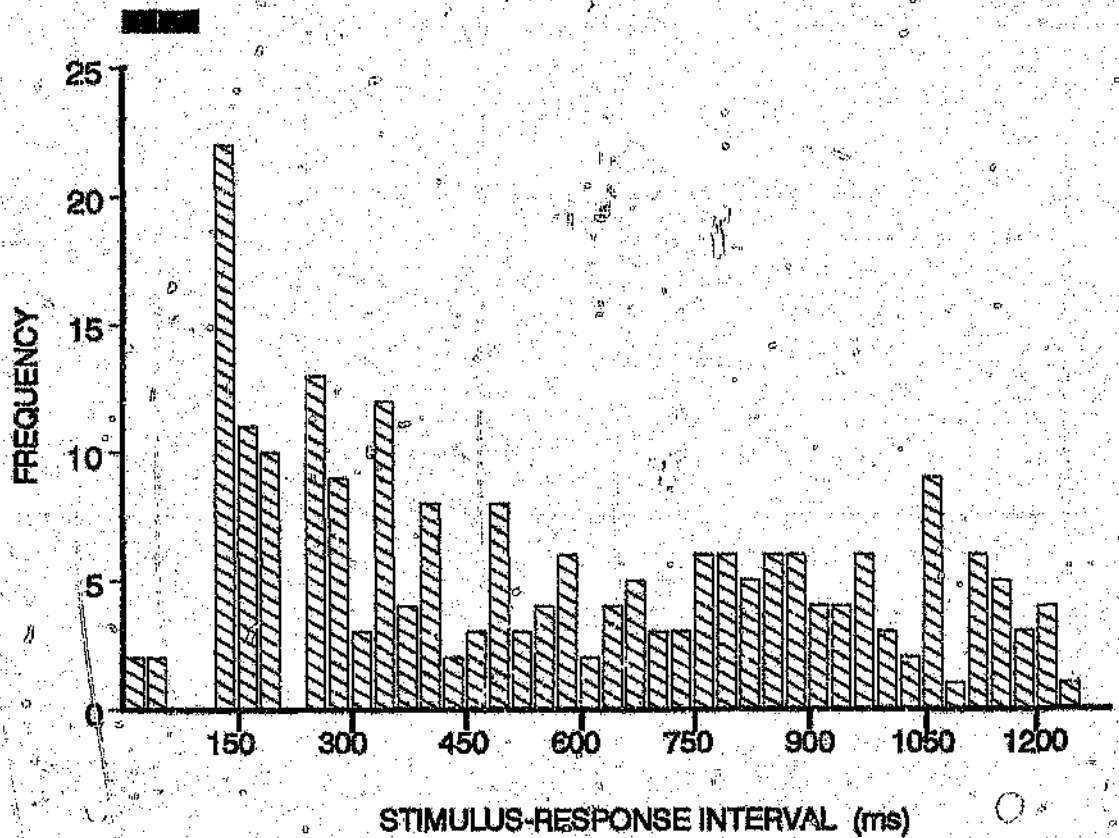


Fig. 4.11 *H. marmoratus* Stimulus-Response intervals ($n = 230$) during a broadcast at an intensity of 106 - 109 dB (7 males). The solid black bar represents the duration and position of the stimulus.

kHz

3

2

1

100 ms

Fig. 4.12 Aggressive call of *H. marmoratus*

Three subjects continued producing advertisement calls throughout the experiment. The lowest intensity broadcast which caused a subject to cease calling was 101 dB, and a further subject stopped calling when presented with a broadcast of 104 dB. At 106 dB three subjects were inhibited from calling and although all the previous subjects which stopped calling assumed a 'low' position, one of the subjects which stopped at 106 dB remained in an active position with the vocal sac partially inflated. This subject continued calling after the broadcast had ceased. Two frogs moved during the broadcast sequence, one moved away from the speaker when presented with a broadcast of 100 dB, and the other moved towards the speaker when presented with a broadcast of 109 dB. Both subjects resumed calling after their move.

There was no significant change in the repetition rate of the subjects' calls throughout the broadcast sequences (Friedman ANOVA, $F = 0.88$, $P = 0.93$, $df = 4$).

4.3.3 *Semnodactylus wealii*

Increasing intensity broadcasts between 88 - 113 dB at the subject's call site were presented to nine *S. wealii*. As the intensity increased, subjects showed a gradual increase in the number of calls produced approximately 500 ms from the end of a stimulus. This resulted in a significant decline in the mean S-R interval with increasing intensity (Spearman's correlation coefficient, $r_s = -1$, $P < 0.001$, [2-tailed], $n = 7$, see Table 4.5). At a relatively low broadcast intensity of 88 - 91 dB, 63% of all the responses were produced within 500 ms from the end of a stimulus. The number of responses in this period steadily increased with increasing intensity, resulting in 81% of the responses occurring in this period at a broadcast level of 98 - 100 dB and up to 99% at an intensity level of 110 - 113 dB (see Figs. 4.13 - 4.19).

TABLE 4.5

Mean S-R intervals ($\pm$ SE) for 9 *S. wealii* ($n = 792$).

SPL of broadcast (dB at subject's call site)	S-R interval (ms)
88 - 91	1224 $\pm$ 105
92 - 94	1090 $\pm$ 98
95 - 97	895 $\pm$ 95
98 - 101	831 $\pm$ 75
101 - 104	714 $\pm$ 46
105 - 109	700 $\pm$ 60
110 - 113	463 $\pm$ 97

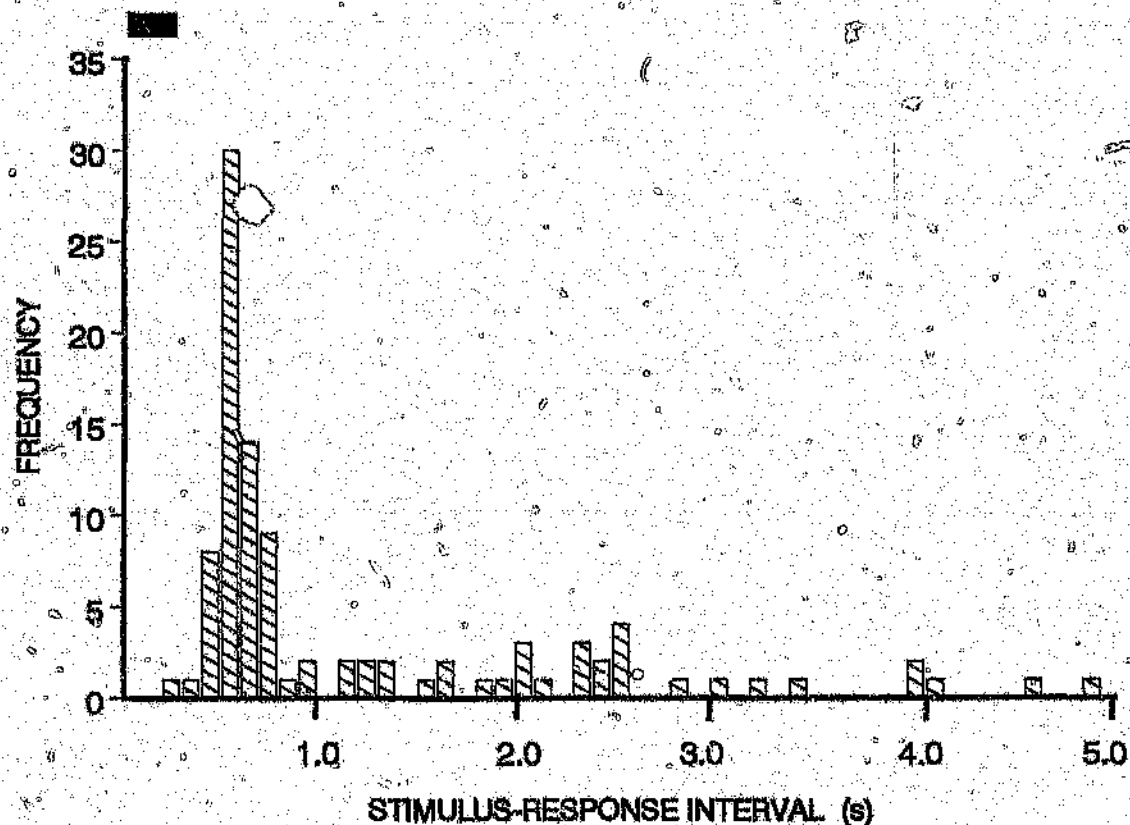


Fig. 4.13 *S. wealii* Stimulus-Response intervals ($n = 99$) during a broadcast at an intensity of 88 - 91 dB (8 males). The solid black bar represents the duration and position of the stimulus.

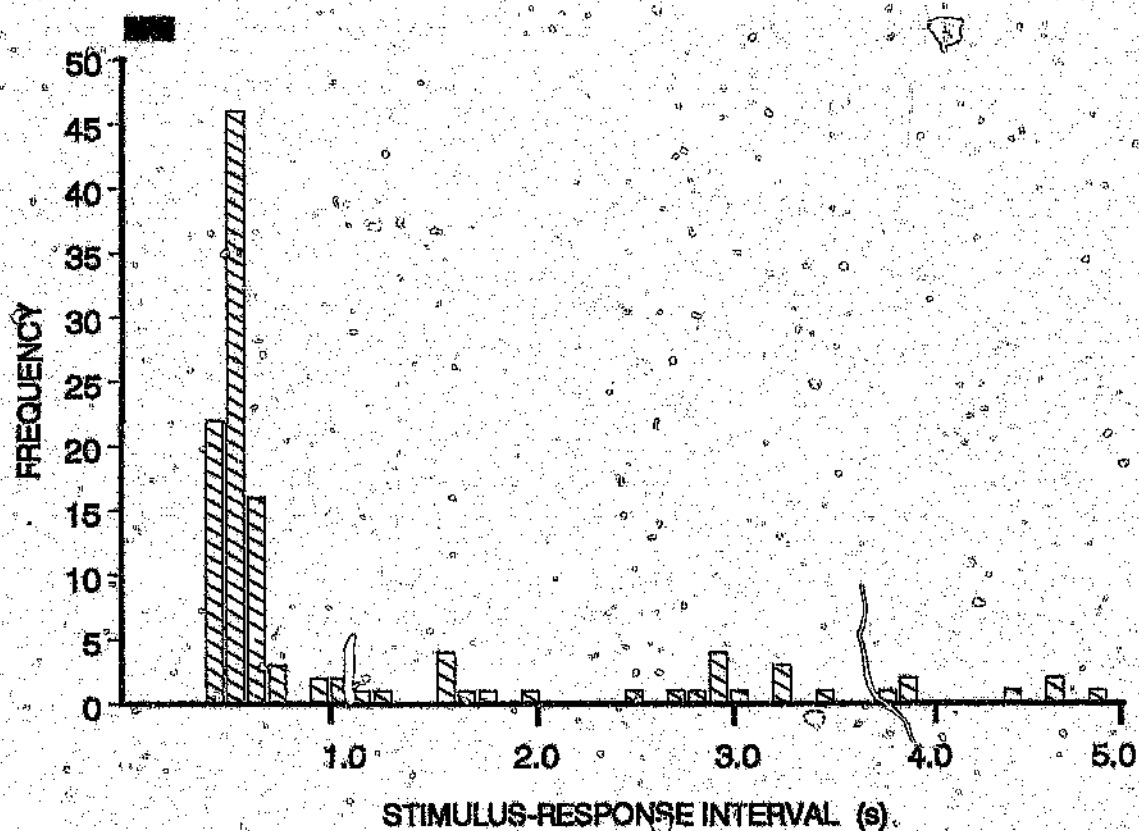


Fig. 4.14 *S. wealii* Stimulus-Response intervals ($n = 120$) during a broadcast at an intensity of 92 - 94 dB (9 males). The solid black bar represents the duration and position of the stimulus.

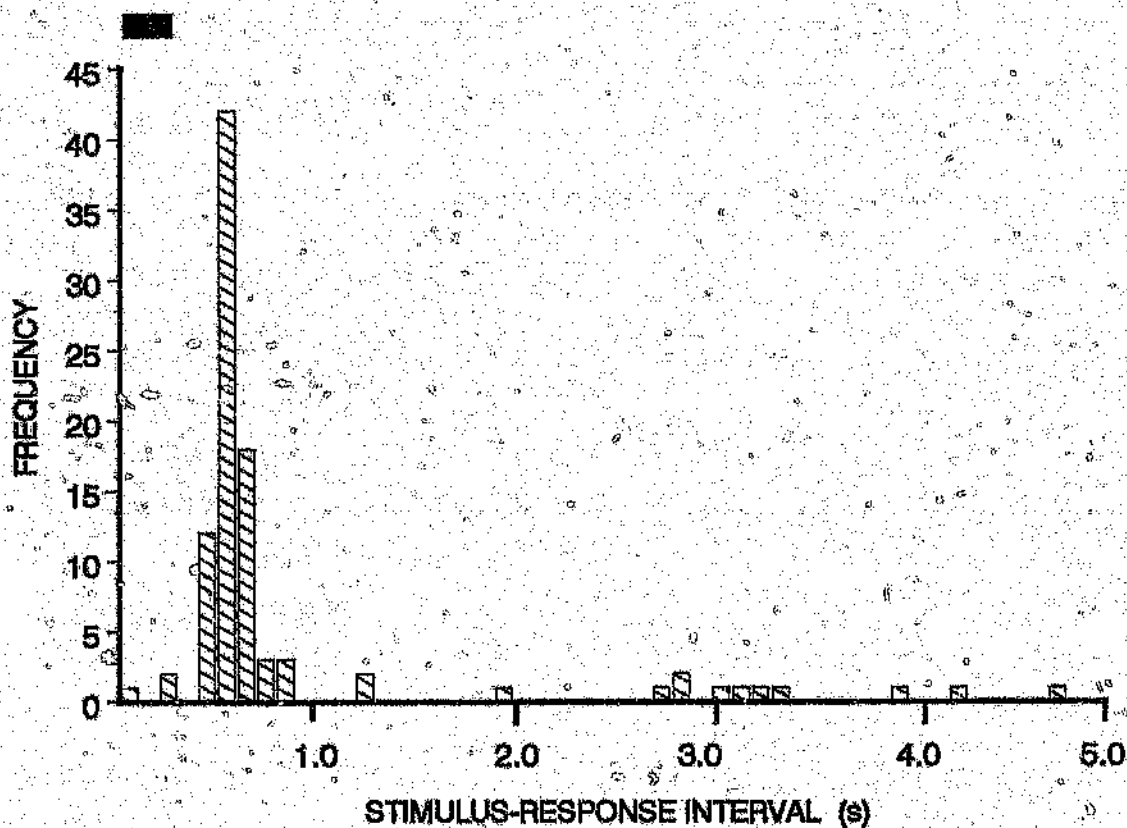


Fig. 4.15 *S. wealii* Stimulus-Response intervals ($n = 95$) during a broadcast at an intensity of 95 - 97 dB (8 males). The solid black bar represents the duration and position of the stimulus.

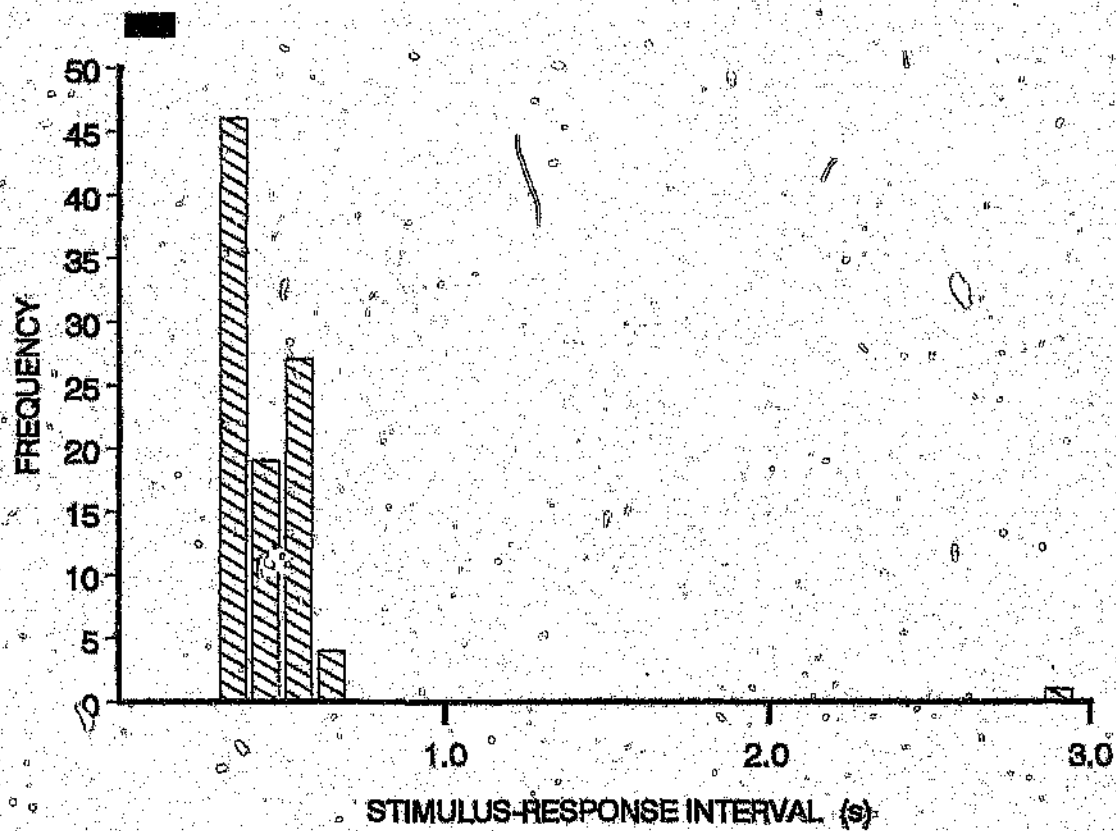


Fig. 4.16 *S. wealii* Stimulus-Response intervals ($n = 95$) during a broadcast at an intensity of 98 - 100 dB (9 males). The solid black bar represents the duration and position of the stimulus.

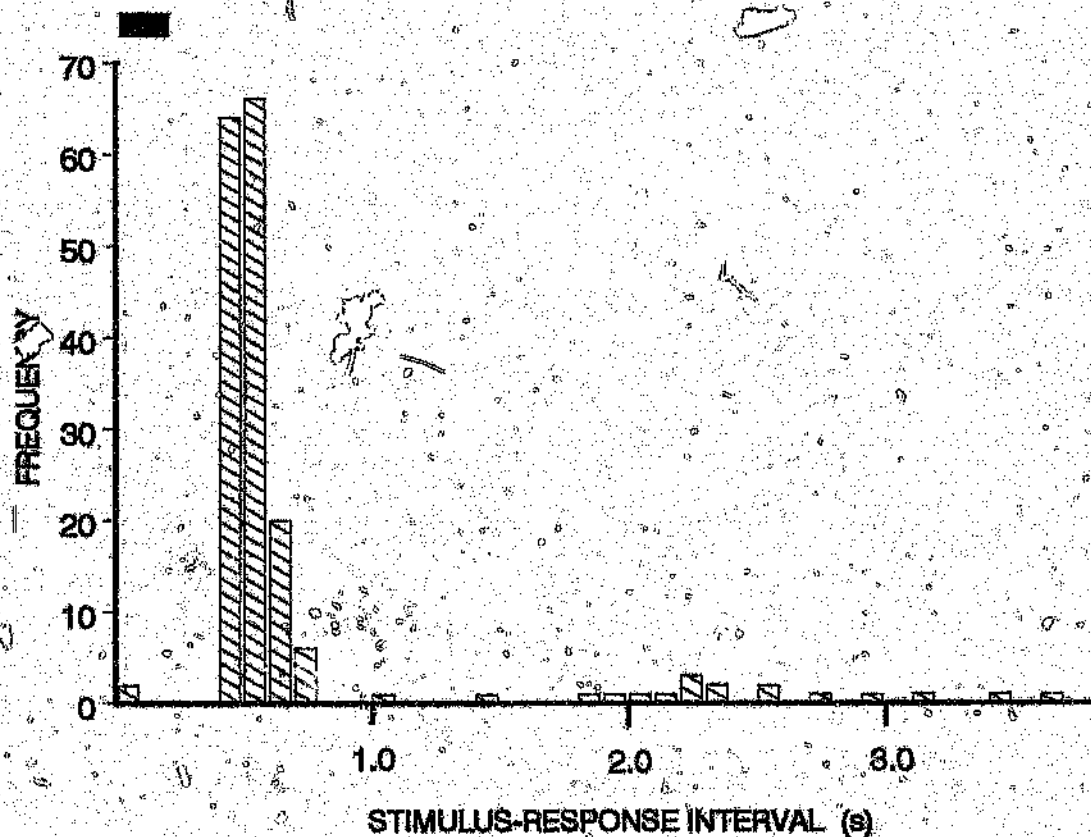


Fig. 4.17 *S. wealii* Stimulus-Response intervals ($n = 176$) during a broadcast at an intensity of 101 - 104 dB (9 males). The solid black bar represents the duration and position of the stimulus.

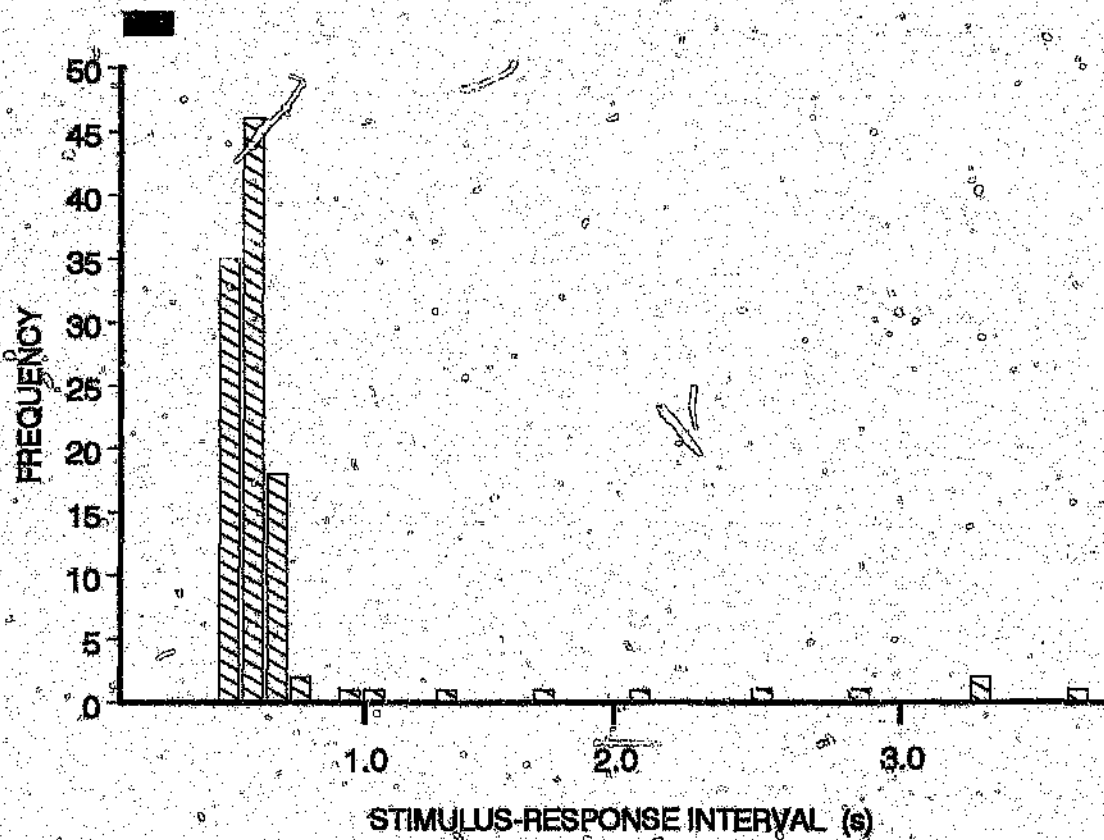


Fig. 4.18 *S. wealii* Stimulus-Response intervals ($n = 111$) during a broadcast at an intensity of 105 - 109 dB (8 males). The solid black bar represents the duration and position of the stimulus.

