

https://dspace.org/

# Aspects of reproduction in the leaf-foldind frog afrixalus delicatus

**Backwell, Patricia Ruth Yvonne**

**2016-06-06**
http://hdl.handle.net/10539/20426

Downloaded from a DSpace repository. https://dspace.org/

# ASPECTS OF REPRODUCTION IN THE LEAF-FOLDING FROG, AFRIXALUS DELICATUS

---

*Patricia Ruth Yvonne Backwell*

Thesis submitted to the Faculty of Science,
University of the Witwatersrand, Johannesburg
in fulfilment of the requirements for the
degree of Doctor of Philosophy.

JOHANNESBURG

January 1991

## ABSTRACT

This work examines aspects of sexual reproduction in the previously little-studied Leaf-folding Frog, Afrixalus delicatus.

The taxonomic status of this species was determined using the Mate Recognition System to delimit the species boundary. Male social behaviour was investigated with particular reference to the structure and functional partitioning of the two-part advertisement call; the maintenance of intermale spacing and the effects of chorus size on the spatial separation of males; chorus organisation; call site selection and fidelity to call sites. The climatic factors influencing male behaviour were also examined. The mating success of calling and satellite males was determined and the possible causes of the variation in mating success were examined.

Female behaviour was also extensively studied. Females were found to produce a small number of large eggs that are protected in leaf nests. Oviposition site requirements were determined, and the concentration of nests examined. Fertilisation success was found to be high. Some females were found to be polyandrous, mating with up to three males. The behaviour of females in the chorus was observed and females were found to generally mate with one of the nearer males irrespective of morphology or behaviour. The potential and actual accuracy of mate localisation was determined.

This study of a species' mating system and its flexibility in relation to ecological, physiological and social pressures allowed for a more thorough understanding of anuran reproductive behaviour and its evolution.

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.

Rockwell

*17th day of January 1991*

*Dedicated to my Mother*

**Maureen Backwell**

## PREFACE

Anurans provide a model system for the study of social behaviour and communication. In spite of increased interest in this field, many aspects of their behaviour have yet to be investigated through detailed field studies. **Afrixalus delicatus** is a small anuran that has received little previous attention. Due to a variety of uncommon behavioural traits associated with mating, it provided a wide scope for both observational and experimental work.

I would like to acknowledge the assistance of my supervisor, Professor Neville Passmore. His encouragement and guidance were greatly appreciated. I recognise that he is responsible for much of my intellectual development and he taught me many valuable lessons. I would like to thank Ian and Jean Garland for the facilities and comforts they provided during the fieldwork. I am grateful to Steven Telford, Phillip Bishop, Mandy Dyson and Michael Jennions for their numerous discussions and constructive advice on this work. I would like to thank Neville Passmore, Steven Telford, Phillip Bishop, Mandy Dyson, Jonathan Brand and David Amm for assistance with fieldwork and the construction of field equipment. I am grateful to Catherine Snow and Lucinda Backwell for proof-reading drafts and assisting in the production of this thesis. Finally, I would like to acknowledge my mother, Maureen Backwell, whose support and understanding has made this work possible.

Animal ethics clearance for this work was obtained from the Animal Ethics Screening Committee, University of the Witwatersrand (clearance number 89-61-2). The author was the recipient of a Senior Bursary from the University of the Witwatersrand and a bursary from the Council for Scientific and Industrial Research. The Communication Biology Research Group, Zoology Dept., University of the Witwatersrand and the Foundation for Research Development, Council for Scientific and Industrial Research, funded the fieldwork.

Various papers reporting the findings detailed in this thesis have been published, are currently in press; or are being reviewed.

"Functional Partitioning of the Two-part Call of the Leaf-folding Frog, **Afrixalus delicatus**" (1988) Herpetologica 44(1): 1 - 7.

"Polyandry in the Leaf-folding Frog, Afrixalus delicatus" (1990) Herpetologica 46: 7 - 10.

"Aggression and Intermale Spacing in the Leaf-folding Frog, Afrixalus delicatus" (1990) S. Afr. J. Zool. 25(2): 133 - 137.

"Male Mating Success in the Leaf-folding Frog, Afrixalus delicatus" (submitted to Herpetologica).

"Sonic Complexity and Mate Localisation in the Leaf-folding Frog, Afrixalus delicatus" (submitted to Herpetologica).

"Classification of the Natal dwarf Afrixalus species" (submitted to J. Afr. Zoology).



## ABBREVIATIONS USED IN THE TEXT

| | |
|---|---|
| C | degrees Centigrade |
| cm | centimetre |
| dB | decibel |
| df | degrees of freedom |
| E | east |
| fig. | figure |
| hr | hour |
| Hz | Hertz |
| Lat. | latitude |
| Long. | longitude |
| m | metre |
| min | minute |
| n | sample size |
| no. | number |
| NS | non-significant |
| mm | millimetre |
| P | probability |
| S | south |
| s | second |
| SPL | sound pressure level |
| SMRS | Specific-Mate Recognition System |
| SVL | snout to vent length |
| W | Watt |
| $\bar{x}$ | mean |

CONTENTS


Title page ..... i
Abstract ..... ii
Declaration by candidate ..... iii
Dedication ..... iv
Preface ..... v
Abbreviations used in text ..... vii
Contents ..... viii
List of figures ..... xiv
List of tables ..... xvi

CHAPTER ONE

GENERAL INTRODUCTION

1.1 Preamble ..... 1
1.1.1 Anuran reproductive strategies ..... 2
1.2 Study species ..... 6
1.3 Study area ..... 8
1.4 Scope and objectives ..... 10

CHAPTER TWO

NATAL DWARF AFRIXALUS

2.1 Introduction ..... 11
2.1.1 General ..... 11
2.1.2 Classification of the genus Afrixalus ..... 12
2.2 Methods ..... 13
2.3 Results ..... 15
2.4 Discussion ..... 22

CHAPTER THREE

TWO-PART ADVERTISEMENT CALL


| | | |
|---|---|---|
| 3.1 | **Introduction** | 23 |
| 3.2 | **Methods** | 25 |
| 3.2.1 | Recording of advertisement call | 25 |
| 3.2.2 | Effect of call components on female phonotaxis | 25 |
| 3.2.3 | Effect of call components on male behaviour | 27 |
| 3.2.4 | Relative abundance of call components at different chorus sizes | 27 |
| 3.2.5 | Effect of female presence on the relative abundance of call components | 30 |
| 3.3 | **Results** | 30 |
| 3.3.1 | Advertisement call | 30 |
| 3.3.2 | Effect of call components on phonotaxis | 33 |
| 3.3.3 | Effect of call components on male behaviour | 33 |
| 3.3.4 | Relative abundance of call components at different chorus sizes | 34 |
| 3.3.5 | Effect of female presence on the relative abundance of call components | 37 |
| 3.4 | **Discussion** | 39 |


CHAPTER FOUR

INTEEMALE SPACING


| | | |
|---|---|---|
| 4.1 | **Introduction** | 42 |
| 4.1.1 | General | 42 |
| 4.1.2 | Maintenance of spacing | 43 |
| 4.1.2.1 | Advertisement call | 43 |
| 4.1.2.2 | Encounter call | 44 |
| 4.1.2.3 | Physical combat | 46 |
| 4.1.3 | Function of spacing | 48 |
| 4.1.4 | Aims | 49 |
| 4.2 | **Methods** | 50 |
| 4.2.1 | Advertisement call intensity | 50 |
| 4.2.2 | Recording and analysis of encounter calls | 50 |

| | | |
|---|---|---|
| 4.2.3 | Aggressive interactions: vocal and physical | 51 |
| 4.2.4 | Nearest neighbour distances | 51 |
| 4.2.5 | Effect of nearest neighbour distance on frequency of aggressive interactions | 52 |
| 4.3 | **Results** | 52 |
| 4.3.1 | Advertisement call intensity | 52 |
| 4.3.2 | Encounter calls | 55 |
| 4.3.3 | Aggressive interactions : vocal and physical | 55 |
| 4.3.4 | Nearest neighbour distances | 65 |
| 4.3.5 | Effect of nearest neighbour distance on frequency of aggressive interactions | 65 |
| 4.4 | **Discussion** | 67 |
| 4.4.1 | General | 67 |
| 4.4.2 | Advertisement call intensity | 67 |
| 4.4.3 | Maintenance of spacing | 68 |
| 4.4.4 | Functions and effects of spacing | 68 |

CHAPTER FIVE

SOME ASPECTS OF MALE BEHAVIOUR

| | | |
|---|---|---|
| 5.1 | **Introduction** | 72 |
| 5.1.1 | General | 72 |
| 5.1.2 | Climatic factors | 72 |
| 5.1.3 | Call sites and fidelity | 73 |
| 5.1.4 | Chorus distribution | 74 |
| 5.1.5 | Chorus organisation | 76 |
| 5.2 | **Methods** | 77 |
| 5.2.1 | Climatic factors | 77 |
| 5.2.2 | Normal call sites and fidelity | 77 |
| 5.2.3 | Chorus distribution | 78 |
| 5.2.4 | Chorus organisation | 79 |
| 5.3 | **Results** | 82 |
| 5.3.1 | Climatic factors | 82 |
| 5.3.2 | Call sites and fidelity | 82 |
| 5.3.3 | Chorus distribution | 85 |
| 5.3.4 | Chorus organisation | 86 |

5.4 Discussion ..... 91
5.4.1 General ..... 91
5.4.2 Climatic factors ..... 91
5.4.3 Call sites and fidelity ..... 91
5.1.4 Chorus distribution ..... 92
5.1.5 Chorus organisation ..... 95

CHAPTER SIX

MALE MATING SUCCESS

6.1 Introduction ..... 97
6.1.1 General ..... 97
6.1.2 Mating success of calling males ..... 97
6.1.3 Satellite behaviour ..... 98
6.1.4 Mating success of satellite males ..... 99
6.1.5 Aims ..... 99
6.2 Methods ..... 100
6.2.1 Male mating success ..... 100
6.2.1.1 Verification from natural breeding area ..... 101
6.2.2 Satellite behaviour ..... 101
6.3 Results ..... 101
6.3.1 Male mating success ..... 102
6.3.1.1 Verification from natural breeding area ..... 108
6.3.2 Satellite behaviour ..... 110
6.4 Discussion ..... 111
6.4.1 Male mating tactics ..... 111
6.4.2 Mating success of calling males ..... 111
6.4.3 Mating success of satellite males ..... 113

CHAPTER SEVEN

MATING AND NESTING BEHAVIOUR

7.1 Introduction ..... 115
7.1.1 Anuran mating behaviour ..... 115
7.1.2 Terrestrial breeding ..... 116

7.1.3 Clutch size and egg characteristics ..... 117
7.1.4 Polyandry ..... 118
7.2 **Methods** ..... 119
7.2.1 Rapid call ..... 119
7.2.2 Mating and nest-building behaviour ..... 120
7.2.3 Nest characteristics ..... 120
7.2.4 Oviposition site requirements ..... 121
7.2.5 Egg characteristics and hatching success ..... 121
7.2.6 Polyandry ..... 122
7.3 **Results** ..... 122
7.3.1 Rapid call ..... 123
7.3.2 Mating and nest-building behaviour ..... 123
7.3.3 Nest characteristics ..... 131
7.3.4 Oviposition site requirements ..... 134
7.3.5 Egg characteristics and hatching success ..... 137
7.3.6 Polyandry ..... 139
7.4 **Discussion** ..... 139

CHAPTER EIGHT

FEMALE BEHAVIOUR

8.1 **Introduction** ..... 144
8.1.1 General ..... 144
8.1.2 Accuracy of mate localisation ..... 144
8.1.3 Female behaviour in the chorus ..... 145
8.1.4 Aims ..... 146
8.2 **Methods** ..... 147
8.2.1 Interaural distances ..... 147
8.2.2 Accuracy of phonotaxis ..... 147
8.2.3 Female behaviour in the chorus ..... 149
8.3 **Results** ..... 149
8.3.1 Interaural distance ..... 149
8.3.2 Accuracy of phonotaxis ..... 149
8.3.3 Female behaviour in the chorus ..... 152
8.4 **Discussion** ..... 154

CHAPTER NINE

CONCLUDING DISCUSSION


| | | |
|---|---|---|
| 9.1 | **Sexual reproduction** ..... | 156 |
| 9.2 | **Reproductive strategy** ..... | 159 |
| 9.2.1 | Male reproductive strategy ..... | 159 |
| 9.2.2 | Female reproductive strategy ..... | 162 |
| 9.2.3 | Effect of chorus density on reproductive strategy ..... | 163 |
| 9.3 | **Conclusion** ..... | 166 |

APPENDIX ONE

Analysis of male distribution patterns in anuran choruses ..... 167

REFERENCES ..... 177

LIST OF FIGURES


Fig. 1.1 : A. delicatus
(a) a calling male and (b) a gravid female ..... 7

Fig. 1.2 : Natural breeding areas of A. delicatus
on Twinstreams farm:
(a) Matatiele pan
(b) Mavungweni pan
(c) Passmore's pan ..... 9

Fig. 2.1 : Sonograms of the three Natal dwarf
Afrixalus species ..... 16

Fig. 2.2 : Photographs of the three Natal dwarf
Afrixalus species ..... 17

Fig. 3.1 : Photograph of cage:
(a) external view
(b) pond inside cage ..... 29

Fig. 3.2 : Wide band (300 Hz filter) sonogram of the
two-part call of A. delicatus ..... 31

Fig. 3.3 : Abundance of call components at different
chorus sites ..... 36

Fig. 4.1 : Wide band (300 Hz filter) sonogram of
A. delicatus encounter call ..... 57

Fig. 4.2 : Flow diagram of aggressive interactions
between A. delicatus males ..... 58

Fig. 4.3 : Aggressive interaction between two males ..... 59

Fig. 4.4 : Nearest neighbour distances at
different chorus sites ..... 62

Fig. 4.5 : Distribution of nearest neighbour distances at different chorus sizes ..... 64

Fig. 5.1 : The measurement of delay periods ..... 81

Fig. 5.2 : Wide band (300 Hz filter) sonogram of zip calls of two neighbouring A. delicatus males showing call overlap and call alternation ..... 88

Fig. 7.1 : Wide band (300 Hz filter) sonogram of the rapid call of A. delicatus ..... 124

Fig. 7.2 : Female approach to calling male ..... 126

Fig. 7.3 : (a) Leaves of Polygonum pulchrum and Ludwegia stolonifera
(b) an amplexing pair ..... 128

Fig. 7.4 : Nest-building behaviour ..... 129

Fig. 7.5 : (a) A completed nest and
(b) an opened nest ..... 130

Fig. 7.6 : A. delicatus tadpoles ..... 132

Fig. 7.7 : Map of Matatiele pan showing areas of Polygonum pulchrum and Ludwegia stolonifera and the occurrence of A. delicatus nests ..... 133

Fig. 7.8 : Histograms of the nest and pan leaf characteristics ..... 135

Fig. 7.9 : Distribution of egg clutch mass ..... 138

Fig. 8.1 : Examples of female approaches ..... 153

Fig. 9.1 : Density effects on the reproductive behaviour of A. delicatus males ..... 165

Fig. A1.1 : Nearest neighbour distances at different chorus sites ..... 171

LIST OF TABLES


Table 2.1 : Call parameters of three Natal dwarf Afrixalus species ..... 18

Table 2.2 : Behavioural comparison of three Natal dwarf Afrixalus species ..... 19

Table 2.3 : Morphological comparison of three Natal dwarf Afrixalus species ..... 20

Table 2.4 : Analysis of advertisement calls of three Natal dwarf Afrixalus species ..... 21

Table 3.1 : Call parameters of A. delicatus advertisement call ..... 32

Table 3.2 : Relative abundance of call components at different chorus sites ..... 35

Table 3.3 : Relative proportion of zips and trills with and without a female present in the chorus ..... 38

Table 4.1 : Call directivity patterns ..... 54

Table 4.2 : Call parameters for A. delicatus encounter call and zip call ..... 56

Table 4.3 : Nearest neighbour distances at different chorus sites ..... 61

Table 4.4 : Multiple-range analysis (Student-Newman-Kuel) of differences between mean nearest neighbour distances ..... 63

Table 4.5 : Frequency of vocal and physical aggressive interactions at three chorus sizes ..... 66

Table 5.1 : Call site fidelity of 25 males ..... 84

Table 5.2 : Intercall intervals for zips and trills ..... 89

Table 5.3 : Delay period between two consecutive calls of neighbouring males ..... 90

Table 6.1 : Spearman's correlation coefficients for all variable combinations ..... 104

Table 6.2 : Three variable partial correlation coefficients for mating success and other variables ..... 105

Table 6.3 : Stepwise Variable Selection Multiple Regression analysis for mating success ..... 106

Table 6.4 : Partial correlation coefficients for the number of nights spent calling ..... 107

Table 6.5 : Size measurements for naturally-captured individuals ..... 109

Table 7.1 : Comparison of A. delicatus zip, trill and rapid call ..... 125

Table 7.2 : Oviposition site requirements for A. delicatus ..... 136

Table 8.1 : Mean jump error angles and statistics for female approaches ..... 151

Table A1.1 : Clark and Evans' (1954) analysis of spacing patterns ..... 172

Table A1.2 : Craig's (1953) analysis of spacing patterns ..... 173

Table A1.3 : Chi-square test for Clark and Evans' analysis ..... 175

Table A1.4 : Chi-square test for Craig's analysis ..... 175

Table A1.5 : Pielou's analysis of spatial distribution ..... 176

# CHAPTER ONE

# GENERAL INTRODUCTION

## 1.1 PREAMBLE

Reproduction in biparental organisms includes three complex adaptations: meiosis, fertilisation and syngamy. Fertilisation is the bringing together of sex-cells of individuals of opposite gender. All biparental organisms have "fertilisation mechanisms" (Paterson, 1985) that include characters involved in signalling between the mating partners or between their sex-cells. The ability to find conspecific mates is an essential requirement of sexually reproducing animals (Passmore, 1981). Effective recognition of potential sexual partners is accomplished by the "Specific-mate Recognition System" (SMRS). This comprises a sequence of steps involving the emission of a signal, its reception by the potential partner, and its processing by the central nervous system. This conditionally releases a response to be similarly received, processed and responded to by the first partner etc. (Paterson, 1977). Individuals that depart radically from the norm would not attract conspecific mates if they fall outside the receiver's range, and the genes governing this radical departure would then not be represented in the following generation. Stabilising selection would act over successive generations and consequently very little genetic variation would underlie the phenotypic expression of the SMRS (Passmore, 1981; Paterson, 1980, 1985). The signals involved in the SMRS are shaped by natural selection to serve the purpose of promoting the meeting of conspecific sexual partners. Thus the signals will be adaptive in the normal habitat of the species and will be most effective in that habitat (Paterson, 1977). There is a wide range of signalling and recognition systems and channels in the animal kingdom. Recognition may be visual- [e.g. fireflies (Buck, 1938), widowbirds (Anderson, 1982)]; chemical- [e.g.

butterflies (Brower (1969), moths (Schneider (1963)]; tactile- [e.g. sticklebacks (Ommanney, 1963), acridid grasshoppers (Otte (1972)], or auditory- [eg. Indigo Buntings (Emlen, 1972), crickets (Alexander, 1961), anurans (Wells, 1977b)].

The mate recognition system of anurans comprises (a) the advertisement call which functions as a long-distance attractant and also conveys information regarding species identity, and (b) the female auditory receptor system, that is tuned to receive such calls (Telford, 1982). The frequency structure of the advertisement call is precisely matched to the best excitatory frequencies of the female's primary hearing organs (Capranica, 1976; Ryan and Rand, 1990), i.e., a close relationship has evolved between the signal structure and the receptor tuning.

The part played by social interactions in anuran reproduction is profound and is an integral part of the mate recognition system (Telford, 1982; Wells, 1977b). In the majority of frog species, social behaviour includes both competitive male-male interactions and access to mates (Telford, 1982). It is important to note that the recognition process does not necessarily imply any form of assessment of genetic quality as a potential parent by either partner of the other (Paterson, 1977).

### 1.1.1 Anuran Reproductive Strategies

Reproductive strategies encompass behaviours and physical adaptations specific to mating, as well as the social consequences of these behaviours (Vehrencamp and Bradbury, 1984). The mating system includes such features as the number of mates acquired, the manner of mate acquisition, the presence of pair-bonds and the patterns of parental care provided by each parent. Anuran reproductive strategies are remarkably diverse, both within and between species. Within species, variation in population density is one factor believed to affect the mating strategy employed by individual males, to the extent of causing a change in the entire mating system of the population (Emlen and Oring, 1977; Wells, 1977b). The density of calling males within a population may affect the intensity of intermale competition, the mate- locating strategies, and the cost of resource defence (Dyson, 1986). Between species, the variation is substantial and may

be split into two broad categories: explosive and prolonged breeding patterns (Wells, 1977b). In general, prolonged breeding covers periods of more than a month, while explosive breeding refers to periods of a few days to a few weeks. This distinction provided an evolutionary framework for understanding the relationship between social behaviour and ecology in anurans. The length of the breeding season determines the density of males at the breeding site and hence the type and intensity of male-male interactions (Wells, 1977b). It also determines the temporal availability of females at the breeding site. Consequently, the length of the breeding season influences the selective pressures that shape the mating system.

Explosive breeding is usually associated with marked spatial clumping around suitable oviposition sites and is characteristic of many species that breed in temporary rain pools or ephemeral habitats (Wells, 1977b). The aggregations of males lead to high-density populations and there is often active searching for females. Social organisation is uncommon and active searching behaviour is a response to the probability that male reproductive success is determined by the rate at which males encounter other individuals (Wells, 1977b). The advantage of encountering an incoming female probably outweighs the disadvantage of repeatedly clasping other males, and thus a calling strategy or the defence of a territory would be inviable, since females would be intercepted by searching males before they reached the calling individual (Wells, 1977b).

Prolonged breeding is probably the more common system. Here males are sedentary and acoustic communication allows the identification of the callers' sex and their reproductive state; it facilitates the location of mates, and it permits the establishment and maintenance of individual distance or territory by males (Arak, 1983b; Telford, 1982; Wells, 1977b; Whitney and Krebs, 1975a). Males vocalise in choruses that probably advertise the locations of breeding sites to females and males in surrounding areas (Bogert, 1960; Wells, 1977b). The more intensified sound source of a chorus may facilitate easier localisation of the breeding area (Wells, 1977b). Breeding aggregations lead to the concentration of both sexes within a small area and increase the chance of

encountering a potential mate (Arak, 1983a). They also provide the potential for females to compare males' qualities and/or resources (Arak, 1983a).

Within the chorus, vocalisations play a role in the attraction of females to males (for review see Wells, 1977a,b) and in the maintenance of a characteristic distance between callers, which allows for effective signalling and may enhance a male's chance of securing a mate (Arak, 1983b; Fellers, 1979a; Whitney and Krebs, 1975a). Since the advertisement call functions in mate recognition, it is necessarily species-specific and relatively invariable in the features required for this recognition. The advertisement call may be variable in other features. Calls have been reported to vary due to both external (e.g. temperature: Bellis, 1957; Brown and Brown, 1977; Littlejohn, 1976; Michaud, 1964; humidity; call site and wind: Bellis; 1957; Wells, 1977b) and internal factors (e.g. body size: Loftus-Hills, 1973; Zweifel, 1968; age and hormonal levels: Bellis, 1957; Wells, 1977b).

Females are presumably preferentially attracted to conspecific calls that are most audible and locatable (Arak, 1983a; Dyson, 1989). A male's relative mating success may increase if, for example, his call is louder than surrounding calls and hence heard by more potential mates (Dyson, 1989). Relative male mating success may also be influenced by behavioural variability [e.g. in the amount of time spent at the breeding site; the reproductive tactic employed; call site fidelity; and other factors (Arak, 1988a; Dyson, 1986; Gerhardt et al., 1987; and other factors)].

The advertisment call is perceived not only by females, but also by conspecific males and may play a role in the social organisation of the chorus (see Whitney and Krebs, 1975a). Chorus organisation involving antiphony and other ordered call patterns may maximise signal efficiency (Whitney and Krebs, 1975a) and allow the discrimination of the signal against background noise. Male-male vocal interactions resulting in the spatial separation of calling males have been paid considerable attention in prolonged-breeding anurans (Arak, 1983b; Fellers, 1979a; Littlejohn, 1977; Whitney and Krebs, 1975a). Intermale spacing may improve an individual male's attractiveness as a mate by maximising his locatability and/or the distinctiveness of his call.

In order to succesfully mate, female anurans must recognise the calls of conspecific males, as well as locate these calls. Studies in many anurans have shown that the female auditory system can process male acoustic cues and be guided to the sonic target with extreme accuracy (Feng et al., 1976; Gerhardt and Rheinlaender, 1982; Passmore et al., 1984). Although the mechanism of localisation is uncertain, the ability of some extremely small anuran species to localise a sound source in three dimensions is impressive (Passmore et al., 1984).

As previously described, anuran reproductive strategies encompass not only adaptations to ensure fertilisation, but also factors which facilitate (a) the survival of offspring, eg. various forms of parental care (Duellman and Trueb, 1986; Salthe and Mecham, 1974); and increased genetic variability of offspring (Gladstone, 1979; Stacey, 1982); (b) coexistence with other species, e.g. differences in advertisement call structure (Gerhardt, 1974; Littlejohn and Martin, 1969); (c) the avoidance of predation, e.g. larval predation (Duellman and Trueb, 1986; Poynton, 1964) and (d) the ability to overcome the physical and environmental restraints on the adult individuals, e.g. breeding energetics (Seymour, 1973; Wells, 1976); length of breeding season (Wells, 1977b); temperature (Arak, 1983a).

Specialisations in oviposition are relatively common in anurans and presumably affect the survival of offspring, particularly in harsh environments (Duellman and Trueb, 1986). The most common and presumably least specialised mode of oviposition is the deposition of a large number of eggs in open water (Duellman and Trueb, 1986; Salthe and Mecham, 1974). Specialisations show a trend towards the withdrawal of development from free environmental water (Lutz, 1948; Poynton, 1964; Salthe and Mecham, 1974). Various species have specialised by laying fewer eggs, but protecting them in nests constructed at the time of spawning (Robertson, 1984; Wager, 1956, 1965), while other species exhibit extreme forms of parental care - e.g. **Pipa pipa** (Salthe and Mecham, 1974). The adaptations involved in these specialisations are presumably a response to predation on early developmental stages (Duellman and Trueb, 1986; Poynton, 1964), or to reduced availability of surface water (Duellman and Trueb, 1986; Robertson, 1984). Another specialisation in reproductive strategy that could

increase the chances of offspring survival is the accomplishment of increased genetic diversity in offspring (Gladstone, 1979; Stacey, 1982). Genetic diversity in a population is a result of recombination and mutation during sexual reproduction. Variation in offspring would allow a greater adaptability against fluctuations in the environment (Gladstone, 1979).

## 1.2 STUDY SPECIES

**Afrixalus delicatus** (Hyperoliidae) usually breeds on emergent vegetation in the eulittoral zone of permanent standing water (Telford, 1982). Males have been found calling on water-lily leaves and reeds (Passmore and Carruthers, 1979) and from emergent eulittoral vegetation (Telford, 1982). Males congregate at the breeding site nightly from September to February each year. They occupy call sites that they defend from intrusion by conspecific males (Telford, 1982). Female arrival is asynchronous and females approach individual calling males and initiate amplexus (Telford, 1982). Oviposition occurs on leaves above water and the eggs are enfolded by a leaf whose opposing faces are glued together to form a protective nest for the development of early stages (Wager, 1956; Pickersgill, 1984; Telford, 1982).

**Afrixalus delicatus** is a small frog [male snout-vent length 15.2 - 19.5 mm and female 17.2 - 21.8 mm](Pickersgill, 1984). Adults have a light dorsum with two darker longitudinal stripes which do not, or only slightly, overlap the upper eyelid (Pickersgill, 1984). The tibia may have an oblique, but narrow transverse band over the lower exposed surface (Pickersgill, 1984). Small dark asperities are normally present on the chest and belly. The dorsal asperities are minute, strongly developed and scattered over the dorsum, but rarely concentrated on the snout (Pickersgill, 1984; Poynton, 1964). The dorsum is a light golden colour, and the throat is yellowish in males and yellowish-white in females. The venter is white and the legs, feet and toes are yellowish-white (pers. obs.). The body is long and slender, the eyes are large with vertical pupils (Passmore and Carruthers, 1979).