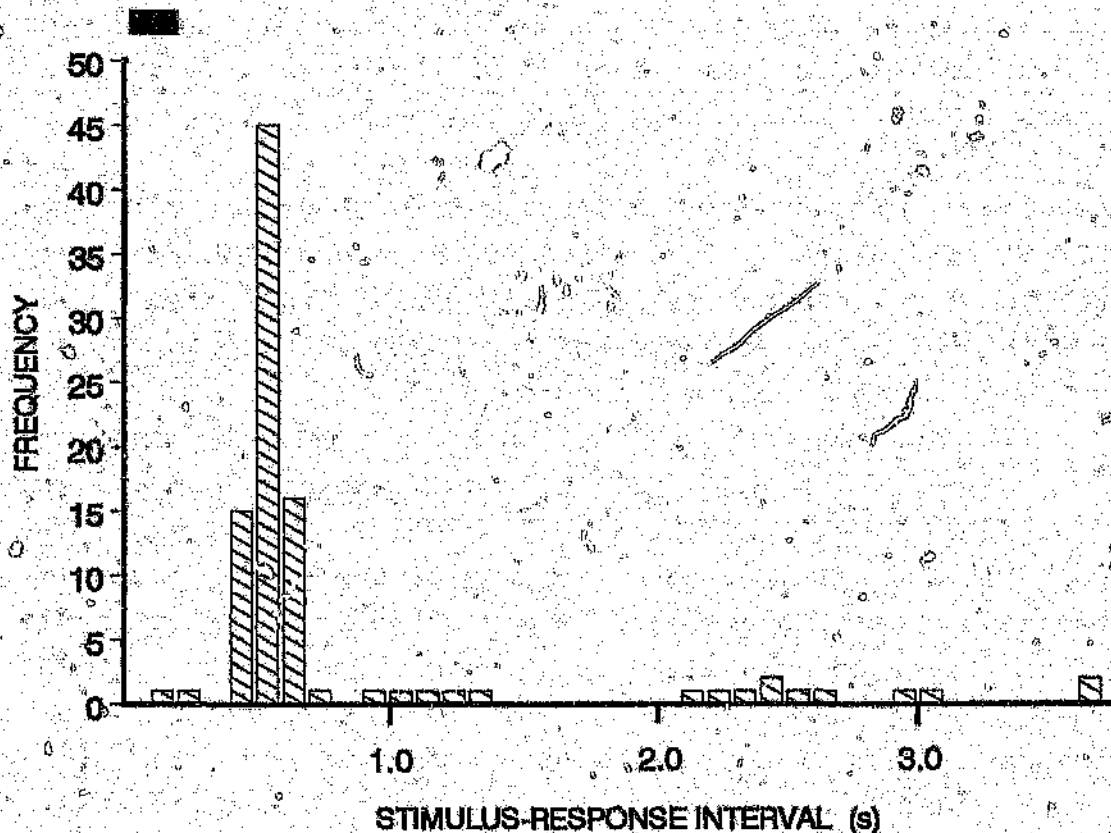


Fig. 4.19 *S. wealii* Stimulus-Response intervals ($n = 97$) during a broadcast at an intensity of 110 - 113 dB (6 males). The solid black bar represents the duration and position of the stimulus.

Three subjects showed no change in the spectral or temporal properties of their calls throughout the broadcasts, however, the other subjects showed a number of changes. The first change to be noted was the production of double responses. These consisted of two advertisement calls, separated by an interval of 500 ms ($SD = \pm 100$ ms, $n = 21$), the first of which followed almost immediately after a stimulus. The second advertisement call was typically 60 ms ($SD = \pm 44$ ms, $n = 21$) shorter than the first (Figure 4.20). Double responses were first produced at an intensity of 90 dB with a total of nine double responses given by four subjects at broadcast intensities below 98 dB. Above 98 dB six individuals produced a total of 39 double responses with 60% of these occurring at 107 dB and above. One individual produced a triple response at a broadcast level of 107 dB and then ceased to call in response to further stimuli.

Three subjects produced aggressive calls (Figure 4.21) the first being produced in response to a broadcast level of 104 dB. Occasionally aggressive calls were produced as the second call in a double response. Only one subject was inhibited from calling and this was when it was presented with a broadcast of 107 dB. Furthermore, only one subject moved during the broadcasts. The movement was away from the loudspeaker and occurred at a broadcast intensity of 113 dB. There was no change in the number of notes with increasing intensity of the broadcast.

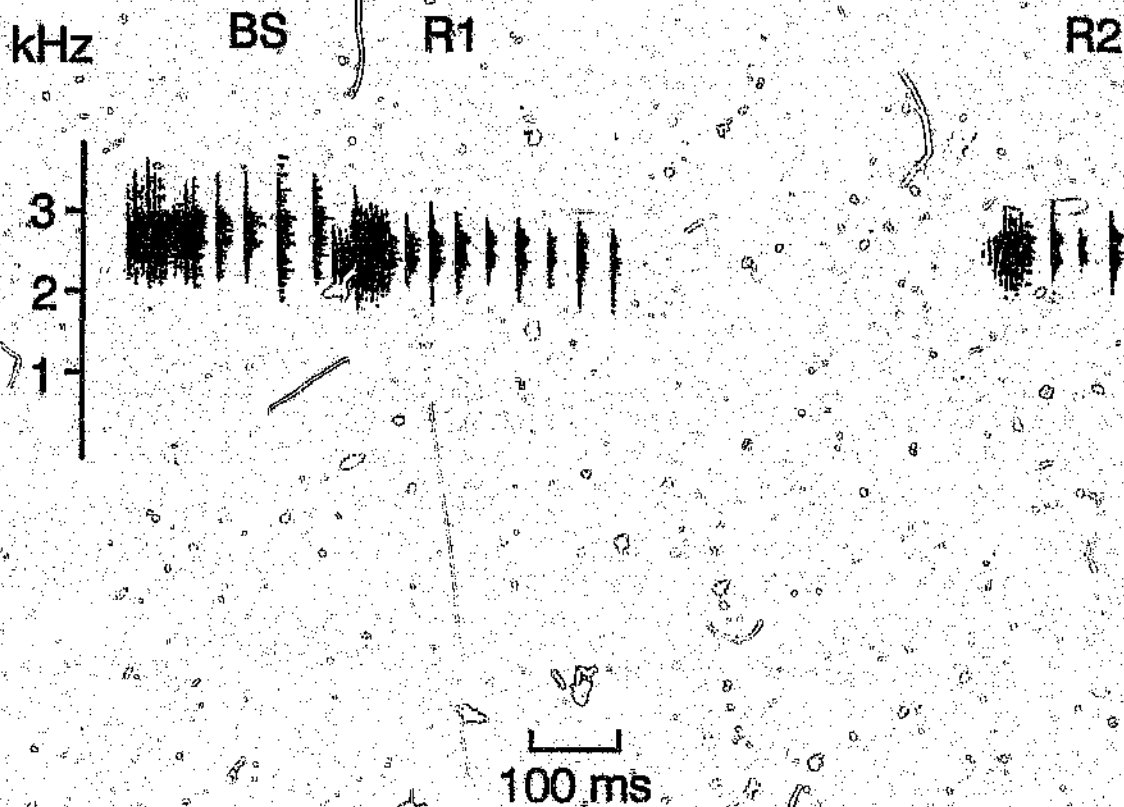


Fig. 4.20 The double response (R1, R2) of *S. wealii* to a broadcast stimulus (BS).

kHz

3

2

1

100 ms

Fig. 4.21 Aggressive call of *S. wealii*

4.4 Discussion

4.4.1 General

Several studies have shown that an increase in the SPL of advertisement calls stimulates a change in the behaviour of the recipient (Bunnell, 1973; Telford, 1985; Schwartz, 1987, 1989). Consequently, males alter their vocal behaviour in response to the proximity of neighbours, which is judged by the perceived SPL of the advertisement call. In this study, the vocal behaviour of the males of all three species was shown to be affected by changes in the intensity of the stimulus. As the stimulus was very similar to a natural call, the broadcast simulated a calling neighbour moving closer to the subject.

At low broadcast intensities the general trend for all species was to continue calling in a pattern similar to that occurring before the broadcast began. However, besides call alternation occurring by chance, some precise call-timing was exhibited by *S. wealii* at low broadcast intensities. Although Narins and Capranica (1976, 1978) suggested that call alternation occurs in *E. coqui* at low intensity broadcasts this was not observed in this study.

As the intensity of the broadcast to *E. coqui* and *S. wealii* was gradually increased, the number of responses which were time-locked to the stimulus increased proportionately, and the temporal relationship between the calls and the stimuli became more precise.

At very high broadcast intensities, in all three species, the males produced aggressive calls instead of advertisement calls. If the broadcast persisted at this

intensity then males often became silent and many approached the loudspeaker. This type of behaviour has been described in other anurans (Brzoska et al., 1982; Robertson, 1984; Wells and Schwartz, 1984b) and crickets (Cade and Otte, 1982). The silence evoked by continuous broadcasts at high intensities may be an artifact of the non-interactive nature of the experiment. The continuous loud stimulus is produced by the loudspeaker irrespective of the evoked aggressive responses of the subject. This represents an unnatural situation, as only in rare instances would an individual continue to produce advertisement calls after being continually threatened by aggressive calls.

Also, as shown by Robertson (1986a) the response to the stimulus may depend upon the relationship of the subject to the stimulus. If the subject was the same weight or heavier than the individual which produced the stimulus then it attacked the loudspeaker. However, if it were lighter then it was observed to retreat. The results obtained in this study were consistent between individuals within a species, although males varied considerably in their SVL. Although subjects were not weighed, it is thought that it is unlikely that a subject's weight, relative to that of the individual from which the source stimulus was made, had any bearing on the behaviour observed in these experiments.

4.4.2 Intensity and spatial information

It appears that calling males may assess their neighbours' positions, relative to their own, by using intensity cues. The results of this study confirm that inter-male spacing in *E. coqui*, *H. marmoratus* and *S. wealii* are vocally mediated and this has been suggested in several other species (Schneider, 1967, 1968; Paillette, 1970; Pierce and Ralin, 1972; Schneider and Nevo, 1972; Allan, 1973; Rosen and Lemon, 1974; Pellers, 1975, 1979a; Whitney and Krebs,

1975a; Brzoska et al., 1982; Telford, 1982; Robertson, 1984; Rose and Brenowitz, 1991). The variation in the intensity of the advertisement call within an individual of a species is quite small, seldom exceeding 2 - 3 dB, while the variation between individuals can be quite large, sometimes as much as 12 dB (Gerhardt, 1975; Brenowitz et al., 1984; but see Lopez et al., 1988).

Consequently, when looking at the spatial organization of calling males of a particular species, the nearest neighbour distances will vary quite considerably reflecting the variation in the intensity of different individuals' advertisement calls. Inter-male spacing within a species will be a direct effect of the complex interactions between the calls of differing intensity.

Telford (1985) provided the first experimental verification of the functional significance of inter-male spacing. He showed that female *H. marmoratus* were significantly more often attracted to loudspeakers which were separated by 50 cm as opposed to 25 cm in phonotaxis experiments. If this were true for most species of anurans which exhibit vocally mediated spacing patterns then the selective pressure acting upon males to adequately space themselves from their near neighbours would be quite considerable.

4.4.3 Territoriality and active space

As mentioned previously, *E. coqui* is the only species in this study which defends an area which can correctly be termed a territory (Hinde, 1956). *E. coqui* do not form aggregations (Narins and Capranica, 1978) but call in fairly low density choruses (M. M. Stewart, personal communication) from distinct territories in which there are defended resources such as oviposition and retreat sites. However, *H. marmoratus* and *S. wealii* only defend specific individual distances (Conder, 1949) which are compressible at high densities (Telford and Dyson, 1988). *E. coqui*

males readily drop the female attractant note (* see footnote) of their call at broadcasts of fairly low intensities (i.e. 83-88 dB) suggesting that in these territorial frogs it is more important to spend time defending their territories and ensuring that their neighbours are sufficiently well spaced relative to themselves, rather than constantly trying to attract a mate.

The results of the increasing intensity broadcast experiments in this chapter suggest that males are intolerant of intruders in their "active space". The active space of an advertisement call is determined by (a) the intensity of the signal (SPL), (b) the amount of attenuation caused by vegetation or the ground and (c) the auditory threshold (and therefore the sex) of the recipient. As the calls of most anurans are only slightly directional, the shape of the active space in an anechoic chamber would be more or less spherical and the attenuation would follow the spherical spreading rule of 6 dB per doubling of distance. However, in the field the shape and size of the active space will vary tremendously depending upon vegetation, climatic conditions and the height of the signaller from the ground.

Due to considerable differences in the tuning of auditory fibres of male and female anurans (Narins and Capranica, 1976; Wilczynski et al., 1984; but see Loftus Hills and Johnstone, 1970), the active space of a male's advertisement call can be divided into two categories dependent upon the sex of the recipient:

* The "gul" note has been shown to play an important role in female attraction, see Narins and Capranica, 1978).

A. Female active space (female recipient).

Since most anurans produce very intense signals and females have relatively low auditory thresholds which are specifically tuned to these signals, the female active space may be very large. *Hyla ewingi* has been shown to have an effective communication distance of up to 100 m (Loftus Hills and Littlejohn, 1971). In an anechoic chamber this distance would be equivalent to the radius of the active space. Unfortunately, the sex of the individual used to determine the auditory threshold of *H. ewingi* was not stated (Loftus Hills and Johnstone, 1970) consequently this can only provisionally be called female active space. Brenowitz et al. (1984) demonstrated that the female active space of a male *Hyla crucifer* advertisement call may be as large as 70 m (in radius), which is 6 times larger than the male individual space (see below). Females are frequently found in a different habitat from males (i.e. in an elevated position rather than at the water's surface). The signal will therefore degrade differently for males and females, producing another sexual difference between the active spaces of advertisement calls. As female active space may be quite large it will suffer from considerable attenuation caused by vegetation and ground effects. Therefore, in most cases female active space will be generally ovoid in shape, with a discontinuous border and a flattened lower limit caused by ground attenuation. Hence a female in an elevated position near the boundary of the active space may accidentally move out of the active space simply by jumping to the ground.

At the boundary of their active space the females exhibit long-range phonotaxis and move in the general direction of the signaller. As they approach the signaller they begin short-range phonotaxis which is characterised by a zig-zag type of approach. The female active space of an individual is not an exclusive zone and may overlap or

contain many other female active spaces and male individual spaces. The parameters which determine the size of female active space are fairly constant during an evening and consequently female active space is an absolute value and is not compressible.

One of the parameters determining the size of the female active space is the intensity of the signal. Furthermore, many authors have shown that, within a species, the intensity of the call is positively correlated with body size. The size of the female active space of a large individual will therefore be greater than that of a smaller individual. However, the correlation between body size and the diameter of the active space will not be very strong, as other parameters such as excess attenuation will play a major role in restricting the size of the female active space.

B. Male individual space (recipient).

Within the female active space there is a smaller, roughly spherical volume surrounding the male. In this report it is termed the male individual space. The size of the male individual space is determined by the intensity of the source signal, chorus density and the behavioural threshold of the recipient. It is a particularly dynamic space and is compressible with increasing densities of chorus participants. It may overlap with or be contained within other female active spaces and is a relatively small volume in which other calling individuals are not tolerated. As a mutually exclusive zone, this space will be defended by aggressive calling and combat against vocalizing conspecifics.

When an individual of either sex enters or calls within the female active space (but outside the male individual space) the behaviour of the signaller remains unchanged.

However, when a female enters or a male calls within a male's individual space then there is an immediate response to the intruder. If the intruder is a female, males will either increase their call rate, turn towards the female or sometimes approach the female. On the other hand if the intruder is a vocalizing male, the resident male will switch to aggressive calling and if the intruder persists, the resident will move towards the intruder and enter into combat. Sometimes silent males are tolerated within the male's individual space as satellite males, but are immediately attacked if they begin calling. On warmer nights, both female active space and male individual space will be larger as the auditory thresholds of the individuals decrease with increasing temperature.

These experiments essentially simulated the approach of a calling conspecific through the female active space and male individual space. Together they have demonstrated an incremental change in response according to call intensity. That is, as the intensity increased, the frogs' behaviour changed from the natural calling pattern, to time-locked responses and aggressive calls, and finally to silence and movements toward or away from the loudspeaker. Aggressive interactions only occurred once the male individual space had been invaded. In conclusion, all the species examined in this section exhibited a graded escalation of time-locked and aggressive responses, linked with increasing call intensity, and hence invasion of active space.

CHAPTER FIVE

INTENSITY AND DISTANCE DISCRIMINATION BY FEMALE *HYPEROLIUS MARMORATUS*

5.1 Introduction

5.1.1 General

The distance over which communication is effective depends upon call intensity, call radiation patterns, hearing thresholds, call propagation, and environmental conditions. The previous chapter highlighted the role of call intensity in male-male interaction and this chapter discusses the significance of call intensity in respect of female behaviour.

5.1.2 SPL and communication distance

One obvious advantage of producing very loud calls is related to the distance over which an individual can communicate. The louder the calls the greater the distance over which communication is effective. There is considerable selective pressure for frogs to communicate over long distances (Passmore, 1981). Most frogs are dependent upon surface water for reproduction and therefore cannot afford to vocalize at any great distance from the water surface. Marten et al. (1977) suggested that the most efficient way animals can increase their effective

communication range is to vocalize from a position at least 1 m above the ground, thereby minimizing excess attenuation due to ground effects. Consequently, although frogs are limited by physiological constraints to vocalizing close to the ground or the water surface, these very intense vocalizations may be an adaptation to long distance communication in close proximity to the ground.

Measurements of natural sound levels coupled with neurophysiological data, enable the determination of the maximum distances over which individuals can communicate effectively. Loftus Hills and Littlejohn (1971) estimated that as *Crinia parainsignifera* has a mean SPL of 87.5 dB (peak at 50 cm) and a hearing threshold of 70 dB, then it can only communicate over a maximum distance of 4 m, while *Hyla ewingi*, with a mean SPL of 100.8 dB (peak at 50 cm) and a hearing threshold of 55 dB, can communicate over a distance of 100 m. *Hyperolius marmoratus* has a mean SPL of 103.5 dB (peak at 50 cm) (Passmore, 1981) and a hearing threshold of 71 dB (Goelst, 1985) which corresponds to an effective communication distance of 32 m.

The numerous applications of sound level measurements warrant the tedious efforts required to record SPL accurately in the field. In many of the earlier behavioural experiments in which male or female anurans were subjected to broadcast calls, the level at which the call was broadcast was chosen subjectively. Gerhardt (1978a) demonstrated the importance of broadcast level on the phonotactic behaviour of female *Hyla cinerea*. He showed that when the broadcast levels were set at 75 or 85 dB, females preferentially selected a call that was entirely pulsed at a depth of 50%. However, when the broadcast level was only 65 dB, this preference was no longer present. It is important to know more about the SPL of animal vocalizations in different habitats, together with sound propagation data, to enable us to predict the extent to which particular signals are adaptive in particular environments. Furthermore, this information

would facilitate the calculation of energy expended, and therefore the cost incurred by the signaller during vocalization.

5.1.3 Call radiation patterns

In studies of female choice and phonotactic behaviour, the call radiation pattern plays an important role. Licht (1976) noted that female *B. americanus* were frequently seen to bypass calling males on their way to a particular caller, and he interpreted this in terms of sexual selection. However, Gerhardt (1975) has characterized male *B. americanus* as directional sound sources, and it is possible that females only appear to bypass males as they do not actually enter the male's directional sound field.

Call radiation patterns may be obtained by taking SPL readings at the same distance from the frog's snout, from the front, side and rear. Several authors have plotted radiation patterns and have found some species to be very directional sound sources (*Hyla chrysoscelis*, *Bufo americanus*, Gerhardt, 1975; *Cacosternum boettgeri*, *Hyperolius pusillus*, *H. argus*, *H. tuberilinguis*, Passmore, 1981; *Philautus leporhinus*, Arak, 1983b), while others act as omnidirectional sound sources (*Hyla crucifer*, Gerhardt, 1975; *Hyperolius marmoratus*, Passmore, 1981; *Uperoleia rugosa*, Robertson, 1984).

As excess attenuation caused by plants may be as high as 7.5 dB at 2 m (Wells and Schwartz, 1982), the above authors made absolute measurements of directivity by either pruning away intervening vegetation or having "line-of-sight clearance" from the microphone of the SPL meter to the calling individual. However, the physical characteristics of the call site can have a profound effect on the sound radiation pattern. Male *Heleioporus* call from breeding burrows and the burrows have been demonstrated to enhance the principal frequency component of the call by resonance

(Bailey and Roberts, 1981). It has also been suggested that the burrow system may compensate for the lack of a vocal sac in *Heleioporus* spp. (Bailey and Roberts, 1981). Greer and Wells (1980) suggested that as most male *Centrolenella fleischmanni* call from the under side of leaves, the leaf may act as a reflector affecting the directionality of the signal. Wells and Schwartz (1982) demonstrated that although *C. fleischmanni* are not directional sound sources, the directional "beaming" of the call was a direct result of the physical nature of the call site. Narins and Hurley (1982) also found that although male *E. coqui* usually had a uniform sound radiation pattern, three out of the 14 individuals studied had directional radiation patterns, with a front-back intensity difference of at least 5 dB. The directional nature of these individuals' calls was directly related to the physical nature of their call sites. An important aspect of directional calls is that they have been suggested to suffer less excess attenuation than non-directional ones (Richards and Wiley, 1980).

5.1.4 Perception of distance

Many authors have demonstrated that the sound pressure level of mating calls in anurans is positively correlated with body size (e.g. Gerhardt, 1975; Wilbur et al., 1978; Berven, 1981; Passmore and Telford, 1983). Also, females of some species exhibit a preference for males with louder calls in experimental situations (Fellers, 1979a; Ryan, 1980; Fairchild, 1981; Dyson, 1985). From the results of these experiments, it has been suggested that considerable selective pressures may be acting on large male body size through female preference for louder calls. This is an attractive idea for advocates of sexual selection theory, but very few studies have examined whether a female can differentiate between quiet calls that emanate from a nearby source and loud calls from more distant points.