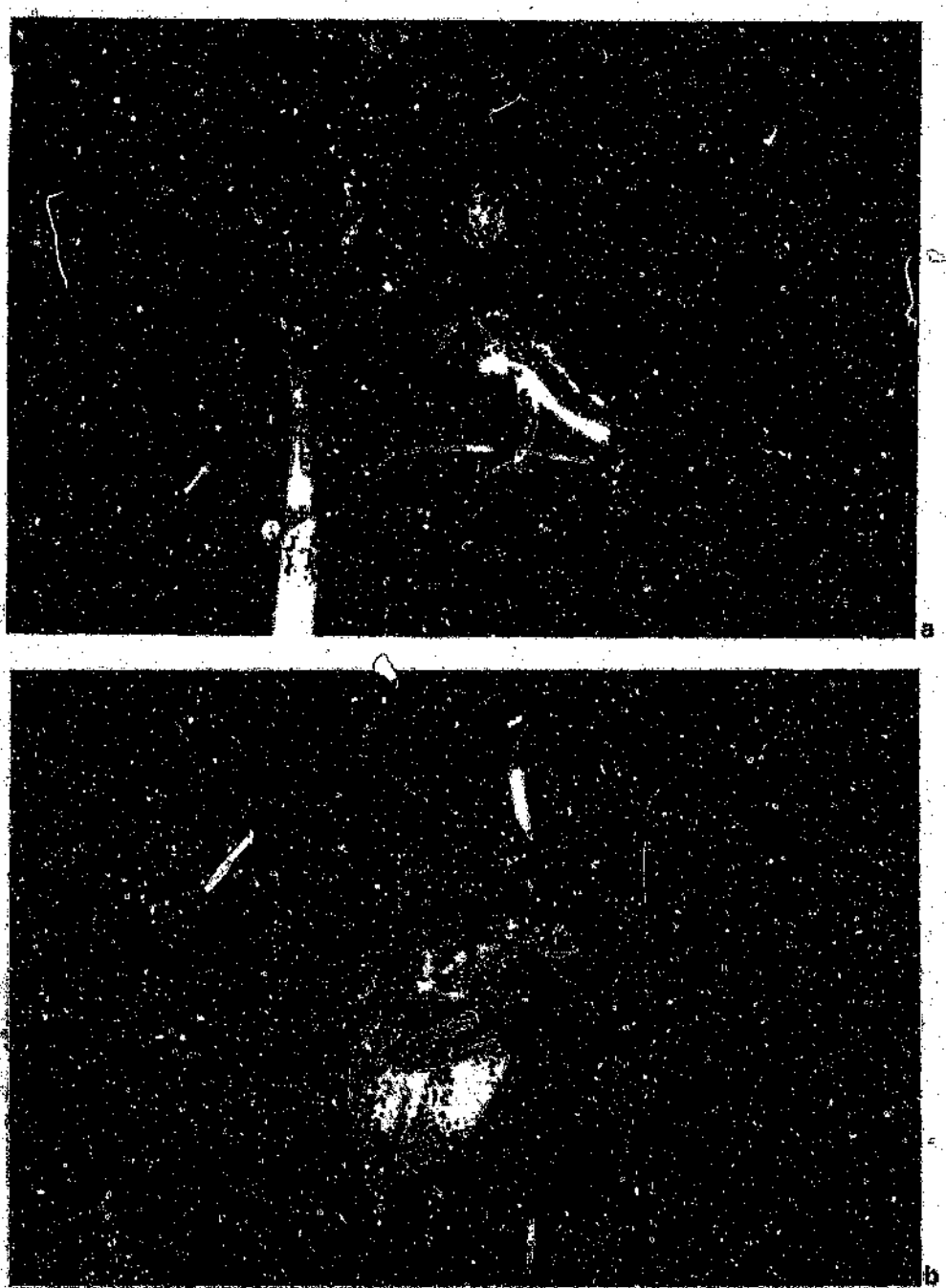



FIGURE 1.1 A. delicatus (a) calling male and (b) gravid female.

## 1.3 STUDY AREA

The study site is situated near Mtunzini (Lat. 28°51'S; Long. 31°46'E) on the north coast of Natal, at the southern extremity of the Mozambique coastal plain. The study animals were collected from three shallow coastal ponds on "Twinstreams Farm" belonging to Mondi Forests (see Fig. 1.2). Matatiele is a natural pond in the coastal dune forest. It is a semi-permanent body of open water approximately 100m long and 30m wide, tapering at each end (see Telford, 1982). Mavungweni pond is man-made and established in 1982. It lies on the border between the coastal dune forest and a sugar cane field. It is approximately 50m long and overgrown in parts by emergent vegetation. Passmore's pond was a shallow pond in a natural depression, on the border between the coastal dune forest and grassland. It was overgrown with emergent vegetation and there was very little open water. This pond was approximately 30m long and 10m wide. Heavy rainfalls flooded this pond in 1988 and it has subsequently provided a more diverse habitat with large areas of open water with dense, floating and emergent vegetation. The ponds are all shallow, seldom exceeding 1m in depth. Although the vegetation at Matatiele is far more diverse than at the other ponds, they all have a pronounced eulittoral zone with fringe vegetation consisting of **Polygonum pulchrum** and **Ludwigia stolonifera.**

The mean annual air temperature is 20,5 C. The rainy season begins in September/October and extends until the end of March. These are also the hottest months. Twenty five anuran species occur in the area, nineteen of which breed at the above-mentioned ponds.

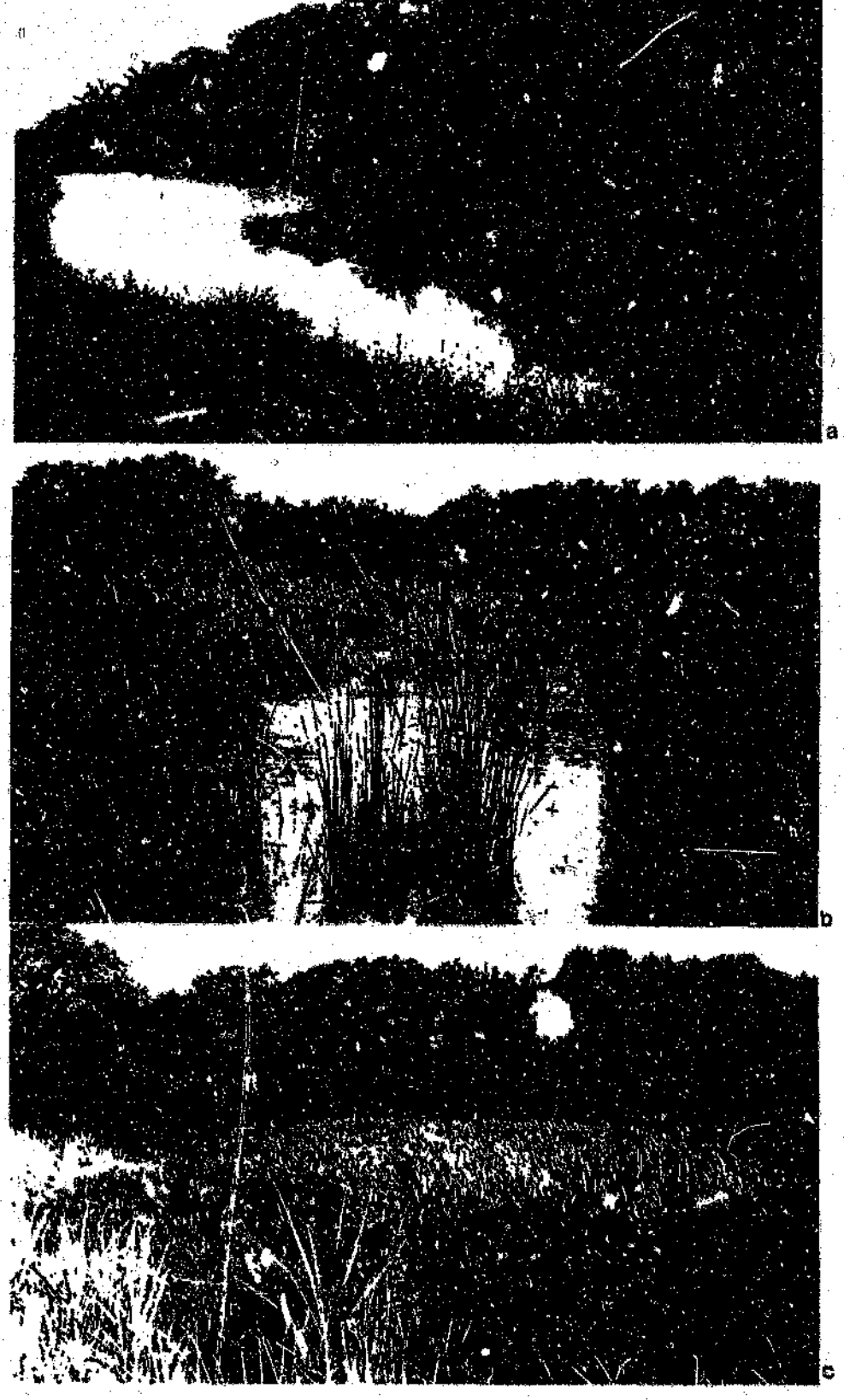



FIGURE 1.2 Natural breeding areas of **A. delicatus** on "Twinstreams Farm"; (a) Matatiele pan; (b) Mavungwani pan and (c) Passmore's pan.

## 1.4 SCOPE AND OBJECTIVES

This thesis is essentially concerned with the adaptations that allow successful reproduction and larval survival in A. delicatus. Both pre- and post-amplexus behaviour were examined in relation to successful and efficient reproduction.

The major questions addressed in this work are:

1) Is there functional partitioning of the two-part call in the context of male-male communication and female attraction?
2) How is spatial separation maintained in a breeding chorus?
3) What ecological and social factors influence male behaviour?
4) Is there variability in male mating success, and if so, are there morphological and/or behavioural correlates of mating success?
5) How and where are eggs deposited and what are the advantages of nest building?
6) How do females behave within the chorus and how accurately can they locate a sound source?

# CHAPTER TWO

# NATAL DWARF AFRIXALUS

## 2.1 INTRODUCTION

### 2.1.1 General

It is widely recognised that anuran advertisement calls are species-specific, with each species' call differing from every other in at least one of the call attributes (Littlejohn, 1977). The advertisement call forms part of the highly characteristic Mate Recognition System of the species and will dictate precisely the limits of a species gene pool by confining matings to within species boundaries (Paterson, 1981; 1985). The definition of a species as a "closed gene pool" is now widely accepted. In using the Mate Recognition System, one can distinguish species using the very same characters that the animals themselves are using to recognise conspecifics (Passmore, 1981). This makes the anuran advertisement call a taxonomic character of the first order (Passmore, 1981).

However, when dealing with congeneric and very similar species, an analysis of the advertisement calls alone may be insufficient in an attempt to identify species boundaries. When the advertisement calls of two populations differ marginally, or when the differences are related to temporal call characteristics, one could erroneously split a species into two taxa. It is then neccesary to examine another component of the Mate Recognition System: the responses of females to the advertisement calls of each population or taxon. If females are attracted to the advertisement calls, they are conspecifics. If females do not respond to the calls, they are heterospecific.

Numerous other features have been recognised as important for identifying anuran

species (Pickersgill, 1984; Schiøtz, 1974; Stewart, 1967). The majority of these are external morphological features, and would be useful in higher level classification (genus, family etc.), and in assigning individuals to species categories. If a morphological feature can be shown to be unique to a particular species, as defined by its Mate Recognition System, then this feature would be useful in the identification of museum specimens.

2.1.2 Classification of the genus Afrixalus

The genus shows some overall similarities to the Reed Frogs (**Hyperolius**), but can be readily distinguished by the vertical pupil (Passmore and Carruthers, 1979). In all South African **Afrixalus** species, the tympanum is concealed; the digits are webbed and terminally expanded into discs; and small dorsal skin asperities are present (Passmore and Carruthers, 1979). There is a clear distinction between **A. fornasini** (a large species with a distinct morphology and advertisement call), and the dwarf **Afrixalus** species. The taxonomy of the dwarf species is presently in a state of disorder. Poynton (1964) recognised **A. spinifrons**; **A. brachycnemis brachycnemis** and **A. brachycnemis knysnae** as the only small **Afrixalus** species in South Africa. He considered **A. b. brachycnemis** and **A. b. knysnae** to be distinct on the subspecific level on account of **A. b. knysnae's** undivided tubercles on the outer fingers and **A. b. knysnae's** greater degree of spinosity. Wager (1965) followed Poynton's (1964) classification and added preliminary advertisement call data to substantiate it. He described the **A. spinifrons** call as a subdued but high pitched "zizzzz" or "preetteee" lasting about 5 s. He found **A. b. brachycnemis** and **A. b. knysnae** morphologically indistinguishable, but each produced a distinct call. **A. b. brachycnemis** produced a call which is "like "zip-zip-zip-zeep-zip-zeep" repeated at intervals" while the **A. b. knysnae** call is "ee-ee-zizzzz", lasting about 5 s (Wager, 1965).

Schiøtz (1974) recognised two dwarf **Afrixalus** species from Southern Africa: **A. brachycnemis** and **A. pygmaeus**. He described the call of **A. brachycnemis** as a brief series of clicks, and that of **A. pygmaeus** as a buzzing sound. Although he found it impossible to separate them morphologically, he claimed that they were clearly

distinguishable by their voices. Loveridge (1957) had previously regarded A. pygmaeus as a subspecies of A. brachycnemis.

Following Poynton (1964), Passmore and Carruthers (1979) listed two dwarf Afrixalus species from South Africa: A. brachycnemis (which included the two subspecies A. b. brachycnemis and A. b. knysnae) and A. spinifrons. Pickersgill (1984; in prep) recently described four cryptic dwarf Afrixalus species from South Africa: A. aureus, A. delicatus, A. spinifrons, and A. knysnae. He stated that A. delicatus is a cryptic species within A. b. brachycnemis (as described by Poynton [part], 1964; Wager [part], 1965; Stewart [part], 1967 and Passmore and Carruthers [part], 1979); and with A. pygmaeus and A. brachycnemis of Schiøtz, 1974. Unfortunately, adequate quantitative call descriptions were not included in his analysis. Lambiris (1988) examined nearly all of the material studied by Pickersgill, but was unable to fully agree with his conclusions. He states that the morphological differences between the taxa that Pickersgill recognises are not clear or cons[illegible], 1988).

In an attempt to clarify the taxonomy of the Natal dwarf Afrixalus species, I have compared the three taxa (A. delicatus, A. spinifrons and A. aureus) with respect to morphology, behaviour, advertisement calls, and the responses of females to these calls.

## 2.2 METHODS

Recordings of advertisement calls of 10 males of each of the three taxa were made in the field from October 1989 - January 1990 using a Sony TCD - 5M tape recorder and a Sony ECM - 16T microphone. Recordings were made at 20-25 C (air temperature). Recordings were analysed on a Uniscan II sound spectrum analyser in the frequency range of 0 - 10 kHz. The upper and lower limits of the emphasised frequency range were measured, as well as the call duration, the number of pulses per call and the pulse repetition rate. For each of these parameters, the mean and ranges were calculated. One-way analyses of variance and Kruskal-Wallis tests were used to compare the calls of the three taxa. A sonogram of a single typical call of each species was made on a Kay model 7800 spectrum analyser.

Each recorded male was photographed, captured and his snout-vent length measured. The following features were also noted: dorsal colouration; chest and throat colouration; presence and width of tibial stripe; and presence and width of lateral stripes. The males were then euthenased using a solution of MS222 (Animal Ethics Screening Committee clearance number: 89-61-2). They were placed in 40% alcohol for five days and in 4% formalin thereafter. The preserved specimens were examined for: dorsal asperities; gular disc size, shape and texture; and snout shape. Specimens were lodged at the Transvaal Museum, Pretoria (accession numbers: 69166-69198).

Observations on the breeding biology of each species were undertaken in its natural breeding habitat. I noted: chorus density; the existence of clusters of males within the chorus; the level of aggression; nest-building behaviour and the plant species used in nest construction; the occurrence of satellite males; calling behaviour; and calling period. The behavioural observations were made between 20h00 and 22h00.

I conducted single-stimulus phonotaxis experiments to determine the extent of between-species recognition. Three acoustic stimulus tapes were prepared by recording an individual male of each species in the field. The stimuli were broadcast using a Sony TCD-5M tape recorder and a Phillips AD 50600 loudspeaker. The loudspeaker was placed on one end of a 2 x 2 m canvas arena, 1 m directly in front of the female release point. Amplexing pairs were captured at the natural breeding areas. Females were separated from their males before the first trial and placed in a perforated container at the release point. Females were left to settle for two minutes after call broadcast commenced. The container was then opened. Females were first presented with broadcast calls of conspecific males (from their own population), and if they responded positively (deliberately approached and made contact with the loudspeaker), they were presented with a broadcast of a "heterospecific" male's call. The conspecific call was then rebroadcast and the female's response again noted. Females were assumed not to have recognised the "heterospecific" call if they approached both the initial and the final call broadcasts, but did not respond to the middle "heterospecific" call. This work was conducted during the 1989/90 breeding season (October - January).

## 2.3 RESULTS

The collection localities of the three species were: **A. aureus** - temporary pond on the roadside 6 km from Emshopi Gate, Mkuzi Reserve, Northern Natal, 27°39'S; 32°10'E; **A. delicatus** - Mavungweni Pan, Twinstreams Farm, Mtunzini, Natal, 28°51'S; 31°46'E; **A. spinifrons** - Passmore's Pan, Twinstreams Farm, Mtunzini, Natal, 28°31'S; 31°46'E. Photographs and sonograms of each species are given in Figures 2.1 and 2.2. Advertisement call, behavioural and morphological data are presented in Tables 2.1, 2.2 and 2.3. **A. delicatus** and **A. spinifrons** produced a two-part advertisement call consisting of a sustained falsetto trill and a short "zip" sound on a rising note. **A. aureus** produced only a trill call component. Statistical analyses of the advertisement calls (Table 2.4) revealed that there were significant differences between the three species for all of the measured call parameters of the trill call component. The zip calls of **A. delicatus** and **A. spinifrons** differed in two of the five measured variables: lower limit of the emphasised frequency and pulse repetition rate. The morphological and behavioural data similarly indicated differences between the three taxa, although many of the characteristics examined showed considerable interspecies overlap.

In the phonotaxis experiments, **A. delicatus** females did not respond to the advertisement call broadcasts of **A. spinifrons** males (n = 10). **A. aureus** did not respond to the broadcast calls of **A. delicatus** (n = 9) or **A. spinifrons** (n = 9) males. All of these females responded to the initial and the final conspecific call broadcasts.

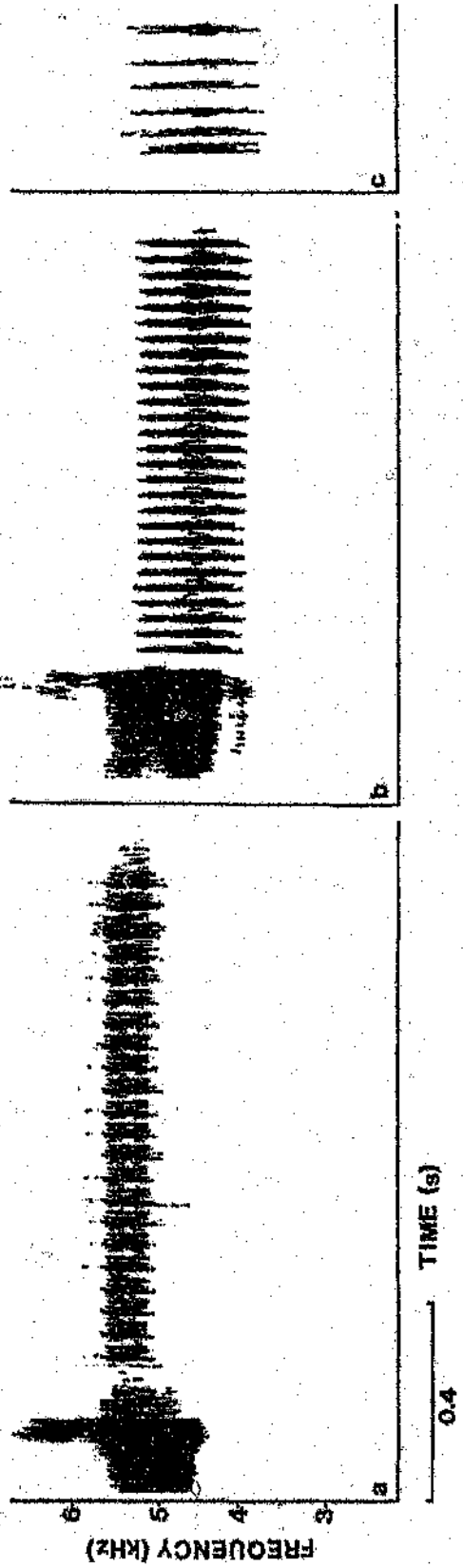



FIGURE 2.1. Sonograms of the three Natal dwarf Afrixalus (a = A. delicatus; b = A. spinifrons; c = A. aureus).




FIGURE 2.2. Photographs of the three Natal dwarf **Afrixalus** species (a = **A. spinifrons**; b = **A. aureus**; c= **A. delicatus**). Photographs a and b by V. C. Carruthers.

TABLE 2.1

Call parameters for the three Natal dwarf Afrixalus (n = 10). Figures indicate mean values and those in parentheses indicate ranges. (A. aureus) did not produce a zip call component).

| | A. delicatus | | A. spinifrons | | A. aureus |
|---|---|---|---|---|---|
| | trill | zip | trill | zip | trill |
| Upper limit of emphaised frequency (kHz) | 5.8 (5.2-6.2) | 5.8 (5.4-6.1) | 5.4 (5.0-6.0) | 5.7 (5.1-6.5) | 5.4 (5.2-5.8) |
| Lower limit of emphasised frequency (kHz) | 4.9 (4.5-5.6) | 4.4 (3.8-5.0) | 3.7 (3.5-4.0) | 3.6 (3.0-4.0) | 3.8 (3.2-4.2) |
| Call duration (s) | 3.3 (1.7-5.9) | 0.2 (0.1-0.3) | 3.3 (1.2-5.2) | 0.2 (0.1-0.4) | 0.5 (0.3-0.7) |
| Number of pulses per call | 39 (13-55) | 18 (12-25) | 29 (18-46) | 15 (8-23) | 9 6-16) |
| Pulse repetition rate (pulses /s) | 19 (6-23) | 139 (116-173) | 8 (4-13) | 81 (49-112) | 22 (16-30) |

TABLE 2.2

Behavioural comparis- . between three Natal dwarf Afrixalus.

| | A. delicatus | A. spinifrons | A. aureus |
|---|---|---|---|
| Abundance of call components | zip more common than trill; zip produced regularly | zip more common than trill; zip produced less regularly than A. delicatus | trill call or no zip call component |
| Chorus period | sundown - 00h30 | sundown - 03h00 | sundown - 04h00 |
| Chorus structure | low density chorus; groups of 4 - 8 males | high density chorus; groups of 4 - 20 males | very high density chorus without group |
| Nests | above water; built on grass or Polygonum or Ludwegia | above water; built on grass or young Phragmites | above water; built on grass |
| Satellite males | about 25% of males are satellites | about 5% of males are satellites | about 50% of males are satellites |
| Aggression level | intermediate | high | very high |

TABLE 2.3

Morphological comparison between the three Natal dwarf Afrixalus (n = 10).

| | A. delicatus | A. spinifrons | A. aureus |
|---|---|---|---|
| SVL $\bar{x}$ | 1.87 | 1.89 | 2.07 |
| range | 1.78-2.02 | 1.79-2.00 | 1.82-2.18 |
| chest and throat colour | golden/pale-yellow | dark yellow | pale-dark yellow |
| dorsal colour | golden yellow | golden brown | golden yellow |
| tibial stripe | sometimes present; variable width | usually absent, always inconspicuous | conspicuous and broad |
| dorsal asperities | present but not conspicuous | large and concentrated on snout | present but not conspicuous |
| snout shape | pointed | rounded | pointed |
| gular disc | opaque and granular | large; white or yellow; granulation variable | white; granulation variable |
| lateral stripe | present; variable and often broad | present; variable but often narrow | present but variable |

TABLE 2.4

Analysis of the advertisement calls of the three Natal dwarf Afrixalus : one way Analysis of Variance (F) and Kruskal-Wallis (K-W) tests. Significance levels in parentheses.

| | Trill | | Zip | |
|---|---|---|---|---|
| | F | K-W | F | K-W |
| Upper limit of emphasised frequency (kHz) | 4.81 (0.02) | 6.66 (0.04) | 0.33 (0.58) | 0.58 (0.45) |
| Lower limit of emphasised frequency (kHz) | 49.23 (0.00) | 20.12 (0.00) | 14.59 (0.00) | 6.82 (0.00) |
| Call duration (s) | 21.11(0.00) | 19.44(0.00) | 0.61(0.45) | 0.34(0.56) |
| Number of pulses per call | 19.96 (0.00) | 19.89 (0.00) | 10.3 (0.32) | 0.77 (0.38) |
| Pulse repetition rate (pulses / s) | 23.89 (0.00) | 16.22 (0.00) | 36.38 (0.00) | 14.30 (0.00) |

## 2.4 DISCUSSION

Based on the results of the phonotaxis experiments, **A. delicatus**, **A. spinifrons** and **A. aureus** are undoubtedly three distinct species. Females are not attracted to the advertisement calls of heterospecific males, and this precludes the possibility of interbreeding.

Further evidence supporting this conclusion comes from the analysis of the trill call components of these species. It is the trill call that is used for female attraction in **A. delicatus** (pp. 33) and **A. aureus** (no other component is present). It is presumably also the trill call that functions in female attraction in **A. spinifrons**. It is therefore the trill call that would be important in species recognition. The trill calls of these three species differed from each other in each of the five measured call variables. This provides strong evidence that the three taxa form distinct and separate species. In **A. delicatus**, the zip call is used for male-male communication and is not involved in mate recognition (pp. 33). The zip calls of **A. delicatus** and **A. spinifrons** differed in two of the five measured call parameters.

The behavioural and morphological characteristics showed considerable overlap between species and were therefore poorer indicators of species identity than advertisement calls. However, the concentration of enlarged asperities on the rounded snout allowed for the identification of **A. spinifrons** individuals. **A. aureus** and **A. delicatus** males were morphologically very similar and no unique features were found to distinguish between them. This underscores the necessity of analysing advertisement calls and female responses to the calls before species identity can be established.

# CHAPTER THREE

# FUNCTIONAL PARTITIONING IN THE TWO-PART CALL

## 3.1 INTRODUCTION

Most anuran species possess a small organised vocabulary (Capranica, 1965). The advertisement call is the most commonly heard component, and it generally serves two functions: to attract gravid females to conspecific calling males (for review see Bogert, 1960; Gerhardt, 1973; Littlejohn, 1977; Wells, 1977a), and to attract males to the breeding site and maintain their relative distributions during calling (for review see Arak, 1983a; Fellers, 1979a; Littlejohn, 1977; Robertson, 1984; Salthe and Mecham, 1974; Whitney and Krebs, 1975a). Thus, within the vocabulary of a species, a particular vocalisation may function in more than one capacity.

The two primary functions of the advertisement call may be combined into one monophasic signal that simultaneously conveys separate messages to males and females (Littlejohn, 1977; Littlejohn and Harrison, 1985; Wells, 1977a), or they may be separated between the components of a biphasic call (Littlejohn, 1977; Littlejohn and Harrison, 1985; Narins and Capranica, 1976, 1978). Biphasic advertisement calls have been reported in a number of species: **Hyla ebraccata** (Wells and Schwartz, 1984); **Hyla microcephala** (Schwartz and Wells, 1985); **Physalaemus pustulosus** (Rand and Ryan, 1981); **Geocrinia laevis** (Harrison and Littlejohn, 1985); **Philautus leucorhinus** (Arak, 1983a) and others.

Narins and Capranica's (1976, 1978) studies of **Eleutherodactylus coqui** were the first to examine the communicative significance of a two-note call. Although both notes

are perceived by males, the first note ("co") is used during male-male encounters and the second note ("qui") serves to attract females. The functional dichotomy of the two notes reflects a difference in the distribution of the best excitatory frequencies of primary auditory neurons for males and females; i.e., the peripheral auditory sensitivity shows a sexual difference (Narins and Capranica, 1976). Littlejohn and Harrison (1985) found that the functions of attraction of mates and repulsion of intruding males are partitioned between the two components of the biphasic call of **Geocrinia victoriana.** The call consists of an introductory note followed by a series of repeated notes. Females are attracted only to the repeated notes, but these have little effect on male calling behaviour. The introductory notes are directed at other males in a territorial context. They found that this differentiation was based on temporal, rather than spectral, properties of the two components.

There seems to have been convergent evolution of complex multi-note calls in chorusing frogs from several different families, but the advantages of complex calls are still unclear (Wells and Schwartz, 1984). In those species which show no clear functional partitioning in the call components, several advantages have been ascribed to the complex call. Tuttle and Ryan (1982) suggested that multi- note calls in **Smilisca** facilitate the overlapping of calls by neighbouring males. This results in a synchronous burst of calling which is confusing to predatory bats. Rand and Ryan (1981) similarly proposed that the call complexity series of **Physalaemus pustulosus** allows a male to effect a compromise between maximum mate attraction and minimum predation risk. A further advantage of the complex call was proposed by Wells and Schwartz (1984), who suggested that the locatability of males by gravid females would be easier in a chorus if a male was repetitious, as it would provide maximum contrast with continuous background noise. Consequently, the secondary click notes of **Hyla ebraccata** would enhance a male's ability to attract a mate.

In those species that have the two functions clearly partitioned between the call components, the advantage would presumably lie in the ability of a male to selectively alter the proportions of the call components in various social contexts (Arak, 1983a).

The advertisement call of the leaf-folding frog, **A. delicatus**, provided an opportunity to study functional partitioning in the context of both mate attraction and male- male communication. I examined: (1) the structure of the advertisement call; (2) the effect of each call component on female behaviour using two-stimulus phonotaxis experiments; (3) the effect of each call component on male behaviour using call playback experiments; (4) the effect of chorus size on the relative proportion of call components; and (5) the effect of female presence on male calling behaviour.

## 3.2 METHODS

### 3.2.1 Recording the Advertisement Call

Recordings of advertisement calls of 30 males were made in the field from October to February 1984 and in October and November 1985, using a Sony TC-185 SD tape recorder and an Adastra electret condensor microphone. Recordings were made at 21 - 25 C (air temperature). The recordings were analysed on a Uniscan II sound spectrum analyser within the frequency range of 0 - 10 kHz. The upper and lower limits of the emphasised frequency ranges were measured, as well as call duration, number of pulses per call and pulse repetition rate. For each of these parameters, the mean and range were calculated. A sonogram of a single typical call was made on a Kay model 7800 spectrum analyser. Calling males and amplexing pairs were collected from the coastal pans. Air temperatures were measured using a Bat - 12 (Bailey Instruments) digital thermometer.

### 3.2.2 Effect of Call Components on Female Phonotaxis

In order to prepare acoustic stimuli, an advertisement call was recorded in the field using a Nagra III tape recorder and an AKG D900 dynamic microphone at an air temperature of 23 C (Bat-12 Bailey Instruments digital thermometer). A segment of this recording carrying a single clear trill or tip call with little background noise was used to make two tape loops. Two stereo tapes of 30 min duration were made using the respective calls on left and right tracks. On stimulus tape 1, the calls were not presented

in a fixed pattern, and there was no set alternation of the two components. Intercall intervals for natural male calls were measured from recordings of natural choruses. By manually interrupting the tape transport mechanism, intercall intervals were varied to resemble the calling pattern of a natural calling male. The intercall intervals for the zip stimulus ranged from 0.7 - 4.8 s and for the trill from 2.0 - 3.1 s. On stimulus tape 2, the calls were presented in a fixed pattern with the repetition rate of the zip call increased, so that the total sound output from the speakers broadcasting the zip and trill calls was equal (each had 2 s "on air" in every 10 s). The intercall interval for the 2 s trill call was 8 s and for the 0.2 s zip call was 0.8 s. A third stimulus tape was prepared (stimulus tape 3) on which one track carried two trill calls in every 20 s (intercall interval = 8 s) and the other track carried one trill and 10 zips in every 20 s (the total sound output on both tracks was equal). Due to the rapid rise time of individual pulses, it was necessary to use a high powered amplifier (Klein and Hummel SB280 140W) to reproduce the calls with adequate fidelity. The stimulus tape was broadcast using a Sony TCD5M tape recorder, the above amplifier and a pair of JVC S-M3 miniature HiFi loudspeakers (18 x 11 x 11 cm). These loudspeakers were placed 2 m apart facing each other on a canvas arena (3 x 2 m). Playback levels were adjusted to the natural sound pressure level (SPL) of the species (97 dB peak at 25 cm) using a Brüel and Kjaer 2209 sound level meter. The arena was illuminated with a single 60 W red light bulb suspended 2 m above ground level. Each female performed a single trial in each of four experiments: (1) the zip component was broadcast from one speaker and the trill from the other using stimulus tapes 1 and 2; (2) the trill was broadcast from one speaker and the whole call (zip and trill) from the other using stimulus tape 3; (3) the zip was broadcast alone as a single stimulus using using one track of stimulus tape 1; and (4) the trill was broadcast alone as a single stimulus using the other track of stimulus tape 1.

Females were separated from males before the first trial and placed in a perforated container at the midway between the two speakers. The female was confined in the container for 2 min while the stimuli were broadcast from opposite ends of the arena. The container was then opened. Trial duration was measured from the moment the female started moving to the moment she made physical contact with one of the

speakers. Experiment 1 was conducted during the 1985-1986 breeding season using tape 1 and during October 1986 using tape 2. Experiments 2, 3 and 4 were conducted during the 1985-1986 breeding season.

### 3.2.3 Effect of Call Components on Male Behaviour

Each track of stimulus tape 1 (see above) was broadcast separately to calling males using a Sony TCD5M tape recorder, a Klein and Hum. el SB280 amplifier and a JVC SM-3 miniature HiFi speaker. The loudspeaker was placed 50 cm from the subject. The SPL of the playback was set at 103 dB peak at 25 cm using a Brüel and Kjaer 2209 sound level meter (6 dB higher than the normal call level). This represented a male 12.5 cm from the caller, which was necessary to initiate aggressive responses. The stimulus and the evoked vocal response were recorded on a second tape recorder (Sony TCD5 PRO).

### 3.2.4 Relative Abundance of Call Components at Different Chorus Sizes

To facilitate changes in chorus size, this study was conducted on a caged population of males. The cage (2 x 3 x 2 m) was constructed using a wooden frame covered with polypropylene netting. Access was gained through a sealed canvas door. An artificial pond 1 x 2.5 x 0.5 m was dug along the length of the cage. Vegetation from the natural pan was planted in the pond and included **Polygonum pulchrum** and **Ludwegia stolonifera**, the plant species favoured by **A. delicatus** as calling sites (see Fig. 3.1).

The number of calling males in the cage was controlled and the chorus was recorded using a Sony TC-185 SD tape recorder and an Adastra electret condenser microphone. The microphone was suspended 1.5 m above water level in the centre of the cage. Ten recordings of each of seven chorus sizes ($n = 2 - 8$ males) were taken at different times on different nights. Each recording was 5 min long. The number of zip and trill components was counted from the recordings. In large choruses (seven or eight calling males), this was facilitated by the chorus organisation (call initiation, bouts and

alternation of calls) found in this species. This study was conducted during the 1984-1985 breeding season.



a



b

FIGURE 3.1 Photographs of cage (a) external view; (b) pond inside cage.

### 3.2.5 Effect of Female Presence on the Relative Abundance of Call Components.

The chorus was recorded 10 min after the introduction of a female into the cage. The change in call composition was calculated as the difference between the number of components produced with a female present and the number of components calculated for the same chorus size in the previous experiment, when no female was present. Between 60 and 90 min elapsed between the two counts. This experiment was conducted six times at a single chorus size (five calling males).

## 3.3 RESULTS

### 3.3.1 Advertisement Call

One part of the call is a rapidly pulsed "zip" sound on a rising note and the other is a sustained falsetto trill of variable duration (0.3 - 11.8 s)(Figure 3.2 and Table 3.1). The two components differ considerably in their pulse repetition rate and their duration, but are similar in other respects. There is no fixed pattern of alternation of the two components, although the zip is given more frequently than the trill. The two components are not linked in a single unit or produced in a set sequence and males may produce one component only for long periods of time.

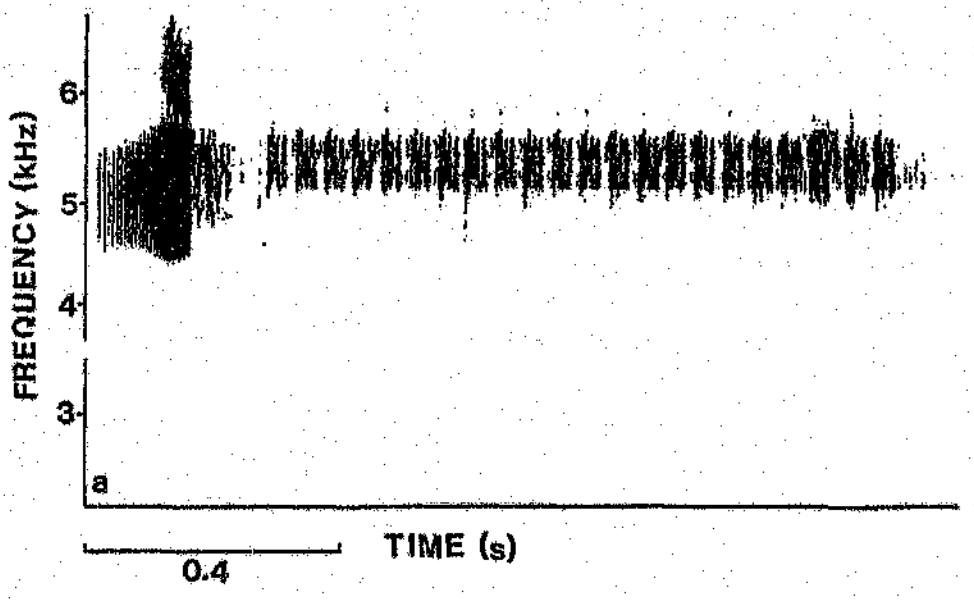



FIGURE 3.2 Wide band (300 Hz filter) sonogram of the two-part call of *A. delicatus*, the zip followed by the trill.

TABLE 3.1

Call parameters of **A. delicatus** advertisement call (n = 30).

| | Zip | | Trill | |
|---|---|---|---|---|
| | $\bar{x}$ | (range) | $\bar{x}$ | (range) |
| Upper limit of emphasised frequency range (kHz) | 5.8 | (5.4-7.0) | 5.7 | (5.1-7.2) |
| Lower limit of emphasised frequency range (kHz) | 4.4 | (3.8-5.5) | 4.5 | (3.5-6.1) |
| Call note duration (s) | 0.2 | (0.1-0.3) | 3.4 | (0.3-11.8) |
| Number of pulses per call | 26 | (16-42) | 69 | (5-247) |
| Pulse repetition rate (pulses/s) | 145.8 | (111.1-192.9) | 20.4 | (15.5-31.5) |

### 3.3.2 Effect of Call Components on Female Phonotaxis

The first 35 females tested either failed to respond or fled the arena. It was therefore necessary to investigate the precise conditions required for female response and to construct the arena to allow easy observation of the individuals. Responses to the broadcast stimuli were obtained on nights when a light drizzle fell and usually after midnight. It was necessary to release the female with extreme care, as any disturbance caused her to remain stationary. In the initial experiment using stimulus tape 1, females were presented with the zip component from one loudspeaker and the trill component from the other. The calls were presented at the natural call rate. The eight females that responded all approached and made contact with the loudspeaker broadcasting the trill (two-tailed binomial probability: $P < 0.05$). The response time for each trial ranged from 160 s to 330 s ($\bar{x}$ = 196 s). The air temperature ranged from 22 - 26 C.

Since females may have responded to the trill because it had more time "on air", the experiment was repeated using stimulus tape 2, in which both components had an equal sound output. Nine of the 25 tested females responded; all approached and made contact with the speaker broadcasting the trill (two-tailed binomial probability: $P < 0.05$). The response time for each trial ranged from 60 s to 455 s ($\bar{x}$ = 156 s). The air temperature ranged from 17 - 24 C.

In experiment 2 (stimulus tape 3), ten females responded to the trill and 12 to the whole call (two-tailed binomial test: $P = 0.5$). In the single zip stimulus trials, each of seven females was tested four times (a total of 28 trials), but on no occasion did a female approach or make contact with the speaker. The single trill stimulus initiated eight positive responses, one each from eight of the 14 females tested.

### 3.3.3 Effect of Call Components on Male Behaviour

Twenty calling males were individually presented with both zip and trill calls as acoustic stimuli over a range of air temperatures (22 - 25 C) during the 1985 - 1986 breeding season and in October 1986. The zip component elicited obvious changes in

calling behaviour. The changes varied from silence (n = 4), through increased zip rate (n = 2), to encounter calling (n = 13). Encounter calls are produced by male, during close-range interactions when the advertisement call has failed to repel intruders that are calling too close to the resident male. This call is a more rapidly-pulsed and slightly longer version of the zip component of the advertisement call at a slightly lower frequency (Telford, 1982). Although the responses were variable, 19 of the 20 males tested must have perceived the broadcasts of the zip calls, because they altered their calling behaviour in response to this stimulus. In contrast, 17 males showed no response (their calling behaviour was unaltered) to the trill, while three males responded by increasing the rate of trill calling.

### 3.3.4 Relative Proportions of Call Components at Different Chorus Sizes.

The mean number of call components per male was calculated by dividing the total number of each call component by the number of participating males. There is a marked decrease in trill calling with an increase in chorus size (Pearson's correlation coefficient: $r = -0.80$) and a marked increase in the zip calling with an increase in chorus size ($r = +0.80$) (Figure 3.3; Table 3.2).

TABLE 3.2

Relative abundance of call components at different chorus sizes ($n = 10$) for each size).

| Chorus size (no. of calling males) | Zips per male in 5 min period $\bar{x}$ ± SD | | Trills per male in 5 min period $\bar{x}$ ± SD | |
|---|---|---|---|---|
| 2 | 39 | 18.0 | 8 | 5.6 |
| 3 | 29 | 17.7 | 4 | 2.6 |
| 4 | 39 | 11.9 | 3 | 0.8 |
| 5 | 33 | 13.1 | 2 | 0.6 |
| 6 | 46 | 18.4 | 2 | 0.6 |
| 7 | 57 | 24.0 | 2 | 0.4 |
| 8 | 51 | 19.4 | 2 | 0.4 |

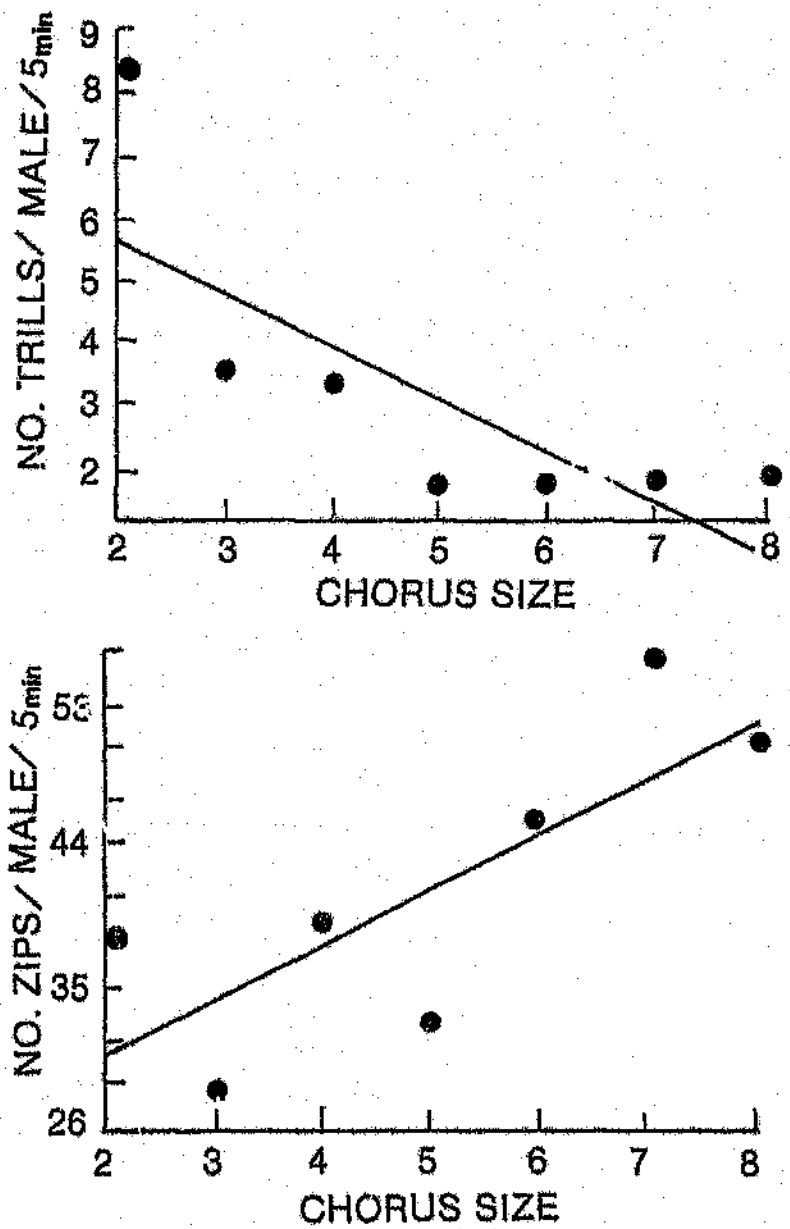



FIGURE 3.3 Abundance of cell components at different chorus sizes (n = 10 for each chorus size).

### 3.3.5 Effect of Female Presence on the Relative Proportion of Call Components.

Six choruses with a single female in each were examined during the 1985 - 1986 breeding season. Each chorus consisted of five calling males. The number of trill and zip components was counted before and after the female was placed in the cage. A Wilcoxon matched-pairs signed-ranks test was conducted on the data using the proportion of trills out of all calls. The two-sided P value (for $T+ > c$) was 0.032, thus the presence of a female in the chorus significantly increased the proportion of trill calls (Table 3.3).

TABLE 3.3

Relative proportions of zips and trills at a chorus size of five, and without a female present in the chorus (n = 6).

| | Zips per male in 5 min period $\bar{x}$ ± SD | Trills per male in 5 min period $\bar{x}$ ± SD |
|---|---|---|
| With female | 27.9 ± 8.6 | 3.0 ± 0.9 |
| Without female | 38.3 ± 13.5 | 1.8 ± 0.5 |

## 2.4 DISCUSSION

Anuran advertisement calls function to indicate the callers' species, sex and locality to gravid female conspecifics (see Wells, 1977 a & b, for review). The call therefore facilitates the meeting of the sexes . A second function of the call is to advertise the callers' position to nearby males (see Littlejohn, 1977, for review). This facilitates the maintenance of interindividual distance between calling males and thus intermale spacing in the chorus.In this study I found that, as in **Eleutherodactylus coqui** (Narins and Capranica, 1978) and **Geocrinea victoriana** (Littlejohn and Harrison, 1985), these two functions are separated between the two components of the call. Unlike these species, the two components of the **A. delicatus** call are not linked in a single unit or produced in a set sequence. Males often produce one component only for long periods of time. For this reason I do not consider this call to be biphasic, but rather to consist of two separate parts, each with a specific function.

In **A. delicatus**, sexual advertisement to conspecific females is facilitated by the trill note. This note is perceived by gravid females and acts as a releaser of the phonotactic response. Females do not respond to the zip component and do not display any preference for the whole call over the trill alone. In previous work on functional partitioning (Littlejohn and Harrison, 1985; Narins and Capranica, 1978), the natural call rate has been used in phonotaxis experiments. A possible criticism of this (raised by an anonymous reviewer) is that the two call components do not have equal time "on air", and the female may respond not to the temporal differences in the call notes themselves, but to the total sound output of the signals. I have shown that, in this species, there is no difference in the responses of females when the alternative stimuli are at the normal call rate and when they have equal total sound output.

When a female is present in the chorus, males alter the relative proportion of the two call components, producing an increased proportion of trill components. The probability of mate attraction is thus enhanced. Since it was observed that the trill component initiates trilling by other males, it is possible that only a few males directly perceive the female and increase their proportion of trills. Other males respond to this

vocal cue by also increasing the number of female- attracting components in their calls.

Males perceived and reacted to the broadcasts of the zip component, but showed no response to the trill. The zip call functions in male-male communication and presumably facilitates male spacing. This spatial separation may improve an individual male's attractiveness as a mate by maximising his locatabiiity and/or the distinctiveness of his call. The most common response to a loud zip call was encounter calling (see pp. 68). In this species, encounter calling has three possible effects: one of the males moves away and continues calling from a more distant position; one of the males becomes silent; or an aggressive interaction occurs between the two males. The aggressive interactions involve physical combat in which one of the males is displaced and the other continues calling. Encounter calling in each of these cases leads to spatial separation of calling males.

Biphasic calls presumably have evolved from the simpler monophasic signals, since they offer added advantages in the efficiency of communication. In functionally partitioned calls (Littlejohn and Harrison, 1985; Narins and Capranica, 1976, 1978), the male is capable of selectively modifying the proportion of call components in different social contexts (Arak, 1983b). This is also clearly evident in the two-part call of **A. delicatus**. Males alter their call composition in different social contexts, presumably to effect a compromise between mate attraction and the repulsion of intruding males in such a way as to maximise the efficiency of (1) their calling time and (2) response to their vocalisations.

The benefit of a functionally partitioned two-part call lies not only in the ability to communicate separately with each sex, but also in the ability to communicate exclusively with one sex. **A. delicatus** males are able to stop giving female-attraction signals and to produce only male spacing signals when an intruder is present. Females would thus not approach the interacting males and the resident would not risk losing her to the intruder (Wells and Greer, 1981). The possession of a functionally partitioned call may enhance the efficiency of vocal communication and hence increase the individual's chance of mating. Possibly the two-part call of **A. delicatus** is more

easily modified to produce a larger repertoire of signals than are the functionally partitioned biphasic calls of other species because the two components are not linked in a single unit or produced in a set sequence.

# CHAPTER FOUR

# INTERMALE SPACING

## 4.1 INTRODUCTION

### 4.1.1 General

In prolonged breeding anurans, a male's reproductive success depends on his ability to attract females to his calling site and to prevent interference from other males (Wells, 1977b). The maintenance of an individual distance may increase a males' reproductive success in three ways: it may enable females to locate individual males more easily by reducing acoustic interference between callers (W... and Krebs, 1975a); it may reduce the number of competitors by preventing new males from calling (Wells, 1977b); and it may may provide a clear pathway for female approach (Whitney and Krebs, 1975a). Males may therefore be under selective pressure to maintain adequate spatial separation (Telford, 1985).

Male spacing is well documented in prolonged breeding anurans (Arak, 1983b; Crump, 1972; Fellers, 1979a; Whitney, 1980). Apart from attracting mates, the advertisement call may inhibit calling by nearby males (Whitn... d Krebs, 1975) and, through mutual avoidance, function in the initial separation of calling males (Gerhardt, 1975; Ryan, 1982; Telford, 1985; Wells, 1977b). Encounter calls and physical combat also play an important role in the agonistic behaviour required to maintain spatial organisation (Arak, 1983b; Tunnel, 1973; Fellers, 1979a; Schwartz ans Wells, 1985; Whitney, 1980).

The distance between each male and his nearest calling neighbour has been used as an index of spatial separation within anuran choruses (Awbrey, 1978; Dyson, 1986; Fellers, 1979a; Robertson, 1984; Rosen and Lemon, 1974; and others). In many species, nearest neighbour distances initially decrease with an increase in chorus density (Dyson, 1986; Fellers, 1979a), but males maintain a specific minimum inter- individual distance at high densities. This often results in an even distribution of calling males in the chorus (Dyson, 1986; Fellers, 1979a; Robertson, 1984).

### 4.1.2 Maintenance of Spacing

There is a three-level system for the maintenance of spacing: (1) the advertisement call; (2) the encounter call; (3) physical combat (Bunnel, 1973; Fellers, 1979a; Robertson, 1984; Wells and Schwartz, 1984).

#### 4.1.2.1 Advertisement Call

Most authors agree that males perceive the calls of conspecifics and respond to them in some way. Whitney and Krebs (1975a) state: "One behaviour that seems to function in maintaining spacing between males is the [advertisement] call; the presence of an [advertisement] call alone in an area can inhibit other males from calling there. This suggests that, in nature, males can use [advertisement] calls as a cue to avoid areas having high densities of calling frogs."

Some species appear to be able to modify their advertisement calls according to the social context in which they are used (Arak, 1983a). Schwartz and Wells (1985) and Pallett and Pa smore (1988) found that males increased the complexity of their advertisement calls in response to conspecific male calls. In a number of species, males have been found to alternate their calls with those of near neighbours (Arak, 1983a; Fellers, 1979a; Jaslow, 1979; Robertson, 1984; Rosen and Lemon, 1974). Wells (1977b) reported that males tend to space their signals so that calls of neighbouring males do not overlap. In some species call alternation is precise and leads to the formation of duets, trios and quartets (Wells, 1977b). Males appear to hear the calls of

other males because they orientate towards them and alternate calls even when these neighbouring males are obscured from view (Jaslow, 1979). Fellers' (1979a) study of **Hyla crucifer** showed that males respond to neighbours' calling by shifting their own calls so that there is no overlap. In playback experiments he found a distinct tendency for a frog to avoid temporal overlap of his call with those of his neighbours by shifting his vocalisation to an interval of silence between successive prerecorded calls.

Awbrey (1978) proposed that individual calling males could determine the proximity of a neighbour, or intruding male, through the intensity of their advertisement call. The results of numerous experiments have provided strong evidence for this (Broska et al., 1982; Robertson, 1984; Telford, 1985; Narins and Hurley, 1982). There is, generally, a threshold intensity above which a male will not tolerate another male's call, and aggression is then triggered. In many species, it has been found that larger males have higher intensity calls than smaller males (Gerhardt, 1987; Given, 1987; Loftus Hills and Littlejohn, 1971; Passmore and Telford, 1983). It is thus possible that larger males may defend larger individual distances than smaller males (Telford, 1985). Other factors, apart from body size, may influence the perceived intensity of a signal. Sound attenuation would depend on the transmission properties of the call site (Robertson, 1984; see also pp. 91); the radiation pattern of the signal (Telford, 1985) and the frequency of the call (Brenowitz et al., 1984). Brenowitz et. al. (1984) further indicated that the sensory threshold of the receiver would be an important factor.

4.1.2.2 Encounter calling

Vocalisations involved exclusively in aggressive behaviour have been reported in many species (Arak, 1983a; Emlen, 1968; Fellers 1979a; Jensen and Preston, 1968; McDiarmid and Adler, 1974; Passmore, 1977; Robertson, 1984; Wells, 1978; Wells and Greer, 1981; Wells and Schwartz, 1984; Whitney, 1980; Whitney and Krebs, 1975a and others). McDiarmid and Adler (1974) suggested the term "encounter call" to describe the vocalisations occurring in close range encounters in territorial species (this call has more widely been termed the "territorial call" although Littlejohn (1977)

termed the territorial call as one used in long range warnings to conspecific intruders and the encounter call as one used in short range aggressive interactions). There are other calls involved in aggressive interactions and the maintenance of intermale spacing. Passmore (1977) described a "chorus call" in some **Ptychadena** species. This call was produced regularly in large aggregations of calling males and was particularly common as the chorus was building up to peak level. He suggested that part of its function could be to influence the distribution of males relative to one another. Fellers (1979a) found similar behaviour in **Hyla versicolor**. Wells (1978) found that male green frogs have four types of vocalisations that are used in territorial advertisement and defence.

Fellers (1979a) reported that agonistic interactions in **Hyla versicolor** were always initiated by an intruder with an encounter or advertisement call. The resident male responded with encounter calls after which the intruder often left without further challenge. He concluded that territories were maintained initially using the encounter calls and ultimately by fighting. Encounter calls are energetically more efficient than physical interactions, but are not effective without the ultimate threat of a fight.

Arak (1983b) described an encounter and a territorial call for **Philautus leucorhinus**. Territorial calls were given during long-range interactions and served as a challenge, leading to further interaction if answered with a territorial call from a rival male. The encounter call, which resembles a long territorial call, was given only during close-range interactions, usually before physical contact was made. Both of these aggressive calls would presumably function to maintain the spacing between calling males.

Encounter calls are generally exchanged between resident and intruder. If the intruding male does not retreat, fighting may occur (Emlen, 1968; Robertson, 1984; Whitney and Krebs, 1975 and others). Encounter calls may also be exchanged during physical combat (Arak, 1983b; Brattstrom and Yarnell, 1968; Wells, 1981 and others).

In some species there tends to be an all-or-none response with males switching directly from the advertisement to the encounter call (Telford, 1982). In others, males

show a graded response by increasing the proportion of encounter calls (Wells and 3Schwartz, 1984). In **Uperolia rugosa**, Robertson (1984) found three distinct behavioural thresholds evoked by particular sound pressure levels. The males responded to the advertisement call playback at 76 dB by calling antiphonally with it. At 84 dB the males began giving aggressive calls and at 91 dB there was a fight or flight response. This adds evidence to Whitney's (1980) claim that "If the mating call fails to repel intruders, males have a second line of defence in the encounter call".

When calling in bouts, males cannot detect the positions of conspecifics during periods of silence, and hence it may be important to establish dominance at the beginning of each bout (Fellers, 1979a). This appears to be effective if a male accentuates his presence with an encounter call (Fellers, 1979a).

Playback experiments have been performed on many species in order to determine the effects of the advertisement and encounter calls on agonistic behaviour. Conspecific encounter calls are perceived by males as distinct from advertisement calls and males give the strongest aggressive responses to the encounter calls (Schwartz and Wells, 1985; Wells and Greer, 1981; Whitney, 1980). Allan (1973) found that playbacks of encounter calls in **Hyla regilla** inhibited calling by nearby males and were often followed by their withdrawal. Fellers (1979a) reported that males "challenge" the speaker during playback of aggressive calls.

The encounter call is more effective than the advertisement call in eliciting agonistic behaviour. If heeded, the encounter call may prevent combat. It is clearly evident that the encounter call plays an important role in maintaining spatial separation of calling males.

4.1.2.3 Physical Combat

Agonistic encounters involving physical contact between conspecific males have been documented in several species (Arak, 1983b; Crump, 1972; Duellman, 1966; Fellers, 1979a; Schroeder, 1968; Wells and Schwartz, 1984; Whitney, 1980). The

form and intensity of this aggressive behaviour is quite variable (Wells, 1977a).

In **Hyla versicolor** males frequently fight by shoving each other with their fore-limbs, butting with their heads, kicking with their hind-limbs and jumping on each other (Fellers, 1979a). Such fights always resulted in one male leaving the area or moving off a few cm and remaining silent. Telford (1982) described physical combat involving wrestling and kicking in **Hyperolius marmoratus**. He found that fighting resulted in displacement of both males in 17.5% of all observations; separation of males and resumption of advertisement call emission by the victor with occasional aggressive calling in 57.9% of observations; or the loser departing or adopting a passive position in 24.6% of observations. Lutz (1960) described grapples between males of **H. faber** where fatal wounds were sometimes inflicted by the sharp pollices which were dug into the opponent. Wounding seems to be rare in anurans and documented fighting generally ends without injury.

Actual combat seems to be the last recourse in the attempt to maintain spatial separation between calling males. Aggressive calls would not be effective without the ultimate threat of a fight (Fellers, 1979a). Bunnell (1973) came to the same conclusion in his study of **Dendrobates pumilio** and stated: "The vocalisations serve as an effective distance advertising mechanism for spacing which maintains its potency by occasional behavioral reinforcement through attack and fighting".

There are accounts of species in which fighting is infrequent. Wells and Schwartz (1984) and Fellers (1979a) found that a relatively low level of physical aggression characterised many hylids that maintain regular spacing in choruses but do not necessarily defend fixed territories night after night. They concluded that fighting seems to be more frequent, more prolonged and more violent in anurans that defend resources such as oviposition sites. There are accounts of physical combat which are not necessarily involved in the spacing of calling males. Veloso (1977) documented agonistic behaviour in **Caudiverba caudiverba**: "As the frog produces an aggressive call, it jumps and attacks any moving object located 20 - 30 cm in its vicinity". The adaptive significance of these encounters seems to be related to the presence of

predators. Altig (1972) also found that the defensive behaviour was directed at both predators and conspecifics in **Rana aerolata**. Whitney (1980) proposed that some frogs attack and others submit due to variability in the physiological state of the individuals, specifically in their level of sex hormones.

In many studies it has been found that one or more males give aggressive calls during physical interactions. It is even more common to find that the fights are preceeded by exchanges of aggressive calls (Arak, 1983a; Brattstrom and Yarnell, 1968; Fellers, 1979a; Telford, 1982; Veloso, 1977; Wells, 1981). The occurrence of physical combat is now well established in anurans. Fighting clearly functions in maintaining spacing in many species. The outcome of the interactions seem generally to be the submission of one participant after which spacing seems to be re-established.