Perhaps females are responding simply to the loudest male because he is the closest, and not necessarily because his call is intrinsically one of the loudest in the chorus. Arak (1983c) demonstrated that female *Bufo calamita*, preferred calls which differed only by 2 dB. However, when the loudspeakers were placed at different distances from the female and their intensities adjusted to be the same at the female release point, there was no preference exhibited. Consequently he suggested that females were simply passively attracted to the call perceived at the highest intensity.

In order for females to mate preferentially with males that produce more intense signals, they would need to be able to assess the distance of a calling male and then calculate his absolute intensity. Ramer et al. (1983) suggested that females may select larger males by using acoustic cues alone. They studied *R. clamitans* which produces (among others) a single note advertisement call. This call can be divided into two frequency ranges: 1) a low frequency range (200 - 450 Hz), and 2) a mid frequency range (500 - 1 000 Hz). The excitatory-inhibitory ratio (EIR) was used by Ramer et al. (1983) for scoring advertisement calls and was obtained by dividing the low frequency intensity by the mid frequency intensity. They found that EIR correlated positively with SVL in *R. clamitans*. Consequently, small males had a low EIR, as the amplitude for the most intense low frequency was considerably smaller than the amplitude for the most intense mid frequency. The opposite is true for large males. Therefore small males had a lot more energy in the mid frequency range than the low frequency range while the opposite occurred in large males. They suggested that a large EIR score would indicate to a female that the call was produced by a large and long lived male, and females should be more attracted to these males. However, as high frequencies attenuate faster than low frequencies (Konishi, 1970) from a distance a small male

would appear to have a higher EIR, as the ratio of low/mid frequencies swings in favour of the low frequency. Consequently females could only use EIR as a cue for large males at close distances.

As most frogs' calls do not have separate elements that degrade predictably with distance, the possibility that a female could calculate absolute intensity from differential frequency attenuation seems unlikely, and was tested using various combinations of intensity and distance in simple two-choice discrimination experiments.

5.1.5 Two-choice intensity discrimination experiments

The two-choice discrimination experiment was first introduced by Littlejohn and Michaud (1959). They tested the ability of gravid female *Pseudacris streckeri* to discriminate between calls of conspecific males and calls of a sympatric species. They broadcast either conspecific calls, or those of a sympatric species, through loud speakers at each end of an enclosure. Females were caught in amplexus and tested after being separated from the male and allowed a short period to become adjusted to the artificial environment. Since that time, the two-choice discrimination experiment has been widely used to test the preferences of female anurans to various synthetic and natural mating calls.

Indeed, many authors have experimentally demonstrated, using the two-choice discrimination experiment, that female anurans preferentially select the louder of two broadcast calls (Fellers, 1979a; Fairchild, 1981; Arak, 1983c; Dyson, 1985). Large male *H. marmoratus* produce significantly louder calls than small males (Passmore and Telford, 1983) and females preferentially approach louder calls in two-choice discrimination experiments (Telford, 1982; Dyson, 1985). However, there seems to be some confusion over the differences in intensity that a female can detect which may be an artefact of the experimental design (see Telford,

1982; Dyson, 1985).

In this chapter I re-examine the preference and discrimination ability of female *H. marmoratus* to conspecific calls varying in intensity and distance in the simple two-choice experiment.

5.1.6 Four-choice discrimination trials

As mentioned above, the results of simple two-choice discrimination experiments suggest that female anurans preferentially select the larger or louder male (Fellers, 1979a; Ryan, 1980; Fairchild, 1981; Arak, 1983c; Dyson, 1985). It has already been mentioned that large males of *H. marmoratus* produce louder calls than small males (Passmore and Telford, 1983), consequently in natural populations females would be expected to exhibit a preference for the larger males. However, in observations of natural pairings of *H. marmoratus* females were not influenced either by size or age in the selection of their mates (Passmore and Telford, 1983; Dyson et al., 1992). Although larger male *H. marmoratus* call louder, and females are preferentially attracted to louder calls in two-choice discrimination trials, these preferences are not reflected in natural matings.

Gerhardt (1982) discovered that when female *H. cinerea* were given a choice of four loudspeakers broadcasting different frequencies, their performance was somewhat reduced when compared to a two loudspeaker choice. The two loudspeaker choice is an unnaturally simple choice for a female to be confronted with, and perhaps more reliable data can be obtained from studies of multiple loudspeaker choices, which are more closely allied to natural conditions.

In this chapter I investigate the effect of increasing the complexity of choice on the intensity preferences and discrimination ability of female *H. marmoratus*. The

results were then compared with those obtained from simple two-choice discrimination trials. The overall objective of this chapter was to determine if female *H. marmoratus* could differentiate between the confusing effects of SPL and distance, and also to examine intensity preferences in simple and more complex discrimination experiments. Towards this main objective the answers to the following questions were sought:-

1) When presented with two calls differing only in intensity do female *H. marmoratus* preferentially approach the most intense call, and if so what is the smallest difference in intensities that they can detect?

2) Is the behavioural preference shown in (1), significantly altered by increasing the complexity of choice in four-choice discrimination trials?

3) Can female *H. marmoratus* distinguish between quiet calls that emanate from a nearby source and loud calls from more distant points in simple two-choice discrimination experiments?

5.2 Methods

5.2.1 General materials

Amplexing pairs of *H. marmoratus* were collected from two shallow ponds near Mtunzini, Zululand during January 1985, (for a detailed description of the study site and species see Chapter one and Appendix B). The frogs were transported soon after capture to the testing arena less than 3 km away, and females were tested within 5 hours of capture. The testing arena was situated in an open outside area, away from any buildings or large trees, and consisted of a 2.5 x 2.5 m flat canvas floor surrounded by low canvas walls 40 cm high. The arena was provided with dim illumination by a single 60 W red bulb suspended 1 m above the female release point.

Air temperature ranged from 18.3 - 26.3 C during the period in which these experiments were conducted.

Each female was gently separated from the amplexing male immediately before the first trial and placed at the release point in the centre of the arena under a plastic mesh release cage. The stimuli were broadcast to the female and after two minutes the release cage was slowly removed without disturbing the female. If the female failed to locate a loudspeaker within 10 min she was discarded and not used again. A positive response was scored when a female approached within 5 cm of a loudspeaker, or contacted a loudspeaker. Once the female had completed a trial she was returned to the release cage and the above procedure was repeated for the next combination of stimuli.

The acoustic stimulus was a synthetic standard call (see Chapter four, section 4.2.2) that was behaviourally

equivalent to a typical natural call (see Dyson and Passmore, 1988a, b; Backwell et al., 1991). Each stimulus had a repetition rate of 60 calls/min which approximates the natural calling rate of males at the pond. The stimulus tape was relayed from a Nagra III tape recorder to a four-channel analogue sequence controller specifically designed for this experiment. The sequence controller was constructed by J Nel (Central Electronic Services, University of the Witwatersrand). The sequence controller allowed the stimulus to be routed to successive Portamon speaker-amplifiers in a regular sequence. It was imperative to utilise the sequence controller as various temporal relationships between broadcast stimuli have been shown to have a strong influence on female preferences in discrimination experiments. If one stimulus overlaps or shortly follows another, females of this species have been shown to prefer the leading stimulus irrespective of frequency and/or intensity differences (Dyson and Passmore, 1988a, b). Consequently, the sequence controller eliminated any possible temporal bias as the same synthetically generated signal was broadcast from each loudspeaker, with an identical intercall interval. The number of sequential outputs could be varied from one to four depending upon the experimental demand. The loudspeaker which broadcast the first call in a trial was randomised utilizing the four-channel sequence controller.

Peak SPLs were measured with a Brüel and Kjaer 2230 precision integrating sound level meter, used in conjunction with a B & K 4165 microphone, a flexible microphone extension rod (B & K UA0196) and a microphone dehumidifier (B & K UA0308).

5.2.2 Two-choice intensity discrimination trials

Female *H. marmoratus* were placed in the centre of the arena and presented with four different pairings broadcast from

loudspeakers placed at equal distances from the release point, (the arrangement of loudspeakers is shown in Fig. 5.1). One loudspeaker always broadcast a call of 104 dB at 50 cm, and again to eliminate any bias, the end which housed this "standard" loudspeaker was frequently alternated and the pairings were presented in an irregular order.

The standard loudspeaker was paired with one of the following for each trial:-

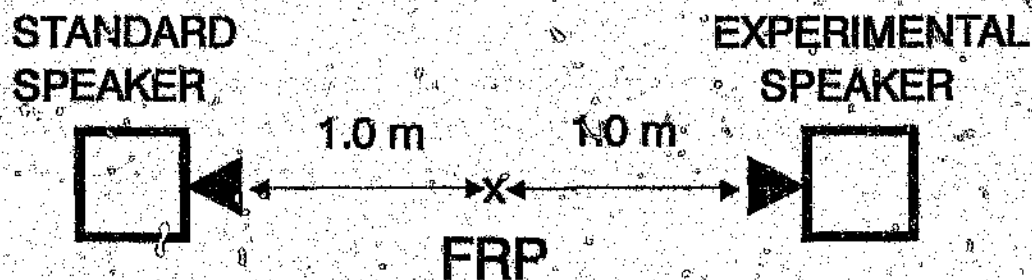
Trial 1: Standard speaker vs Experimental speaker with a broadcast call of 101 dB (peak SPL at 50 cm). This call attenuated to a SPL of 93 dB at the female release point.

Trial 2: Standard speaker vs Experimental speaker with a broadcast call of 98 dB (peak SPL at 50 cm). This call attenuated to a SPL of 90 dB at the female release point.

Trial 3: Standard speaker vs Experimental speaker with a broadcast call of 92 dB (peak SPL at 50 cm). This call attenuated to a SPL of 85 dB at the female release point.

Trial 4: Standard speaker vs Experimental speaker with a broadcast call of 104 dB (peak SPL at 50 cm). This call attenuated to 98 dB (peak SPL) at the female release point.

Trial 4 represents a control pairing, as both loudspeakers are broadcasting calls at the same peak SPL (i.e. 104 dB at 50 cm), and are equal distances from the female release point.



FRP = FEMALE RELEASE POINT

Fig. 5.1 Two-choice intensity discrimination trials

5.2.3 Four-choice intensity discrimination trials

Female *H. marmoratus* were placed in the centre of the arena and presented with eight trials of four calls broadcast at equal distances from the female release point, (the arrangement of loudspeakers and a diagrammatic representation of the equipment is shown in Fig. 5.2). In each of the eight trials at least one of the loudspeakers was broadcasting a call at a peak SPL of 104 dB at 50 cm. The order in which the eight trials were presented to the female was irregular to exclude any possible bias. Each series consisted of the standard speaker linked with one of the following arrangements:-

Trial 1: Standard speaker vs three speakers all broadcasting calls at a SPL of 101 dB.

Trial 2: Standard speaker vs three speakers all broadcasting calls at a SPL of 98 dB.

Trial 3: Standard speaker vs three speakers all broadcasting calls at a SPL of 92 dB.

Trial 4: Standard speaker vs one speaker broadcasting a call at a SPL of 101 dB, one speaker broadcasting a call at a SPL of 98 dB, the other speaker broadcasting a call at a SPL of 95 dB.

Trial 5: Standard speaker vs one speaker broadcasting a call at a SPL of 98 dB, one speaker broadcasting a call at a SPL of 92 dB, the other speaker broadcasting a call at a SPL of 86 dB.

Trial 6: Standard speaker vs two speakers broadcasting calls at a SPL of 101 dB, the other broadcasting a call at a SPL of 104 dB.

Trial 7: Standard speaker vs two speakers broadcasting calls at a SPL of 98 dB, the other broadcasting a call at a SPL of 104 dB.

Trial 8: Standard speaker vs three speakers all broadcasting calls at a SPL of 104 dB. This choice acted as the control choice.

All SPLs quoted above were peak SPL measured at a distance of 50 cm, and their corresponding attenuated values at the female release point can be seen in Table 5.2.

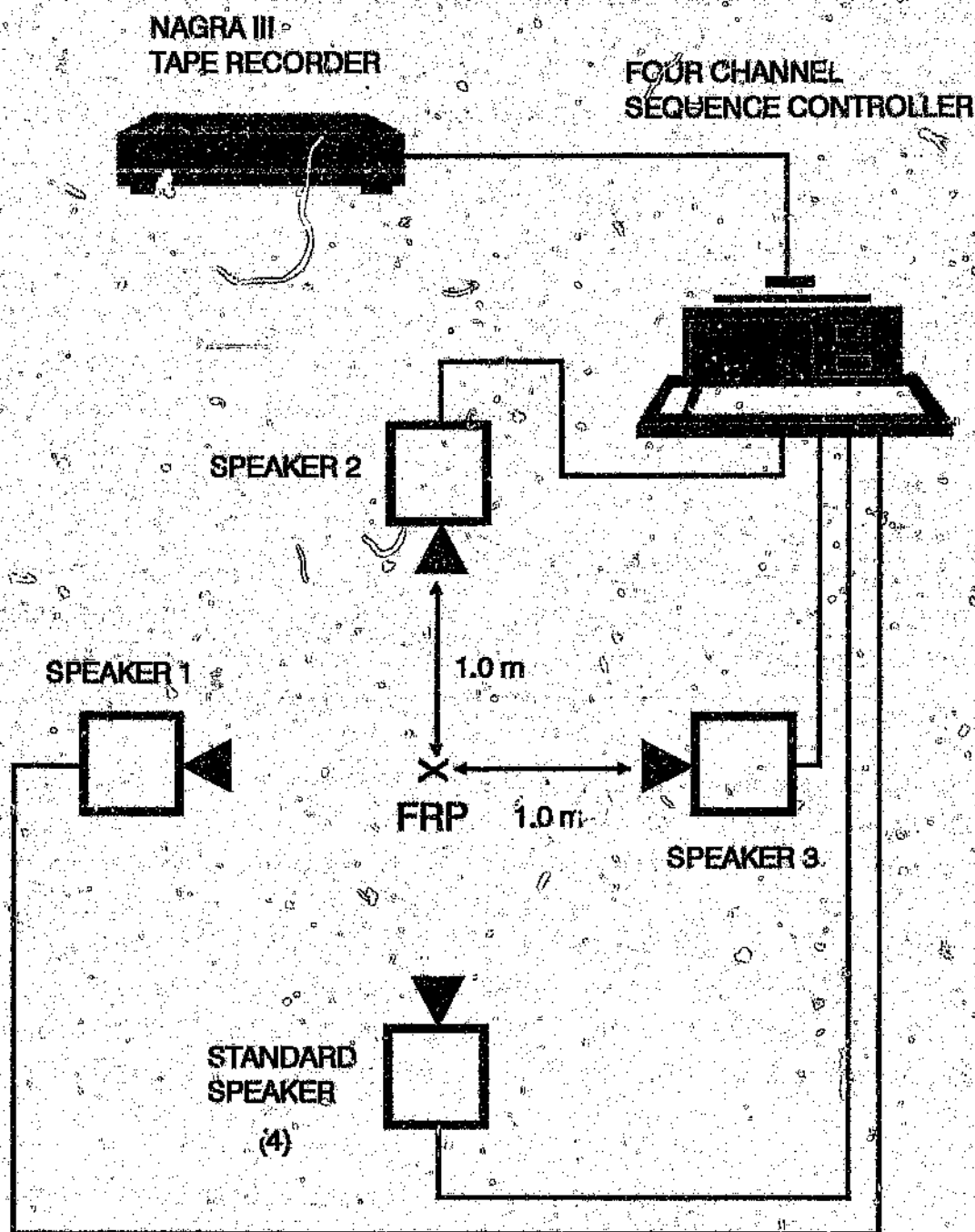


Fig. 5.2 Four-choice intensity discrimination trials

5.2.4 Distance versus intensity discrimination trials

The females were presented with seven different stimulus pairings in which one loudspeaker always broadcast a call at 104 dB SPL at 50 cm and was at a fixed position 1 m from the female release point (standard speaker see Fig. 5.3). This call attenuated to give a SPL of 98 dB at the female release point. In order to eliminate any possible bias, the ~~egg~~ which housed the standard loudspeaker was frequently changed, and the order with which a female was presented with the seven stimulus pairings was randomised. The standard speaker was paired with one of the following for each trial:-

Trial 1: Standard speaker vs Experimental speaker with a broadcast call of 109 dB (peak SPL at 50 cm), placed 2 m from the female release point. This call attenuated to 98 dB (peak SPL) at the female release point.

Trial 2: Standard speaker vs Experimental speaker with a broadcast call of 110 dB (peak SPL at 50 cm), placed 2 m from the female release point. This call attenuated to 99 dB (peak SPL) at the female release point.

Trial 3: Standard speaker vs Experimental speaker with a broadcast call of 115 dB (peak SPL at 50 cm), placed 2 m from the female release point. This call attenuated to 102 dB (peak SPL) at the female release point.

Trial 4: Standard speaker vs Experimental speaker with a broadcast call of 104 dB (peak SPL at 50 cm), placed 1 m from the female release point. This call attenuated to 98 dB (peak SPL) at the female release point.

Trial 5: Standard speaker vs Experimental speaker with a broadcast call of 104 dB (peak SPL at 50 cm), placed 1.16 m from the female release point. This call attenuated to 95

dB (peak SPL) at the female release point.

Trial 6: Standard speaker vs Experimental speaker with a broadcast call of 104 dB (peak SPL at 50 cm), placed 1.4 m from the female release point. This call attenuated to 93 dB (peak SPL) at the female release point.

Trial 7: Standard speaker vs Experimental speaker with a broadcast call of 104 dB (peak SPL at 50 cm), placed 2.07 m from the female release point. This call attenuated to 90 dB (peak SPL) at the female release point.

Trial 4 represents a control pairing, as both loudspeakers are broadcasting calls at the same SPL (i.e. 104 dB at 50 cm), and are equal distances from the female release point. The arrangement of the loudspeakers is illustrated in Fig. 5.3.

5.2.5 Statistical methods

With discrimination trials that only involved two speakers the Binomial test was used to determine levels of significance. The results obtained in the four-speaker trials were compared with the respective two speaker trials and Fisher's exact test was used to determine if any significant differences existed at the 0.05 probability level. The Chi-square test was used to determine if the distribution of female responses to the four loudspeakers was significantly different from a uniform distribution.

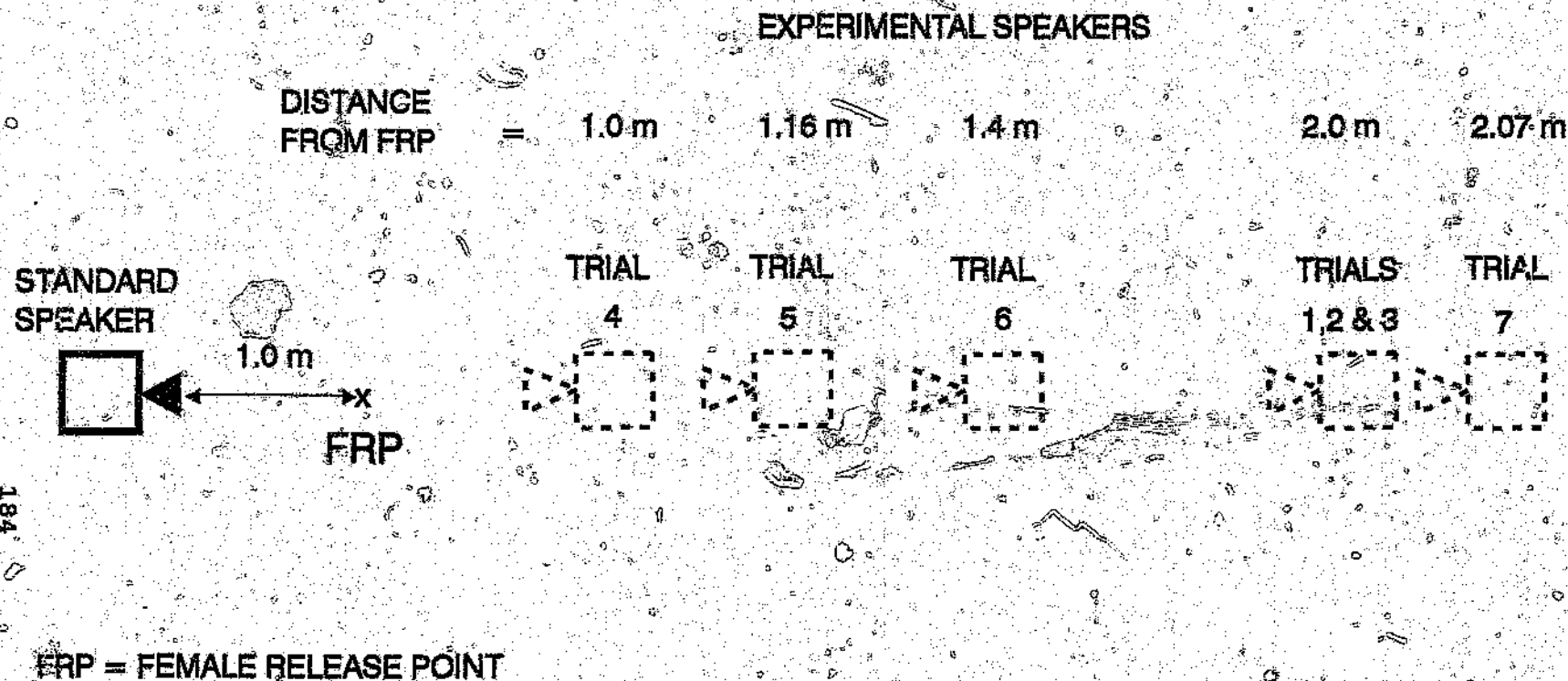


Fig. 5.3 Intensity vs distance discrimination trials

5.3 Results

5.3.1 Two-choice intensity discrimination trials

Thirty-five two-choice intensity discrimination trials, using 21 females, were conducted. The results are summarised in Table 5.1. In this experiment both the loudspeakers were kept at a fixed position of 1 m from the female release point (see Fig. 5.1). When the difference between the SPL of the loudspeakers was 5 dB or more at the female release point the females showed a significant preference for the loudest call, (Binomial test, $P < 0.05$).

TABLE 5.1

Results of two-choice intensity discrimination trials

Trial no.	Standard speaker	Experimental speaker		
	Score	Score	SPL	
1	<u>11</u>	2	101	(93)
2	<u>11</u>	1	98	(90)
3	<u>10</u>	0	92	(85)
4	9	11	104	(98)

The standard speaker was set at a SPL of 104 dB at 50 cm which attenuated to 98 dB at the female release point.

SPL = peak SPL (dB) at 50 cm in front of speaker, peak SPL (dB) at the female release point in parentheses.

Score = Number of females positively responding to a particular speaker. Each speaker placed 1 m from female release point (see Fig. 5.1). Significant results are underlined (Binomial $P < 0.05$).