4.1.3 Function of Spacing

Various functions of intermale spacing have been proposed. It is important to distinguish between spacing as a result of site-specific territoriality and that which arises from the maintenance of an individual distance (Telford, 1982). Site-specific territoriality occurs when intolerance of other individuals centres around particular locations (Wells, 1977b). Individual distance is a result of intermale spacing without site attachment (Telford, 1982).

Anuran territoriality involves site attachment as well as the intolerance of intruders (Crook, 1973; Wells, 1977b). The particular location (territory) is defended with aggressive behaviour and may contain one or more of the following resources required for survival and/or reproduction: oviposition site; courtship area; feeding site; shelter; source of moisture (Wells, 1977b). The possession of a territory would be advantageous to a male if it gives him exclusive or priority access to a resource that is in short supply (Wells, 1977b). In some cases it may give a male direct access to females in an area or may enhance his attractiveness to prospective mates in terms of offspring survival and/or increased audibility (Wells, 1977b). Howard (1978a) found that male mating success of **Rana catesbeiana** depends on the oviposition site quality and on the ability

ability of the male to defend the site from intruders. In summary, the territorial defence of resources may provide an advantage to the holder in terms of survival and/or reproductive success.

Although it is often difficult to distinguish between the maintenance of a territory and that of an individual distance, the two types of behaviour may have different functions (Wells, 1977a). Individual distances are maintained through hostility without site attachment. Males may occupy different call sites on different nights (Whitney and Krebs, 1975a) and there is no defence of a resource which is in short supply. The maintenance of an individual distance and hence a minimum distance between calling males, may reduce interference between callers and enable a female to localise an individual male more easily (Whitney and Krebs, 1975a). It may also reduce the number of competitors by preventing nearby males from calling; males would not compete for calling sites but rather for the opportunity to call (Wells, 1977b). Both territoriality and the maintenance of an individual distance would limit the density of calling males and may force "excess" males to adopt alternative mating strategies or to establish sub-optimal call sites (Telford, 1982).

### 4.1.4 Aims

The aim of this chapter is to examine the social organisation in **Afrixalus delicatus** with reference to intermale spacing. Answers were sought for the following questions:

1) Is there spatial separation between calling males in the chorus?
2) Is the spacing a result of territoriality, or the maintenance of an individual distan
3) How is the spacing maintained?
4) How does chorus size affect the spacing?
5) What are the functions and effects of spacing in this species?

## 4.2 METHODS

### 4.2.1 Advertisement Call Intensity

The natural peak sound pressure levels (SPL) of each call component were measured using a Brüel and Kjaer 2209 precision Sound level meter. A foam windshield covered the microphone during all measurements. The microphone was placed at a horizontal distance of 25 cm directly in front of the calling male. This distance was measured with a metal tape. Vegetation intervening between the caller and the microphone was pruned away, and nearby calling males were removed. Peak SPLs were measured to the nearest 0.5 dB, with 10 readings being taken for each male.

The mean SPL was calculated from these readings. It was not neccessary to convert the readings into microbars before averaging them because the variability in SPL was low (Broch, 1967). The SPL of the zip call was measured for 16 males, and the trill call for 13 males.

Call directivity patterns of both call components were determined by measuring peak SPL (as above) from directly in front of the male ($0^{\circ}$), directly behind the male ($180^{\circ}$), and from one side ($90^{\circ}$, $270^{\circ}$). This was done separately for zips ($n = 7$) and trills ($n = 6$).

The ambient noise level was measured on 25 nights. The microphone of the SPL meter was held horizontally, 30 cm above ground level, at a distance of 5 m away from the chorus and directed away from calling males. Readings of the background SPL were used to gauge the relative intensity of the **A. delicatus** advertisement call.

### 4.2.2 Recording and Analysis of Encounter Calls

Recordings of encounter calls of 26 males were made in the field during 1984, 1985 and 1986. The recordings were made on a Sony TC-185SD tape recorder using an Adastra electret condenser microphone or a Sony TCD5M tape recorder using a Sony

ECM-16T electret condenser microphone. Recordings were made at air temperatures of 22 - 26 C.

The recordings were analysed on a Uniscan II sound spectrum analyser within the frequency range of 0 - 10 kHz. The upper and lower limits of the emphasised frequency range, the call duration, number of pulses per call and the pulse repetition rate were measured. The mean and range were calculated for each parameter. A sonogram of a single typical call was made on a Kay model 7800 spectrum analyser. The natural sound pressure level (SPL) of the calls of six individuals was measured to the nearest 0.5 dB, using a Brüel and Kjaer 2209 sound level meter. The microphone was held 25 cm in front of the caller and 10 readings were taken for each male. The mean SPL was calculated directly from the 50 readings. It was not neccessary to convert the readings to microbars before averaging them because the variability in SPL was low (Broch, 1967).

### 4.2.3 Aggressive Interactions: Vocal and Physical

Calling males were collected from the natural breeding areas (pp. 8) and transported to the cage, which was illuminated with a single 60 W red light bulb suspended 1.5 m above water level. Choruses were closely observed during November and December 1985. Twelve interactions were observed from the initial approach of the intruding male and a further 16 from the onset of encounter calling. The spatial positions of the calling males, their movement, the occurrence of vocal interactions and the form of physical combat were documented. Time measurements were made using a stopwatch and the outcome of the interactions was noted with reference to the position of the resident and the intruder before and after the interaction.

### 4.2.4 Nearest Neighbour Distances

The shortest distance from each calling male to his nearest calling neighbour was measured for five choruses at each of seven chorus sizes (2 - 8 males). The measurements were made using a 2 m flexible tape measure which allowed accuracy to

the nearest cm. At each chorus size, the five readings were taken from different choruses on different nights. A linear regression and a one-way analysis of variance was performed on the data. A Student - Newman - Kuels test was performed to calculate the significance levels of the differences between the mean nearest neighbour distances at each chorus size. Histograms were drawn to show the frequency of nearest neighbour distances at each chorus size. In order to determine the distribution patterns of the choruses, four tests were conducted: Clark and Evans' (1954) test; Craig's (1953) test; chi-square test and Pielou's (1962) test.

### 4.2.5 Effect of Nearest Neighbour Distances on the frequency of Aggressive Interactions

This experiment was conducted on a caged population of males during November 1986. Nearest neighbour distances were measured (see above) for five choruses at each of three chorus sizes (3, 5 and 8 calling males). The number of encounter calls and physical interactions was counted in each chorus over a 30 minute period. At each chorus size, the five readings were taken from different choruses on different nights. Readings were always taken between 21h00 and 22h00 to avoid the possible effect of time of night, which has been shown to influence the level of aggression in **Hyperolius marmoratus** (Dyson, 1989).

## 4.3 RESULTS

### 4.3.1 Advertisement Call Intensity

The mean peak SPL of the zip call component was 95.1 dB at 25 cm ($n = 16$; SD = 2.96). The trill component had a mean peak SPL of 94.1 dB at 25 cm ($n = 13$; SD = 3.01). Individual variation in call SPL was low for both call components, with the largest individual range of 1.0 dB. Variability between individuals was also low (coefficient of variation; zip = 3.16%, $n = 16$; trill = 3.33%, $n = 13$). There was no difference between SPL readings taken from 0 ; 90 and 180 for either the zip or trill

components (Table 4.1). This indicates that the sound envelope around the male is roughly spherical and uniform.

The nightly ambient noise level was found to vary considerably between nights and ranged from 68.5 dB to 117.5 dB ($\bar{x}$ = 87 dB; n = 25; SD = 13.6). It is, however, relatively intense in comparison with the **A. delicatus** advertisement call. The **A. delicatus** call is produced at a low intensity relative to both ambient noise and the advertisement calls of sympatric species (see Passmore, 1981).

TABLE 4.1

Call directivity patterns of zip and trill call components at three positions around the calling males.

| | position | $\bar{x}$ SPL | n | SD |
|---|---|---|---|---|
| ZIP | 0 | 94.5 | 10 | 3.65 |
| | 90 | 93.0 | 8 | 3.28 |
| | 180 | 92.5 | 7 | 2.99 |
| TRILL | 0 | 9.25 | 7 | 3.44 |
| | 90 | 92.8 | 6 | 3.12 |
| | 180 | 93.5 | 6 | 2.30 |

### 4.3.2 Encounter Call

The encounter call is produced at a higher intensity than the zip and trill component of the advertisement call ($\bar{x}$ = 101.0 dB; 95.1 dB and 94.4 dB peak at 25 cm respectively). Analysis of variance showed a significant difference between the zip and encounter call SPL ($F = 34.3$; DF num = 1; DF den = 10; $P < 0.01$), and between the trill and encounter call ($F = 33.2$; DF numerator = 1; DF denominator = 10; $P < 0.01$). The lower limit of the emphasised frequency range of the encounter call is 1.1 kHz lower than that of the zip and the call is, on average, double the length of the zip (see Table 4.2 and Figure 4.1). The encounter call has been accurately described as a more rapidly pulsed and slightly longer version of the zip component of the two-part call at a slightly lower frequency (Telford, 1982).

### 4.3.3 Aggressive Interactions: Vocal and Physical

In the twelve interactions observed from the initial approach of the intruding male, it was always near neighbours that interacted. The intruding male was either calling too close to the resident ($n = 8$) or was silent but within 30 cm of the resident ($n = 4$). The intruding male generally approached the resident and was always within 15 cm of him before the resident emitted encounter calls. In each of the 28 observed interactions, vocal aggression preceded physical combat. Initially the encounter calls of both males are inserted between zip calls. On no occasion were trill calls given by either male once encounter calls had been emitted. After both males had emitted encounter calls there was an escalation of aggressive behaviour with the males turning to face each other and even looking over the edge of the call site leaf while calling directly at the other male ($n = 9$). It was generally the resident who moved to the intruder to initiate physical combat ($n = 11$), see Figure 4.2 and 4.3.

TABLE 4.2

Call parameters for A. delicatus encounter call and zip call.

| | Encounter call (n = 26) $\bar{x}$ | (range) | Zip call (n = 30) $\bar{x}$ | (range) |
|---|---|---|---|---|
| Upper limit emphasised frequency range (kHz) | 5.6 | (2.8-8.9) | 5.8 | (5.4-7.0) |
| Lower limit emphasised frequency range (kHz) | 3.3 | (1.4-4.0) | 4.4 | (3.8-5.5) |
| Call note duration (s) | 0.3 | (0.1-0.7) | 0.2 | (0.1-0.3) |
| Number of pulses per call | 48 | (19-108) | 26 | (16-42) |
| Pulse repetition rate (pulse/s) | 153.9 | (115.4-193.2) | 145.8 | (111.1-192.9) |
| SPL (dB peak at 25 cm) (n = 6) | 101.0 | 97.0-107.0 | 96.1 | (94.0-97.1) |

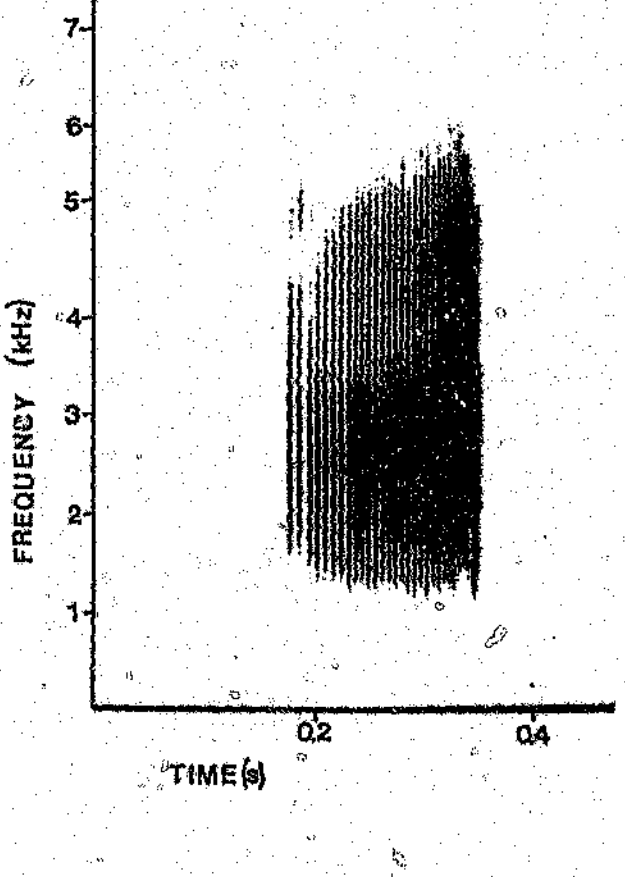



FIGURE 4.1 Wide band (300 Hz filter) sonogram of A. delicatus encounter call.

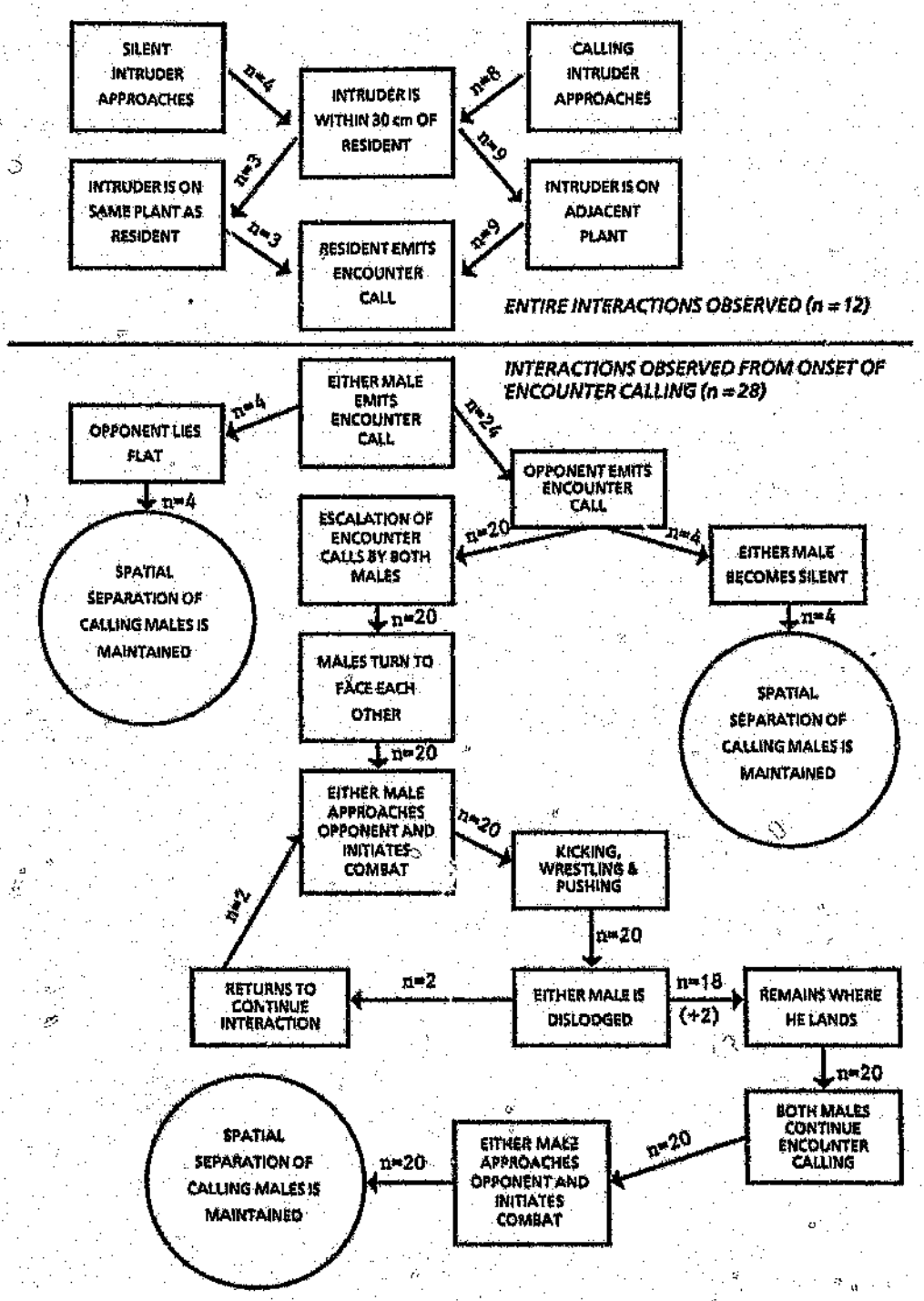



**FIGURE 4.2** Flow diagram of aggressive interactions between **A. delicatus** males.

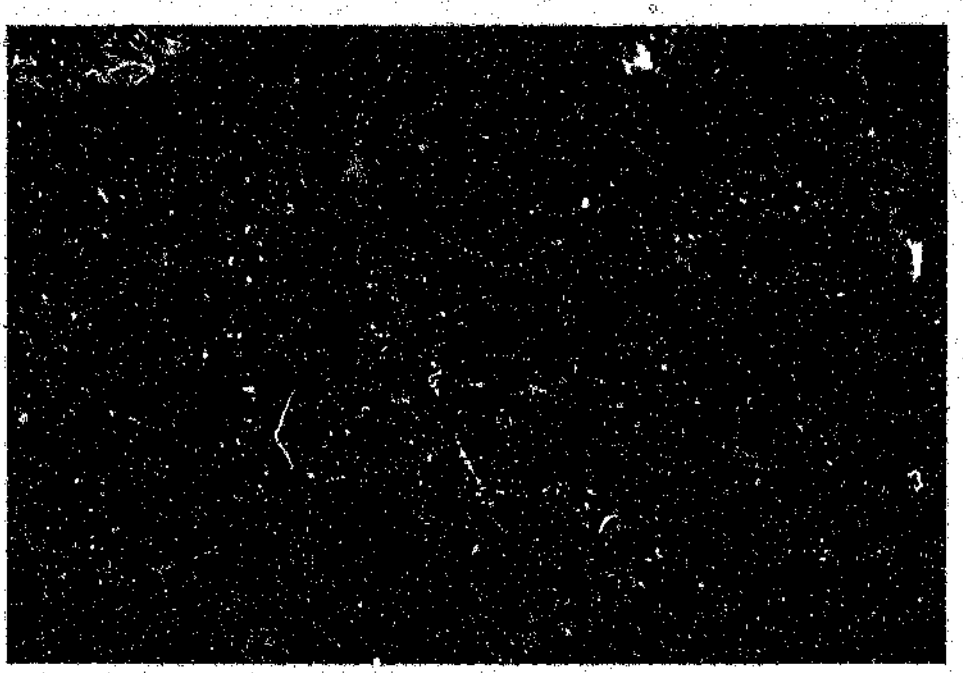


FIGURE 4.3 Aggressive interaction between two **A.delicatus** males.

Encounter calls are given by both males alternately. Only encounter calls are emitted throughout the physical interaction. The males grapple, grabbing each other with their fore and hind limbs (see Figure 4.3). Males were observed kicking, particularly at the face of the opponent (n = 18). One male is generally dislodged from the site, and unless he returns to continue the interaction (n = 2), he remains where he lands but emits encounter calls irregularly. Eventually the defeated and displaced male ceases encounter calling and remains silent for a long period (3 - 7 min) before moving away or resuming normal calling. The successful male also eventually ceases encounter calling and remains silent before resuming normal calling.

Resident males succeeded in displacing the intruder in 12 of the 14 interactions and retained their call sites. The interacting males were always found at least 40 cm apart after a physical interaction, and always further removed from each other than before the interaction. The aggressive interactions lasted 2.5 min (range = 0.5 - 3.5 min) although physical combat was generally brief and lasted 1.0 min (range = 0.5 - 2.5 min).

TABLE 4.3

Nearest neighbour distances (NND) at different chorus sizes (CS).

| CS | n | $\bar{x}$ NND (cm) | $\pm$ SD |
|---|---|---|---|
| 2 | 10 | 88.2 | 15.3 |
| 3 | 15 | 67.7 | 33.3 |
| 4 | 20 | 52.8 | 29.3 |
| 5 | 25 | 33.4 | 20.1 |
| 6 | 30 | 35.7 | 26.0 |
| 7 | 35 | 31.7 | 24.9 |
| 8 | 40 | 31.3 | 18.9 |

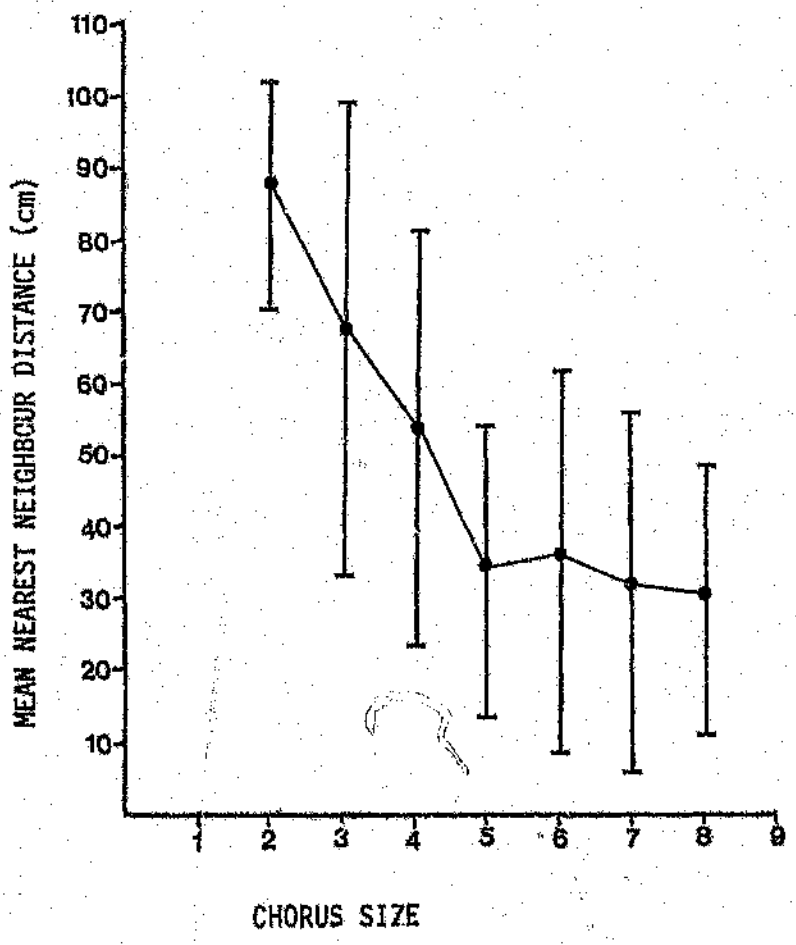



FIGURE 4.4 Nearest neighbour distances at different chorus sizes (n = 5 choruses at each chorus size).

TABLE 4.4

Multiple-range analysis (Student-Newman-Kuel) of differences between mean nearest neighbour distances at different chorus sizes.

| CHORUS SIZE | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|
| 3 | 0.01 | | | | | |
| 4 | 0.01 | 0.05 | | | | |
| 5 | 0.01 | 0.01 | 0.05 | | | |
| 6 | 0.01 | 0.01 | 0.05 | NS | | |
| 7 | 0.01 | 0.01 | 0.05 | NS | NS | |
| 8 | 0.01 | 0.01 | 0.05 | NS | NS | NS |

CHORUS SIZE

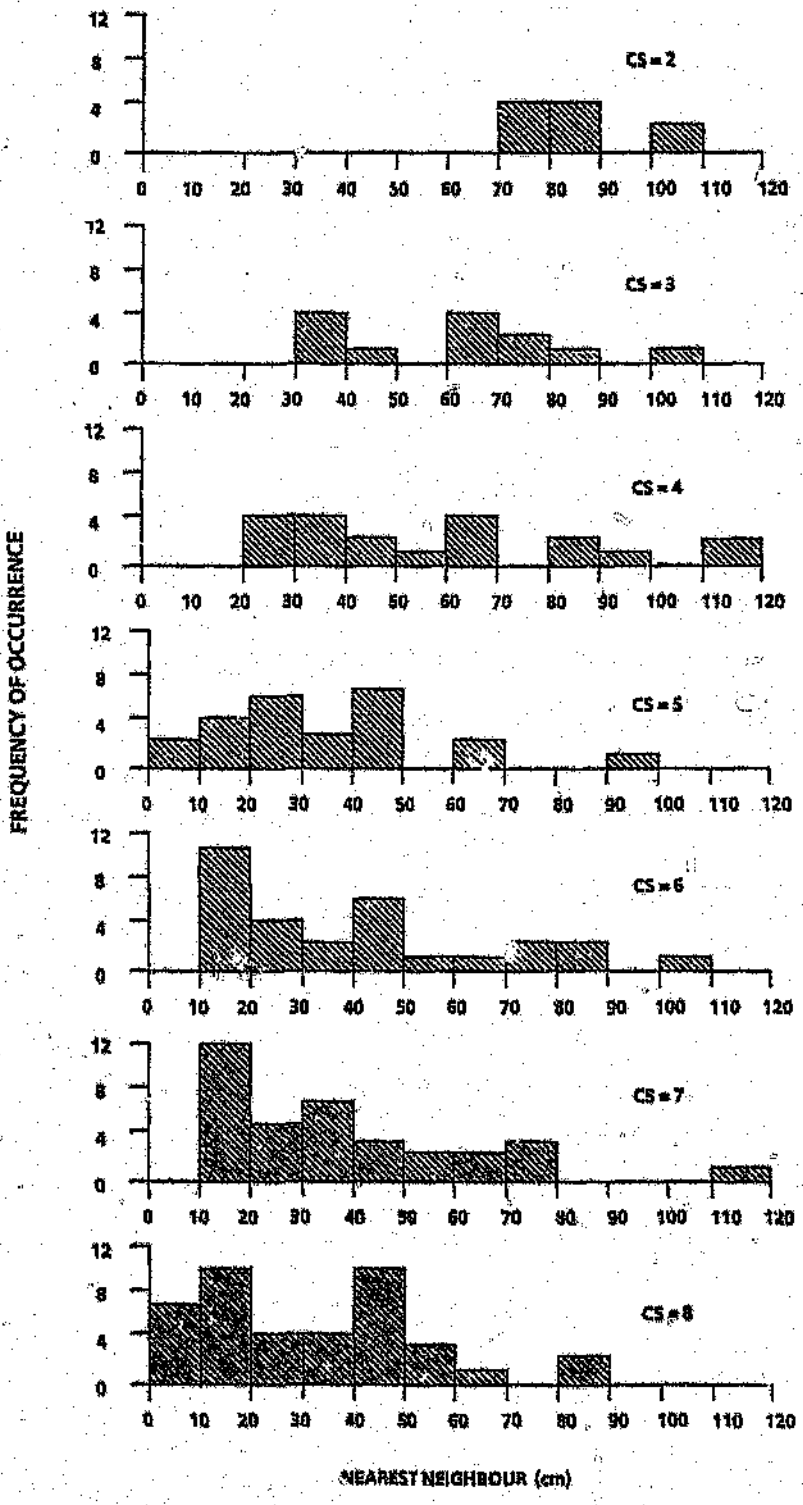



FIGURE 4.5 Distribution of nearest neighbour distances at different chorus sizes (CS = chorus size).

### 4.3.4 Nearest Neighbour Distances

An increase in the chorus size led to a decrease in the nearest neighbour distances ($r = 0.91$; $DF = 6$; $P < 0.01$) - see Table 4.3 and Figure 4.4. One way analysis of variance revealed significant differences between the means ($F = 12.77$; DF num = 6; DF denom = 168; $P < 0.01$). A Student- Newman- Kuels test revealed that there are no significant differences in spacing in chorus sizes of 5; 6; 7 and 8 but that significant differences exist between chorus sizes of 2; 3 and 4 as well as between each of these low chorus sizes and all other chorus sizes (see Table 4.5). The histogram of nearest neighbour distances at each chorus size show that males call increasingly closer together as chorus density increases. The histograms also depict the variability in nearest neighbour distances (see Figure 4.5).

The analysis of male distribution patterns in **A. delicatus** revealed conflicting results for each of the four methods employed to determine them. A critical examination of the methods was undertaken and is included in Appendix 1 (pp. 167).

### 4.3.5 Effect of Nearest Neighbour Distance on the Frequency of Aggressive Interactions

As the chorus size increased and the nearest neighbour distances decreased, the number of vocal and physical aggressive interactions increased. There were no aggressive interactions at a chorus size of three calling males (see Table 4.5).

TABLE 4.5

Frequency of vocal and physical aggressive interactions (FAI) over a 30 min period for three chorus sizes (CS).

| Cs | (N)n | $\bar{x}$ NND | FAI | |
|---|---|---|---|---|
| | | | vocal | physical |
| 3 | (5) 15 | 59.4 | 0 | 0 |
| 5 | (5) 25 | 39.4 | 0.4 | 0.2 |
| 8 | (5) 40 | 28.9 | 1.8 | 1.4 |

## 4.4 DISCUSSION

### 4.4.1 General

**Afrixalus delicatus** displays prolonged breeding behaviour where the male attracts females to his calling site using vocalisation (see Wells, 1977b). A male's reproductive success probably depends on his ability to attract females (Arak, 1983a; Wells, 1977b) and there would be strong selective pressure on the male to be heard and easily located by females. **Afrixalus delicatus** displays spacing behaviour characteristic of many other anurans (Arak, 1983a; Bunnel, 1973; Fellers, 1979a; Robertson, 1984; Wells, 1977b and others). Chorusing groups are found within the natural breeding area and interactions between males generally centre around the defence of call sites and intermale spacing.

In this species, oviposition does not occur at the call site and there is no resource defence by males. Thus intermale spacing is due to the maintenance of an individual distance rather than territoriality (see Crook, 1973; Telford, 1982; Wells, 1977b; Whitney and Krebs, 1975a).

### 4.4.2 Advertisement Call Intensity

The advertisement call of this species is produced at a relatively low intensity when compared to sympatric anuran species (see Passmore, 1981; Telford, 1982) and to the levels of background noise. Intraspecific variation in advertisement call intensity has been reported in numerous species (see Telford, 1982), but was negligible in **A. delicatus**. Although it is possible for males to judge the distance to near neighbours using the intensity of the advertisement call (Gerhardt, 1975), it is difficult to determine whether larger males defend larger individual distances based on their increased call intensity. Variation in the behavioural threshold that elicits aggression, chorus density and time of night all influence nearest neighbour distances (Dyson, 1989; Telford, 1985) and may obscure the small effect that intensity differences may have, particularly in this species where variation in intensity is low.

The call directivity pattern of a male could be an important factor in both female attraction and intermale spacing. Passmore (1981) suggested that the nature of the directivity pattern may explain reported observations of females bypassing males while apparently responding to a certain individual only. It would, similarly, be important to determine the distances separating calling males. If the call intensity behind a male was lower than that in front of him, neighbours could space at shorter distances if, for example, they were facing away from each other. The circular sound envelope found in **A. delicatus** precludes this effect.

4.4.3 Maintenance of Spacing

Spatial separation between calling males is presumably maintained through the three level system reported in many other species (Bunnel, 1973; Fellers, 1979a; Robertson, 1984; Wells and Schwartz, 1984 and others). The zip component of the two-part call presumably functions in the initial separation of calling males (pp. 39 - 41). The encounter call is similar to the zip but is produced at a higher intensity. This may enhance its audibility over the background of zip calls. It is possible that the encounter call evolved from the zip (Telford, 1982). The encounter call is emitted during aggressive interactions and together with physical combat, or the threat of combat, maintains the spatial separation between calling males. Vocal aggression precedes physical combat in this and many other species (Arak, 1983a; Brattstrom and Yarnell, 1968; Telford, 1982; Wells, 1981). Vocal aggressive interactions are more common than physical combat since the encounter call is often sufficient to chase away the intruding male. The form of combat in **A. delicatus** is similar to that found in other species (Bunnel, 1973; Fellers, 1979a; Telford, 1982 and Wells, 1978) and involves wrestling, kicking and pushing, although no wounding was observed (as reported by Lutz (1960) in **Hyla faber**). Physical combat seems to be the last resort in the attempt to prevent other males from calling nearby.

Despite considerable documentation of social spacing behaviour in anuran choruses, very little attention has been paid to the possible effects of chorus density on spacing patterns (Telford, 1985). Fellers (1979a) found a tendency for frogs to call increasingly

closer to one another as density increases. His analysis shows that spacing changed from uniform to random at high densities. Telford, Dyson and Passmore (in press) also found that spacing breaks down as an effect of the breakdown of chorus organisation at high densities. They concluded that: "Spacing can only be maintained in socially organised choruses where individuals are capable of alternating their calls with one another. Through the maintenance of optimal spacing, males increase their probability of attracting a mate but as density inceases, chorus organisation is affected and spacing is disrupted". It is predictable that spacing would break down at high densities if one considers the function of the advertisement call in this process. Bishop's (in prep.) evidence that call alternation functions to allow **Hyperolius marmoratus** males to estimate the proximity of near neighbours using the relative call sound pressure levels suggests that when call alternation is possible, males may maintain uniform spacing. As density increases and call alternation is no longer possible, near neighbour's calls no longer provide an indication of distance, and spacing would become random.

In **A. delicatus** the nearest neighbour distance decreases with increasing chorus density. Unlike Dyson (1986) and Fellers (1979a), I found that the distances decrease only up to a point, and that males then defend an individual distance of approximately 30 - 35 cm. At low chorus sizes (2 - 4 males), males are spaced maximally and very few aggressive interactions occured between them. At higher chorus sizes (from 5 - 8 males) aggressive interactions are required to maintain a preferred minimum individual distance. As the chorus size increases, more aggressive interactions are required to maintain spacing. Choruses of nine or more males were extremely rare (found only on three occasions irrespective of the number of males placed in the cage). It is proposed that at a chorus size of eight males, no more males were accommodated in the chorus and additional males were inhibited from calling. Dyson (1986 and pers. comm.) found that additional males were accommodated in the chorus of **Hyperolius marmoratus** and that spacing mechanisms broke down once the chorus reached a high density (approximately 8 males/m$^2$). The responses of males in these two species are obviously different.

The analysis of male distribution patterns in **A. delicatus** as well as a critical

examination of the methods employed, is included in Appendix 1 (pp. 167). Due to the uncertainty of the methods for analysing distribution patterns, conclusions regarding such patterns will not be made here.

### 4.4.3 Functions and Effects of Spacing

The spacing behaviour exhibited by **A. delicatus** may reflect the ability of males to reduce the number of potential competitors (see Fellers, 1979a; Wells, 1977b) under conditions of limited area. Under natural breeding conditions, space is not limiting and additional males would be accommodated on the perimeter of the chorus. The limitation of competition may be an effect of the maintenance of spacing under certain natural conditions (e.g. at a small breeding pond, where space is limiting). Wells (1977b) proposed that the maintenance of spacing would reduce competition, even under conditions of unlimited space since newly arrived males would have to search for calling sites at suitable distances from other calling males, and in so doing, would lose valuable mate-attraction time. The extent to which this would affect a resident male's reproductive success is questionable.

The probable function of spacing lies in the increased male reproductive success gained through: (1) the decreases of acoustic interference between near neighbours (Whitney and Krebs, 1975a), which results in an increase in a male's locatability and the distinctiveness of his call; and (2) the provision of a clear pathway for female approach (Whitney and Krebs, 1975a), which prevents neighbouring males from intercepting approaching females.

Telford (1982, 1985) postulated that spacing evolved as a result of the limited resolving powers of the female auditory system. He demonstrated experimentally that there is a selective advantage to males in maintaining a minimum individual distance in

closer distances up to the point where the advantage of being spatially separated is matched by the disadvantage of spending increased time in aggressive interactions (Telford, 1982; 1985). Dyson (1986) found that additional males were accommodated in **H. marmoratus** choruses since no minimum individual distance was maintained, thus there may be a compromise. However, in **A. delicatus**, the advantage of being spatially separated outweighs the disadvantage of spending increased time in aggressive behaviour at all chorus sizes, and no compromise is made.

# CHAPTER FIVE

# SOME ASPECTS OF MALE BEHAVIOUR

## 5.1 INTRODUCTION

### 5.1.1 General

The differences in mating systems of anuran species are largely due to differences in ecology, physiology and social behaviour. The mating system of a species generally reflects aspects of its evolutionary and natural history. Within species, there is often considerable flexibility in the mating system, and the extent to which a species can be said to have a "typical mating system" is questionable (Arak, 1983a).

The male reproductive strategy can be viewed as a consequence of the way in which individuals interact in response to various social and ecological pressures (Arak, 1983a). Autecology provides a framework for the evolution of reproductive strategies (Salthe and Mecham, 1974), but the role played by social interactions is a profound one. In order to formulate an overall view of the mating system of a species, one must necessarily examine individual aspects of behaviour. The purpose of this chapter is to reveal the collective behaviours of males in response to some aspects of ecological and social pressures, namely: climatic factors, call sites, distribution at the natural breeding area, call site fidelity, and chorus organisation.

### 5.1.2 Climatic factors

Climatic factors may dictate the seasonal availability of breeding sites and may,

therefore, affect the breeding behaviour of an anuran species (Telford, 1982). Many early studies of anuran ecology have demonstrated that calling activity is influenced by weather (Bowker and Bowker, 1972; Schneider, 1977; van Gelder and Hoedmaekers, 1971), and rainfall appears to exert the greatest influence. Telford (1982) found that the level of breeding activity of 13 sympatric anurans decreased as the number of days since the last rainfall increased. Furthermore, air as well as water temperature have been shown to be important variables influencing breeding activity. Telford (1982) found that the air temperature had no significant effect on individual species calling activity above 16 C, although the level of activity was greatly reduced below 16 C. Schneider (1977) similarly found that European hylids did not call unless the air temperature exceeded a lower limit, but calling behaviour did not correlate with ambient temperature above this threshold. There is very little documentation on the effect of humidity on nightly calling activity, but humidity could perceivably influence male behaviour.

The effect of temperature, rainfall and humidity on the level of calling activity was investigated in **A. delicatus**. The purpose of this work was to reveal the extent to which climatic variables determine the level of calling activity and hence the availability of the pan as a suitable breeding area on a nightly basis.

### 5.1.3 Call Sites and Call Site Fidelity

Anurans with prolonged breeding seasons generally call from stationary positions around or near the breeding pool (Arak, 1983a). Some species call from a wide range of sites, e.g., **Hyperolius argus**, while others select particular sites, e.g., **Leptopelis natalensis** (Telford, 1982). Subtle variations of habitat suitability within chorus locations may make some calling sites better than others for attracting females (Arak, 1983a). For instance, Fellers (1979b) reported that males of **Hyla versicolor** that occupied certain perches had an advantage in attracting mates. These perches were horizontal and surrounded by relatively little vegetation, thus creating less attenuation of the advertisement call. Greer and Wells (1980) reported a similar increase in attractivness in male **Centrolenella fleischmanni**, where males with call sites over 0.6 m above ground level obtained more mates than those on lower sites.

In those territorial species where call site is also used as an oviposition site, there will obviously be strong selection on the males to possess an optimal site with respect to both its suitability as an oviposition site and to its sound propagation properties.

Call site fidelity has been reported in numerous anuran species and is usually explained in terms of territorial defence (Emlen, 1968; Mc Vey et al., 1981; Schneider, 1977). Mc Vey et al. (1981) suggested that call site fidelity may have arisen as a consequence of site familiarity contributing to predator avoidance or food gathering efficiency in non-territorial species. Telford (1982) suggested that if non-territorial males returned to the same call sites, they would not waste time and energy on locating suitable sites each night. He also predicted that selection pressures causing call site fidelity would be more intense in high density populations.

A preliminary investigation of the selection of call sites and the level of call site fidelity was undertaken for **A. delicatus**. I attempt to answer the following questions: Are particular call sites chosen, and if so, what are their characteristics? Is call site fidelity displayed, and if so, at what level?

### 5.1.4 Chorus distribution

Prolonged breeding male anurans generally vocalise in choruses, and it is believed that the more intense sound source of a chorus may facilitate easy localisation of the breeding area by females (Wells, 1977b). However, chorusing may have the effect of decreasing the conspicuousness of individual males' signals. A compromise between the two alternatives could be achieved if males formed small groups within the chorus. The advantages of chorusing would then presumably be maintained, while the signals of individuals retain their conspicuousness because call overlap could be avoided, either actively or by chance. Within a small group, call overlap may be avoided if the participating males actively place their calls between the calls of other males.

The optimal group size for the avoidance of call overlap would be limited by the call duration and repetition rate (Brush and Narins, 1989). In **Eleutherodactylus coqui**,

the optimal group size of 3 - 4 males would probably allow the maintenance of total acoustic avoidance (Brush and Narins, 1989).

Three theories have recently been proposed to explain how and why males form groups or clusters within a chorus:

1) Female preference model (Bradbury, 1981)
Males gain no intrinsic advantage from spatial clustering, but clustered males are favoured by females since it allows a female to compare mate quality.

2) Hotspot model (Bradbury and Gibson, 1983)
Male clustering is produced by the sequential settlement of males onto sites or pathways preferentially used by females. This implies that some sites are preferential in terms of their mate attraction potential. Newly arriving males can either cluster at suitable sites, or settle solitarily at sites where access to females is reduced although exclusive.

3) Hotshot model (Beehler and Forester, 1988)
This model was formulated due to the authors' belief that the previously proposed models were inadequate to explain much of the variation in male clustering systems; were inaccessible to empirical testing; and were over-emphasising the role of female choice. The Hotshot model highlights the importance of male dominance interactions and downplays the the importance of female choice based on male phenotype. The model claims that, certain males, because of behavioural and/or morphological attributes, are extremely successful in attracting mates. Other, less successful males, cluster around these "hotshots" and so obtain a greater probability of mating than they would have were they to have displayed alone.

critical examination of the three approaches, it is relatively easy to eliminate the Fem reference Model since it proposed that female choice is the driving force. The existence of female choice needs to be irrefutably demonstrated before this model becomes a viable proposition. The Hotspot Model is conceivably plausible and would be particularly applicable to species in which females return to their "usual" mating site

when seeking a new partner (which could possibly be the case in A. delicatus, since polyandrous females -see pp. 142- may return to the same area on subsequent nights). The flaw of the Hotspot Model lies not in its logical validity, but in its inaccessiblity to empirical testing: do clusters form around hotspots or are hotspots formed in the clusters? The Hotshot Model is an attractive alternative but its applicablity to individual anuran species must be examined.

I conducted an investigation into the distribution of males within a natural chorus in order to determine whether males form distinct patches, and if so, what the characteristics of these patches were.

5.1.5 Chorus Organisation

The most commonly reported form of temporal chorus organisation is the avoidance of call overlap with the calls of neighbouring males (see Wells, 1977a for review). It is evident that call alternation is a form of social interaction in many species (Awbrey, 1978). It is generally viewed as a means of decreasing acoustic interference and so maximising a male's signal efficiency (Wells, 1977a). Passmore and Telford (1981) experimentally demonstrated that the temporal separation of calls did not enhance their locatability in **Hyperolius marmoratus**. They proposed that call alternation may be important in the spatial distribution of males rather than in the ability of females to locate males. This was verified by Bishop (in prep.) who has shown that, in **H. marmoratus**, call alternation allows males to estimate the proximity of near neighbours. A male cannot perceive the calls of a neighbouring male during his own call emission. Thus it is only by antiphonal calling that males can hear their neighbours. He has also shown that call alternation is probably not due to social interaction. Chance alone may be sufficient to prevent continued call overlap. Social interactions may be based on the sound pressure levels of the calls rather than on the temporal features.

A preliminary examination of chorus organisation was undertaken in **A. delicatus** in order to determine whether males had set call rates irrespective of neighbours' calls; whether call triggering occurred; and whether call alternation was a regular occurrence.

## 5.2 METHODS

### 5.2.1 Climatic Factors

The number of calling males present at Mavungweni Pan was counted over 27 successive nights during October and November 1988. Counts were made between 20h00 and 21h30 to prevent the possible bias of time of night which has been reported to influence the calling activity in a sympatric species (Dyson, 1986). The relatively low population size of the species allowed for an accurate count to be taken, by following a set route through the vegetation each night.

Nightly ambient temperatures were taken at 21h00 using a Bat-12 Bailey Instuments digital thermometer. Humidity readings were taken nightly using a Barigo Hair-hygrometer. The occurrence of rainfall was noted over the entire 27 day period.

Spearman's Correlation analyses were performed on the data and the significance levels of the correlations were calculated.

### 5.2.2 Normal Call Sites and Call Site Fidelity

As a preliminary investigation, 28 calling males were studied at Matatiele pan during December 1983 and January 1984. The call sites used by these males were examined using the following parameters: the plant species used as a call site; the height of the call site above water level; the position of the call site relative to open water and the occurrence of vegetation around the call site. From these data it was found that the call sites were highly specific and a more comprehensive study was therefore undertaken in the cage during January and February 1985.

Fifty one plants providing call sites were present in the cage. These carried 251 leaves of varying shapes and sizes which provided a wide range of potential call sites. The following measurements were taken (to the nearest mm) for each leaf: width at widest point; length from stem to apex and the height above water level. Calling

males were collected from Matatiele pan and transported to the cage. Once a stable chorus was established (usually after two nights), the call sites of 41 males were studied over 10 nights. The leaves used as call sites were measured using the parameters listed above. A t-test for the difference between the two sample means was conducted on the data for each leaf parameter.

In order to investigate call site fidelity, calling males were collected from the natural breeding areas and branded with distinguishing marks on their hind limbs before being placed in the cage. The call sites of the branded males were noted for five successive nights following their release by drawing the brand-mark of the male on the underside of the leaf used as a call site. The males were considered to be displaying call site fidelity if the sites used on different nights were no more than 15 cm apart. It was often possible to identify branded males without catching or disturbing them although it was necessary to catch a few of the males for identification. A total of 41 males was observed. This work was conducted over the 1984/85, 1987/88 and 1988/89 breeding seasons.

5.2.3 Chorus Distribution

The chorus of calling males present at Mavungweni Pan was examined over 19 successive nights during October and November 1988. The chorus was found to be divisible into distinct groups of males (patches). The number of males present in each patch was noted and the nearest neighbour distances within each patch were measured (see pp. 51 for methods). The distance to the nearest patch was measured using a 3 m flexible tape measure. The number of nests present in each patch area was counted each night. The patch fidelity was examined by recording the position of all patches present on each of the 19 nights, and "patch fidelity" was said to occur if a group of males occupied the same area as a group of males from the previous night. A 50 cm error margin was allowed. [Note that it was not determined whether the same individuals were displaying patch site fidelity or not]. Chorus groups were observed for a total of 45 min each night in order to determine if inter-male interactions (in the form of vocal and

physical interactions) occurred exclusively within a patch or whether chorus group members interacted with males from adjacent patches.

Readings were taken nightly between 20h00 and 21h00. Ambient temperatures ranged from 16.9C - 28.4C ($\bar{x}$ = 19.5C), and the relative humidity ranged from 43 - 88% ($\bar{x}$ = 71%).

Pearson's Correlation coefficients, as well as the significance levels of the correlations, were calculated for the following data:

1) the total number of males present at the pan and the number of patches present;
2) the total number of males present at the pan and the distance to the nearest neighbouring patch;
3) the number of males within a patch and the mean nearest neighbour distance within that patch;
4) the mean nearest neighbour distance within a patch and the distance to the nearest neighbouring patch;
5) the total number of males at the pan and the mean nearest neighbour distance for each night.

A t-test was conducted on the data for:

1) the number of males within patches that contained new nests and patches that contained no new nests;
2) the number of males within parches that displayed patch site fidelity and patches that did not display fidelity.

5.2.4 Chorus Organisation

Approximately 150 sound recordings of choruses containing 2 - 14 males were made during the 1984/1985 and 1985/1986 breeding seasons using a Sony TC-185SD tape recorder and an Adastra electret condenser microphone. From these, 15 were randomly selected and analysed on a Uniscan II sound spectrum analyser within the 0 - 10 kHz range. Intercall intervals were measured for successive calls of each male

[separately for trills (n = 25) and zips (n = 17)]. The possible existence of call triggering and call alternation were examined by measuring the "delay period" between the calls of two neighbouring males (see Figure 5.1). A single typical sonogram of the zip calls of two neighbouring males was made on a Uniscan II sound spectrum analyser.

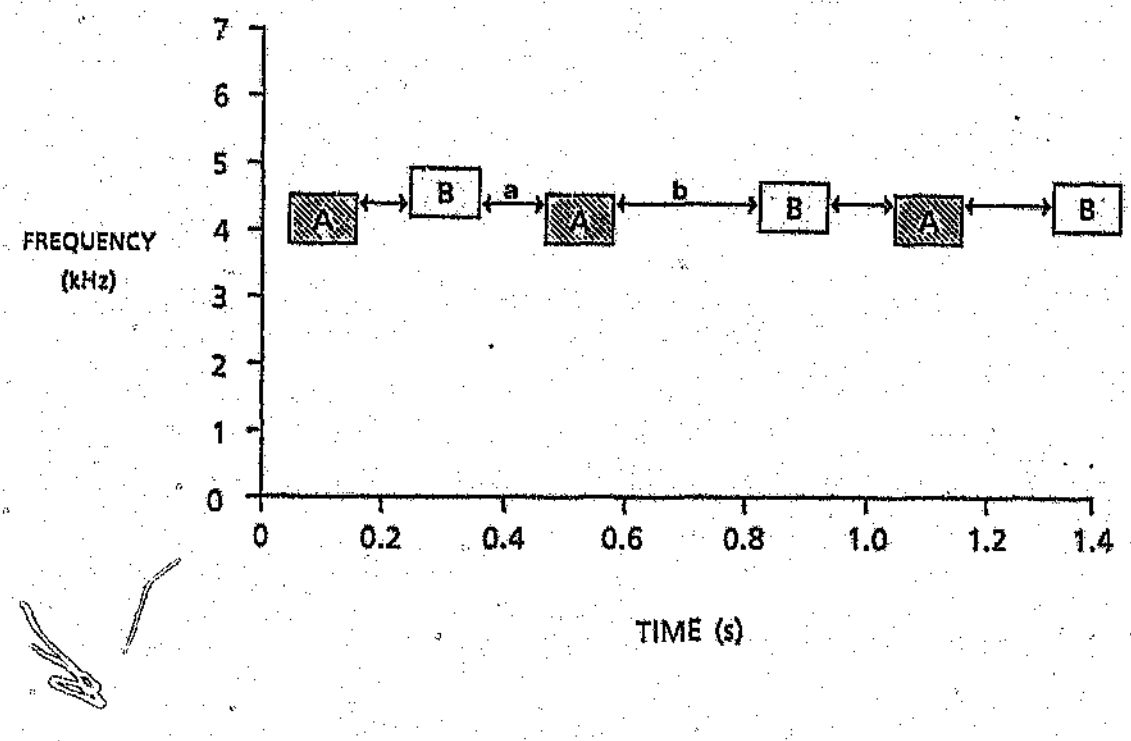



**Figure 5.1** The measurement of "delay periods" between the calls of two neighbouring males. (a = "delay period" for male A; b = "delay period" for male B).

## 5.3 RESULTS

### 5.3.1 Climatic Factors

Over the 27 night period, a mean of 7.4 males called on each night (range 0 - 25; SD = 7.6; n = 27 nights). Rain fell on seven occasions with a maximum of six days between rainfalls (x = 3 days; n = 6).

There was no significant correlation between the number of calling males present and air temperature ($r = 0.316$; $P > 0.05$; $n = 27$). There was also no significant correlation between the number of calling males and the relative humidity ($r = 0.28$; $P > 0.05$; $n = 27$). There was a significant negative correlation between the number of calling males and the number of days since the last rain ($r = -0.55$; $P < 0.01$; $n = 27$).

### 5.3.2 Call Sites and Call Site Fidelity

Calling occurs on the leaves of the plant species **Polygonum pulchrum** and **Ludwegia stolonifera.** The leaves of these plants are also used as oviposition sites (pp.151). Of the 28 natural call sites examined at Matatiele pan, 20 were on the leaves of **Ludwegia stolonifera** and eight on **Polygonum pulchrum.** (Since **Ludwegia** is approximately twice as common as **Polygonum** at this pan, there seems to be no preference for either plant species.) The height of the call sites above water level ranged from 2.5 cm to 37.0 cm ($x = 21.5$ cm; $n = 28$). The call sites were all in the eulittoral zone of the pan or in patches of low eulittoral zone vegetation surrounded by reed clumps and other taller vegetation. Small chorusing groups were distributed around the pan.

Males selected particular leaves as call sites, and the preference was for the shorter, wider leaves of the population. The difference in leaf width between the population and the sample means ($x = 1.63$ cm, $n = 251$; $x = 2.11$ cm, $n = 41$ respectively) was significant ($t = 4.81$; $DF = 40$; $P = 0.001$). Similarly, the difference in leaf length between the population and sample means ($x = 9.11$ cm, $n = 251$; $x = 8.11$, $n = 41$

respectively) was significant ($t = 2.08$; $DF = 40$; $P < 0.01$). For each leaf, the width was multiplied by the length to give a leaf area index. A t-test on leaf areas revealed a significant difference between the population and the sample means ($\bar{x} = 16.23$ cm$^2$, $n = 251$; $\bar{x} = 13.9$ cm$^2$, $n = 41$ respectively; $t = 3.03$; $DF = 40$; $P < 0.01$) which indicates a preference for smaller leaf area. The height of the leaf above water level did not significantly influence the selection of call site (population: $\bar{x} = 18.90$ cm, $n = 251$; sample: $\bar{x} = 21.50$ cm, $n = 41$; $t = 0.57$; $DF = 40$; $P > 0.1$).

Although the leaves selected by males as call sites and those selected by females as oviposition sites (p. 151) were the shorter, wider leaves in the population, a comparison between call site and oviposition site leaves revealed significant differences between leaf width ($t = 3.65$; $DF = 95$; $P < 0.001$) but not leaf length ($t = 0.57$; $DF = 95$; $P > 0.2$).

I noted that not all males observed over a five night period called on each night (see Table 5.1). Of the 40 observed males, 14 displayed no call site fidelity and called at different call sites on each night spent calling, ten displayed total fidelity and nine displayed incomplete fidelity. Males displayed a mean level of 50 % call site fidelity (see Table 5.1).

TABLE 5.1

Call site fidelity of 25 males over a five-night period.

| Male no. | No. nights calling | No. call sites used | Max. no. nights at single site | % Fidelity |
|---|---|---|---|---|
| 1 | 1 | 1 | 1 | - |
| 2 | 1 | 1 | 1 | - |
| 3 | 1 | 1 | 1 | - |
| 4 | 1 | 1 | 1 | - |
| 5 | 1 | 1 | 1 | - |
| 6 | 1 | 1 | 1 | - |
| 7 | 1 | 1 | 1 | - |
| 8 | 2 | 2 | 1 | 0 |
| 9 | 2 | 2 | 1 | 0 |
| 10 | 2 | 2 | 1 | 0 |
| 11 | 2 | 2 | 1 | 0 |
| 12 | 2 | 2 | 1 | 0 |
| 13 | 2 | 1 | 2 | 100 |
| 14 | 2 | 1 | 2 | 100 |
| 15 | 3 | 3 | 1 | 0 |
| 16 | 3 | 3 | 1 | 0 |
| 17 | 3 | 3 | 1 | 0 |
| 18 | 3 | 3 | 1 | 0 |
| 19 | 3 | 3 | 1 | 0 |
| 20 | 3 | 2 | 2 | 67 |
| 21 | 3 | 2 | 2 | 67 |
| 22 | 3 | 1 | 3 | 100 |
| 23 | 3 | 1 | 3 | 100 |
| 24 | 3 | 1 | 3 | 100 |
| 25 | 4 | 4 | 1 | 0 |
| 26 | 4 | 4 | 1 | 0 |
| 27 | 4 | 4 | 1 | 0 |
| 28 | 4 | 3 | 2 | 50 |
| 29 | 4 | 2 | 3 | 75 |
| 30 | 4 | 2 | 3 | 75 |
| 31 | 4 | 1 | 4 | 100 |
| 32 | 4 | 1 | 4 | 100 |
| 33 | 4 | 1 | 4 | 100 |
| 34 | 4 | 1 | 4 | 100 |
| 35 | 4 | 1 | 4 | 100 |
| 36 | 5 | 5 | 1 | 0 |
| 37 | 5 | 2 | 4 | 80 |
| 38 | 5 | 2 | 4 | 80 |
| 39 | 5 | 2 | 4 | 80 |
| 40 | 5 | 1 | 5 | 100 |
| $\bar{x}$ | 3 | 2 | 2 | |

5.3.3 Chorus Distribution

Males form distinct patches within the breeding area. There was a mean of 7.9 m[illegible]s at the pan per night (range = 0 - 25; n = 19 nights), and a mean of 2.9 patches per night (range = 0 - 8; n = 19). Each patch contained 1 - 8 calling males ($\bar{x}$ = 2.7; n = 57). The mean nearest neighbour distance within patches was 41.5 cm (n = 137) and the mean distance separating patches was 2.33 m (n = 51).

The number of patches present was correlated with the total number of males present at the pan (r = 0.89; P < 0.01; n = 15). There was also a positive correlation between the mean nearest neighbour distance and the distance to the nearest patch (r = 0.3; P < 0.05; n = 39). No significant correlations were found between:

1) the number of males present in the patch and the distance to the nearest patch (r = -0.21; P > 0.05; n = 48)
2) the mean nearest neighbour distance within a patch and the number of males in that patch (r = -0.23; P > 0.05; n = 42)
3) the total number of males present at the pan each night and the mean nearest neighbour distance for all patches on that night (r = -0.17; P > 0.05; n = 15).

Patches in which nests occurred had significantly more males than [illegible] in which no nests were found (t = 2.80; P < 0.05; n = 22; 35). There was a non-significant difference in the number of males constituting patches in which patch fidelity was displayed and patches in which no fidelity was noted (t = 0.69; P > 0.05; n = 20; 32).

In the majority of cases (75%), nests were present in patches that displayed fidelity. In 23% of patches, no nests were found although patch fidelity had been displayed; and in 2% of patches, there were old nest sites although males had not exhibited patch fidelity.

On no occasion (n = 19 nights; 14 hours of observation), was a male observed interacting with males from another patch. No vocal or physical aggression occurred between patches and the distance separating patches was presumably large enough to prevent call interference (e.g. call overlap) between males from neighbouring patches. A relatively large number of aggressive interactions occurred between males within a single patch (n = 51).

### 5.3.4 Chorus Organisation

There is no fixed call rate in this species. The intercall interval varies between successive calls for both zips and trills (see Table 5.2). The zip calls of near neighbours were found to alternate for a period of time, but then to be emitted closer and closer until the calls overlapped before again approaching alternation (see Figure 5.2). This pattern was irregular and variable according to the variation of the participating individuals' call rates. There was no obvious call triggering of zips and the delay periods between zips of neighbouring males were variable. Trilling occurred in bouts between long periods when no trilling occurred. Trilling seemed to initiate trilling by other males although strict call triggering with set delay periods was not found. The trill calls of neighbouring males were found to overlap in 26 of the 48 cases analysed. In

the remaining 22 cases there was a variable intercall interval but in 21 of these cases the calls followed each other very closely (see Table 5.3).