5.3.2 Four-choice intensity discrimination trials

Two hundred and forty-three four-choice intensity discrimination trials, using 37 females, were conducted. The results are summarised in Table 5.2. When females were presented with the choice in trial 1 (i.e. one loudspeaker at a SPL of 104 dB at 50 cm and the other three at a SPL of 101 dB at 50 cm; equivalent to a 5 dB difference at the female release point), there was no significant preference for any loudspeaker. Also, with the choice in trial 2, equivalent to a 8 dB difference at the female release point, there was no significant preference for the louder call. Trial 1 and trial 2, differ significantly (Fisher's exact test, $P < 0.05$), from trial 1 and trial 2 of the two-choice discrimination experiments. This indicates that although the difference in SPL is the same, the female's behaviour has been significantly altered by the addition of speakers or in other words by increasing the complexity of choice. Only when there was a 13 dB difference at the female release point (trial 3) did females exhibit a distinct preference for the loudest speaker.

When there was a step-wise 3 dB or 6 dB difference at 50 cm in front of each speaker (trials 4 and 5), the females showed a considerable preference for the loudest broadcast. If two loudspeakers were kept at 104 dB at 50 cm, and the other two at 101 dB or 98 dB at 50 cm (trials 6 and 7), then there was a preference for the loudest broadcast, although these results were not as clear-cut as the corresponding trials in the two-choice discrimination experiment.

If all the loudspeakers were broadcasting calls at the same intensity (trial 8) then the females did not show a preference for a particular loudspeaker and the distribution of female responses was not significantly different from a uniform distribution (Chi-square test $\chi^2 = 0.35$, $P > 0.9$, $df = 3$).

TABLE 5.2

Results of four-choice intensity discrimination trials

Trial no.	Experimental speaker numbers			Standard speaker
	1	2	3	4
1	SPL 101 (93)	101 (93)	101 (93)	104 (98)
	Score <u>6</u>	<u>11</u>	7	8
2	SPL 98 (90)	98 (90)	98 (90)	104 (98)
	Score 7	6	8	8
3	SPL 92 (85)	92 (85)	92 (85)	104 (98)
	Score 7	1	1	19
4	SPL <u>95 (87)</u>	98 (90)	101 (93)	104 (98)
	Score <u>6</u>	2	5	17
5	SPL 86 (78)	92 (85)	98 (90)	104 (98)
	Score 0	3	6	22
6	SPL 101 (93)	101 (93)	104 (98)	104 (98)
	Score 6	2	9	14
7	SPL 98 (90)	98 (90)	104 (98)	104 (98)
	Score 4	3	10	14
8	SPL 104 (98)	104 (98)	104 (98)	104 (98)
	Score 7	7	9	8

SPL = peak SPL (dB) at 50 cm in front of speaker, peak SPL (dB) at the female release point in parentheses.

Score = Number of females positively responding to a particular speaker.

Each speaker placed 1 m from female release point (see Fig. 5.2). Results that differ significantly from the corresponding two-choice intensity discrimination trials are underlined (Fisher's exact test $P < 0.05$).

5.3.3 Distance versus intensity discrimination trials

One hundred and nineteen distance-versus-intensity discrimination trials, using 42 females were conducted. The results are summarised in Table 5.3. In the control experiment (trial 4), where females were presented with calls from the same distance at equal intensities no preference was shown for either speaker. In trials where the difference between the SPL of the loudspeakers was 3 dB or less at the female release point, females failed to show a significant preference for either call. However, when the difference in SPL at the female release point was 4 dB or greater the females showed a significant preference for the loudest call irrespective of its distance from the release point, or its absolute SPL at 50 cm from the loudspeaker. For example, in trial 3, there was a 4 dB difference at the release point, and the females showed a significant preference (Binomial test, $P < 0.05$) for the louder call even though it was twice the distance of the opposing call. In trial 6, there was a 5 dB difference, and females significantly chose the loudest broadcast, which in this case was the closest loudspeaker. (Binomial test, $P < 0.05$).

Females respond significantly to the call which is perceived to be 4 dB or greater than the other call at the female release point, irrespective of absolute SPL.

TABLE 5.3

Results of distance vs intensity discrimination trials

Trial no.	Standard speaker	Experimental speaker		
	Score	Score	SPL	Distance
1	10	11	109 (98)	2.0
2	7	10	110 (99)	2.0
3	5	13	115 (102)	2.0
4	9	11	104 (98)	1.0
5	9	8	104 (95)	1.16
6	9	1	104 (93)	1.4
7	13	3	104 (90)	2.07

SPL = peak SPL (dB) at 50 cm in front of speaker, peak SPL (dB) at the female release point in parentheses.

Score = Number of females positively responding to a particular speaker.

Distance = Distance of experimental speaker from female release point.

Significant results are underlined (Binomial Test, $P < 0.05$)

5.4 Discussion

5.4.1 Female intensity preferences in a two-choice situation

The results in Table 5.1 show that female *H. marmoratus* are significantly more attracted to the louder of two calls when the difference between the calls, at the female release point, is 5 dB or more. The response can be seen to be graded so that the larger the intensity difference the greater number of females choosing the louder call.

These results support the findings of Dyson (1985) which are in conflict with those of Telford (1982) who found that female *H. marmoratus* sometimes exhibited a clear-cut preference for calls that differed by 3 dB at 50 cm from the loudspeaker, while at other times only exhibited this preference when the calls differed by 6 dB or more, at 50 cm from the loudspeaker. Unfortunately, neither of these authors measured the actual SPL perceived by the female but simply assumed the inverse square law to hold true under field conditions. When they were comparing female responses to differences in intensities of 3 dB, at 50 cm from the loudspeaker, this difference was probably 4 - 6 dB at the female release point, dependent upon the many factors involved in excess attenuation of signals close to the ground (see section 5.1.1). Consequently this may explain why Telford (1982) obtained confusing results with a 3 dB difference at 50 cm but a clear-cut response at a 6 dB difference at 50 cm. In the latter case this difference was probably as much as 7 - 9 dB perceived by the female.

In the experiments described here very precise measurements were made at the position of the female's head in order to calculate the absolute differences perceived by the female

under the experimental conditions. Each of these measurements was repeated at least 10 times in order to eliminate any errors caused by climatic changes. However, the SPL measured by an SPL meter may tell a very different story from what a female hears and physiologically responds to (see Zelick and Narins, 1985b). In addition the design of two choice experiments is such that as soon as a female begins to approach the louder call, the intensity of the other call will diminish with distance. This has the effect of increasing the SPL difference of the calls reinforcing the phonotactic behaviour of the female to the call she first responds to.

Passive attraction of females to the call perceived at the loudest intensity may be attributed to the physical properties of their auditory system. For example, a call perceived at a low SPL just above the auditory threshold would provide a relatively low level stimulus when compared to calls perceived at a SPL much higher than the auditory threshold. Feng (1981) studied the directional response characteristics of single neurons in the torus semicircularis of *Rana pipiens* and discovered that there was an overall increase in the mean number of spikes per second (firing rate), in a single unit, with increasing intensity. He showed that when the stimulus intensity was just above threshold (32 dB), the firing rate was slightly above the spontaneous firing rate, however with a 20 dB elevation in stimulus intensity there was at least a three fold increase in firing rate. Capranica and Moffat (1975) studied the response properties to different frequencies and intensities of single auditory nerve fibres in the eighth nerve of a spadefoot toad (*Scaphiopus couchii*). They discovered that as the intensity of the stimulus was increased, low-frequency and high-frequency units increased their discharge rate monotonically over a range of about 30 - 40 dB above threshold. For example, at a stimulus intensity of 80 dB SPL one low-frequency unit had a firing rate of 28 spikes/s, at 90 dB SPL it had a firing rate of

70 spikes/s and it reached a peak of 125 spikes/s at 110 dB SPL. These authors have demonstrated that a louder call will produce a high level stimulus in the auditory system, compared with a call just above threshold level. This suggests that the reason why females prefer calls which are 5 dB louder than other calls is due to the increase in firing rate within their auditory system. Consequently females are simply choosing the call which produces the highest level of stimulus in their auditory system.

5.4.2 Effects of confounded four-choice discrimination trials on the intensity preferences of females

In the two-choice discrimination experiments (see Table 5.1) and the distance vs intensity discrimination experiments (see Table 5.3) it was shown that females displayed a significant preference for the louder of two calls, when the difference in intensities perceived by the females was only 4 - 5 dB. This preference was shown to be independent of the absolute intensity of the signal and the distance of the source from the female. However, when the females were presented with a series of three quiet calls of the same intensity and one loud call (Section 5.2.3, trials 1, 2 and 3), there was no preference for the loud call when it was 5 - 8 dB (Section 5.2.3, trials 1 and 2) louder than any of the quiet calls. The preference for the louder call was only present when this intensity difference was elevated to 13 dB at the female release point.

In the four-choice discrimination experiment, where each call is at least 20 dB above the hearing threshold for *H. marmoratus* (trials 1 and 2), there will be a high level stimulus in the auditory nerves for each call. As the

firing rate increases proportionally with increasing intensity (Capranica and Moffat, 1975; Feng, 1981) then at a signal intensity of only 15 dB above threshold (85 dB in trial 3) there will be a considerably reduced firing rate when compared with trials 1 and 2. As the female is presented with four calls, all of which constitute a high level stimulus in the auditory system (in trials 1 and 2), then she may be confused with respect to differentiating the slightly higher-level stimulus and selects the calls at random. When the difference in firing rates produced by the calls becomes greater as the intensity difference increases, then females are able to differentiate between quiet calls and loud calls (trial 3, see Table 5.2). When females are presented with many calls at similar intensities she is unable to distinguish which calls are slightly louder, possibly as a result of the physical properties of her auditory system. However, when this difference is sufficiently large to produce a substantial difference in firing rate in the auditory system then females are passively attracted to the calls which produce a high level stimulus within the auditory system.

In all the other trials of the four-choice discrimination experiment, females preferentially selected the loudest call. This is probably due to the fact that in trials 4 and 5 the female was given a range of SPL and this consequently led to a range from low-level to high-level stimuli in the auditory system which facilitated determination of the loudest call. In trials 6 and 7, the calls presented to the females produced an equal ratio of low-level and high-level stimuli in the auditory system and females were able to easily differentiate between the quiet calls and the loud calls. These latter two trials actually represent a doubling of the simple two-choice experiments where females could easily distinguish between two calls differing by 5 dB (see Table 5.1).

Unfortunately the relationship between call intensity and individual fibres' discharge rate within the torus semicircularis is unknown for *H. marmoratus*. In addition, the discriminatory ability of their auditory apparatus to differentiate between many calls of similar intensities has not yet been examined. Neurophysiological data of this nature would be necessary to substantiate the above suggestions but unfortunately fall outside the scope of this thesis.

Gerhardt (1982) compared the ability of female *H. cinerea* to discriminate between stimuli of differing low frequency peaks in two- and four-choice situations. He found that in four-choice situations "contrary to their performance in the two-stimulus situation, the animals did not prefer the 900 Hz-signal over the 700 Hz-call". He suggested that the female's performance is reduced in the four-choice or more complex situations, especially when the differences among the stimuli are small. In the experiments reported here, when a two-choice situation was made more complex by the addition of speakers playing broadcasts at the same low intensity, the female's performance was considerably reduced. The females only preferred the louder call when it was over four times louder than the quiet calls, whilst in the two-choice situation, females preferred the louder call when it was less than twice the intensity of the quiet calls.

In natural populations of *H. marmoratus* inter-individual variation in SPL of mating calls was found to be only 5 dB (Passmore and Telford, 1983) and as males call in dense clusters, then it is likely that females will be confronted with many males calling at similar intensities. Trials 1 and 2 (of the four-choice discrimination experiment), are the experimental conditions that most closely represent the natural situation. Consequently this would explain why mating was found to be random with respect to size and therefore call intensity (Passmore and Telford, 1983).

In summary, authors should be very wary of making assumptions of the importance of various call parameters from the results of simple two-choice phonotaxis experiments without supporting evidence from field observations or more complex phonotaxis experiments.

5.4.3 Discrimination between call intensity and distance by females

In many field studies females have been found to mate preferentially with larger males and the body size differences between unmated males and mated males have often been ascribed to the effects of active female choice (Davies and Halliday, 1977; Wilbur et al., 1978; Fellers, 1979a; Ryan, 1980, 1983a; Fairchild, 1981; Gatz, 1981a, b). Several of these authors suggest that the increased mating success of large males is mainly due to females choosing mates on the basis of certain call parameters and little attention has been given to the effects of certain male traits known to influence mate choice, for example, male-male competition.

Growth in frogs is assumed to be indeterminate and larger males are thought to be older males. It has been demonstrated that a distinct relationship exists between the SPL, call frequency and male body size in anurans (Zweifel, 1968; Gerhardt, 1975; Oldham and Gerhardt, 1975; Wilbur et al., 1978; Ryan, 1980; Berven, 1981; Passmore and Telford, 1983). Consequently in most anurans, larger males produce louder calls with lower frequencies. Females have been shown to preferentially approach the louder broadcast call in simple two-choice experiments (Fellers, 1979a; Arak, 1983c; Dyson, 1985 and this study). In the light of these experimental observations many authors have suggested that the older, larger, males are "fitter" than the smaller males and that females actively choose these fitter males as mates, on the basis of certain call parameters. The

genetic qualities of the fitter males are assumed to be inherited by their offspring, (although both Borgia (1979, 1981) and Arak (1983c) consider this unlikely.

In *H. marmoratus* larger males have been demonstrated to produce louder calls with a lower frequency (Passmore and Telford, 1983) and females preferentially approach louder or lower frequency calls (Dyson, 1985; Telford et al., 1989). Consequently, it would be logical to predict that in natural populations of *H. marmoratus*, females would mate preferentially with larger males and sexual selection would act in favour of large male body size. However, in extensive field studies on *H. marmoratus* (Passmore and Telford, 1983; Dyson et al., 1992), there was no relationship between age and body size of males and mating was found to be random with respect to age and body size. In order for a female to actively choose a mate which has an intrinsically louder call she must be able to differentiate between signals broadcast from a close male and a distant male. Hence, the female needs to be able to assess the absolute intensity of a male's signal and also to calculate his distance from her. The results summarized in Table 5.3 indicate that females are only responding to differences in intensity perceived at the female release point irrespective of absolute intensity. When the difference in SPL at the release point was 3 dB or less (trials 1, 2, 4 and 5), females did not show a preference for either loudspeaker, although the difference in absolute SPL of the speakers was sometimes as much as 6 dB, i.e. one being twice as loud as the other (trial 2). In these results females appeared to be unable to assess the distance of a signal (and therefore the absolute SPL) and were simply passively attracted (*sensu* Parker, 1982, 1983) to the loudest call perceived at the female release point. If the call contained several different frequency components, then perhaps the female could assess the

distance from a calling male by detecting the differential attenuation of these frequency components. However, due to the fairly short distances over which a female actually responds to an individual call, these differences in attenuation of the different frequency components will be minute and probably too small to detect. The call of *H. marmoratus*, as described in Chapter one, does not have extensive frequency modulation and, therefore, the assessment of distance by differential attenuation seems very unlikely in this species.

In a similar study on *Bufo calamita* (Arak, 1983c), females did not respond preferentially to louder calls when the SPL of the loudspeakers were identical at the female release point. In his experiments Arak found that females preferentially chose the louder call when the difference in SPL at the release point was only 2 dB. Also Fellers (1979a) discovered that female *Hyla versicolor* preferentially approached the louder of two speakers when the difference in SPL at the centre point of the arena was again 2 dB.

The results summarised in table 5.3 may be used to explain the conflict between experimental results and natural observations of matings in *H. marmoratus*. Although female *H. marmoratus* are passively attracted to louder calls in simple two-choice experiments, in the field females are confronted with many males at different distances from them. They would be passively attracted to the ones which they perceived to be calling at least 4 dB louder than neighbouring males, irrespective of the male's distance from the female. Consequently, as the preference for louder calls is attributable to passive attraction and not active female choice, then random mating with respect to size would be expected in natural populations. Also, in these experiments, females only showed a significant preference for calls that differed by 4 - 5 dB. Further,

as the maximum variation between individuals in this population was only 5 dB ($n = 21$) (Passmore and Telford, 1983) there will only be a small number of males in the natural population which are calling at a sufficiently high intensity to gain an advantage over the other males. However, as mentioned previously males call at elevated positions in distinct clusters and it is likely that size related vocal cues such as intensity will be confounded. Females approaching clusters will be presented with similar sized males producing similar calls at different distances from the females. Therefore, it is very unlikely that a loud calling male will be at any advantage over a quieter male with respect to female choice. Active female choice may play an important role in species which have a greater inter-individual variation in SPL and call at ground level from the perimeter of a pond.

Non-random mating with respect to size has been documented for many species (Licht, 1976; Davies and Halliday, 1977, 1979; Wells, 1977a, b, 1979; Howard, 1978a, b, 1980; Wilbur et al., 1978; Ryan, 1980; Berven, 1981; Gatz, 1981a, b; Fairchild, 1981; Lee and Crump, 1981; Woodward, 1982a, b) and it is still uncertain what roles inter-male competition and active female choice play in determining the variation in male mating success.

If females are displaying active choice for a particular call parameter such as intensity or frequency, then this preference should persist irrespective of changes in other call parameters. However, Telford and Passmore (1985) have demonstrated that the low frequency preference of female *H. marmoratus* can be reversed by increasing the intensity or repetition rate of the least preferred call, and Gerhardt (1978b) extinguished the preference for entirely pulsed calls by female *Hyla cinerea* by decreasing the broadcast level. Also, Ehret and Gerhardt (1980) discovered that female *H. cinerea* chose a continuous noise broadcast, as often as they chose the unmasked synthetic mating call when

the SPL of the noise was increased from 40 dB to 50 dB. Consequently these results suggest that neither intensity nor frequency are used as criteria by which females actively choose mates, and they support the notion that females are passively attracted to certain stimuli as a result of the neurophysiological design of their auditory system.

CHAPTER SIX

CALLING BEHAVIOUR AND MATE CHOICE IN *HYPEROLIUS MARMORATUS*

6.1 Introduction

6.1.1 General

It has been suggested that males may try to out-signal competitors (Parker, 1983), thereby increasing their chances of securing a mate. Within a breeding assemblage of male anurans there are several ways in which a male may out-signal his competitors:

- 1) Simply by increasing the number of nights in which he participates in the chorus, a male may influence his mating success (e.g. Greer and Wells, 1980; Gatz, 1981b; Arak, 1983c; Godwin and Roble, 1983; Jacobson, 1985; Gerhardt et al., 1987; Morris, 1989; Ritke and Semlitsch, 1991).

- 2) Also, by increasing the amount of time he spends calling within a night (calling persistence) a male may attract more mates. Forester et al. (1989) found that significantly more females were attracted to speakers that were "on the air" for 80% of the test period, rather than 20 - 60%.

- 3) By increasing his call duration a male may spend more time "on the air" and females of some species are more attracted to longer calls (Klump and Gerhardt, 1987).

- 4) By increasing the intensity of his call a male may be able to communicate over a longer distance, thereby

increasing his active space (see Chapter four) and may enjoy differential mating success (Arak, 1983c, 1988b; Forester and Czarnowsky, 1985; Gerhardt, 1987).

5) By increasing call rate, a male may obviously out-signal his rivals, and it has been shown that many species, in two-choice discrimination tests, prefer faster repetition rates (Forester and Czarnowsky, 1985; Gerhardt, 1987, 1988; Schwartz, 1987; Sullivan, 1987).

Most of these female preferences have been demonstrated in laboratory experiments or acoustically simple field situations. Two-choice discrimination tests, as described in the previous chapter, have been extensively used in laboratory experiments to demonstrate various female preferences (e.g. Sullivan, 1983; Wells and area 1984a; Klump and Gerhardt, 1987; Wells, 1988; Lopez and Narins, 1991). As pointed out in the previous chapter the results of laboratory experiments, such as two-choice phonotaxis, do not always reflect the outcome of mate choice in the field. The ability of females to detect changes in male behaviour and thereby exhibit preferences for certain call parameters, is dependent upon: 1) females being able to make similar choices in acoustically complex environments at the breeding site, (Morris and Yoon, 1989), and 2) intra-individual consistency in the male's call parameter that is responsible for the mating preference, over the female sampling period (Searcy and Andersson, 1986; Sullivan, 1990; Sullivan and Hinshaw, 1990).

6.1.2 Call rate preferences

Directional female mating preferences for males producing courtship signals at higher rates have been documented in numerous taxa, including mammals (McComb, 1991), birds (Andersson, 1989), insects (Simmons, 1988) and frogs (Gerhardt, 1991). Martof and Thompson (1964) were the first to test the effects of call rate on female choice in

frogs, and surprisingly found that females preferred rates that were about the same as a typical natural rate. However, several other authors have subsequently investigated the effect of increasing call rate on female behaviour and all have found that females prefer the faster rate (e.g. Schneider, 1982; Sullivan, 1983; Gerhardt, 1987; Klump and Gerhardt, 1987; Wells, 1988). Field-choice experiments, in which females were presented with a 'natural' choice between two calling males in the field, were conducted by Morris and Yoon (1989). Their results showed that significantly more females chose the male with the higher call rate. However, studies on the relationship between call repetition rate and male mating success in natural breeding assemblages are limited. In order for females to preferentially select high call rates there presumably should be consistent differences in male call rate over the female's sampling period (Sullivan and Hinshaw, 1990).

Certain male *B. woodhousei* have been demonstrated to consistently call more frequently on successive nights than other males and females show a significant preference for these males (Sullivan, 1982b). In similar studies of natural populations of two other species, males with a higher mean call rate achieved more matings than males with lower call rates (*P. crucifer*, Sullivan and Hinshaw, 1990; *E. coqui*, Lopez and Narins, 1991).

6.1.3 Female sampling period

Sullivan (1990, 1994) noted that certain male characters used by females for mate choice vary over the time period in which a female is seeking a mate. This may play an important role when considering such male characters as display rate which is known to change rapidly over relatively short periods of time. Certain anurans call in bouts, where males call rapidly for short periods of time and then remain silent until calling resumes in another

bout (Schwartz, 1991). A bout caller may not have an advantage over a male that calls consistently, especially when the female's sampling period is quite long, as the call rate of the bout caller and the consistent caller, will be perceived as equivalent. However, even though the call rates may be equivalent over a certain time period, this does not necessarily preclude mate choice, as this may still occur based on the temporal pattern of calling. Females might discriminate against bout callers if the ability to call in a regular consistent manner is more indicative of male quality.

This chapter describes my investigation into the calling behaviour of males in a natural population, the call rate preferences of females in natural populations and in two-choice discrimination trials, and the time period over which females sample call rate. The answers to the following questions were sought:-

- 1) Do males in natural populations exhibit consistent differences in call rate?
- 2) Do females show a significant preference for faster call rate stimuli in two-choice discrimination trials?
- 3) If females do show a preference for faster call rates, over what period of time are they sampling for rate?
- 4) Do the results of (2) reflect the situation found in the natural population?
- 5) Do males exhibit differential calling persistence in the field?

Special acknowledgements

The work presented in this chapter has been published (or submitted, see Preface for details) and I feel it is important to acknowledge the input of the co-authors at this juncture. Special thanks are due to Pat Backwell, Neil Caithness, Michael Jennions and Neville Passmore.

6.2 Methods

6.2.1 Call rate and calling persistence

The study site for this experiment was a shallow temporary pond near Mtunzini, Zululand (for a detailed description of the study site and species see Chapter one and Appendix B). This study was conducted over 19 nights during December 1989 and January 1990. Air temperature ranged from 18.5 C - 23.5 C during the period in which the experiments were conducted.