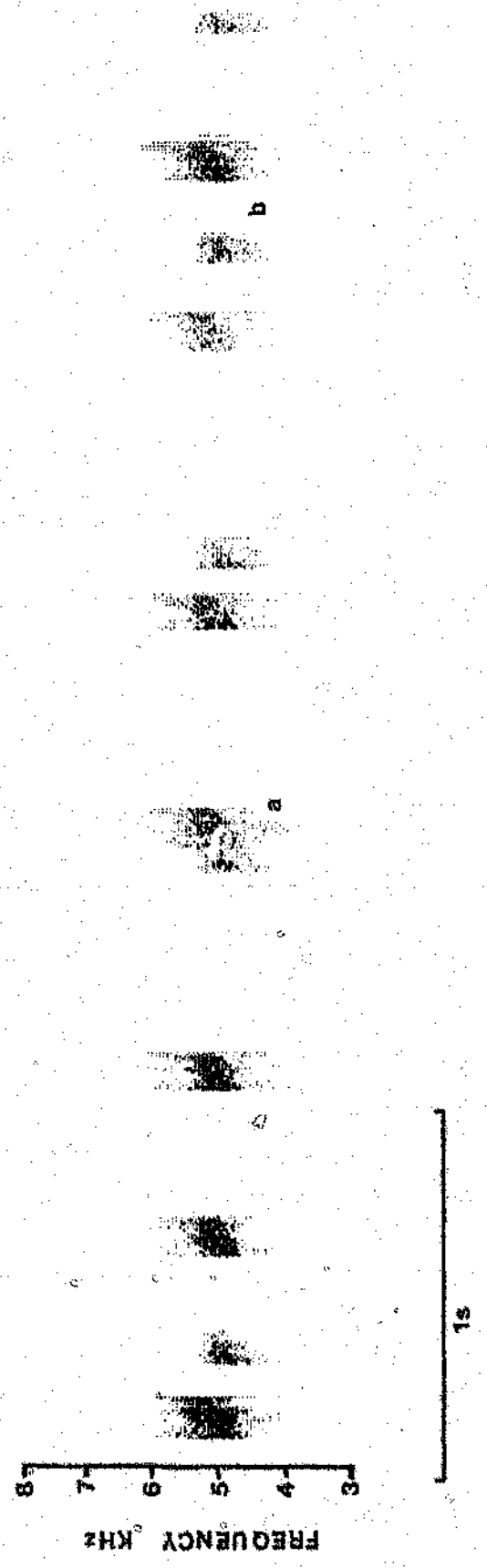



Figure 5.2 Wide band (300 Hz filter) sonogram of zip calls of two neighbouring *A. dellcatus* males showing call overlap (a) and call alternation (b).

TABLE 5.2

Intercall intervals between successive calls of individual males (n = 20).

| Male number | Intercall intervals (s) | |
|---|---|---|
| | Zip | Trill |
| 1 | 3.1 | 14.2 |
| 2 | 7.2 | 24.8 |
| 3 | 0.4 | 8.0 |
| 4 | 1.9 | 23.1 |
| 5 | 1.5 | 2.2 |
| 6 | 0.8 | 8.0 |
| 7 | 1.0 | 15.1 |
| 8 | 1.9 | 15.9 |
| 9 | 0.9 | 45.3 |
| 10 | 1.3 | 5.3 |
| 11 | 9.5 | 38.7 |
| 12 | 3.1 | 12.0 |
| 13 | 9.6 | 24.4 |
| 14 | 9.7 | 8.0 |
| 15 | 3.9 | 6.7 |
| 16 | 1.1 | 10.7 |
| 17 | 4.3 | 12.0 |
| 18 | 0.7 | 3.6 |
| 19 | 5.4 | 5.3 |
| 20 | 1.9 | 1.8 |
| x̄ | 3.46 | 14.26 |
| SD | 3.16 | 11.76 |
| SE | 0.71 | 2.63 |

TABLE 5.3

Intercall intervals between the calls of two neighbouring males (n = 17 for zips; 48 for trills).

| Zips | | | Trills | |
|---|---|---|---|---|
| Male no. | x | (range) | Male no. | x |
| 1 | 9.8 | (4.9 - 17.3) | 1-26 | 0 or <0 |
| 2 | 17.8 | (13.0 - 22.2) | 27 - 46 | <0.5 |
| 3 | 63.5 | (16.0 - 22.2) | 47 - 48 | 23.99 |
| 4 | 50.7 | (37.3 - 80.0) | | |
| 5 | 48.8 | (24.4 - 64.4) | | |
| 6 | 67.0 | (44.4 - 88.8) | | |
| 7 | 12.9 | (11.1 - 14.2) | | |
| 8 | 13.8 | (6.7 - 33.3) | | |
| 9 | 12.0 | (5.3 - 20.0) | | |
| 10 | 10.7 | (7.1 - 13.3) | | |
| 11 | 9.7 | (5.0 - 17.8) | | |
| 12 | 11.2 | (6.4 - 13.3) | | |
| 13 | 6.4 | (4.9 - 8.5) | | |
| 14 | 8.5 | (2.1 - 29.3) | | |
| 15 | 23.1 | (12.4 - 42.2) | | |
| 16 | 15.1 | (5.2 - 24.9) | | |
| 17 | 13.9 | (7.5 - 22.2) | | |
| x̄ | 23.28 | | | |
| SD | 20.83 | | | |
| SE | 4.93 | | | |

## 5.4 DISCUSSION

### 5.4.1 General

The mating strategy employed by males of any anuran species would necessarily reflect the physiology and ecology of the species. Social factors may also be expected to play a profound role. It is not surprising that mating strategies show a high level of flexibility both between and within species. This chapter reveals the extent to which selected ecological, physiological and social factors influence the male mating strategy in A. delicatus.

### 5.4.2 Climatic Factors

It appears that many frog species are capable of detecting climatic changes, and that these changes influence the level of calling activity. In A. delicatus, climatic variables may influence the length of the breeding season (Telford, 1982), but appear to have a limited effect on calling activity during peak season. The number of males calling at the natural breeding area was not affected by air temperature or relative humidity. Rainfall did exert a significant effect, with calling activity being highest during or shortly after rain. This is not surprising when considering the effect of rainfall on the nests of this species (see pp. 139).

### 5.4.3 Call Sites and Call Site Fidelity

Males call from stationary sites around or near the breeding pool. Particular sites

were selected and are generally surrounded by vegetation, which may create greater sound attenuation (Fellers, 1979a), but would presumably offer advantages in their inaccessibility to predators. The leaves preferred as call sites were the wider, shorter leaves in the population although the reason for this is not clear. The height of the call site above water level was lower than that for other sympatric species (apart from those calling at ground level (Telford, 1982)). Some call sites were better than others for attracting mates (as proposed by Arak, 1983a; Fellers, 1979a and Wells, 1980; see Chapter 5).

Call site fidelity is displayed by approximately 50% of all males and would presumably confer an advantage in familiarising a male with his surroundings which would contribute to predator avoidance (see Mc Vey et al., 1981). Telford (1982) further suggested that if males returned to the same call site each night, they would conserve energy and there since they would not have to select a suitable site each night.

### 5.4.4 Chorus Distribution

In Ar. dalbatus, the chorus is distinctly divided into small groups of males. These patches do not appear to interact with each other but rather function as independent choruses. The distance between neighbouring patches was, on average, 5.5 times greater than the distances between neighbouring males within a patch. The number of males constituting a patch does not appear to increase indefinitely as more males enter the breeding area, but rather, the additional males appear to form new patches.

In anuran choruses, calling sites are often associated with particular vegetation types, the distribution of which may have the effect of limiting the distribution of the associated anuran species. The spatial arrangement of males may simply be the effect of vegetation distribution and call site preference. It is important to point out that the patches found in the A. delicatus choruses did not correspond to vegetation distribution, and clusters of males were found within areas of homogeneous vegetation. Within these homogeneous vegetation areas, there was no detectable difference in resource availability and thus the patches were not separated by unsuitable breeding areas.

The consequences of clustering were examined by Brush and Narins (1989). They proposed that individual signals would be most conspicuous to females when they are not acoustically interfering with each other. If males were uniformly dispersed (as opposed to clustered), they would interact with only their close neighbours and consequently, their calls would be distinct relative to those males only. However, there would be geometric areas within the chorus where call interference would occur. These areas would also on the borders of interacting groups, where males would need to avoid call overlap within their group as well as with males of neighbouring groups. Clustering may enhance the attractiveness of female attraction by enabling males to interact only with the males in their cluster.

Although patches that contained nests had significantly more males present than patches in which no nests were found, this could be due to the increased probability that at least one of the constituent males would mate (i.e. a patch has the summed probabilities of each of its constituent males' probability of mating).

It also appears that the number of males constituting a patch does not influence the level of patch site fidelity, and so patches that contained a greater number of males were not necessarily reused on following nights.

The relationship between the occurrence of nests within a patch and the display of fidelity to that patch indicates that: either males preferentially select patch sites in which mating had previously occurred (i.e., the presence of nests resulted in the fidelity); or that the presence of nests is an obvious result of the fact that males display fidelity (i.e., the fidelity results in the presence of nests). The fact that 23% of patches in which fidelity had been displayed contained no nests (as opposed to the 2% of patches in which old nests were found but where fidelity had not been evident), indicates that the presence of nests probably exerts little influence on the display of fidelity to a patch.

It appears that patches that are most widely separated from other patches are also those in which the males (within the patch) are most distant from each other. This is not influenced by the number of males constituting the patches, and these patches are not peripheral. I am unable to explain these results and further investigation of the phenomenon is required.

When considering the proposed models on the evolution of clustering, it is difficult to determine which of the alternatives best fit these data. Further extensive investigation is required. This preliminary investigation has, however, pointed out two important factors:

1) In order for the Hotshot Theory to explain clustering, males must necessarily judge calling males' attractiveness in the same way that females judge such attributes.

Presumably there is a continuum of male attractiveness, and this would necessitate that males acutely perceive the attractiveness of a caller relative to his own attractiveness. 2) The Hotspot Theory may be a plausible explanation of clustering in A. delicatus in that females may return to previous mating/oviposition sites on subsequent nights if they display polyandry (see pp. 139). Males that cluster around such sites may be at a mating advantage. This would explain the high level of call site fidelity and occurence of old nests within patch sites.

Clustering may also be an anti-predator adaptation that makes each individual harder to locate within the chorus (Wells, pers. comm.).

### 5.4.5 Chorus Organisation

Dyson (1986) proposed that spacing can be maintained in socially organised choruses only where individuals are able to alternate their calls with near neighbours. As chorus density increases, call alternation is no longer possible. Since males cannot hear a call at the instant their own call is sounded (Bishop, in prep.), chorus organisation is affected and spacing breaks down. Call alternation and chorus organisation are therefore essential components in the facilitation of spacing (Dyson, 1986).

Intercall intervals are variable in A. delicatus and calls do not form a regular train as they do in many other species. Call alternation as well as call overlap occur. There appears to be no call trigg[illegible] of "zips" although trill calls do appear to stimulate other males to trill. Further investigation is required, but this study has revealed that apparent call alternation and chorus organisation may be due to chance rather than social

interaction. Bishop (in prep.) has clearly demonstrated that careful examination is required before any conclusions can be drawn regarding the influences of chance and/or social interaction on chorus organisation. Whether temporal chorus structure is due to chance or social interaction, it plays a fundamental role in the spatial separation of males in anuran choruses.

# CHAPTER SIX

# MALE MATING SUCCESS: CALLERS AND SATELLITES

## 6.1 INTRODUCTION

### 6.1.1 General

The nightly operational sex ratio of most prolonged breeding anurans is male-biased (Emlen and Oring, 1977). The aggregation of males into breeding choruses provides a forum for male-male competition (Telford and Dyson, 1988) and increases the potential for male mating success to vary (Emlen and Oring, 1977). This results in males being subject to intense selection pressure in attempting to secure matings. Males generally use one of three methods to obtain females: stationary calling; satellite behaviour and opportunism (Howard, 1978a). Stationary calling is by far the most common tactic employed. Males call to defend territories or individual distances and to attract females. Satellite males do not call and do not defend an area. They remain close to calling males and attempt to intercept females attracted by the territory-holder. Opportunistic males call from specific sites but do not defend these areas.

Male *A. delicatus* employ stationary calling and satellite tactics. This chapter examines the variation in mating success within and between these alternative methods.

### 6.1.2 Mating Success of Calling Males

Variation in male mating success has received considerable attention in studies of anuran breeding choruses. The focus of earlier studies of male attributes that may influence mating success was on male size (Dyson, 1986; Howard, 1978a; Ryan, 1980; 1983; Whitney and Krebs, 1975b). More recent studies have attempted to identify other

factors that predict mating success, e.g. call characteristics (Fellers, 1979b; Gerhardt, 1987; Klump and Gerhardt, 1987; Sullivan, 1987); age (Howard, 1978; Wilbur et al., 1978); changes in the number of call notes (Schwartz, 1986; Wells and Bard, 1987); calling persistence (Gerhardt, 1987, Jacobson, 1985; Woodward, 1982); call site characteristics (Brenowitz et al., 1984; Wells and Schwartz, 1984); call site fidelity (Gerhardt et al., 1987; Telford, 1982); spacing behaviour (Dyson, 1989) and call timing (Dyson, 1989; Schwartz and Wells, 1984).

It is important to recognise that a correlation between mating success and a particular male trait may be accounted for by:

* active female choice of male quality (Fairchild, 1984; Ryan, 1982; Wilbur et al., 1978);
* active female choice of male resources (Howard, 1978; Wells, 1977a);
* passive female selection in relation to male-male competition (Greer and Wells, 1980; Telford and Dyson, 1988; Whitney and Krebs, 1975a);
* passive female selection in relation to male audibility and/or locatability (Arak, 1983b; Capranica and Moffat, 1975; Feng, 1981);
* male-male competition alone (Arak, 1983b; Howard and Kluge, 1985; Sullivan, 1983)

or a combination of these factors.

### 6.1.3 Satellite Male Behaviour

Satellite behaviour has been reported in numerous anuran species. In some, it appears that the males are waiting for call sites to be vacated (Arak, 1988a; Robertson, 1986). More commonly, satellite males appear to wait for females to approach their calling neighbour and then attempt to intercept and secure a mating (Arak, 1988a; Perrill, 1984; Sullivan, 1982). In many species (although not all), it is the smaller males that adopt the satellite tactic (Arak, 1988a; Gerhardt et al., 1987; Howard, 1984; Robertson, 1986a). It is possible that small size influences a male's ability to secure a call site (Howard, 1984), or his ability to sustain energetically expensive calling behaviour (Gerhardt et al., 1987). It is also possible that small males have weak advertisement calls and would have

a higher probability of mating by adopting the satellite tactic (Arak, 1988b).

In the majority of anuran species, males switch between calling and satellite behaviour (Arak, 1988a; Perrill, 1984; Robertson, 1986). Shifts from one tactic to the other are thought to be due to changing energetic costs of resource defence and mate locating strategies (see Dyson, 1989). This may be associated with density dependant changes in the intensity of intermale competition (Dyson, 1989).

### 6.1.4 Mating Success of Satellite Males

In some species, the mating success of satellite males is lower than that of callers (Arak, 1988a; Dyson, 1989; Howard, 1978); but equal in others (Gerhardt et al., 1987; Perrill et al., 1978; Sullivan, 1982). If the two mating tactics have unequal pay-offs, they may be maintained if the alternatives are the optimal solutions for different individuals (Arak, 1988b; Maynard-Smith, 1975). If the pay-offs are more-or-less equal, the alternative tactic would reduce the selection intensity on characters that might otherwise be correlated with fitness (Arak, 1988b).

### 6.1.5 Aims

In this chapter, I examine the relative success of the two mating tactics employed by A. delicatus males. The following questions were addressed:

1) Is there variation in calling males' mating success?
2) What morphological and/or behavioural traits correlate with mating success?
3) Is there size or mass assortative mating?
4) What is the frequency of the two mating tactics?
5) What is the relative effectiveness of the alternative tactics?
6) Are satellite males waiting for call sites to be vacated or do they attempt female interception?
7) Do morphological/behavioural traits determine the tactic employed?

8) Do satellite males select larger callers as target males?

9) Are males consistent in the mating tactic employed or do they switch between tactics?

## 6.2 METHODS

The work was conducted on caged populations. The advantages of examining a caged population were two-fold: (i) it prevented males from moving to other breeding sites, so confounding chorus attendance data; and (ii) the possible influence of sympatric species was eliminated and presented the subjects with the limited sonic complexity of the small group of conspecifics being examined.

### 6.2.1 Male Mating Success

A total of 48 males was monitored, each for a period of 5 nights, during October - February 1989/90. The nightly choruses contained 5 - 8 calling males and 0 - 4 satellites. Observations were made between 20h00 and 22h30 to avoid the possible bias of time of night. Males were individually bordered on a hind limb, and mass and snout-vent length (SVL) were recorded. Male mass was measured using a Mettler PE 1600 digital balance, and individuals were first submerged in water for 10s and blotted dry. To avoid the confounding effect of egg mass, females were measured after oviposition. (It is possible that some females still carried eggs, see pp.139. Close examination of females renderred this unlikely; however, it cannot be discounted as a possible source of error). A recording of each caller's advertisement call was made using a Sony TCD 5M recorder and a Sony EMC-16T microphone. The following data were recorded for each male:

1) Nearest neighbour distance(NND): the distance between a subject and his nearest calling neighbour
2) Call site height(CSH): the vertical distance between the subject and water level
3) Presence and tactic: active participation as opposed to remaining on the cage walls where the frogs spend the days; and the tactic employed (calling or satelliting)
4) Satellite neighbour: the presence or absence of a satellite male associated with the calling subject

5) Call site fidelity (CSF): positive if the male was within 20cm of his previous night's call site

6) Aggression: the number of aggressive vocal interactions by the subject during the period 20h30 - 21h30

7) Mating success: females were individually released into the chorus from a central point 1m away from the pond. Males that went into amplexus were given a +1 score.

Advertisement call recordings were analysed on a Uniscan II sound spectrum analyser in the frequency range 0 - 10kHz. The mid-point between the upper and lower emphasised frequency of the zip call was measured.

Statistical analysis

Statistical analyses for calling and satellite males were done separately. Spearman's Rank Correlation Coefficients were calculated for all variable combinations. Three-variable Partial Correlations (with the effect of the number of nights spent calling partialled out) were conducted for mating success vs. all other variables. A multiple Step-wise Variable Selection Regression was conducted on all variables to obtain a model with the smallest set of variables that significantly influence mating success.

6.2.1.1 Verification from the natural breeding area

Unpaired males and amplexing pairs were captured from the natural breeding areas. The SVL and mass of each male was measured as above. Spearman's Rank Correlation Coefficients were calculated for the mass and SVL readings of the males and females constituting pairs. A Mann-Whitney U test was performed on paired and unpaired males with respect to mass and SVL.

6.2.2 Satellite Behaviour

Four approaches were taken in investigating this phenomenon:

i) Thirty six silent males located within 20cm of a calling male were observed over a

five-night period during the 1987 - 1988 breeding season. Their position relative to callers, body posture, calling activity (if any), aggressive interactions (if any), behaviour on the arrival of a female and mating success were recorded.

ii) Twenty nine male removal experiments were conducted in which the calling male was removed and the subsequent behaviour of the satellite recorded. This work was conducted during the 1987/88 breeding season.

iii) The SVL of 38 callers and their associated satellites was measured at the natural breeding site during the 1987/88 and the 1988/89 breeding seasons. The SVL of males with satellites ($n = 18$) and those without satellites ($n = 14$) was measured and compared using Mann - Whitney U tests.

iv) The 11 satellites included in the mating success experiment (see above) were analysed with respect to mating success, chorus attendance, aggressive interactions and nearest neighbour distance. (Call site height and call site fidelity were dependant on the associated caller and were not statistically analysed).

## 6.3 RESULTS

### 6.3.1 Male Mating Success

Mating success over a five night period varied widely ($\bar{x} = 1.2$ matings; $SD = 1.33$; range = 0 - 4; $n = 31$). From Table 6.1 it is clear that there were a large number of significant correlations between variables. Note that call mid-frequency correlated with SVL and mass, and mass and SVL correlated. Mating success correlated with calling persistence (the number of nights spent calling), and both of these variables correlated with NND, call site fidelity and the presence of associated satellites.

The Three-Variable Partial Correlation analysis (see Table 6.2) indicated that when the effect of calling persistence is eliminated, mating success did not correlate with any of the other measured variables. Similarly, the Step-wise Multiple Regression analysis (see Table 6.3) shows that it is only calling persistence that significantly influences mating success, explaining 57% of the variance in mating success. All other variables (when forced into the model) explain only a further 11% of the variance. The remaining

variance in mating success (38%) could be explained by either stochastic factors or unmeasured parameters.

There was a large amount of variation in calling persistence ($\bar{x}$ = 3.03 nights; SD = 1.38; range = 1 - 5 ; n = 31). The data were then re-examined in order to determine if any of the measured parameters explained this variability in calling persistence. Partial correlations on all variables were conducted. The results (see Table 6.4) indicated that the variability in calling persistence correlated strongly with both mating success and call site fidelity. This is not surprising since both of these characters are summed nightly. There was also a significant correlation (although weaker) between calling persistence and NND. Since there was no correlation between mating success and NND (r = 0.02), this correlation may have resulted from the obvious relationship between call site fidelity and NND. If males display call site fidelity, their NNDs would be expected to remain fairly constant.

TABLE 6.1

Spearman's Correlation Coefficients for all variable combinations for calling A. delicatus males (n = 31). Significance levels in parentheses.

| | CF | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| NNC | 0.21 (0.25) | NNC | | | | | | | |
| MS | 0.29 (0.28) | 0.84 (0.00) | MS | | | | | | |
| SVL | 0.77 (0.00) | 0.25 (0.17) | 0.16 (0.37) | SVL | | | | | |
| MASS | 0.39 (0.03) | 0.34 (0.06) | 0.33 (0.07) | 0.58 (0.00) | MASS | | | | |
| AGG | -0.12 (0.50) | 0.11 (0.54) | -0.41 (0.82) | 0.14 (0.44) | 0.10 (0.57) | AGG | | | |
| NN | 0.29 (0.11) | 0.65 (0.00) | 0.62 (0.00) | 0.34 (0.06) | 0.21 (0.24) | -0.37 (0.84) | NN | | |
| SN | -0.06 (0.75) | 0.36 (0.05) | 0.39 (0.03 | 0.12 (0.53) | 0.12 (0.52) | -0.33 (0.86) | 0.29 (0.12) | SN | |
| CSF | -0.12 (0.53) | 0.72 (0.00) | 0.56 (0.00) | 0.04 (0.84) | 0.34 (0.06) | 0.24 (0.18) | 0.44 (0.02) | 0.23 (0.21) | CSF |
| CSH | 0.20 (0.29) | -0.21 (0.25) | -0.14 (0.45) | 0.22 (0.23) | 0.33 (0.08) | -0.17 (0.34) | -0.40 (0.03) | -0.17 (0.35) | -0.07 (0.71) |

NNC = number of nights called
SVL = snout to vent length
NN = nearest calling neighbour
CSF = call site fidelity
CF = call frequency
MS = mating success
AGG = aggressive interactions
SN = satellite neighbour
CSH = call site height

TABLE 6.2

Three-Variable Partial Correlation Coefficients (with the number of nights spent calling partialled out) for mating success vs. other measured variables for calling *A. delicatus* males (n = 31; DF = 28).

| variable | r | R | P |
|---|---|---|---|
| mass | 0.095 | 0.515 | >0.05 |
| aggression | 0.149 | 0.811 | >0.05 |
| NND | 0.183 | 1.002 | >0.05 |
| call site fidelity | 0.112 | 0.661 | >0.05 |
| SVL | 0.096 | 0.578 | >0.05 |
| call mid-frequency | 0.041 | 0.980 | >0.05 |
| satellite to him | 0.179 | 0.980 | >0.05 |
| call site height | 0.071 | 0.383 | >0.05 |

TABLE 6.3

Stepwise Variable Selection Multiple Regression analysis for variables affecting mating success of calling A. delicatus males (dependent variable = mating success).

| | Part. Corr. Coeff. | Part Reg. Coeff. | F | P |
|---|---|---|---|---|
| Variables in model | | | | |
| calling persistence | 0.76 | 0.73 | 40.15 | 0.00 |
| Variables not in model | | | | |
| call mid-frequency | 0.12 | (0.84) | (4.17) | (0.05) |
| SVL | 0.02 | (-0.81) | (0.51) | (0.49) |
| mass | 0.02 | (0.12) | (0.07) | (0.79) |
| aggression | 0.32 | (-0.25) | (2.68) | (0.11) |
| NND | 0.19 | (0.00) | (0.29) | (0.60) |
| satellite to him | 0.26 | (0.21) | (2.04) | (0.16) |
| call site fidelity | 0.09 | (0.02) | (0.00) | (0.95) |
| call site height | 0.06 | (-0.01) | (0.51) | (0.49) |

Figures in parentheses indicate statistics for each of the excluded variables when included into the model.

Multiple $R^2$ adjusted = 0.57.

TABLE 6.4

Partial Correlation Coefficients for the number of nights spent calling and all other measured variables for calling A. delicatus males (n = 31; DF = 28).

| variable | part. corr. coef. | P |
|---|---|---|
| call mid-frequency | -0.04 | >0.05 |
| mating success | 0.56 | <0.01 |
| SVL | -0.05 | >0.05 |
| mass | 0.16 | >0.05 |
| aggression | 0.22 | >0.05 |
| NND | 0.31 | <0.05 |
| satellite to him | 0.05 | >0.05 |
| call site fidelity | 0.40 | <0.01 |
| call site height | 0.06 | >0.05 |

6.3.1.1 Verification from natural breeding site.

Paired and unpaired males collected in the wild did not differ in either SVL or mass (Table 6.5). Similarly, there was no correlation between mass or SVL of males and femal. constituting naturally formed pairs (Table 6.5). In summary, there was no size or mass assortative mating, and mating was random in these .espects.

TABLE 6.5

Size measurements and statistics for naturally-captured A. delicatus males and amplexing pairs.

| | $\bar{x}$ (SD) unpaired males (n = 56) | $\bar{x}$ (SD) paired males (n = 25) | $\bar{x}$ (SD) paired females (n = 25) | U(P) paired (n = 25) & unpaired (n = 56) males | r(P) paired males and females (n = 25) |
|---|---|---|---|---|---|
| SVL | 1.90 (0.08) | 1.88 (0.08) | 2.22 (0.13) | 1.28 (>0.1) | 0.25 (>0.1) |
| mass | 0.33 (0.05) | 0.35 (0.04) | 0.51 (0.06) | 1.32 (>0.1) | 0.05 (>0.1) |

6.3.3 Satellite Behaviour

i) Of the 36 satellites observed in the field, 24 (67%) remained silent over the entire five night period. The mean distance between satellites and their associated callers was 9.3cm (n = 11). Satellites were found only in choruses with more than 6 males, and no aggressive interactions involving satellites were observed. No satellites were observed to mate, although on 12 occasions satellite males attempted to clasp approaching females. All such attempts failed. Satellites also attempted to displace males from amplexus (n = 7), but were also not successful. Satellites adopted a "flat" posture with the head held against the substrate (as opposed to the "upright" posture of callers, where the head and chest are held off the substrate).

ii) Of the 29 satellites in which associated callers were removed, 14 (48%) moved to within 20cm of a second calling male shortly after the removal and continued behaving as satellites. Nine (31%) remained motionless and did not alter their posture or call. The other six (21%) remained in the same position and called at irregular intervals. Each of these six males adopted the "upright" posture, even when not calling.

iii) Satellite males were significantly smaller than calling males (x SVL of callers = 2.0 cm, n = 38; x SVL of satellites = 1.8cm, n = 38; U = 4.05; P < 0.01). Calling males who had associated satellites (n = 18) were indistinguishable from those who had no satellites (n = 14) with respect to SVL (U = -0.21; P = 0.8); mass (U = -0.69; P = 0.5) and call mid- frequency (U = 0.78; P = 0.43).

iv) During the observation periods for the 11 satellite males included in the mating

success experiment, no satellite was found to mate (as opposed to the 58% of calling males which achieved amplexus). Similarly, no satellite was found to engage in a vocal aggressive interaction (as opposed to the 68% of callers who gave encounter calls). Chorus attendance was conspicuously lower for satellite males than for callers, with satellites a mean of 2.2 nights in the chorus (out of a possible 5 nights); and callers spending a mean of 3.0 nights. The mean distance between callers and their associated satellites was 8.0 cm (n = 11).

## 6.4 DISCUSSION

### 6.4.1 Male Mating Tactics

Stationary calling is the most common mating tactic employed by A. delicatus males. Seventy-four percent of males attending the chorus adopted this tactic. Of the remaining males, 21% called once the resident male was removed and so appeared to be waiting for call sites to be vacated, 31% were non-active males and 48% displayed satellite behaviour in which female interception and/or male displacement were attempted. The majority of males employed a fixed mating tactic over the five night observational period.

### 6.4.2 Mating Success of Calling Males

Although there was variability in calling males' mating success, there was no evidence of size assortative, mass assortative, or size dependent mating. As in many similar studies on anurans, variation in male mating success was largely explained by

the variability in the amount of time spent calling (Arak, 1988a; Dyson, 1989; Gerhardt et al, 1987; Jacobson, 1985; and others). Some studies have indicated that increased presence at the breeding site is associated with large male size (Dyson, 1989; Morris, 1989; Gatz, 1981; Sullivan, 1983), but there was no such relationship in A. delicatus. It remains to be tested whether mating itself induces males to call on subsequent nights.

Although a large number of potential correlates of mating success were examined, they explained very little of the variation. There was no evidence of female selection for increased body size, spacing or call site fidelity, nor for any particular call site height, call frequency or level of aggression. (That is not to say that such selection pressures do not exist, they may be important in male-male competition).

6.4.3 Mating Success of Satellite Males

As in many other anurans, satellite males were smaller than callers (Arak, 1988b; Howard, 1984; Fairchild, 1984), and attended the chorus less regularly (Morris, 1989). There was no difference between target and non-target males, which would be expected since all callers have an equal chance of mating on any particular night, and there would be no advantage in satelliting the larger males of the population. On no occasion were satellite males observed to mate. Attempted interception of females and displacement of amplexed males was always unsuccessful.