A network of paths were cut through the emergent vegetation allowing easy access to many calling individuals. Once the males had established fixed calling sites, eight easily accessible males with different dorsal colour patterns were selected. These males were not usually neighbours and represent an arbitrary sample of the population of calling males. A small dynamic microphone (Acustica M31, hyper-cardioid, painted black) was carefully positioned, using a monopod, within 10 cm of each male's call site. Screened microphone cables, supported on overhead pylons, relayed the males' calls back to an 8 - channel event recorder in a mobile laboratory at the perimeter of the pond. Each channel had an adjustable audio switch (indicated by a flashing light-emitting diode). A multiplexer analogue-digital converter identified the active channels and relayed a digital signal to an acquisition card (D8255, Oscar Electronics Ltd.) in the personal computer (see Fig. 6.1).

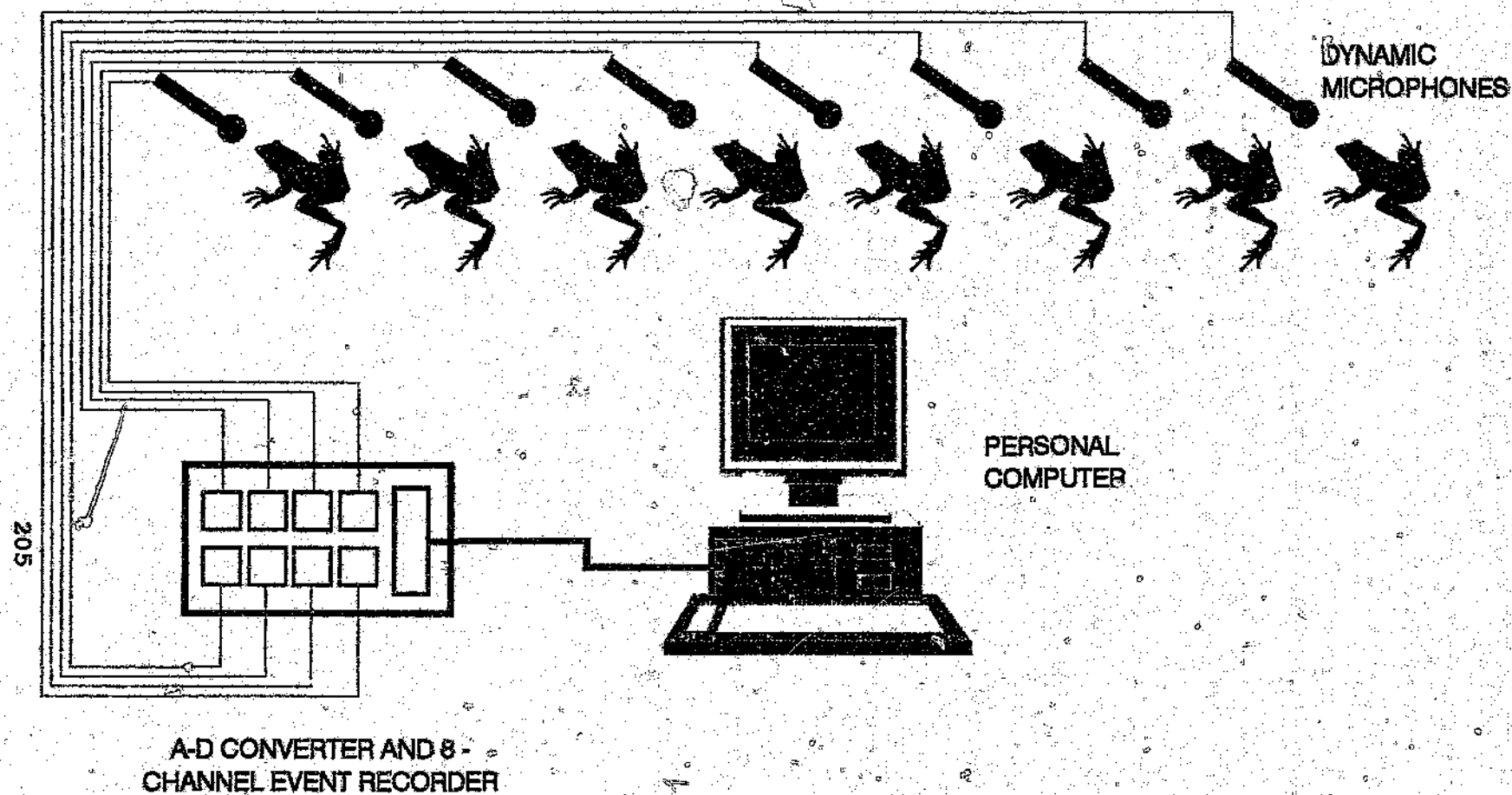


Fig. 6.1 Diagrammatic representation of equipment used in field study

The event recorder logged the time of occurrence of every call made by the subjects and a flashing signal on the computer screen for every call made, together with histograms of calls/min, provided a complete visual record for each frog. This enabled any changes in calling behaviour to be immediately identified and promptly investigated using dim red light. Males that were in amplexus, had been attacked by a predator, or were leaving their call site were collected immediately; those that were silent but still occupying call sites were observed until they either left the site or had remained silent for 30 min. Fights between males were noted and if the subject had been displaced from his original position, but resumed calling close by, the microphone was repositioned. After calling had ceased, each male was captured, heat branded (see Appendix D for details), photographed, and measured with vernier callipers (to the nearest 0.1 mm SVL).

6.2.2 Phonotaxis

The procedure for phonotaxis experiments has already been outlined in Chapter five, Section 5.2.1. The study site for these experiments was the same as Chapter five.

6.2.2.1 Repetition rate experiments

The repetition rate phonotaxis experiments were carried out during December 1990 and January 1991. Air temperature ranged from 18.6 C - 24.3 C during the period in which these experiments were conducted.

The acoustic stimulus was a synthetic standard call (see Chapter four, section 4.2.2) that was behaviourally equivalent to a typical natural call (see Dyson and Passmore, 1988a, b; Backwell et al., 1991). Stimuli differing in repetition rate were broadcast in pairwise combinations using 2 Rebis RA digital samplers (8 bit, 32 kHz sampling rate, Rebis Audio Ltd., England), a Klein and

Hummel SB280/II stereo audio amplifier and two Philips AD50600 4-inch diameter loudspeakers. The loudspeakers were placed facing each other, 1.0 m on either side of the female release point (see Fig. 5.1 for the arrangement of speakers). The call repetition rates chosen for this study were well within the normal range for this population (45, 50, 55, and 60 calls/min).

6.2.2.2 Sampling period experiments

These phonotaxis experiments were carried out during December 1993 and January 1994. Air temperature ranged from 18.7 C - 24.9 C during the period in which these experiments were conducted.

The acoustic stimulus was the same synthetic call, as used previously (see Chapter four, section 4.2.2), and was loaded onto four Rebis RA226 digital samplers from a Nagra IV stereo tape recorder. The digital samplers enabled the temporal relationship between the stimuli to be accurately set, and relayed to a Nagra E tape recorder. Tape loops were made of the appropriate length and recorded onto a Nagra E and used as the 8 stimulus tapes. The temporal relationship between successive stimuli, where the rate is equalized over 10 s, is described below and illustrated in Fig. 6.2.

Sequence 1: Regular call rate, with every call having an ICI of 1000 ms.

Sequence 2: Fast rapid bout, with ten calls separated by an ICI of 506 ms followed by 5446 ms of silence.

Sequence 3: Medium rapid bout (A), with ten calls separated by an ICI of 737 ms followed by 3418 ms of silence.

Sequence 4: Medium rapid bout (B), with five calls

separated by an ICI of 737 ms, followed by 2094 ms of silence and a further five calls with an ICI of 737 ms.

Sequence 5: Two speed bout, with five calls separated by an ICI of 506 ms, followed by five calls with an ICI of 1507 ms.

Sequence 6: Alternating ICI bout (A), ten calls with ICI alternating from 506 ms to 1000 ms followed by 2470 ms of silence.

Sequence 7: Alternating ICI bout (B), ten calls with ICI alternating from 506 ms to 1494 ms.

Sequence 8: Irregular bout, with successive stimuli separated by the following ICI: 1000, 743, 2987, 600, 350, 300, 512, 1127, 800, 1494 ms.

As the stimuli used in each pairing had different ICI, it was impossible to retain a consistent temporal relationship between the stimuli of different stimulus tapes. In order to prevent the establishment of any leader-follower type relationships the stimulus tapes were not synchronized in any way. As sequence 1 was used in every trial, the end of the arena which housed this speaker was alternated between trials.

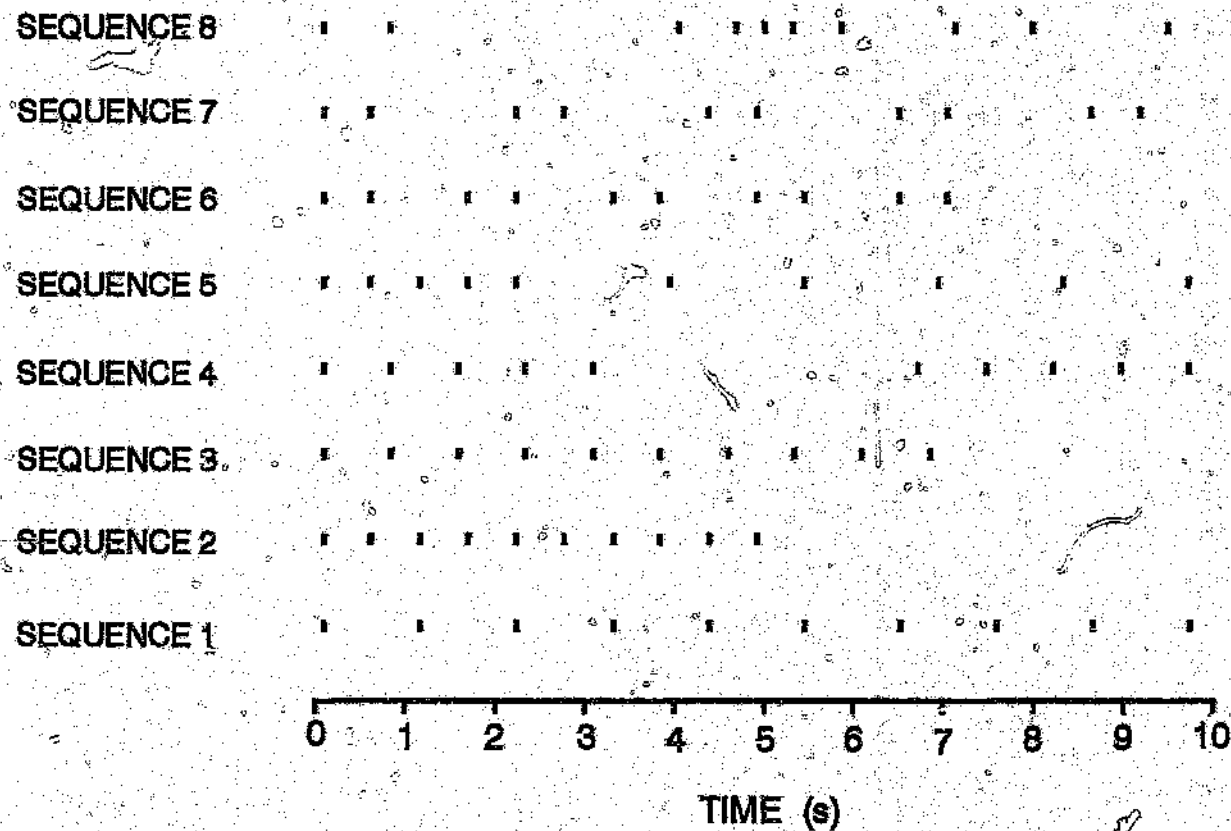


Fig. 6.2 Temporal position of stimuli used in the sampling period experiments

6.2.3 Statistical methods

Kendall's coefficient of concordance W (Siegel, 1956) was used to evaluate whether the call repetition rate rank order was consistent within nights. The influence of call repetition rate on mating success was evaluated by dividing the deviation of the calling rate of each mated male from the mean rate at the time of mating (and 2 additional time frames) by the standard deviation (transformation to z-scores).

Correlations were determined by using either Pearson product-moment or Spearman's correlation coefficient depending on whether the data was normally distributed or not. Differences between the means were determined using the Student's t -test. Responses of females in the phonotaxis experiments were compared using the Binomial test.

6.3 Results

6.3.1 Call rate and calling persistence

Before males take up fixed call sites there is a great deal of movement and aggressive vocalizations, and as the microphones were only placed in position once the males had "settled" down, any calls made before this time were not included in this study. The minute by minute record of the calling behaviour in this study comprised more than half a million advertisement calls produced by 111 males over 12459 min.

6.3.1.1 Time of matings

Twenty one of the 111 males mated during this study, and the distribution of the time of mating is illustrated in Fig. 6.3. As females initiated mating over a period of more than two hours (20.20 - 22.40 h) the number of calls made by a male prior to mating was extremely variable ($\bar{x} = 2137 \pm 1866$, range 9 - 7286 calls, $n = 21$)

6.3.1.2 Calling period

All records in which calling was interrupted by external factors such as rain, predation or mating were excluded. Complete calling records were obtained for 73 males, of which, 60 (82%) males called beyond the period of mating (see Fig. 6.4). The mean calling period was 160 min (± 40 , range 80 - 236 min), and there was a slightly significant correlation between male SVL and the duration of the calling period (Pearson product-moment correlation, $r = 0.26$, $n = 65$, $P = 0.04$). Air temperature was not significantly correlated with the duration of the calling period (Pearson product-moment correlation, $r = 0.41$, $n = 16$, $P > 0.05$).

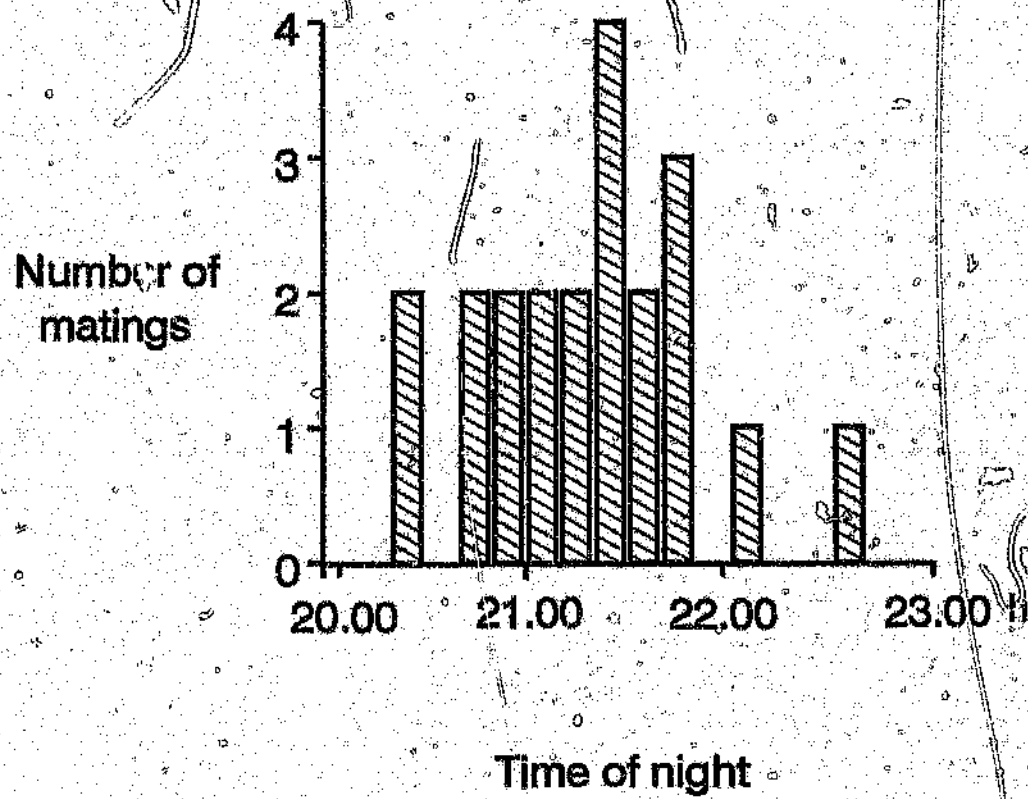


Fig. 6.3 Distribution of the time of matings

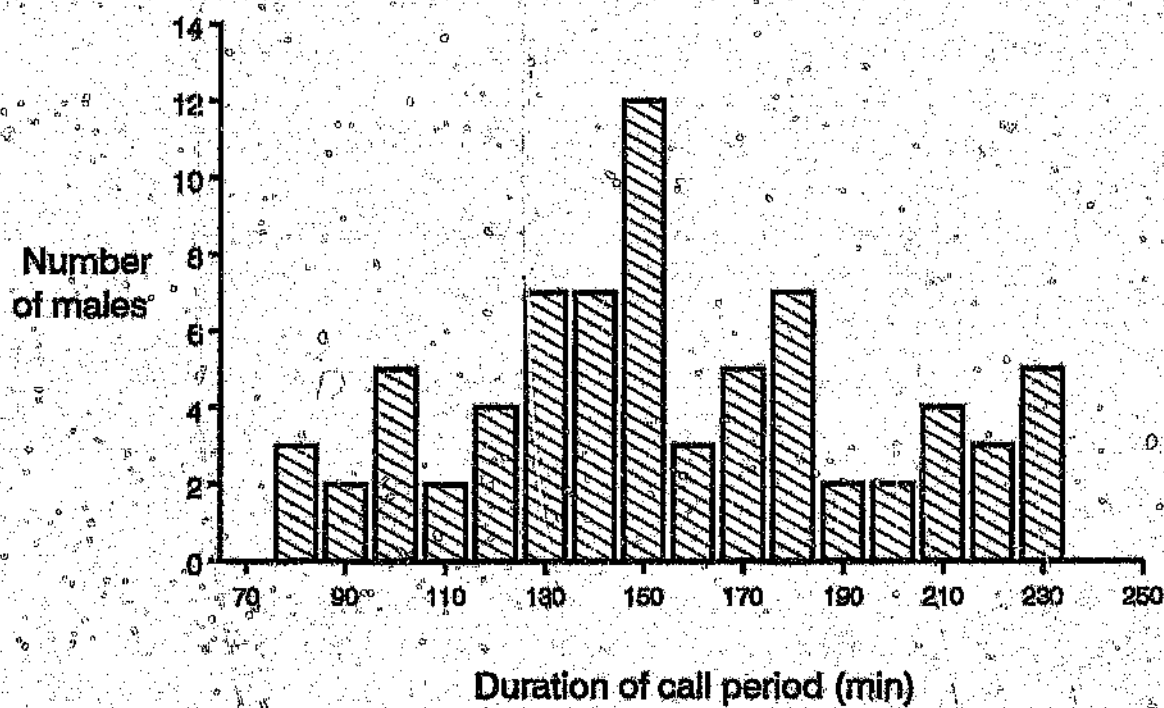


Fig. 6.4 Distribution of call period duration ($n = 73$)

6.3.1.3 Calling persistence

Periods of silence during the peak calling period were uncommon and most males called during every minute of their calling period (see Fig. 6.5). On average males were silent for 3.3% of their calling period (range = 0 - 37.5%, $n = 110$). During silent periods males remained still with a partially inflated vocal sac. Aggressive calling and fighting occurred during the monitored calling period of 14 males (out of 111 = 12.6%). These aggressive encounters were normally short-lived ($\bar{x} = 5.8 \text{ min} \pm 8.1$, range 1 - 35 min, $n = 14$) and seldom repeated. None of the 21 males that mated were involved in aggressive encounters. The mean SVL of males that fought (29.6 mm) was not significantly different from that of males that did not fight (29.2 mm) (Student's t -test, $t = 0.79$, $n = 111$, $P = 0.43$).

6.3.1.4 Call repetition rate

Call repetition rate, within the calling period, displayed a consistent pattern with time. Males normally began with a high call rate and this was sustained for 1 - 1.5 h, followed by a gradually and then more steeply declining rate (see Fig. 6.6).

The very small temperature differences between the beginning and the end of the call period (0.1 °C on 5 nights, 0.2 - 1.0 °C on 9 nights, 1.1 - 1.5 °C on 4 nights and 1.6 - 2.0 °C on 1 night) precludes temperature as the factor responsible for this decline in rate. There was a highly significant positive correlation between average air temperature and mean calling rate of males on a given night (Pearson product-moment correlation, $r = 0.84$, $n = 17$, $P < 0.01$). Call rate was not correlated with body size when the effect of air temperature on call rate was removed (partial correlation coefficient = 0.003).

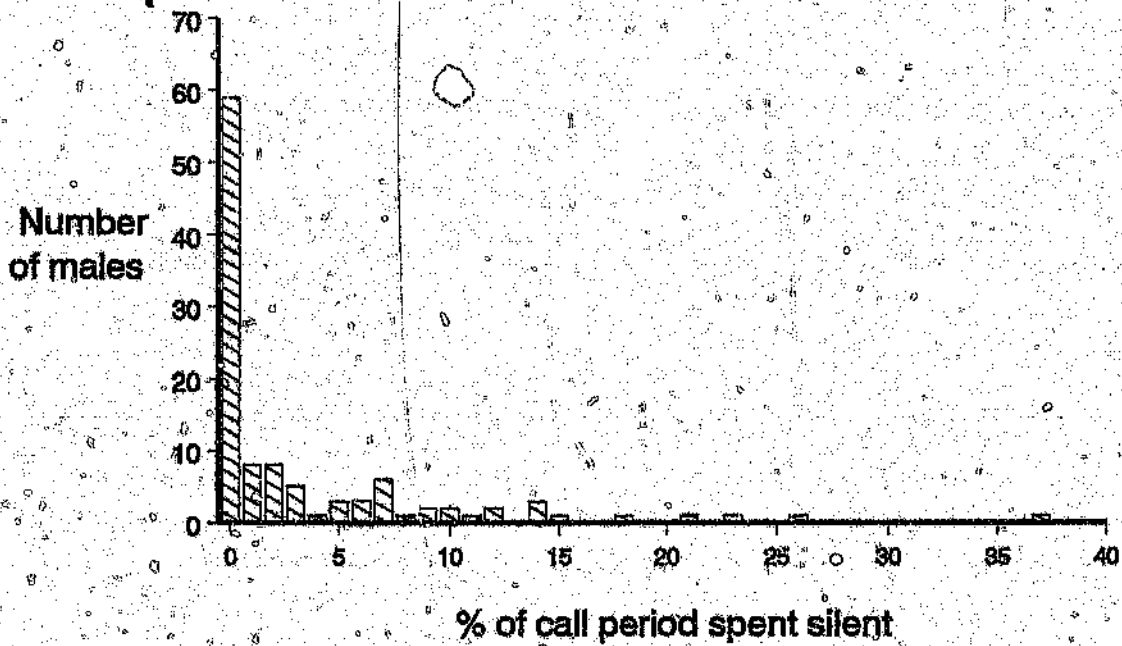


Fig. 6.5 Distribution of the percentage of the call period that males spent silent ($n = 110$)

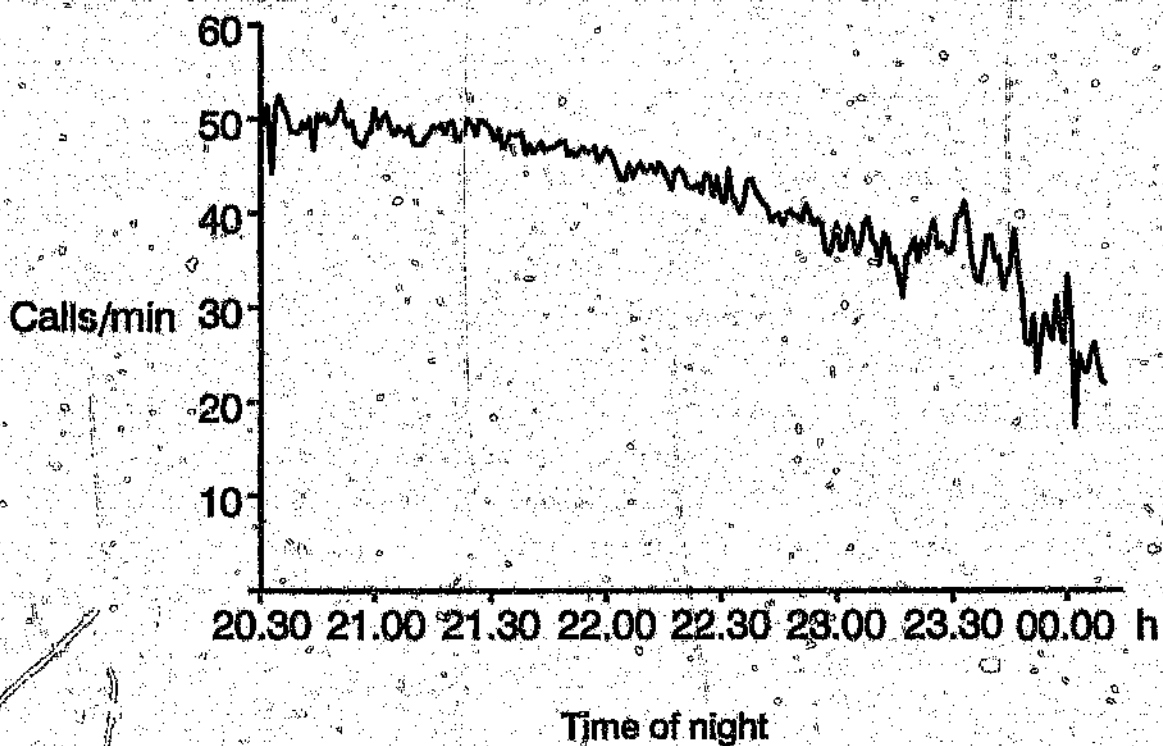


Fig. 6.6 Change in mean call rate with time of night

The call rate of the monitored males varied considerably from minute to minute. The range in call rate over the course of a typical single night is shown in Fig. 6.7. As there was a strong correlation between mean inter-call interval (ICI) and coefficient of variation for ICI (Spearman's correlation coefficient, $r_s = 0.58$, $n = 26$, $P < 0.01$), males with faster average call rates showed less variability in ICI.

The average difference between the highest and lowest rates during the time that matings occurred was 15.8 calls/min. During the period that females were present (see Fig. 6.3), and there were four or more males calling, males were ranked by call rate within minutes and the ranking of individuals in successive minutes was compared. There was a high level of agreement between the ranks of males in different minutes (Kendall's coefficient of concordance, $W = 0.4 - 0.86$, $n = 17$, $P < 0.01$). Consequently, the relative call rates of individuals were largely sustained over time, and different but consistent call rates of males generated the spread of values observed.

6.3.1.5 Mating success

The call repetition rates of mated and unmated males were compared in three different time frames; 1) the minute immediately preceding mating, 2) the last 5 min prior to mating, and 3) the last 15 min prior to mating. Figure 6.8 illustrates that a disproportionate number of mated males had an above average call rate (reflected by a large number of positive z-scores) when compared to the population of calling males.

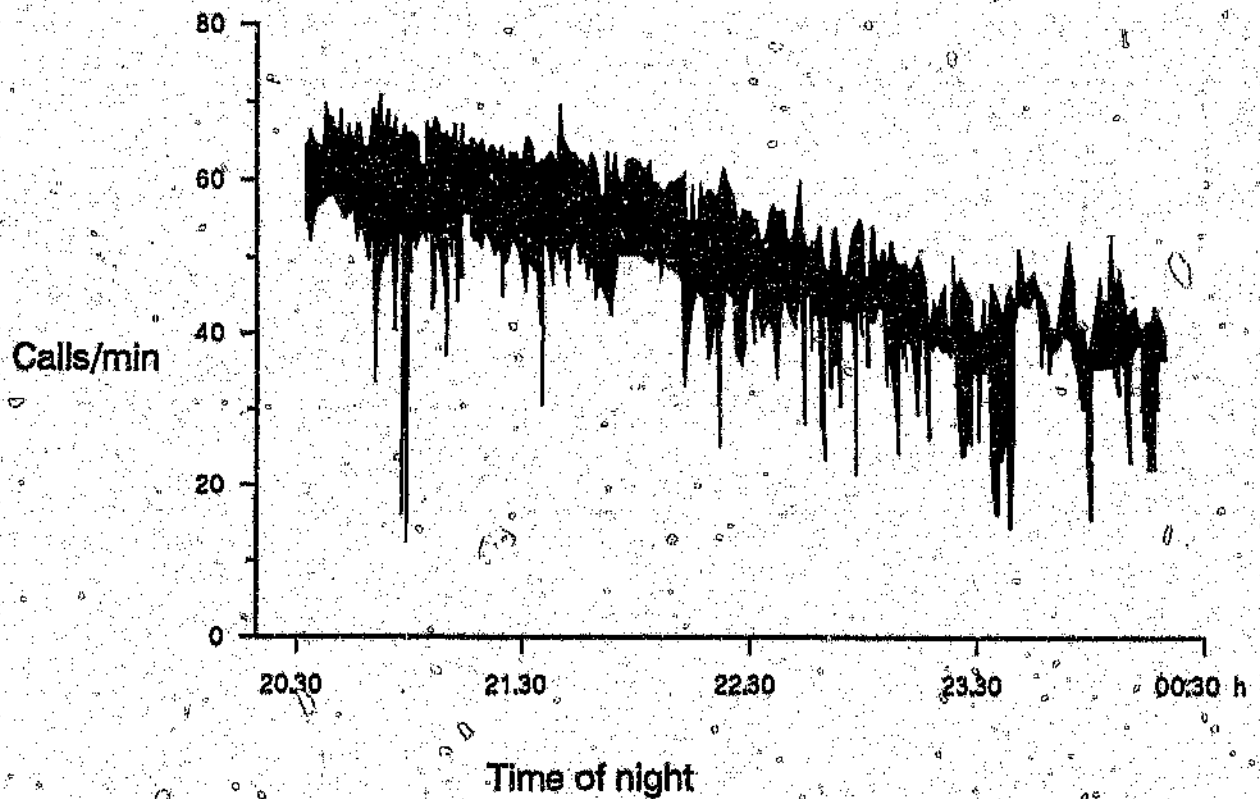


Fig. 6.7 The difference between the highest and lowest call rates, during each min, on a typical night (6 males participated until 23.00 h, 4 between 23.00 - 23.30 h, and 2 thereafter)

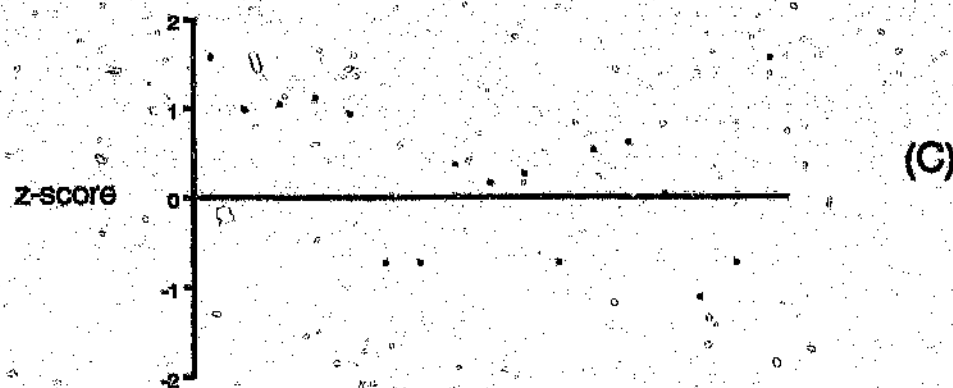
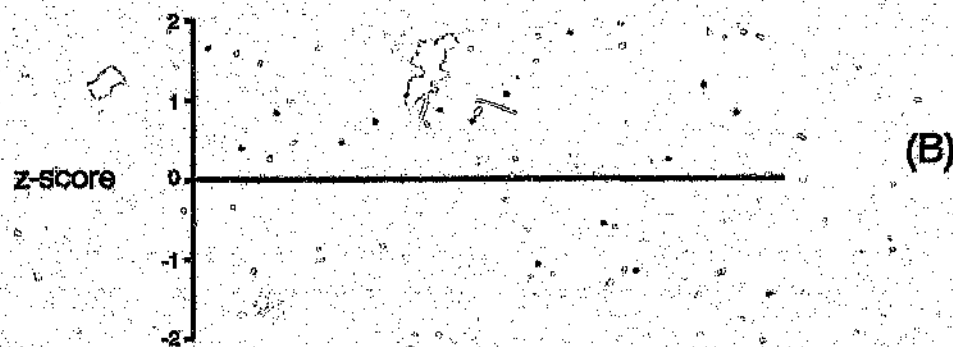
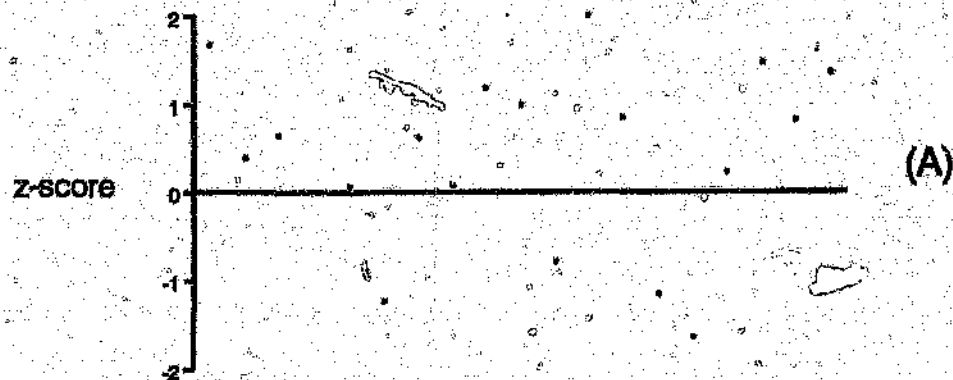


Fig. 6.8 Call rate z-scores for mated males
(A) Scores in the min immediately preceding mating
(B) Scores in the last 5 min immediately preceding mating
(C) Scores in the last 15 min immediately preceding mating

6.3.2 Phonotaxis

6.3.2.1 Repetition rate experiments

The results of the repetition rate phonotaxis experiments are summarised in Table 6.1. Females consistently showed a preference for the faster rate stimuli when the difference between the rates was about 10 or more calls/min. In trials 4 - 7 more than twice as many females selected the fast rate rather than the slow rate, and although these differences were not significant, they suggest that some females can discriminate between two rates varying by 5 calls/min.

6.3.2.2 Sampling period experiments

The results of the sampling period phonotaxis experiments are summarised in Table 6.2. Females only showed a significant preference for the regular rate versus the fast rapid bout (Sequence 2). In all other pairings, no clear preferences for either of the presented alternatives were shown. The time taken by females to contact the loudspeaker was not significantly different in any of the trials (Friedman ANOVA, $F = 1.97$, $P = 0.39$, $df = 6$) (see Table 6.3).

TABLE 6.1

Results of repetition rate discrimination trials

Trial no.	Speaker	
	1	2
1 Rate	60	40
Score	<u>10</u>	1
2 Rate	55	60
Score	<u>10</u>	1
3 Rate	60	50
Score	<u>10</u>	1
4 Rate	55	45
Score	10	3
5 Rate	60	55
Score	9	5
6 Rate	55	50
Score	8	4
7 Rate	50	45
Score	11	4
8* Rate	60	60
Score	5	5
9* Rate	50	50
Score	3	7

For all trials peak SPL (dB) at 50 cm in front of speaker = 104dB, which attenuated to 98 dB at the female release point.

Score = Number of females positively responding to a particular speaker.

Significant results are underlined (Binomial Test $p < 0.05$).

* Control pairings.

TABLE 6.2

Results of sampling period discrimination trials. In all trials the regular rate (Sequence 1) was paired against one of the other sequences. Call rate is equalised over a 10 s period (10 calls/10 s).

Alternative sequence	Regular rate speaker score	Alternative speaker score
2 - Fast rapid bout	<u>15</u>	5
3 - Medium rapid bout (A)	10	10
4 - Medium rapid bout (B)	10	10
5 - Two speed bout	12	8
6 - Alternating ICI bout (A)	9	11
7 - Alternating ICI bout (B)	8	12
8 - Irregular bout	7	13

For all trials peak SPL (dB) at 50 cm in front of speaker = 104dB, which attenuated to 98 dB at the female release point.

Significant results are underlined (Binomial Test, $P \leq 0.05$).

TABLE 6.3

Time taken by females to contact the loud speaker (mean $\pm$ SE)

Alternative sequence	Response time (s)
2 - Fast rapid bout	107.6 $\pm$ 21.4
3 - Medium rapid bout (A)	183.8 $\pm$ 63.4
4 - Medium rapid bout (B)	164.5 $\pm$ 43.1
5 - Two speed bout	100.4 $\pm$ 14.3
6 - Alternating ICI bout (A)	164.5 $\pm$ 34.1
7 - Alternating ICI bout (B)	160.5 $\pm$ 43.3
8 - Irregular bout	97.1 $\pm$ 12.7

6.4 Discussion

6.4.1 Male calling behaviour

Previous studies of female mate choice may not have examined the process thoroughly. In this regard, the need to study temporal changes in male characters that females are assessing, and the time window over which females sample males is of utmost importance (Sullivan, 1990, 1994). As Sullivan (1990, 1994) pointed out, most studies of female mate choice tend to use an "instantaneous snapshot" of the existing variation and this may not reflect the true amount of information utilized by the female in making her choice. In this study the automated call monitoring technique provides a minute by minute record of all the males over the whole period of their vocalization. Moreover, it allows the analysis of call rate over the period when females are present in the chorus, and during the time window when females are sampling males. However, data for the period in which females are sampling males in the field is very difficult to obtain for most species (Sullivan, 1990) and in the present study it was estimated at less than 15 min. This is based upon extensive field observations in which females have not been observed to remain unpaired for longer periods.

This study shows that males vocalized for much longer periods than the time window when females were present in the chorus (see Figs. 6.3, and 6.4). The average number of calls produced by a male in the calling period (6110) exceeds the average per mating (2137) almost by a factor of three. As a result, it is unlikely that males which call for long periods of time gain any mating advantage at all. Often, when males were observed leaving the chorus in the early hours of the morning, they appeared to be in a state

of exhaustion. As the mating success of males has been shown to be influenced by the number of nights they are present in the chorus (Dyson et al., 1992), from an energetic viewpoint, a male should benefit from calling for short periods of time on many nights, rather than long periods of time on a few nights.

Males of many species have been shown to either call in bouts (Rosen and Lemon, 1974; Whitney and Krebs, 1975a; Schwartz and Wells, 1983a; Schwartz, 1991) or call sporadically (Forester et al., 1989) and this has been suggested to play an important role in mate choice or reduction of acoustic interference. However, *H. marmoratus* was shown to call consistently with few, if any, interruptions (see Fig. 6.5), hence the potential for variation in calling persistence to influence mating success or acoustic interference is very limited. Call rates are sustained over time and the relative rankings of the males are consistent. Consistent call rate differences have been shown in several other species in the wild (e.g. Sullivan and Leek, 1986; Sullivan and Wagner, 1988; Sullivan and Hinshaw, 1990).

6.4.2 Female preferences, call rate and mating success

The results of the two-choice discrimination experiments confirm that female *H. marmoratus* share the same preference for faster call rates that is prevalent in other species tested under experimental conditions (see review by Gerhardt, 1988; Lopez and Narins, 1991) or in field discrimination tests (Morris and Yoon, 1989). The preference for faster rates was sustained over a variety of stimulus rates but was strongest when the difference between rates was large (see Table 6.1). Even the largest difference between the stimulus rates was evident in the natural population of calling males during the time window when females were present in the chorus.

The preference for high call rates persists in the field,

resulting in males with above average call rates achieving disproportionately more matings than males with below average rates (see Fig. 6.8). In the field experiment this preference is particularly strong, as the rates that the mated male are compared with, come from an arbitrary sample of calling males rather than the males that the female may have sampled. If the sample of comparative rates included high values not sampled by the female then the potential exists for rate-dependent preferences to be obscured. However, in spite of this, a clear mating advantage associated with high call rate is evident. As male *H. marmoratus* call from fixed call sites, then females entering a chorus would be presented with consistently different call rates emanating from a stable array of points within the chorus. High call rate males, in the chorus, may achieve more matings by rendering themselves more acoustically, and therefore spatially, conspicuous to sexually responsive females (Gerhardt, 1987).

6.4.3 Female sampling period

As mentioned previously in this chapter, the actual period that a female samples males in the chorus is very difficult to determine (Sullivan, 1990, 1994). Female *H. marmoratus* usually take less than 15 min to sample males. However, in the light of the above findings that females prefer fast rates in experimental and field conditions, females must be able to assess rate over a particular time period. Schwartz (1991) thought that males might attract more females by calling periodically at a fast rate (in bouts) rather than consistently at a slower rate. However, in his study he failed to show this preference and suggested that females may be able to integrate sound energy, in which case both his stimuli would be regarded as equal. In the female sampling period experiments in this study similar results were found when the call rate was equalised over a ten second period, except when the calls were

arranged in a fast rapid bout sequence. This sequence (Sequence 2, Fig. 6.2) consisted of ten calls with very short ICI followed by nearly 5.5 s of silence. During observations of natural matings, males were frequently heard to produce a courtship call when females were in close proximity. These courtship calls consisted of normal advertisement calls repeated at a very fast rate, similar to the fast rapid bout (Sequence 2) in this experiment. Perhaps the reason why females failed to show a preference for these calls in phonotaxis studies is due to the fact that these types of calls are only produced when the female is in close proximity to the male (< 20 cm) and the females rapidly respond by initiating amplexus. In the phonotaxis experiments when the females were presented with this stimulus, they often orientated toward the fast rapid bout but during the interbout periods of silence, after failing to locate a nearby male, they re-orientated and began to approach the steady regular stimulus. This process of re-orientating to the different stimuli continued throughout most of the trial until the female was quite close to the regular stimulus speaker. In these trials females approached the regular speaker in a "three steps forward, two steps backward" type of progression.

In all the other pairings with the regular sequence, there was no preference, indicating that female mate choice was not influenced by variability in the temporal pattern of calling. Furthermore, given that females in this study were shown to have a strong preference for faster calling males, and faster calling males were shown to have less variability in ICI, then these phonotaxis experiments show that females are choosing the fast rate males by calls per unit time rather than by consistency of ICI. These experiments suggest that females are not using successive ICI to assess rate, until a critical length of ICI is reached (i.e. > 3418 ms, Sequence 3) and a complex relationship may exist between calls per unit time and

continuous stimulation.

As these stimuli did not differ in their rates over a 10 s period, the female sampling period is probably longer than 10 s. Further experiments, utilising different combinations of calls per unit time, are necessary to elucidate the exact period of time over which females are assessing rate.

6.4.4 Summary

Male *H. marmoratus* call consistently at very high rates over long periods of time and there are consistent differences between the call rates of different males. Females preferred the faster of two rates when presented with a simple two-choice situation and this preference is reflected in the disproportionately large number of matings achieved by high rate calling males in natural populations. Faster calling males may enhance their conspicuousness to sexually responsive females, thereby influencing their mating success. When call rate is equalised over a ten second interval during phonotaxis experiments females only discriminated against sequences with long periods of silence. This suggests that there is a complex interaction between calls per unit time and frequency stimulation.

CHAPTER SEVEN

CONCLUDING DISCUSSION

7.1 Acoustic playback experiments in studies of animal communication

7.1.1 Historical perspective

In the late 1940's workers in the field of acoustic communication were becoming aware of the significance of playbacks of conspecific calls in altering the behaviour of animals (Bogert, 1947; Roth, 1948). Since these earlier experiments, playbacks have been carried out on a variety of taxa from insects, through fish and amphibians, to birds and mammals (Falls, 1992). Bogert (1947) was the first worker to conduct playback experiments on anurans, and he discovered that both male and female *Bufo terrestris* were attracted to broadcasts of a conspecific chorus. In the 30 years following Bogert's report, as the acoustic broadcast equipment improved and became more portable, an increasing number of playback studies on males and females were carried out (e.g. Littlejohn and Michaud, 1959; Blair and Littlejohn, 1960; Capranica, 1965; Gerhardt, 1974a, b). However, it was not until 1976 that intricate playback experiments designed specifically to address a complex set of questions were performed (Narins and Capranica, 1976).

These authors were the first to identify sexual differences in the peripheral auditory sensitivity of a vertebrate. By combining acoustic playback experiments and two-choice discrimination experiments they were able to demonstrate a "functional dichotomy" in the two-note call of *H. coqui*. This experiment paved the way for future workers to embark upon increasingly more sophisticated playback experiments, as evidenced by the ever growing use of computers and digitized stimuli (Gerhardt, 1991; Schwartz, 1991; Brenowitz and Rose, 1994).

7.1.2 Acoustic playback experiments

The vast majority of the experimental data collected in this thesis are the results of acoustic playback experiments. Acoustic playback experiments fall into two general categories. Firstly, they may be of the two (or more) speaker discrimination experiment type (Chapters five and six); or, secondly, they may take the form of various stimuli broadcast to naturally calling males in the field (Chapters two, three and four). In either case the accurate measurement of SPL at the position of the test subject is extremely important. The perceived intensity of the stimulus has a very strong influence on the behaviour of the subject and can confuse experimental results if not taken into full consideration. An example of conflicting results due to inappropriate SPL measurements are represented by Telford's (1982) data relating to the intensity discrimination ability of female *H. marmoratus*. He discovered that in 1981 certain females could discriminate between calls that varied by 3 dB (at 50 cm from the loudspeaker), while in 1982 he found that females could only discriminate against the softer call when there was a 6 dB difference. If, however, he had measured the SPL at the female release point and adjusted the SPL accordingly (thereby avoiding problems caused by excess ground attenuation, see Chapter five), the

differences in SPL may have reflected those perceived by the female in executing her choice.

Although, call discrimination experiments have long been a useful tool for determining the effects of various male call characteristics on female behaviour, authors should be very wary of making assumptions based on the results of these experiments without supporting evidence from field studies (see Chapter five).