6.4.4 Conclusion

Fifty eight percent of the caged calling males mated. Although this figure is artificially high (the number of females released into the cage was disproportionately large to the natural nightly operational sex ratio), it is nonetheless in stark contrast to the fact that no caged satellite male was observed to mate. This provides strong evidence of selection on males to call (as opposed to satellite). Since phenotypic characteristics of callers did not predict mating success, it is likely that, if satellites called, they would increase their probability of mating. It is possible that these males were energetically incapable of calling (possibly due to their small size), or incapable of calling for some other reason (possibly due to underdeveloped gular pouches that may be age related.

The fact that satellite males were never observed to mate (in neither the cage nor the natural breeding area), raises the question of this behaviour can justifiably be termed a "mating tactic". However, the behaviour of these males was comparable to that found in satellites of many other species and suggests that it is a mating tactic, however unsuccesful it may be. The relatively high frequency of satellite behaviour, together with the extremely low payoff, makes it difficult to explain why this tactic persists. The costs of satellite behaviour are presumably low in terms of energetic output (the males do not call), risk of predation (the males are generally stationary) or loss of foraging time (nocturnal foraging was never observed). I suggest that the tactic persists because it is a low cost - low reward behaviour, and may be the optimal solution for these males (see Maynard- Smith, 1975). This is not unique in anurans. Howard (1978) found that the

mating success of satellite males was also extremely low in **Rana catesbeiana** (2 out of 73 satellite males were successful).

In conclusion, it is apparent that males can increase their probability of mating by calling regularly, but within a single night a calling male's probability of mating may depend largely on chance rather than morphological or behavioural traits.

# CHAPTER SEVEN

# MATING AND NESTING BEHAVIOUR

## 7.1 INTRODUCTION

### 7.1.1 Anuran Mating Behaviour

Anurans have a surprising diversity of reproductive behaviours (Wells, 1977a). Social interactions occur almost exclusively during the breeding season (Wells, 1977b) when breeding aggregations, containing many individuals, form in a relatively small area (Arak, 1983a). In some species courtship is simple but in others there are elaborate interactions between males and females involving visual, tactile and auditory signals before pair-formation (Wells, 1977a). Several anuran species have been reported to give calls that are distinct from the normal advertisement call, when females approach (see Wells, 1977a). Heinzman (1970) called these "excitement" calls and Pengilley (1971) called them "courtship" calls. **Afrixalus delicatus** has a call that is distinct from the two-part call and which is given when females are near (Telford, 1982). I will refer to this vocalisation as the "rapid" call. Wells (1977a) pointed out that there is little evidence to suggest that males can distinguish the sex of an approaching individual. Close-range courtship signals occur in many insects and may provide additional directional cues to females at close range (Alexander, 1975). Accurate descriptions of mating behaviour have been made for only relatively few anuran species (Salthe and Mecham, 1974). Males lead females to oviposition sites in some species (e.g. Crump, 1972; Davis, 1941; Silverstone, 1976), but females lead males in others (Silverstone, 1973). The pair may inspect many oviposition sites prior to mating. This phase of courtship generally lasts from a few minutes to several hours (Wells, 1977a). In

**Eleutherodactylus coqui**, pairs may stay together for several days and visit many potential oviposition sites before mating (Drewry, 1974).

**Afrixalus delicatus** displays normal prolonged breeding behaviour. Courtship and mating behaviour were observed and documented for this species and are reported here. The structure and function of the rapid call was also examined.

### 7.1.2 Terrestrial Breeding

Anuran specialisations in oviposition show a trend towards the withdrawal of early development from water (for reviews see Lutz, 1948; Poynton, 1964; Salthe and Mecham, 1974; van Dijk, 1971). The emancipation of non-feeding and larval stages from free environmental water is viewed as an adaptive response to predation (Poynton, 1964; Tihen, 1960; Van Dijk, 1971). The existence of an aquatic larval stage and a terrestrial adult stage in anurans has the disadvantage of exposing the individuals to two successive sets of predators. The evolution of terrestrial breeding would partially overcome the problems of predation on the early developmental stages.

Nest construction below and above water occurs in a number of species, e.g. **Hyla faber, Pseudophryne australis** (Salthe and Mecham, 1974); **Chiromantis xerampelina, Hyperolius pusillus** (Povnton, 1964); **Afrixalus delicatus** (Wager, 1956): **Phyllomedusa** (Salthe and Mecham 1974); some Hylidae (Lutz, 1948). In Hylidae, **Phyllomedusa** and in **Afrixalus**, oviposition occurs on vegetation and the offspring spend part of their development in a leaf nest.

Wager (1956) was first to describe the nesting behaviour of **A. delicatus** : "The eggs are stuck to a leaf beneath [or above] the water, and the edges are then bent over, drawn together and glued in place, making the eggs invisible and protecting them until the tadpoles are formed... Some ten days later the tadpoles, with very long external gills, wriggle out of the nest and into the water." For the nests above water it is the very adhesive oviducal secretion that is used to glue the opposing leaf faces together (Passmore and Carruthers, 1979) and this seal is evidently loosened by rain or moisture

in the air (Schiotz, 1963). The folded leaf acts as a protective device which could overcome the difficulties of exposure to the elements and the transpiration of the nest leaf may maintain a humid microenvironment for the early stages of development (van Dijk, 1971). A description of nest-building behaviour and nest characteristics in **A. delicatus** was undertaken and is documented here.

### 7.1.3 Clutch Size and Egg Characteristics

Clutch size is affected by the mode of reproduction. As the reproductive mode becomes more specialised, the clutch size decreases (Duellman and Trueb, 1986). A decrease in egg number is often offset by parental care and the fact that the young are removed from aquatic predation (Crump and Kaplan, 1979; Salthe and Duellman, 1973; Simon, 1983; Townsend et. al., 1984). Futhermore, as the female body size increases within any mode of reproduction, clutch size also increases (Crump, 1974; Duellman and Trueb, 1986; Salthe and Mecham, 1974). Larger species are obviously able to produce and carry more eggs than smaller species. There is also a trend towards a decrease in egg size with an increase in the size of the clutch (Duellman and Trueb, 1986). In species that have some form of terrestrial breeding, the eggs are often large, non-pigmented and few in number (Inger, 1958). The fact that eggs are large suggests that the larvae may complete part or all of their development within the egg capsule (Brown, 1952).

Salthe and Mecham (1974) review the almost perfect correlation between exposed egg sites and the presence of melanin on the animal hemisphere of the eggs (also reported by Duellman and Trueb, 1986; Martin, 1967). The discrepancies in the correlation between hidden egg sites and the absence of melanin, they claim, are attributable to the recent adaptations to current sites of development, i.e. the melanin is in the process of being lost. Experimental evidence shows that the melanin functions in the resistance to UV irradiation as well as the absorbtion of heat (Salthe and Mecham, 1974). Consequently the eggs of species that construct leaf nests would not require melanin since they have overcome these problems in alternative ways, i.e., they are protected from UV irradiation and heat absorption by the leaf nest. **Afrixalus delicatus**

is reported as having large, non- pigmented eggs that are few in number (Passmore and Carruthers, 1979; Schiotz, 1963; Wager, 1956). The clutch size, egg characteristics and hatching success were documented for this species and are reported here.

7.1.4 Polyandry

Anuran mating systems are characterised by an operational sex ratio skewed towards males (Emlen and Oring, 1977; Woodward, 1984), the absence of pair bonds (see Wilson, 1980), and the lack of parental care in most species (McDiarmid, 1978; Wells, 1977a, 1981). An operational sex ratio skewed towards males indicates that there are a large number of sexually active males coupled with a low number of fertilisable females at any given time. Polygyny would be a logical prediction under these conditions and is a widespread phenomenom in anuran species. The parental investment by the male is small; this leads to the possibility that a low percentage of males could account for a high percentage of the fertilisations in the population (Emlen, 1976).

The fact that most anuran offspring do not require parental care frees the parents of post-copulation responsibility and potentially allows them to immediately pursue futher matings (this is particularly applicable to the male since sperm are easily replaceable, see Trivers, 1972). Polygyny would predictably be the most common mating pattern in anurans.

The female's parental investment is substantially larger than the male's since she invests far more stored energy in each gamete (Trivers, 1972). A female usually needs to copulate with only one male to fertilise all of her eggs, however she need not copulate with only one male unless mating with more than one incurs some cost to her (see Stacey, 1982). A single mating that produces inviable or sterile offspring would claim a large part of a female's reproductive effort. Polyandry may be a mechanism by which she ensures her clutch is fertilised by more than one male which may incidentally lead to an increased genetic diversity of offspring (Gladstone, 1979; Stacey, 1982).

A female mating with more than one male on the same or successive nights has never, to my knowledge, been reported in an anuran species. Females that mate more than once a season have been reported in numerous species (Howard, 1978a; Wells, 1977a). In these cases of muliple clutching, females develop additional egg clutches during the course of the breeding season, but each clutch is fertilised by a single male. There are reports of one male displacing another from amplexus (Arak, 1983a; Davies and Halliday, 1979; Howard and Kluge, 1985) but this usually occurs before egg deposition begins. However, if the female was releasing eggs when in amplexus with the first male and she then mated with the second, she would have, in effect, been polyandrous. However, since this would be due to chance rather than the female's choice, these cases cannot be considered true polyandry. True polyandry has, however, been observed in **A. delicatus** on several occasions and is reported here.

## 7.2 METHODS

The courtship and mating behaviour of **A. delicatus** was first observed under natural breeding conditions at Matatiele pan, one of the natural breeding areas (see pp. 8). These observations were extremely difficult to conduct as they involved standing in water for long periods of time and avoiding disturbing the animals with the flashlight. It was therefore necessary to study a caged population of animals. The cage was sufficiently large and presented a habitat sufficiently similar to the natural breeding area to allow the assumption that the animals were not affected by the surroundings. The cage was illaminated with a single 60 W red light bulb suspended 1,5 m above water level. My presence in the cage did not disturb the animals but allowed easy observation of breeding behaviour.

### 7.2.1 Rapid Call

Recordings of rapid calls of thirteen males were made in the field during 1984, 1985, 1986 and 1988. The recordings were made on a Sony TC-185 SD tape recorder with an Adastra electret condenser microphone or on a Sony TCD5M tape recorder and a Sony ECM-16 T electret condenser microphone. Air temperatures ranged between 20 - 26 C.

The recordings were analysed on a Uniscan II sound spectrum analyser within the frequency range 0 - 10 kHz. The upper and lower limits of the emphasized frequency range were measured as well as the call duration and intercall interval. The mean and range were calculated for each parameter. A sonogram of a single typical rapid call was made on a Kay model 7800 spectrum analyser.

### 7.2.2 Mating and Nest-building Behaviour

Calling males were collected from the natural breeding areas and transported to the cage. Once a stable chorus of calling males was established (usually after two nights), gravid females were released individually into the cage. Twenty-four females were observed and their behaviour documented. This included an account of the phonotactic approach of the female to the calling male, amplexus, the time a female takes to go into amplexus and their behaviour during this time. The duration of amplexus and the interactions between the pair and individual calling males were documented. Nesting behaviour was also observed and included an examination of the plant species used for nests, the number of nests built by each female and the time taken to build each nest. Observations were made nightly from 19h00 to approximately 04h00 during the 1984, 1985 and 1986 breeding seasons. Accurate time measurements were taken using a stopwatch.

### 7.2.3 Nest Characteristics

The nests were observed for a maximum of seven days after their construction. The time taken for the nests to open ($n = 12$), the stage of development of the tadpoles when leaving the nest ($n = 12$) and the effect of rain on nest opening ($n = 7$) were studied. Nests found in Matatiele pan ($n = 18$) were described with respect to their position relative to the open water and surrounding vegetation.

### 7.2.4 Oviposition Site Requirements

Fifty-one plants providing oviposition sites were present in the cage. These carried 251 leaves of varying shapes and sizes which provided a wide range of possible nest sites. Each leaf was measured with a ruler to the nearest mm, using the following parameters: width of leaf at widest point; length of leaf from stem to apex; and the height of leaf above water level.

The oviposition site requirements were established by allowing pairs to construct nests and later opening the nests and measuring the leaves used in their construction. A total of 56 nest leaves was measured using the same parameters as above. A t-test for the difference between the sample mean and the population mean was conducted on the data for each leaf parameter. This experiment was conducted during January and February 1985.

### 7.2.5 Egg Characteristics and Hatching Success

During the day following mating, the nests were examined. A total of 60 nests was opened and the number of eggs in each were counted. Thirty two of the opened nests were placed individually in plastic containers of pondwater and the number of larvae to hatch from each nest was counted. The eggs were examined for the presence of melanin and the diameter of 15 eggs, each from a separate female, was measured with vernier callipers (although this did not provide an accurate measure, it allowed an estimate of ovum diameter). A further investigation was undertaken in order to determine the number of eggs deposited in the first and subsequent nests constructed by each of 15 females. The number of eggs deposited in each nest was compared.

An estimation of the mass of females' egg clutches was calculated by measuring the mass of gravid females before egg laying had occurred, and the mass of the females once all the eggs had been deposited. (see pp. 100 for methods of mass determination). Forty-two females were measured using a Mettler PE 1600 digital balance (accurate to the nearest 0.01 g). The difference between the two readings was used as an estimate

of the clutch mass. Correlation analyses (parametric and non-parametric) were performed on the data and clutch masses were plotted on a histogram and compared to a theoretical normal distribution.

### 7.2.6 Polyandry

For the experiments in which polyandry was examined, approximately 100 gravid females were collected over the three year period and released into the cage. After a female had mated, laid eggs and broken amplexus with a male, she was captured and examined for remaining eggs which were visible through the lateral and ventral body walls. If the female was still carrying eggs, she was captured, individually marked on the hind limb and placed back in the cage. The marked females (n = 15) were observed for a maximum of four successive nights. Each male that mated with a marked female was captured and marked upon breaking amplexus. Females were only removed from the cage once I was satisfied that no eggs were being carried. This work was conducted during the 1984, 1985 and 1986 breeding seasons (October -February).

## 7.3 RESULTS

The observations of breeding at the natural pan gave an overview of natural mating behaviour. It also confirmed that the behaviour of the experimental animals was not affected by the conditions in the cage as there were no observable differences in behaviour between the animals in the cage and those in the natural pans. Female arrival at the pan was erratic and seemed to depend on a wide range of environmental conditions, probably the most important being rainfall. The majority of females were collected on nights during which a light drizzle fell. Low temperatures did not deter mating behaviour and pairs were found at a wide range of temperatures (16 - 27 C). Although calling began as early as 18h00, females were generally found after 21h00. The leaves of two plant species, Polygonum pulchrum and Ludwigia stolonifera play an important role in the breeding biology of A. delicatus. Males call from stationary positions on these leaves (see pp. 91) and oviposition and nest building occurs on these plants.

### 7.3.1 Rapid Calls

The rapid call is produced by males only when a female is in close proximity. The call is given at a rapid rate (intercall interval: $\bar{x} = 2.1$ s; range = 0.8 - 4.4 s; $n = 13$) for a short period (approximately 12 calls). The mean call duration is 0.2 s (range = 0.14 - 0.28 s; $n = 13$). The mean upper limit of the emphasised frequency range is 6.2 kHz (range = 5.9 - 6.4 kHz; $n = 13$) and the lower limit is 4.0 kHz (range = 3.6 - 4.2 kHz; $n = 13$). See Figure 7.1 and Table 7.1. The rapid call is distinct from the trill component of the two-part call (Table 7.1) but is structurally similar to the zip component. It covers a wider frequency range than either of these calls and the intercall interval is much shorter than that for the zip or trill (see Table 7.1).

### 7.3.2 Mating and Nest-building Behaviour

Twenty four gravid females were individually observed after their release into the cage. They often spent long periods of time (10 - 60 min) motionless. Females sat in characteristic "alert" postures with their heads horizontal and their forelimbs extended (see Figure 7.2). Although sideways head movements were common, females were not observed to look directly at calling males. Once a female began an approach to a calling male, her behaviour seemed to become more deliberate. She moved directly to the male in as near a straight line path as the vegetation allowed ($n = 24$). Females generally jumped from plant to plant and seldom ($n = 5$) moved into the water. In order to contact the male, females jumped onto the call site leaf and the male would immediately react by turning to the female and scrambling over or around her and grasping her within a very short time (too short to be accurately measured). The male ceased calling at this point. Amplexus was axillary, the male placing his fore-limbs behind and under the fore-limbs of the female (see Figure 7.3).

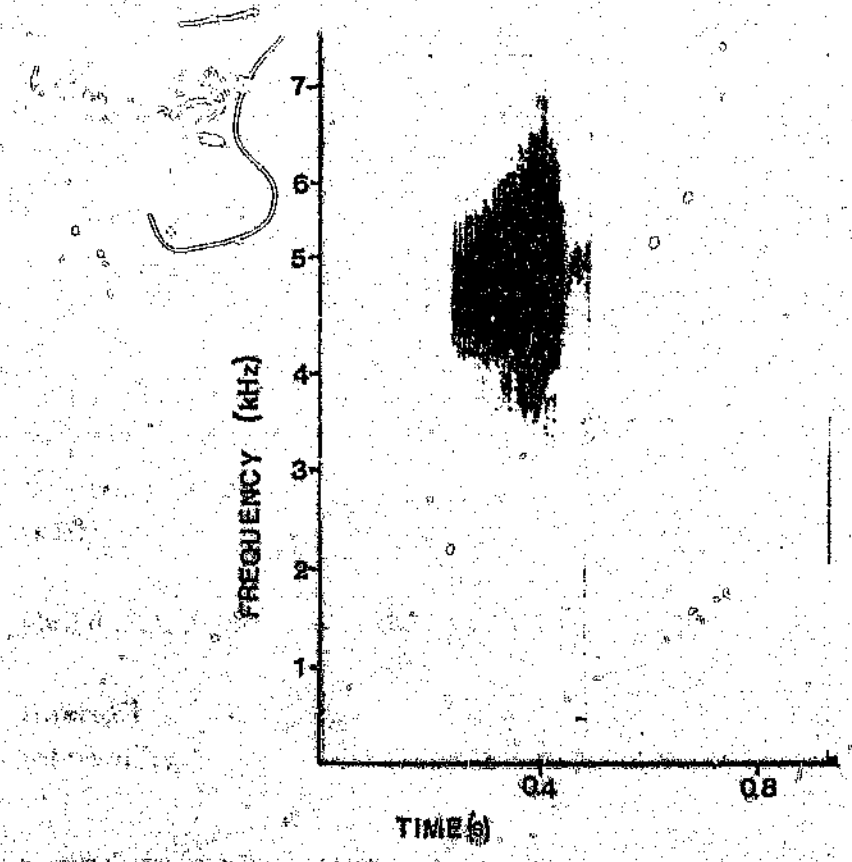



**FIGURE 7.1 Wide band (300 Hz filter) sonogram of the rapid call of A. dilicatus.**

TABLE 7.1

Comparison of zip, trill and rapid calls.

| | Rapid $\bar{x}$ (range) n = 13 | Zip $\bar{x}$ (range) n = 30 | Trill $\bar{x}$ (range) n = 30 |
|---|---|---|---|
| Upper limit of emphasised frequency range (kHz) | 6.2 (5.9-6.4) | 5.8 (5.4-7.0) | 5.7 (5.1-7.2) |
| Lower limit of emphasised frequency range (kHz) | 4.0 (3.6-4.2) | 4.4 (3.8-5.5) | 4.5 (3.5-7.2) |
| Call duration (s) | 0.2 (0.1-0.3) | 0.2 (0.1-0.3) | 3.4 (0.3-11.8) |
| Intercall interval (s) | 2.1 (0.3-4.4) | 23.2 (4.1-200.0) | 24.0 (0-90.0) |

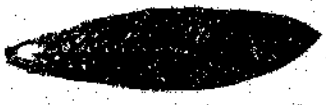


FIGURE 7.2 Female approach to a calling male.

The pair then moved around the vegetation, generally visiting surrounding plants. Presumably the weight of the male made it difficult for the female to jump between plants since the pair usually moved into the water and swam between neighbouring plants. The distance the pairs moved ranged from 20 - 150 cm ($\bar{x}$ = 63 cm; n = 24). During this stage of moving around, the pair was often harassed by calling males. On 15 occasions single males were observed following pairs from plant to plant and calling continuously. On 4 occasions a single male kicked at the paired male and initiated an aggressive interaction in which the paired male, still clasping to the female, kicked back at the interfering male. On no occasion did I observe a single male dislodge the paired male from the female. The time the pair spent selecting an oviposition site ranged from 7 - 70 min ($\bar{x}$ = 48 min; n = 24). During this period of oviposition site selection, it was the female who actively led the male. The male did not seem to "steer" the female in any direction, but rather passively followed her, using his hindlimbs only for balance and support. Once the oviposition site was selected, the amplexing pair positioned themselves on the tip of the leaf facing the stem. The female grasped the leaf margins with her fore- and hind-limbs and the male with his hind- limbs only. The weight of the pair forced the leaf into a vertical position. The leaf margins were pulled together by both partners as the eggs are laid along the centre of the leaf. The oviducal secretion around the eggs glued the leaf margins together. (see Fig. 7.4 and 7.5) The nest took form as the pair moved upwards towards the base of the leaf. On no occasion did the pair use the call site as an oviposition site and on only one occasion were the call and oviposition sites on the same plant. The time taken to build a nest varied considerably due to the variation in the number of eggs laid and the size of the leaf used. The time ranged from 7 - 36 mins ($\bar{x}$ = 19.2 mins; n = 12). After the first nest was built, the pair moved either onto another leaf of the same plant (n = 11)or onto a neighbouring plant (n = 7), and constructed a second nest. It was possible for the pair to break amplexus after the first nest was built, in which case the male began calling again and the female either left the breeding area or started approaching another calling male, (see pp. 139 for data). Females built 1 - 3 nests each ($\bar{x}$ = 1.75; n = 20). Pairs remained in amplexus for the duration of oviposition only ($\bar{x}$ = 198 min; n = 13). It is possible that females mated and constructed nests prior to their capture, thus individual females may construct more than the observed three nests.



LUDWEGIA STOLONIFERA



POLYGONUM PULCHRUM

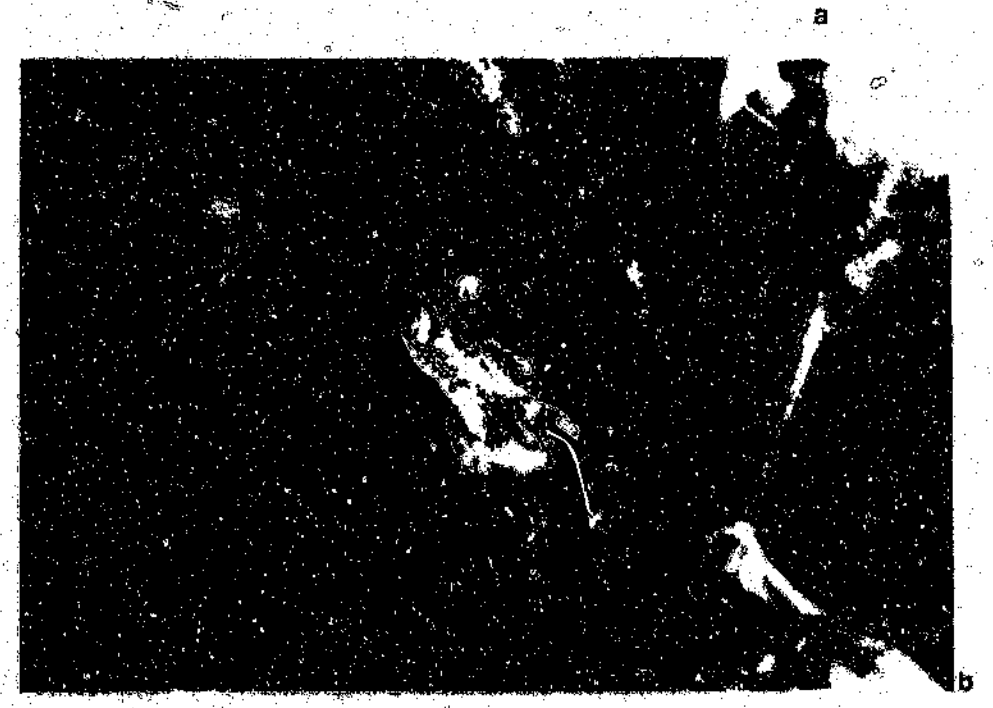



FIGURE 7.3 (a) The leaves of Polygonum pulchrum and Ludwegia stolonifera; (b) an amplexing pair.



FIGURE 7.4 Nest building behaviour.



FIGURE 7.5 (a) A complete nest and (b) an opened nest.

### 7.3.3 Nest Characteristics

In undisturbed nests it was found that it took 2.5 - 6 days for the embryos to leave the leaf nest, ($\bar{x}$ = 3.4; n = 12). Heavy rain affected the nest opening and caused the release of immature embryos into the water (n = 7). Light rain had a less immediate effect on the nests but generally loosened the seal and the nests opened shortly after the rain (within the next two days). Some nests were constructed with the glued leaf margin uppermost, and others with the midvein uppermost and the glued margins facing down. It was found that the nests with upward facing margins were more affected by rainfall since the rain drained off those nests that had the midvein upwards. When no rain occurred, the embryos developed inside the nest until their movement and increased size forced the nest open. The embryos were found to be long and "shark-like" as described by Pickersgill (1984), with terminal mouthparts (see Figure 7.6).

A total of 18 nests was observed and studied at Matatiele pan, 15 of which were found to be surrounded or partially surrounded by vegetation, mostly Polygonum pulchrum and Ludwegia stolonifera. The other three nests were in exposed positions with little or no surrounding vegetation. All nests were found in the eulittoral zone and were in the areas of the pan in which these two plant species occurred (see Figure 7.7).

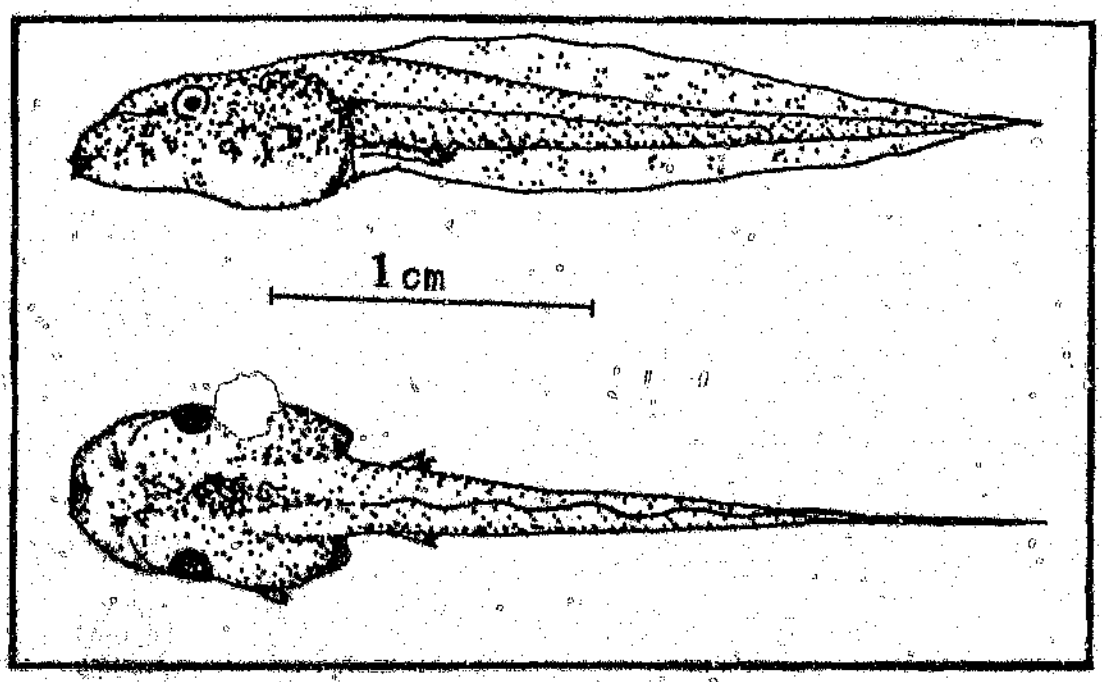



FIGURE 7.6 A. dulloatus tadpoles (after Pickersgill, 1984)

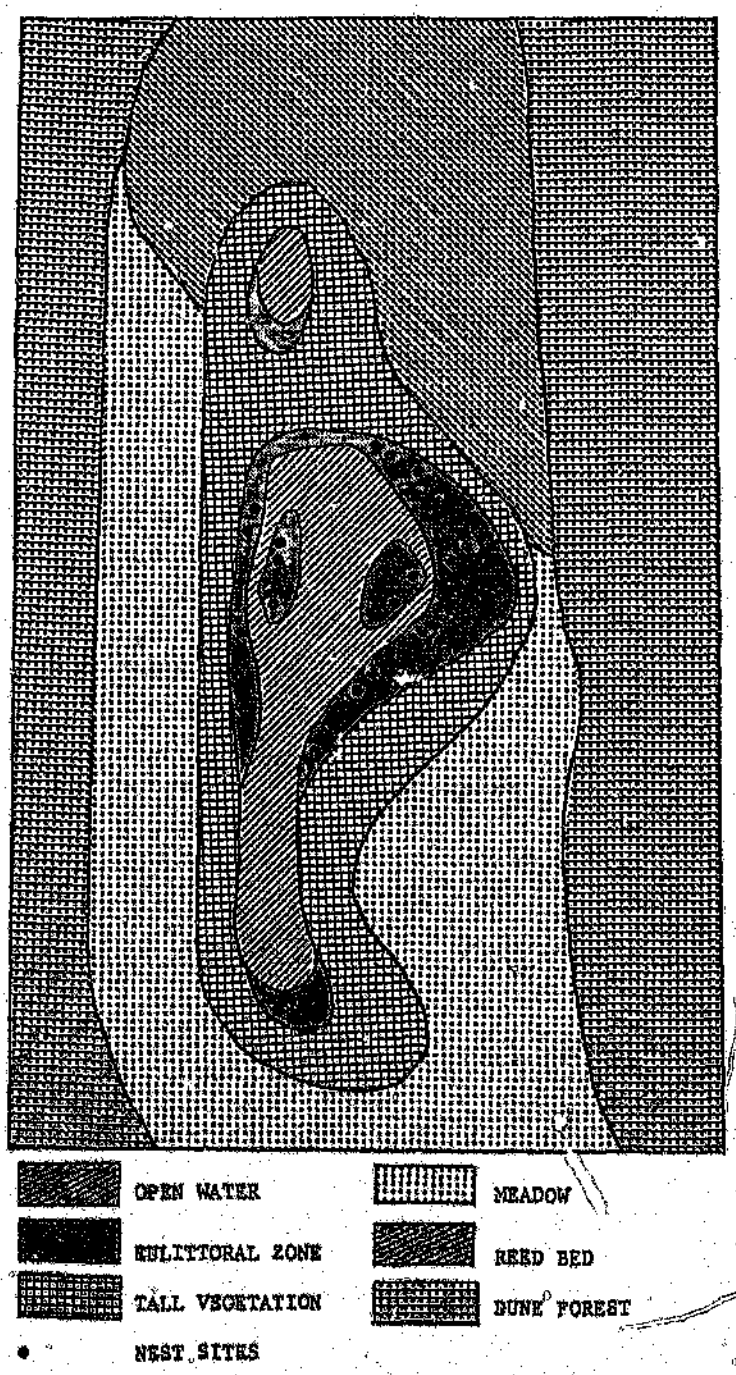
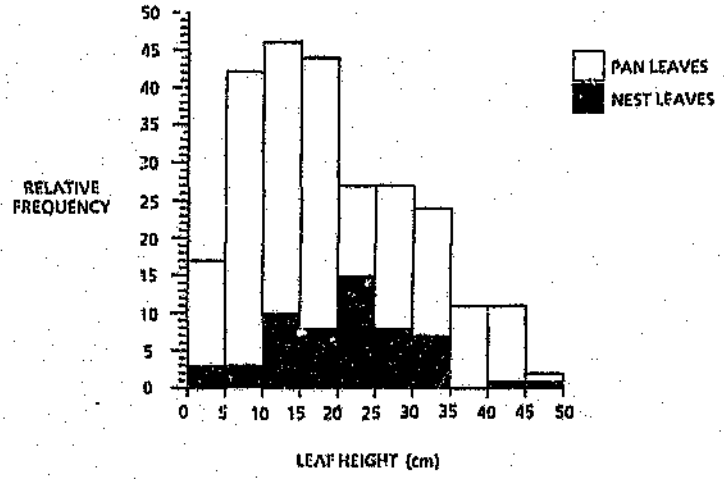


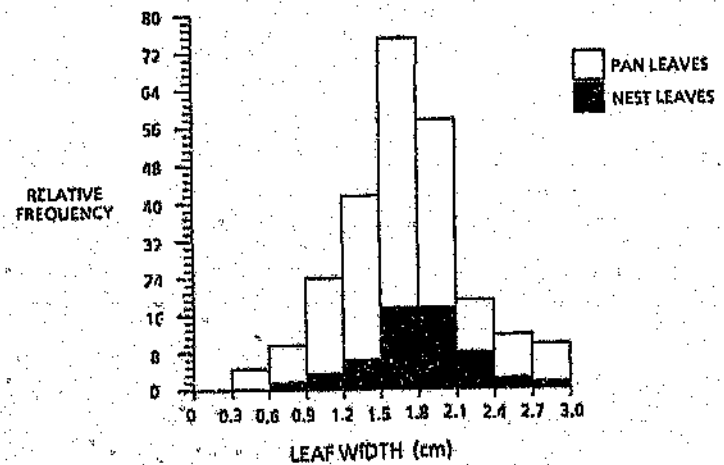

**FIGURE 7.7 Map of Matatiele pan showing areas of *Polygonum pulchrum* and *Ludwegia stolonifera* and the occurrence of *A. delicatus* nests.**

7.3.4 Oviposition Site Requirements

In the natural breeding area **Ludwigia stolonifera** is more common than **Polygonum pulchrum** (approximately 2:1) but there seems to be no preference for either plant species, (the ratio of nests was also approximately 2:1). The leaves of both plants are elongated and flexible and easily manipulated by the frogs during nest building.