The broadcast of specific stimuli to calling males from loudspeakers has been used on many occasions to study patterns of acoustic interactions between calling frogs (e.g. Narins and Capranica, 1978; Narins, 1982a, b; Wells and Schwartz, 1984a, b; Moore et al., 1989; Schwartz, 1991; Brenowitz and Rose, 1994). As most of the male broadcast experiments in this thesis were performed at the beginning of the study, the stimuli used were analogue recordings of natural exemplars of advertisement calls. Later in the study, as technology advanced, synthetic digitized stimuli became more readily available and standard analogue tape recorders were replaced with digital samplers and computers. Most previous studies of male-male acoustic interactions have been limited to two individuals at a time. However, the use of a custom built encoder enabled Brush and Narins (1989) to investigate the acoustic interactions of up to five calling males. These sorts of investigations involving many individuals, are very important in elucidating the true dynamics of choruses, as most previous reports assumed that the chorus was simply an extension of the interactions between two males. Utilizing an 8-channel event recorder and personal computer (as described in Chapter six), I am presently investigating the complexity of chorus dynamics (as outlined in Chapter two) by studying the acoustic interactions between up to eight individuals in the laboratory as well as in the field.

7.2 Social organization in anurans

Most of the social interactions in anurans occur almost exclusively during the breeding season. Typically, much of this social behaviour centres around competition among males for access to mates. Most anurans communicate during these social interactions, by means of species specific sounds. The production of loud calls has evolved to enable anurans to communicate effectively over long distances, whilst being constrained by the need to be in close proximity to the ground. These calls are seldom uttered at random and often a clear type of organization exists. Several different forms of chorus organization have been proposed and the results of Chapter two clearly indicate that the different types of chorus organization exist as a continuum, based upon the delay from when a frog hears a call to when he replies with a response. The species studied in this thesis exhibited three arbitrary classes (i.e. call-triggering, antiphonal calling and synchronous calling) within this continuum, with a further class being possible, but not represented in these species (see Fig. 2.35). There have been several reports on the mechanisms involved in call timing (Loftus Hills, 1974; Lemon and Struger, 1980; Narins 1982a; Zelick and Narins, 1982; Moore et al., 1989) which all seem to be in agreement that following an acoustic stimulus there is an absolute behavioural refractory period (BRP). During this BRP an external stimulus cannot elicit a response. The results presented in this thesis confirm the existence of an absolute BRP in *H. marmoratus* where it was found to have a mean duration of 32 ms (see Chapter three, Table 3.5). However, in contradiction to other published results, Lemon and Struger (1980) suggested that a stimulus occurring in the absolute BRP and even during the production of a call, will influence the duration of the call-cycle period. The results reported here do not lend any support to this suggestion as males who were presented with stimuli during

the production of a call, or shortly thereafter, failed to show any behavioural recognition of the stimulus. The next period to occur after the absolute BRP is the relative BRP, during which time a call is elicited by the perception of a stimulus (Narins, 1982a). If a stimulus is not presented to the frog during the relative BRP, this period is terminated by the spontaneous production of a call. In addition several authors have suggested the presence of call suppression, as there are fewer responses than expected from the onset, through the duration, to shortly after the end of the stimulus (Zelick and Narins, 1982; Moore et al., 1989; Klump and Gerhardt, 1992). Shortly preceding a call itself is a period of excitation, where the neural circuitry has been activated and the production of a call is inevitable, irrespective of any acoustic stimulus perceived.

The sheer complexity of interactions that occur within a natural chorus hamper similar detailed studies being carried out. In most cases the responses of isolated individuals to acoustic playback experiments are studied instead of individual interactions. There is no reason to believe that these studies cannot be extrapolated to embody the chorus as a whole. However, detailed studies of how individuals interact with each other in the chorus would be necessary to substantiate some of the proposed mechanisms of call timing.

7.3 Mating success

Over the last decade the social behaviour of anurans has received a great deal of attention from behavioural ecologists. Certain aspects of their breeding behaviour have made them particularly suitable subjects to test various theories relating to sexual selection and mate choice. Firstly, they form large aggregations which enable repeated observations of social interactions. Secondly, fertilization is external thus providing unambiguous

parentage in most species (however, multiple spawning has been suggested to occur in *Chiromantis xerampelina* by Jennions et al., 1992), and thirdly they can be easily marked, approached and observed with little disturbance. The literature covering all the aspects of sexual selection and mate choice in anurans is exhaustive (see Gerhardt, 1988 for review), nevertheless a summary of the call parameters that influence mating success which directly impinge on the work reported in this thesis, are presented here.

7.3.1 Temporal aspects

Chapter two identified that most anurans organize their choruses in some way or another. It has been suggested that by organizing their calls with respect to time a male can maximise the number of un-masked calls he produces, thus increasing his locatability. However, several authors have shown that simultaneous or overlapping calls are as easy to locate by females as are alternating calls (e.g. Forester and Harrison, 1987; Schwartz, 1987; Dyson and Passmore, 1988a, b; Klump and Gerhardt, 1992; Ibáñez, 1993).

Consequently, in Chapter three, it was suggested that the ubiquitous phenomenon of call timing in males has not evolved as a result of selection pressures imposed by the constraints of the females' auditory system. Rather, it is a mechanism used by males to effect spatial organization which may, in turn, influence their mating success. However, the inhibitory resetting strategy utilized by male *Neoconocephalus spiza*, which has probably evolved as a result from the selective pressures exerted by female preference for leading calls (Greenfield and Roizen, 1993; Sheridan et al., 1993), has not yet been described for any anurans.

7.3.2 Frequency

Several authors have suggested that differential mating success may be achieved by active female choice for size-related variation in the males' calls (e.g. Ryan, 1980, 1983a; Fairchild, 1981; Sullivan, 1983; Forester and Czarnowsky, 1985; Robertson, 1986b). The main parameter of a male's call that is correlated (inversely) with size is the dominant frequency component, and in two-choice discrimination trials many authors have shown that females preferentially select the lower frequency alternative (Ryan, 1980, 1983b; Forester and Czarnowsky, 1985; Robertson, 1986b). If this occurred in natural populations there would be non-random mating with respect to size. However, size-dependent mating success has been convincingly demonstrated in only four species of anurans (Howard, 1980, 1988; Ryan, 1980, 1983a; Robertson, 1986b). Furthermore, in two-choice discrimination trials with female *H. marmoratus* Telford et al. (1989) have shown a strong preference for lower frequency calls, yet in natural populations mating is random with respect to size (Telford et al., 1989; Dyson et al., 1992). Gerhardt (1982) discovered a similar scenario with *Hyla cinerea* and suggested that the inconsistent behaviour of females in laboratory experiments and the natural environment may be explained by differences in the complexity of the acoustic environment. Chapter five highlighted a similar problem involving call intensity (see Section 7.3.3 below), where the ability of the females to discriminate between differences in SPL was impaired when the complexity of choice was increased. Obviously, as the complexity of the acoustic environment changes so do the temporal relationships between the calls of individuals. Dyson and Passmore (1988b) demonstrated that although females preferentially selected the lower frequency call when the two calls were alternating, they responded at random when the calls were simultaneous, and preferred the leading call

of a pair of stimuli that overlapped, irrespective of frequency (within certain limits). Their results explain why random mating with respect to size is observed in natural populations, and highlight the danger of extrapolating the results of two-choice discrimination trials to natural populations.

7.3.3 Call intensity

Advertisement call intensity is the only other call parameter that is correlated with male body size (Gerhardt, 1975; Wilbur et al., 1973; Berven, 1981; Arak, 1983c; Passmore and Telford, 1983). However, Ryan (1983a) suggested that SPL was unlikely to be a reliable predictor of male size due to excess attenuation from vegetation and microclimatic changes. Interestingly, an almost universal preference by females for high intensity calls has been demonstrated using two-choice discrimination trials (Fellers, 1979a; Fairchild, 1981; Telford, 1982; Arak, 1983c; Dyson, 1985). Also in Chapter five it was shown that in simple two-choice discrimination trials females preferentially selected the loudest of two calls when the perceived difference in intensity was as small as 4 - 5 dB. However, this preference was not so evident when the complexity of choice was increased. Furthermore, it has been established that if the intensity of the preferred low frequency call was reduced, females then selected the louder high frequency call in two-choice discrimination trials (Schwartz, 1986; Telford et al., 1989). Additional experiments on the combined effect of intensity and temporal relationships of the stimuli, resulted in the leader of two calls being preferred over the follower, even when the following call was louder (Dyson and Passmore, 1988a). Females were unable to assess the absolute intensity of the stimuli in discrimination trials (Arak, 1983c; this study, Chapter five) suggesting that females are passively attracted to the call perceived at the

highest amplitude, which in many natural situations will be the closest male.

All the above results suggest that there is an extremely complex relationship between call frequency, call intensity and the temporal position of the call with respect to other calls. The choice exhibited by females in simple discrimination trials may be very different from those choices made in the acoustically complex natural breeding assemblage.

7.3.4 Call repetition rate

Call repetition rate preferences have been demonstrated using two-choice discrimination trials in several species (see Gerhardt, 1988 for review; Wells, 1988; Lopez and Narins, 1991). Also, in simple two-choice experiments with naturally calling males, females were shown to prefer the faster caller (Morris and Yoon, 1989). In this study (Chapter six) females were found to preferentially select the faster rate in two-choice discrimination trials and this preference was reflected in the natural population, as faster calling males were more successful in securing a mate than slower calling males. This appears to be a straight forward case of females exhibiting a real preference, which has been confirmed by field studies. However, Schwartz (1986) discovered that in *Hyla microcephala*, although females showed a preference for the faster rate in two-choice discrimination trials, this choice could be negated and even reversed by decreasing the SPL of the faster rate stimulus. Therefore, it seems likely that SPL also plays a vital role in fast repetition rate preferences of females.

7.4 Conclusion

This work identified unambiguous social interactions in several species of frogs and highlighted the importance of SPL on these interactions. It also demonstrated that females showed a preference for loud fast calls and were unable to compute absolute intensity. However, as discussed above, under natural conditions there is an extremely complex interaction between call frequency, call intensity, call repetition rate and the temporal position of a call. In simple two-choice trials, females may show strong preferences for lower frequency calls, louder calls, faster calls and leading calls. These parameters are inter-related in a complex way in the field, such that the preferences exhibited in laboratory experiments may bear little or no relation to the choices made in natural breeding assemblages.

It is felt that this study provides valuable insight into the function and significance of the ubiquitous phenomenon of chorus organization. Furthermore, this study promotes a better understanding of the nature of acoustic interactions between animals, as well as resolving some of the problems surrounding mate choice in the field.

Appendix A

The call repertoire of *Eleutherodactylus coqui*.

Most of the calls illustrated here were obtained in response to the broadcast stimuli presented to the frogs during the increasing intensity experiments, and represent the full array of "coqui +" notes as described in Chapter four. However, the two very long multi-note calls (Fig. A1.3) were emitted by frogs in the early hours of the morning at daytime retreat sites, and were not in response to broadcast calls.

For further details of these calls see Stewart and Rand (1991, 1992) and Stewart and Bishop (1994).

Appendix A

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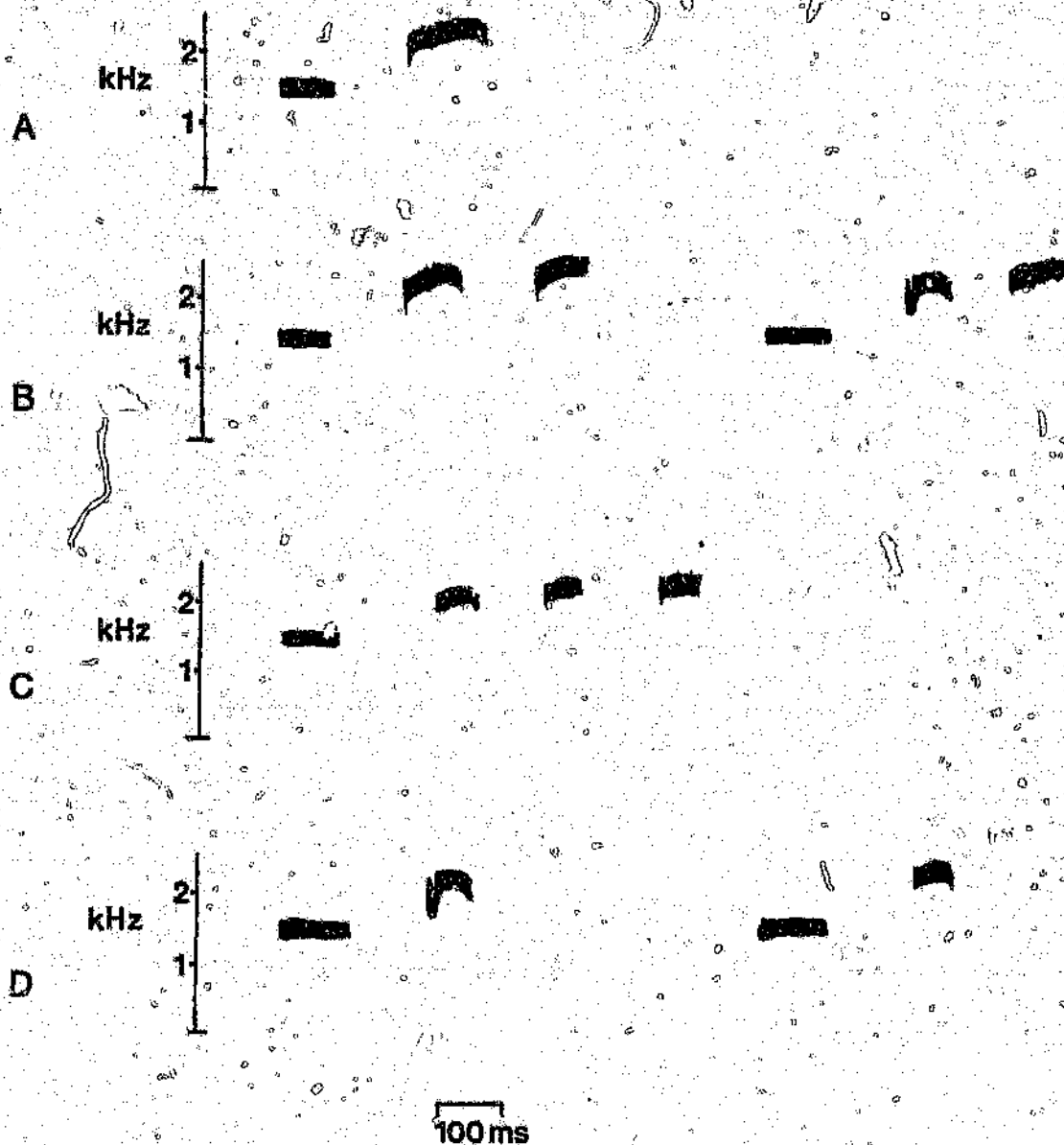


Fig. A1.1 Call repertoire of *E. coqui*.

A - Normal "co-qui" advertisement call

B - "Co-qui-qui" followed by "co-quik-qui"

C - "Co-qui-qui-qui"

D - Two "co-quik" calls

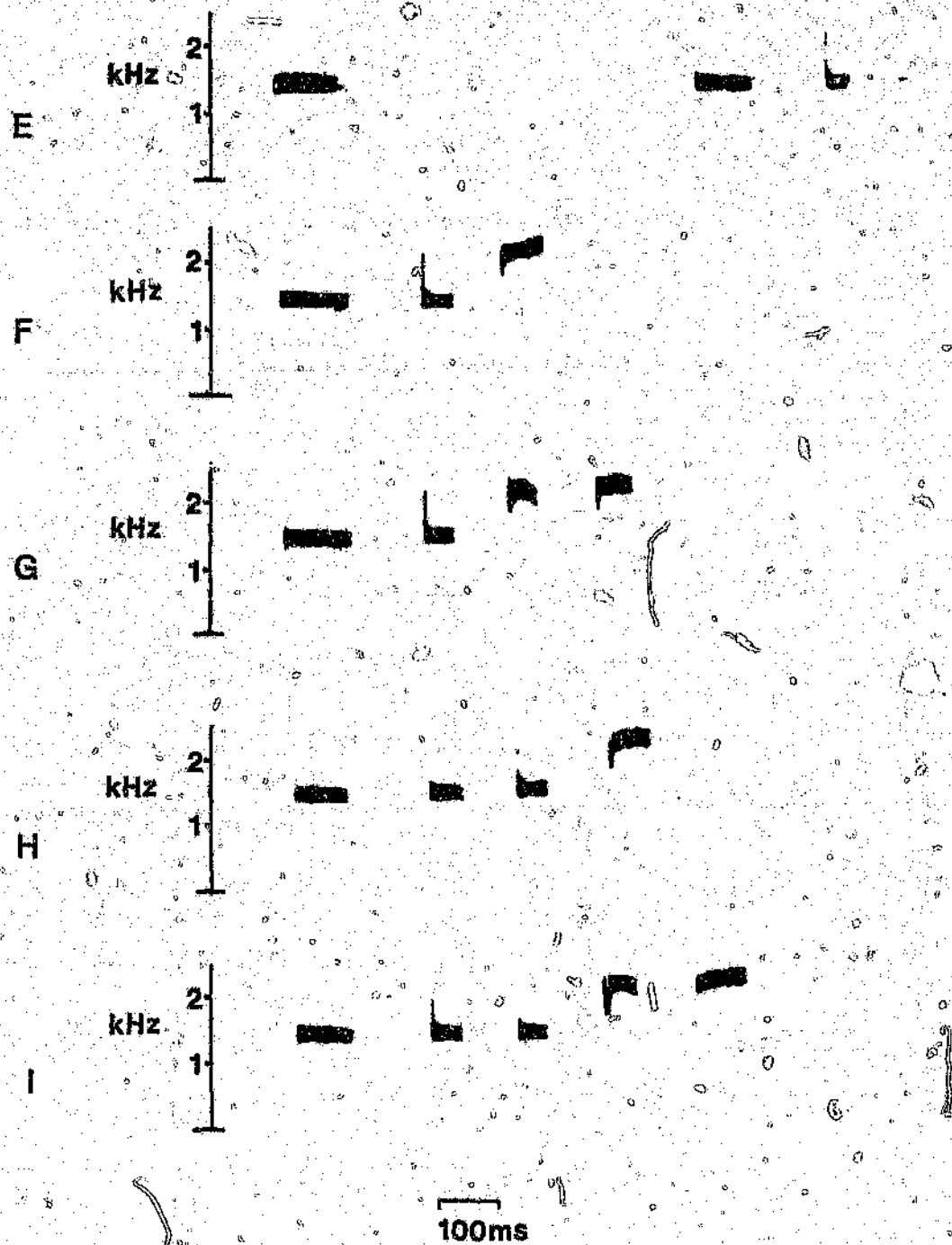


Fig. A1.2 Call repertoire of *E. coqui*.

E - "Co, co-co"

F - "Co-co-qui"

G - "Co-co-qui-qui"

H - "Co-co-co-qui"

I - "Co-co-co-quik-qui"

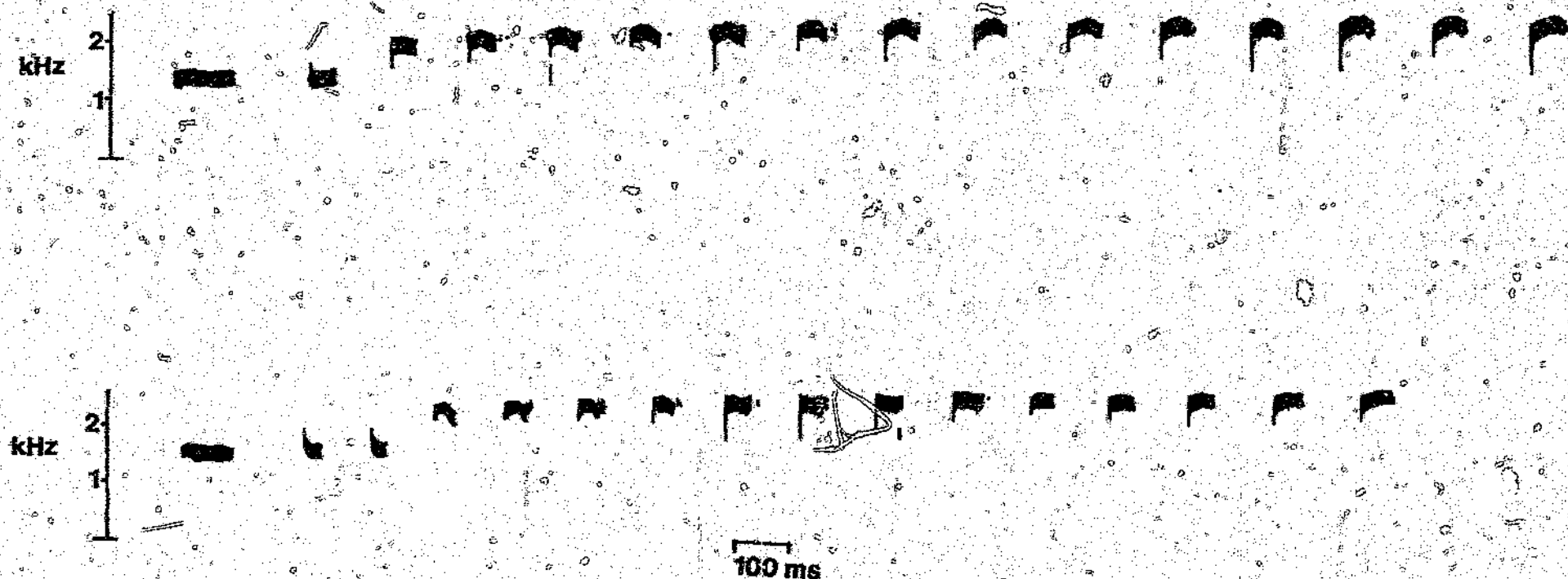


Fig. A1.3 Call repertoire of *E. coqui*.
Two multi-note aggressive calls

Appendix B

Classification and detailed description of the species studied.

1. *Afrixalus fornasinii* (Bianconi, 1849)

Classification: Order Anura, Family Hyperoliidae,
Subfamily Hyperoliinae.

Species description: A large *Afrixalus*, with a body length up to 41 mm (Poynton and Broadley, 1987). The males and females are covered on the dorsal surface by black asperities which are visible to the naked eye and are accentuated in the dark regions by being surrounded by light areas. There is a median, broad, dorsal band which tapers to a point between the eyes and does not join with the dorso-lateral bands posteriorly. The ground colour varies with the incident light from a cream colour to a dark grey-brown at which point the median dorsal band becomes difficult to distinguish (Fig. 1.1).

2. *Eleutherodactylus coqui* Thomas, 1966

Classification: Order Anura, Family Leptodactylidae,
Subfamily Telmatobiinae.

Species description: A medium-sized *Eleutherodactylus* reaching a maximum length of 62 mm. (Lopez and Narins, 1991). The dorsal surface is grey to grey-brown sometimes with an ill-defined "W" behind the eyes, and scattered dark mottling (Fig. 1.3). Often there are light stripes which run from the snout, over the eye, laterally to the vent.

3. *Hyperolius marmoratus* Rapp, 1842

Classification: Order Anura, Family Hyperoliidae,
Subfamily Hyperoliinae.

Species description: A medium-sized *Hyperolius* with a maximum body length of about 33 mm (personal observations). The adult colour pattern is extremely variable and has led to many systematic and nomenclatural uncertainties about this "superspecies" (Poynton and Broadley, 1987). The species studied in this work is recognised, on the basis of laryngeal morphology, as *H. marmoratus marmoratus* (Lambiris, 1992) and further discussion on the current taxonomic position of this species falls outside the scope of this thesis. At the breeding sites used in this study the adults were often striped with yellow and dark brown irregular stripes which sometimes broke up into spots of colour (Fig. 1.5). The juveniles were brown with sometimes darker brown stripes and usually a thin silvery lateral stripe.

4. *Kassina maculata* (Duméril, 1853)

Classification: Order Anura, Family Hyperoliidae, Subfamily Kassiniinae.

Species description: A large, robust *Kassina* reaching a maximum size of 68 mm (Poynton, 1964). The dorsal surface is covered in irregular dark brown spots with a pale outline on a silvery-brown ground colour (Fig. 1.7). The ground colour and pale outlines are replaced by a brilliant scarlet in the axilla, waist, and inner thigh regions (Fig. 1.7).

5. *Kassina senegalensis* (Duméril and Bibron, 1841)

Classification: Order Anura, Family Hyperoliidae, Subfamily Kassiniinae.

Species description: A medium-sized *Kassina* reaching a maximum size of 52 mm (Poynton, 1964). The dorsal surface typically has a unbroken, vertebral, dark stripe and two broken lateral dark stripes (Fig. 1.9). The ground colour varies from yellow through olive to dark brown and in the latter case the stripes are barely discernible.

6. *Semnodactylus wealii* (Boulenger, 1882)

Classification: Order Anura, Family Hyperoliidae,
Subfamily Kassiniinae.

Species description: A small to medium sized Kassina reaching a maximum size of 44 mm (Poynton, 1964). The dorsal surface has dark stripes which are typically divided longitudinally (Fig. 1.11). The ground colour is usually a silvery-beige colour and the hands and feet are yellow.

Appendix C

Correlation between call repetition rate, SVL and ambient temperature in *Hyperolius marmoratus* ($n = 28$)

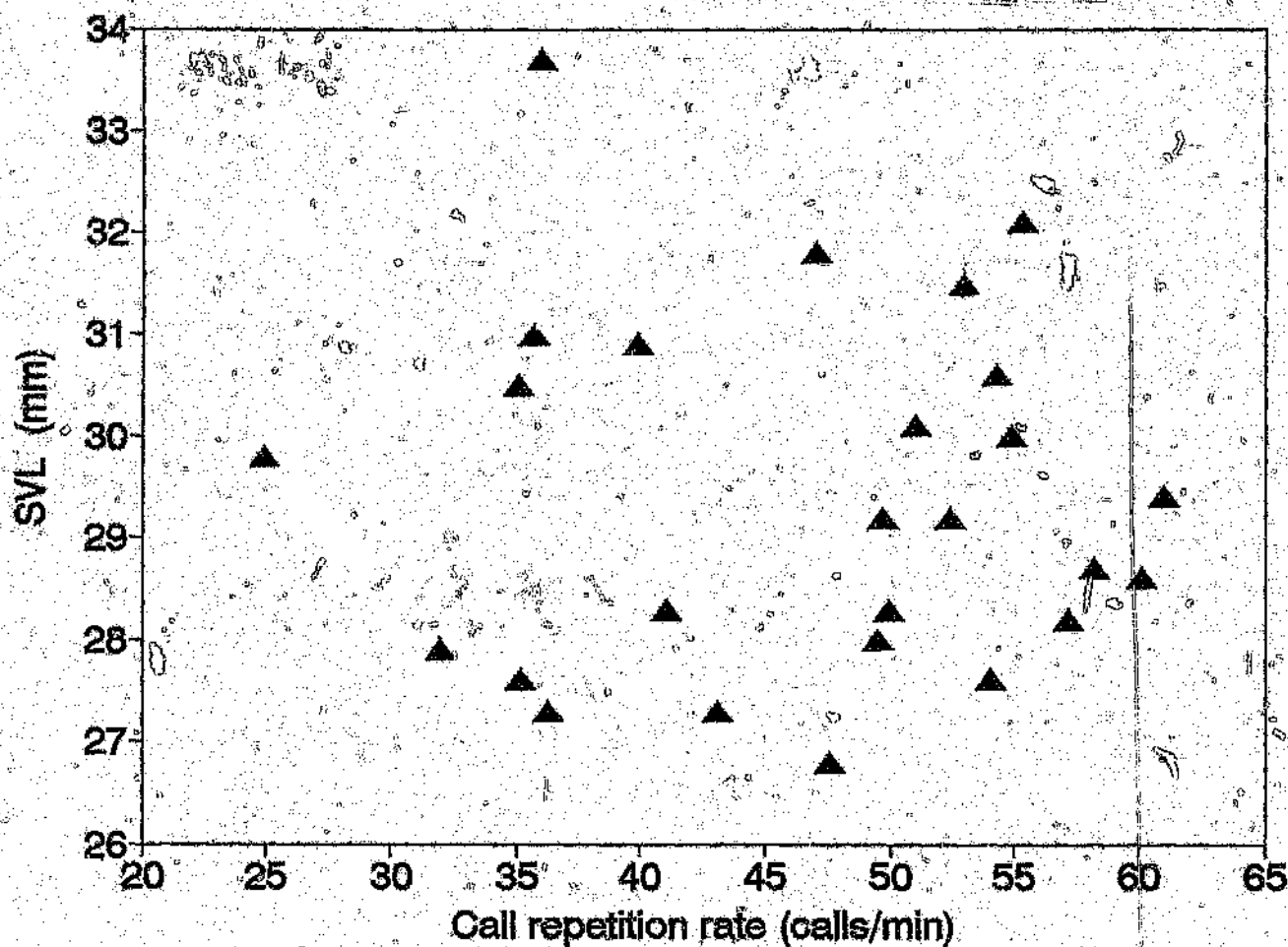


Fig. C1.1 SVL vs repetition rate (Pearson's correlation coefficient, $r = 0.045$, $P = 0.83$)

Appendix C

Correlation between call repetition rate, SVL and ambient temperature in *Hyperolius marmoratus* ($n = 28$)

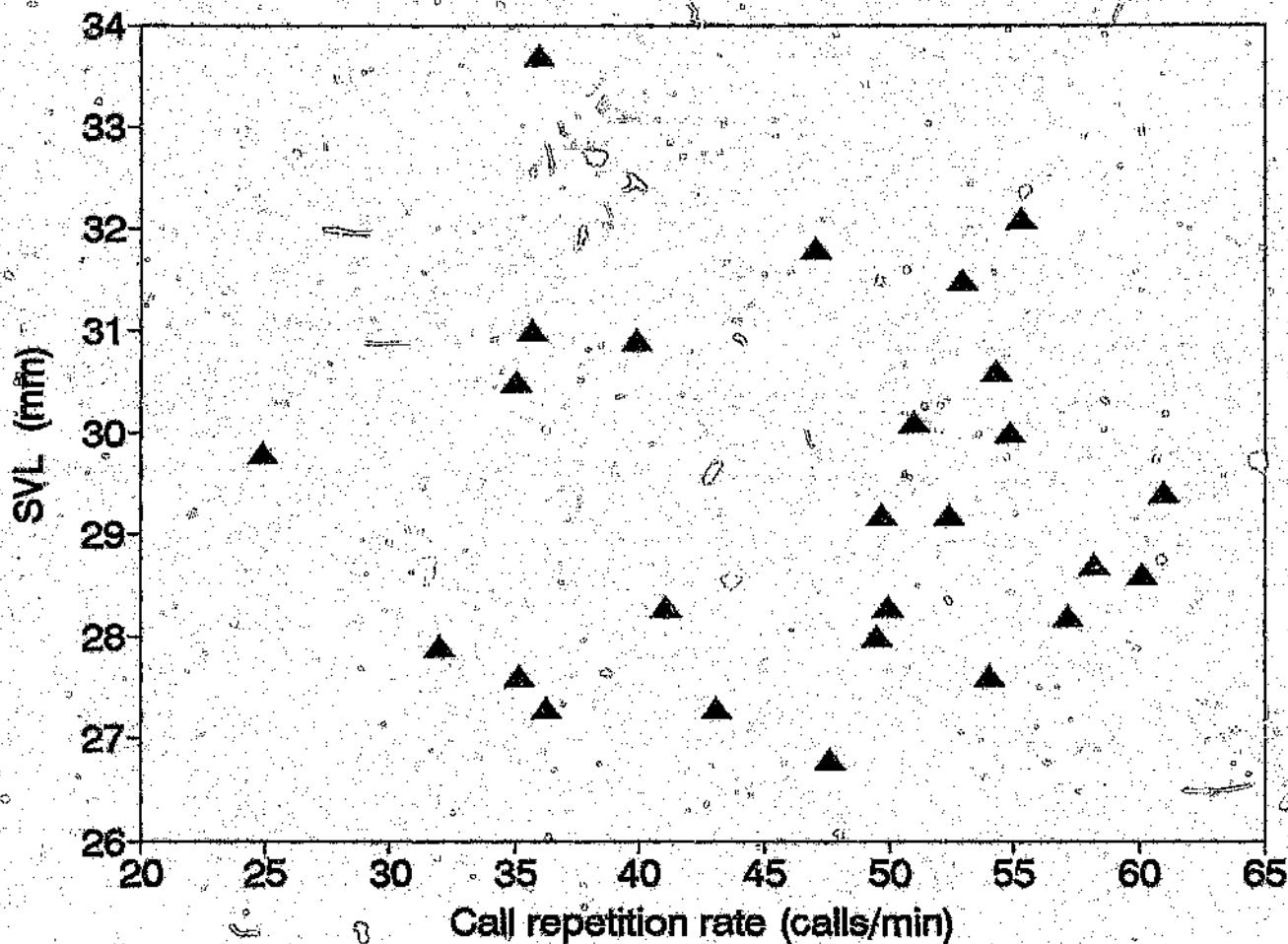


Fig. C1.1 SVL vs repetition rate (Pearson's correlation coefficient, $r = 0.045$, $P = 0.83$)

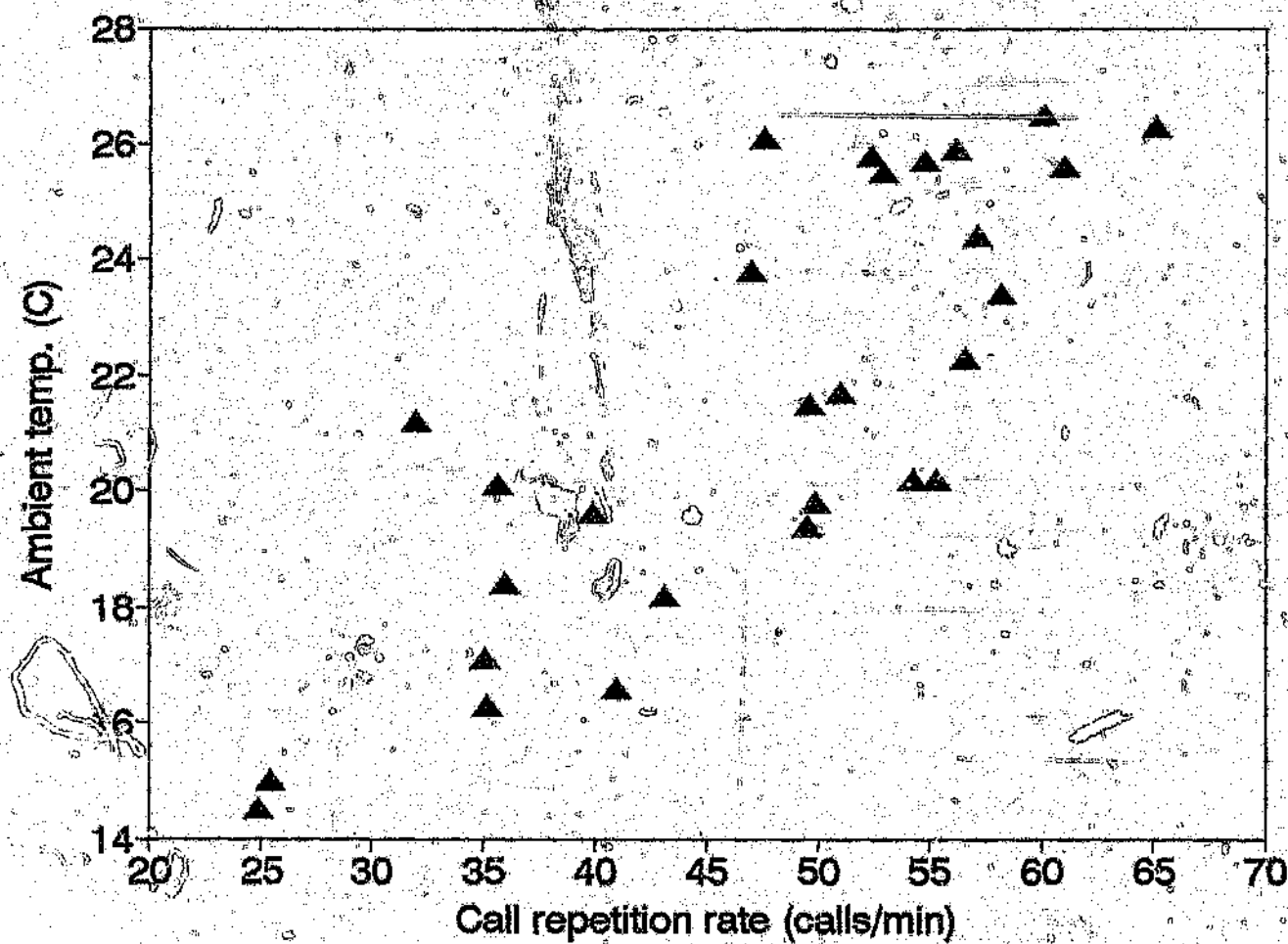


Fig. C1.2 Ambient temperature vs repetition rate
(Pearson's correlation coefficient, $r = 0.806$, $P < 0.001$)

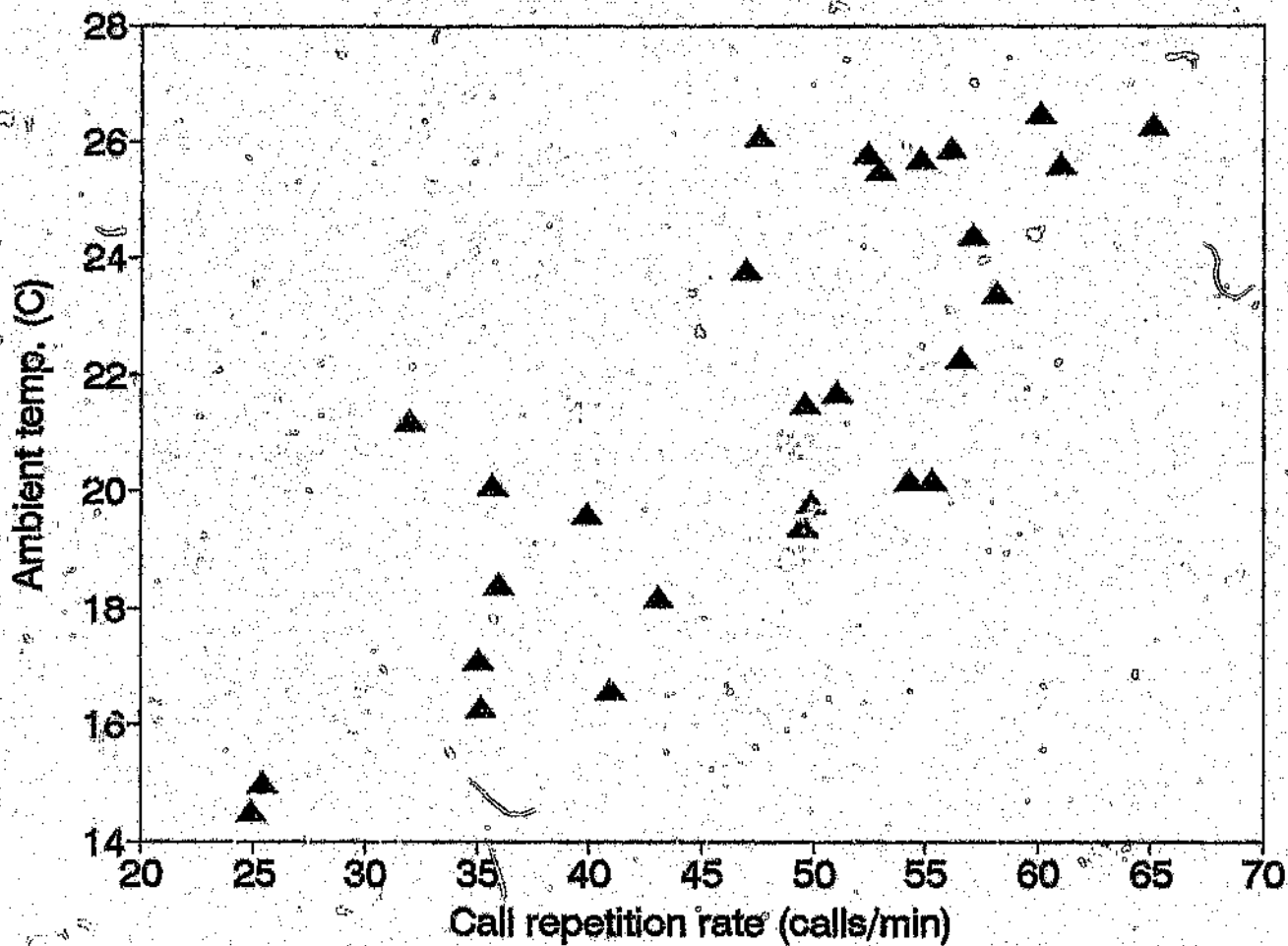


Fig. C1.2 Ambient temperature vs repetition rate
(Pearson's correlation coefficient, $r = 0.806$, $P < 0.001$)

Appendix D

Angle branding method of marking amphibians

The historical method of marking amphibians has been toe-clipping. However several authors have reported considerable blood loss following toe-clipping (see Clark, 1971). This method was thought to be totally impractical in species of frogs which are mainly arboreal, such as *H. marmoratus*. I have successfully branded over 5500 male *H. marmoratus* in the field, using a portable gas burner, and the individual identification of these males has played a vital role in various publications (Telford and Dyson, 1988, 1990; Dyson et al., 1992; Passmore et al., 1992).

Two different brands were used, one the shape of 'I', and the other 'L'. For small amphibians (<30 mm), the length of the upright part of the brand was 3 mm. Using the system shown in Fig. D1, the number of amphibians which can be marked is limited by the area of ventral surface which can be utilized. In an amphibian of SVL 30 mm, four clear brands can be applied allowing up to 9999 individuals to be marked.

Brands were made of NiCo wire and applied according to Clarke (1971). After the brand was applied the mark was immediately painted with mercurochrome and was very obvious. Individuals showed no signs of discomfort, males resumed calling within minutes of the application of the brand, and in captivity, with an *ad lib.* diet of house flies (*Musca domestica*), 80% gained weight. The marks had totally healed within a week and were durable up to a period of three months, at which time some fading occurred and rebranding was necessary.

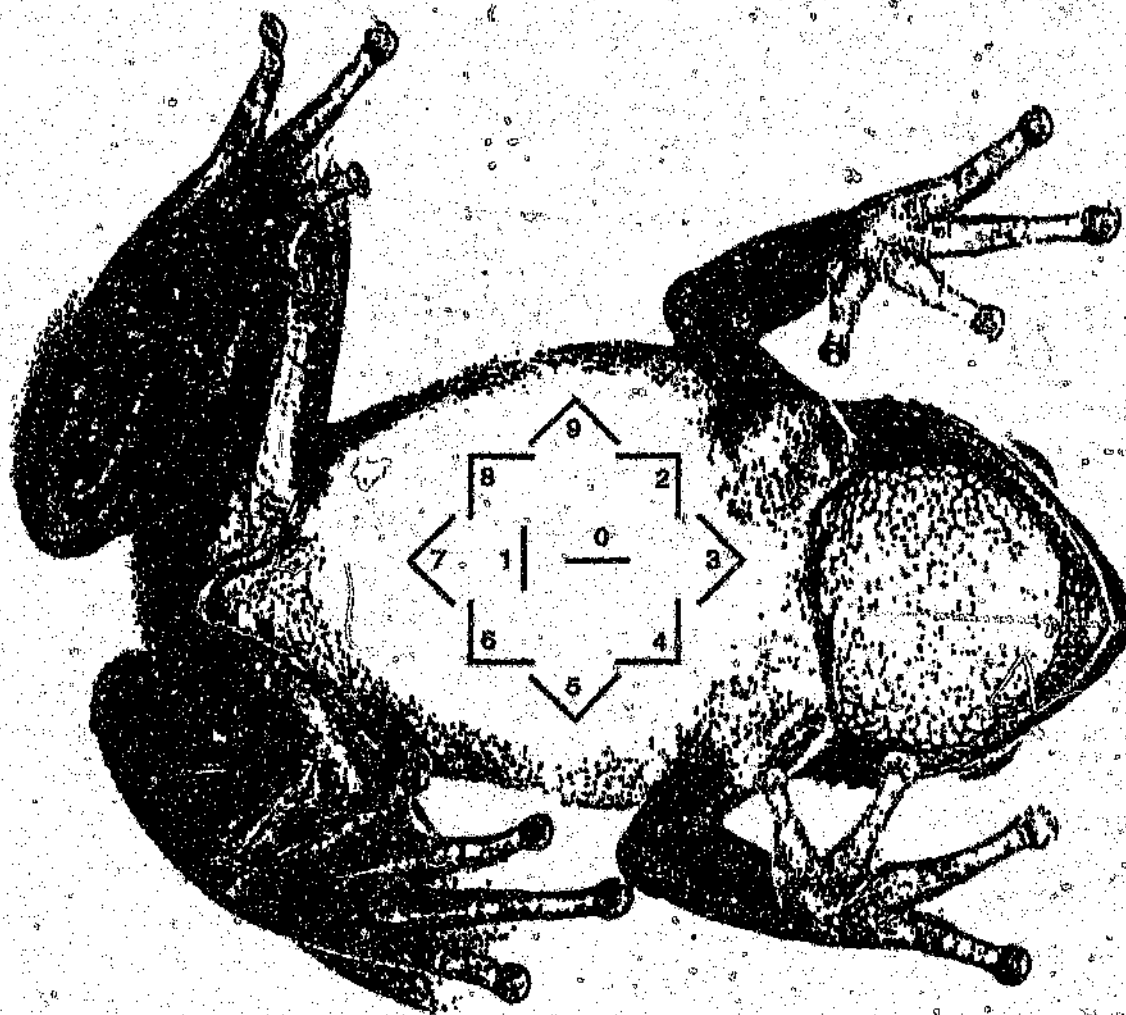


Fig. D1 The position of the brands in the angle branding method of marking amphibians

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