There are certain oviposition site requirements for nest building in this species (Table 7.2). It was found that the leaves used in nest construction were selected on the basis of their width ($t = 1.89$; $P < 0.05$; $n = 56$) and length ($t = 4.09$; $P < 0.01$; $n = 56$). The shorter wider leaves were selected as oviposition sites. Neither the height of the leaf above water ($t = 1.22$; $P > 0.05$; $n = 56$) nor the leaf age ($t = 0.59$; $P > 0.1$; $n = 56$) were factors influencing the selection of an oviposition site, (see Figure 7.8).



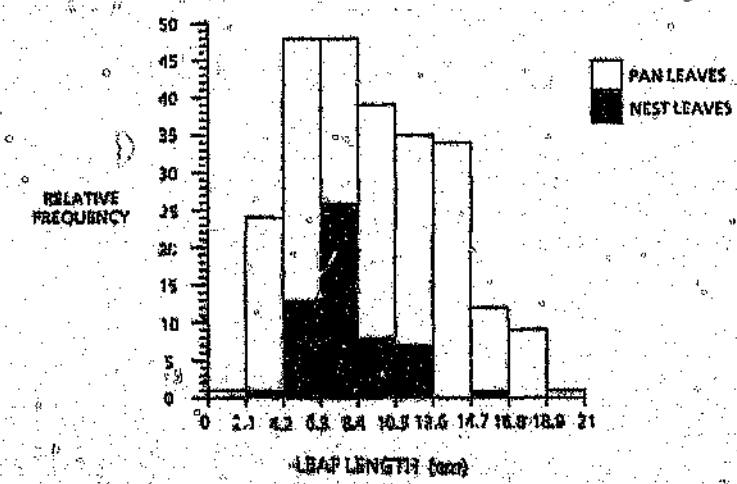




**FIGURE 7.8** Histograms of pan and nest leaf characteristics.

TABLE 7.2

Oviposition site requirements for A. delicatus.

| | Pan $\bar{x}$ | (SD) | Nest $\bar{x}$ | (SD) | t | P |
|---|---|---|---|---|---|---|
| Leaf length (cm) | 9.1 | (4.0) | 7.8 | (2.4) | 4.09 | <0.01 |
| Leaf width (cm) | 1.6 | (0.5) | 1.7 | (0.4) | 1.89 | <0.05 |
| Height of leaf above water (cm) | 16.9 | (10.9) | 20.4 | (9.8) | 1.22 | >0.05 (NS) |

### 7.3.5 Egg Characteristics and Fertilisation Success

The number of eggs laid in each nest varied from 1 to 89 ($\bar{x} = 35$; $n = 60$). The eggs were large (1.54 - 1.58 mm; $n = 15$), yellowish-white and lacked melanin in the animal hemiphere. The hatching success of the eggs was calculated for 32 nests (total of 1078 eggs). There was 100% hatching success for 19 of the nests and the mean hatching success was 94% (range = 0 - 100%). There was no significant difference in the number of eggs deposited in the first, second and third nests of each female ($F = 0.43$; $n = 15$; $P = 0.65$).

The estimated mass of an egg clutch ranged from 0.01 - 0.25 g ($\bar{x} = 0.08$ g; $n = 42$; SD = 0.06). There was a significant positive correlation between clutch mass and the mass of the female before egg deposition ($r = 0.53$; $n = 42$; $P < 0.05$; $r_s = 0.44$; $n = 42$; $P < 0.01$), with heavier females depositing heavier egg clutches. Since it was possible that the mass of the egg clutch was responsible for the additional mass of the female before egg deposition (and therefore responsible for this strong correlation), correlations were conducted on the data for female mass after egg deposition had occurred and clutch mass. These revealed non-significant correlations ($r = 0.37$; $n = 42$; $P > 0.05$; $r_s = 0.35$; $n = 42$; $P > 0.05$). From this it can be concluded that the mass of the female does not significantly affect the mass of the egg clutch she deposits. The clutch masses of 42 females are graphically represented in Figure 7.9. From this graph, it is clear that clutch masses are not normally distributed but rather fall into distinct categories.

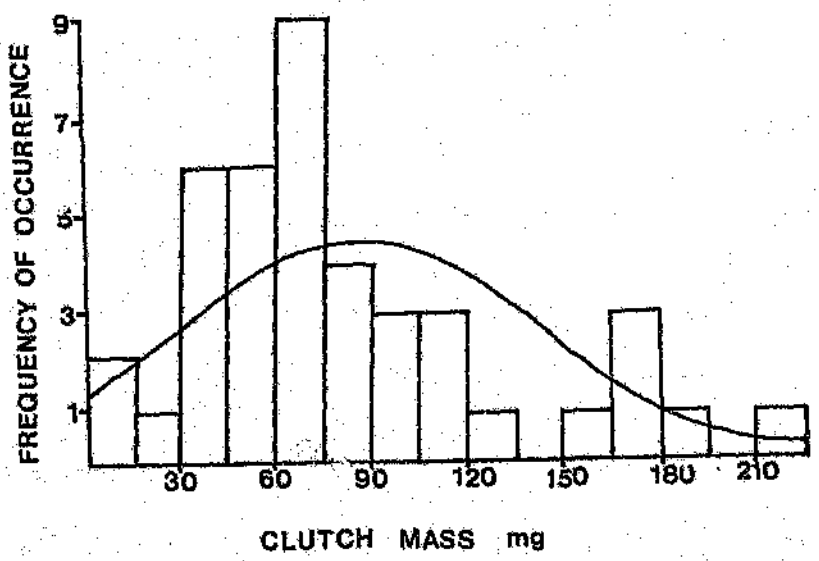



FIGURE 7.9 Distribution of egg clutch masses with normal curve overlaid.

### 7.3.6 Polyandry

Polyandry was observed on seven separate occasions. In the majority of cases (n = 5) females were observed mating with a male and laying eggs in one nest prior to breaking amplexus. The following night each mated with a second male and deposited eggs in a second nest. Amplexus was again broken and no mating occurred on the following two nights. One female mated and constructed a nest within 45 min of being placed in the cage. Amplexus was broken and after 30 min the female had gone into amplexus with another male and a second nest was built. Another female was observed mating with three males, one on the first night and one each on the third and fourth nights after release into the cage. On eight additional occasions I observed a pair breaking amplexus while the female still carried eggs. Although no further matings were observed, these eight females probably deposited additional eggs later.

## 7.4 DISCUSSION

The courtship behaviour of A. delicatus was found to be relatively simple and similar to the common prolonged anuran courtship behaviour as described by Wells (1977a), i.e., female arrival at the breeding site is asynchronous, resulting in heavily male-biased sex ratios on any one night; males use vocalisations to attract females who approach individual calling males with whom they initiate amplexus. Males produce a rapid call when females are nearby (approximately 5 cm). This call presumably acts as a close-range attraction and/or localisation signal. The rapid rate of the call could perhaps facilitate easy localisation of the male. The rapid call is structurally similar to the zip call and may be a modified zip that conveys a different message depending on the context (Wells, pers. comm.).

The behaviour of the female prior to amplexus is interesting in the light of Arak's (1983a) prediction that females would necessarily have to compare or sample several males if she is "choosing" a mate. Afrixalus delicatus females often remain motionless within the chorus before they finally approach and mate with a male. Their behaviour during this time may provide an opportunity for mate selection, or it may be a period

of stimulation during which time a female is "excited" to eventual response. It may also be indicative of the female searching for suitable oviposition sites prior to mating.

The juxtaposition of cloacae due to axillary amplexus would presumably increase the efficiency of fertilisation and may be partially responsible for the extremely high fertilisation success found in this species. Another factor affecting the fertilisation success may be the construction of leaf nests. The sperm and egg cells are restricted within the closed nest. Presumably the mobility of the sperm cells would facilitate the fertilisation of any remaining unfertilised eggs. The high degree of hatching success indicates not only a high level of fertilisation success but also the survival of early developmental stages. There would presumably be a loss of individuals due to predation on later developmental stages, once the larvae have left the nest.

Predation on the non-feeding and larval stages was presumably the cause of the evolution of terrestrial breeding in this species. The emancipation of early development from free water would partially overcome the disadvantage of exposing the vulnerable larval stages to pond life (Crump and Kaplan, 1979; Duellman and Trueb, 1986; Lutz, 1948; Simon, 1983; Townsend et al., 1984). A further advantage of nesting behaviour and the consequent protection of the offspring from predation would be the facilitation of a decrease in egg numbers, particularly important in this small species. Whether the small size of this species facilitated or was facilitated by terrestrial breeding is unknown. Salthe and Mecham (1974) claim that with a terrestrial mode of egg deposition, there is little to be gained by continual increase in the species body size beyond a certain point because ovum size cannot be further increased, and an increase in the clutch size is irrelevant if not disadvantageous. In A. delicatus, female body size is not correlated with the egg clutch mass, thus there would be no advantage to increased female body size in this respect.

Although one would expect a normal distribution of egg clutch masses within the population, my work demonstrates that the clutch masses are not normally distributed but rather fall into separate categories. A possible explanation of this lies in the exhibition of polyandry in this species.

Nest-building was similar to that described by Wager (1956), although nests were always construc' d above water level. The selection of specific leaves as oviposition sites is presumably the result of the physical requirements of the leaf in producing an efficient nest. Wide, short leaves would facilitate easy manipulation during nest building and would be neccessary to adequately cover the eggs to prevent desiccation and exposure to the elements. The pair spends a great deal of time and effort in selecting an oviposition site at a time when they are presumably very vulnerable to predation. It is possible that the selection of an oviposition site may affect the chances of survival of the offspring, thus necessitating the choice of site by the parents. Further investigation of larval predation and survival is neccessary before the function of the prolonged period of oviposition site selection can be determined.

The reproductive behaviour of A. delicatus seems to be stimulated by rainfall. The majority of mating occurs on, or shortly after, rainy nights and chorus size increases on such nights. A possible explanation of this lies in the effect of rain on the nests of this species. Rainfall occurs at regular intervals (see Telford, 1982). By mating and constructing nests during or after rain, the pair may effectively be ensuring that the larvae remain in the nest for a sufficient time to allow development before the next rainfall washes them into the open water.

The fact that single males follow and interact with mated pairs may be a consequence of polyandry. Unmated males may increase their chance of mating by following a pair since they may be able to secure a mating with the female once she breaks amplexus with her current mate.

Polygyny is widespread in anurans. It is the predominant mating system in A. delicatus. Polyandry is also exhibited by this species. In the cases where females did not display polyandrous behaviour, they mated and constructed 1 - 3 nests with the same male, indicating that females could lay all of their eggs without being polyandrous but that some females did not do so. Some females may have mated prior to their capture, thus polyandry may be more common than reported here.

The observed polyandry was not an artifact of overcrowded caged conditions. Caged and natural breeding males maintain a minimum interindividual distance that results in the even distribution of callers and prevents additional males being accommodated in the chorus once a maximum density is reached (see pp. 68).

In most anuran species, a female's clutch is fertilised by one male and is deposited during a single mating. Hormonal as well as extrinsic stimuli initiate ovulation (Salthe and Mecham 1974). It is obvious from this work that A. delicatus is capable of witholding eggs after the initial hormonal stimulus for ovulation has taken effect. A possible explanation for the origin and development of this polyandry is that selection has favoured multiple nests in this species. Females would necessarily evolve the ability to temporarily withold oviposition for short periods of time while further suitable nest sites were found. This would preadapt females for mating with more than one male on the same night. If laying subsequent batches could be delayed for as long as one or two nights, mating with different males on subsequent nights would be possible.

Although various explanations regarding the adaptiveness of polyandry have been offered, no proximal explanation for this behaviour in A. delicatus is evident. Theoretically, polyandry may increase a female's genetic representation in future generations either as a means of reducing the risk of leaving inviable or no offspring, or as a result of increased genetic diversity of offspring that potentially would allow greater adaptability against fluctuations in the environment (Gladstone, 1979; Janzen, 1977; Stacey, 1982). Williams (1975) examined the latter possibility and proposed that the increased genetic diversity would be only a minor factor because within progeny diversity is high even in a monogamous system. He suggested that male quality rather than number should be the dominant consideration in the female strategy. The rarity of polyandry in A. delicatus and the high progeny diversity reported in monogamous systems suggests that the genetic diversity hypothesis alone is unlikely to account for polyandry in this species.

An alternative explanation is that males may be selected to leave their mates after the first batch of eggs is fertilised, particularly if the chances of obtaining a "fresh" female

is high. Males are clearly capable of fertilising an entire clutch and the fact that they release gravid females may indicate an adaptive advantage to this behaviour. Polyandrous females may be smaller than average, but this would not necessarily influence the number or size of eggs produced since female mass does not correlate with egg clutch mass. If the first egg batch is larger than subsequent batches, there would similarly be an advantage in releasing females after the first egg batch was deposited. However, I have shown that the number of eggs deposited in a female's first, second and third batch does not differ. The extent of the male's influence on polyandry requires further attention.

It is also possible that the observed polyandry was not an adaptive strategy. A physiological limitation may prevent some females from depositing their entire clutch at one time, possibly due to differential egg maturation [illegible]es may leave the breeding area after their mature eggs had been laid, re[illegible]n remaining eggs had matured. They would then mate with a new male and, in effect, be polyandrous. However, this seems unlikely as the monogamous females (approximately 93%) laid multiple egg batches with one male on the same night suggests that polyandrous females could potentially have been monogamous. Furthermore, a female was observed mating with a second male only 30 min after breaking amplexus with the first male. The rarity of polyandry in this species argues against its being viewed as an adaptive reproductive tactic, but further investigation is required before a plausible explanation of this behaviour can be formulated.

# CHAPTER EIGHT

# FEMALE BEHAVIOUR

## 8.1 INTRODUCTION

### 8.1.1 General

In the large mixed-species choruses of the African tropics, female anurans locate males in a noisy, complex environment. They are confronted with multiple temporally overlapping sound sources varying in frequency, intensity and duration. In order to achieve amplexus, females must make sense of this sonic complexity as well as avoid predation while negotiating perches under dim lighting. This chapter examines the way in which A. delicatus females move through a chorus of conspecific males.

### 8.1.2 Accuracy of Mate Localisation

Many anurans are able to locate a sound source with extreme accuracy (Feng et al., 1976; Gerhardt and Rheinlaender, 1982; Passmore et al., 1984; Rheinlaender et al., 1979). Females probably use a pressure-gradient receiver mechanism (Gerhardt and Rheinlaender, 1982), in which directional sensitivity is facilitated by the interaction of incident and transmitted sound waves on each of the tympanic membranes.

In measuring the accuracy with which a female's auditory system can process the male's auditory cues and be guided to the sonic target, the experimental procedures employed by many authors may eliminate several factors that would be present under

natural conditions.

Recently, a great deal of criticism has focused on the use of phonotaxis experiment results in predictions of the natural breeding behaviour of anurans (Arak, 1988a; Dyson, 1986; Halliday, 1983; Telford and Passmore, in prep.). The complexity of the sonic and physical environment is thought to influence a female's behaviour to such an extent that the behaviour exhibited in phonotaxis experiments need not be exhibited under natural conditions (Dyson, 1986; Telford and Passmore, 1985). In studies of phonotactic accuracy in **Hyperolius marmoratus**, it has been shown that females locate a sound source more accurately on a two-dimensional arena than on a more natural three-dimensional arena (Passmore et al., 1984). It was predicted that the accuracy under natural conditions may be even lower (Passmore et al., 1984).

Although it is useful to know the precision with which a female is able to locate a sound source, it is probably of greater interest to know the precision that is exhibited under natural conditions and to investigate the influence of sonic and physical complexity on the ability of a female to locate a mate.

### 8.1.3 Female Behaviour in the Chorus

Anurans provide a model system for the study of social behaviour. In spite of increased interest in this field, many aspects of their behaviour have yet to be investigated through detailed field studies. Much of the recent work on anuran social behaviour has focused on studies of mate choice. Active female choice of optimally fit males has been widely invoked to explain non-random mating patterns (Dyson, 1989). There seems to be good evidence for female choice in some species, but interpretations are confounded by several factors including mate recognition, design constraints of female auditory systems, and intrasexual selection (Dyson, 1989). "If there are advantages to females in choosing a particular mate, then we would expect to see females behaving in nature as if they were comparing several males before making a choice. Moreover, in a very complex acoustic environment, sequential sampling rather than simultaneous comparison is probably necessary to discern differences between

males" -( Arak, 1983a). Some species are reported to behave in this way (Duellman, 1966; Fellers, 1979a; Howard, 1981). However, there is the problem of distinguishing between female preference for a male's genes or for the resources he possesses (Arak, 1983a). The structural design constraints on the female's auditory system may bias her ability to localise certain sorts of calls. Also, because anurans are ectothermic, levels of motivation, time to physiological responsiveness and the accuracy of coupling of sender - receiver mechanism may be temperature dependant. These factors may affect female preference and the readiness with which a female will approach a certain male (Arak, 1983a). Also, the female must rely on some phenotypic characteristic in assessing fitness, thus she would have to be able to discriminate between phenotypic characteristics. It is also unknown whether sufficient genetic variation can be maintained in a population to allow female preference to persist or if favoured traits would be rapidly spread and fixed in the population (Arak, 1983a).

There has been very little work on female behaviour and even less on the relative importance of male and female behaviour in the mating system (Arak, 1988a; Howard, 1988; Morris, 1989). It is clear that observations of female behaviour prior to amplexus are required in order to provide an overall picture of the mating system (Morris, 1989).

Once a female has located and approached a chorus, she is faced with the problem of locating an individual conspecific male. The observation of female behaviour at this stage may provide evidence of the mechanism employed to do this. If mating is non-random and females reject certain males even when placed close to them, or successively sample males, it may indicate active female choice (although not always - see Arak, 1983a). If females mate randomly with close-by males, irrespective of morphology or call characteristics, it may indicate a role for passive attraction.

### 8.1.4 Aims

The aim of this chapter is to provide a more thorough understanding of female behaviour in the context of mate localisation. The following questions were addressed:

1) What is the potential accuracy of phonotaxis in this small anuran?
2) How is this potential influenced by the complexities characteristic of natural breeding assemblages?
3) Do females mate with the nearest male or do they move through the chorus bypassing males, and mate with a specific male only?

## 8.2 METHODS

### 8.2.1 Interaural Distances

The interaural distances of 16 **A. delicatus** females were measured during November 1989. Verner callipers were placed across the females' heads to measure the distance between the tympana.

### 8.2.2 Accuracy of Phonotaxis

The accuracy of females' phonotactic approaches were examined under five categories of sonic and environmental complexity during the 1988/89/90 breeding seasons. For categories 1- 4, the testing arena consisted of a cloth floor (2 x 3 m) on which was drawn a 5 x 5 cm numbered grid. A 60 W red light bulb was suspended 2 m above ground level in the centre of the arena. Stimulus tapes were prepared using a single call recorded in the field. The stimulus covered the normal frequency range of the species and was played at the normal repetition rate. The stimuli were broadcast using a Sony TCD 5M tape recorder, a Klein and Hummel SB 280 amplifier and Phillips AD 50600 8 inch diameter loudspeakers. Playback levels were adjusted to the natural sound pressure level of the species using a Brüel and Kjaer 2209 sound level meter.

Category 1: The stimulus tape carried the trill component of the two-part call on the left track. The intercall interval was 16.8 s. The stimulus was broadcast by a single loudspeaker located 1 m from the female release point.

Category 2: The stimulus tape carried both components of the call on the left track. The call components were separated by an 8 s interval (the intertrill interval was therefore

identical to that in category 1). The stimulus was broadcast by a single loudspeaker located 1 m from the female release point.

Category 3: Identical to category 1, but carrying the same stimulus on both left and right tracks of a stereo tape. Left and right tracks alternated precisely. Two loudspeakers (one for each track) were placed at the same end of the arena, 1 m in front of and facing the release position. The loudspeakers were 50 cm apart.

Category 4: Identical to category 3, but with the calls on left and right tracks exactly simultaneous. The two loudspeakers were positioned as in category 3.

Amplexing pairs were collected from the natural breeding sites and females were separated from males immediately before their first trial and placed in a perforated plastic container at the release point. This was removed 2 min after call broadcast had commenced. A positive response was scored if the female made a deliberate approach to, and made physical contact with the loudspeaker. Each female was scored once in each category. The duration of the trial was recorded and each trial was mapped using the coordinates on the arena surface. The accuracy of each approach was quantified in terms of the angular deviation of the jump direction from the target axis. The mean jump error angle was calculated for each trial.

Category 5: Females were individually released into a caged chorus of males (pp. 27). Calling males were collected from the natural breeding area and released into the cage. Choruses consisted of 4 - 8 calling males. A 5 x 5 cm labelled grid, was constructed using twine spanned over the pond. This enabled females' paths through the chorus to be plotted. The approaches were analysed two-dimensionally since the plants in the cage are low, emergent species and the vertical component of females' approaches was negligible.

The jump error angles for all jumps in each of the five categories were compared using a Kruskal-Wallis One-way Analysis of Variance by Ranks. This test was also used to compare the trial durations and the number of jumps in each approach (categories 1 - 5 , as well as the approaches of females in choruses of 4, 5, 6 and 7 males within category 5). For the majority of approaches mapped in category 5 (n = 15), the mass

and snout-vent length (SVL) of the amplexed males were measured. Furthermore, the advertisement calls of these males were recorded on a Sony TCD 5M tape recorder and a Sony EMC-16T microphone. The calls were analysed on a Uniscan II Sound Spectrum Analyser, and the mid-frequency of the advertisement call was measured. The correlations between the accuracy of female approach and these variables (mass, SVL and call mid-frequency) were examined using Spearman's Rank Correlation analyses.

### 8.2.3 Female Behaviour in the Chorus

Twenty eight gravid females were individually released into choruses of males in the cage from a position on the edge of the pond. The females were closer to some males than others. The path of the female through the chorus was plotted (as were the positions of the calling males), using the co-ordinates of a 5 cm labelled grid (see above). The behaviour of females was observed during the approaches. For the majority of approaches mapped, the mass and SVL of the calling males was known. This work was conducted during the 1989/90 breeding season.

## 8.3 RESULTS

### 8.3.1 Interaural distance

The mean interaural distance of **A. delicatus** females was 0.54 cm (SD = 0.04; n = 16).

### 8.3.2 Accuracy of Phonotaxis

Females were able to localise a calling male (category 5) or a broadcast call (categories 1 - 4) with extreme accuracy (mean jump error angle [MJEA] for all approaches = 32.2°; n = 82 approaches). From Table 8.1, it is clear that there were no significant differences between the five categories of approach for trial accuracy, trial durations or numbers of jumps. The zip call component (of categories 1 and 2) did not aid or hinder accuracy. The addition of a second, alternating stimulus (category 3) and

the exact temporal overlapping of the additional stimulus (category 4) also did not influence the accuracy of the females' approaches, trial duration or number of jumps. The increased sonic and environmental complexity of a natural, caged chorus also did not influence the females' accuracy of approach. There was no difference in the accuracy of approaches when 4, 5, 6 or 7 males were present in the chorus ($H = 1.538$; $P = 0.67$; $n = 5$ for chorus sizes of 4, 5 and 7 males, $n = 6$ for choruses containing 6 males).

There was no significant correlation between the accuracy of approach and the mated males' SVL ($r = -0.107$; $P = 0.688$; $n = 15$); mass ($r = -0.399$; $P = 0.136$; $n = 15$) or call mid- frequency ($r = -0.022$; $P = 0.936$; $n = 15$) in category 5 approaches. Females do not appear to localise larger, heavier males with lower frequency calls with increased accuracy.

TABLE 8.2

Mean jump error angles (xJEA), trial durations and number of jumps per trial for the five categories of approach; and the Kruskal-Wallis Analysis of Variance (H) between the categories.

| | | category 1 | category 2 | category 3 | category 4 | category 5* | H | P(H) |
|---|---|---|---|---|---|---|---|---|
| JEA | $\bar{x}$ | 31.57 | 32.47 | 32.17 | 33.42 | 31.96 | 0.32 | 0.99 |
| | SD | 8.62 | 9.11 | 9.33 | 9.39 | 16.98 | | |
| | n | 17 | 17 | 10 | 10 | 28 | | |
| Trial Duration | $\bar{x}$ | 299.80 | 410.69 | 301.67 | 333.50 | 624.55 | 6.97 | 0.1 |
| | SD | 203.77 | 302.26 | 113.19 | 198.13 | 483.89 | | |
| | n | 15 | 16 | 9 | 10 | 11 | | |
| Number Jumps | $\bar{x}$ | 11.82 | 12.59 | 12.70 | 13.60 | 11.32 | 3.76 | 0.4 |
| | SD | 3.91 | 5.67 | 3.68 | 4.95 | 6.30 | | |
| | n | 17 | 17 | 10 | 10 | 28 | | |

* = x distance covered = 0.78 m (n = 28)

8.3.3 Female Behaviour in the Chorus

Of the 28 female approaches mapped, nine females (32%) mated with the nearest male; 17 (61%) mated with one of the two nearest males; and 24 (86%) mated with one of the three nearest males. Fifteen females (20%) mated with the largest male irrespective of of whether he was closest or not. In the trials in which the females did not mate with the nearest male and the SVL and mass of the callers was known (n = 9), four of the females mated with a male who was smaller (mass and SVL) than the nearest male. In the cases where more than one female was released into the chorus on any given night (n = 12), only three (25%) of the males who mated first were the largest males in the population.

In 23 of the 28 trials (82%), the female approached the target male in a fairly direct fashion (Fig. 8.1a), although four of these females bypassed (within 15cm) a calling male during the approach (Fig. 8.1b). In the remaining five approaches (18%), the female appeared to have "visited" a male that was not the eventually succesful mate (Fig. 8.1c). A female was said to have "visited" a male if she appeared to be approaching him, came within 15cm of him, but did not initiate amplexus and altered her direction of approach towards another male. In four of these trials the mass and SVL of the callers was known, and in two of them (50%), the visited male was larger (mass and SVL) than the eventually mated male.

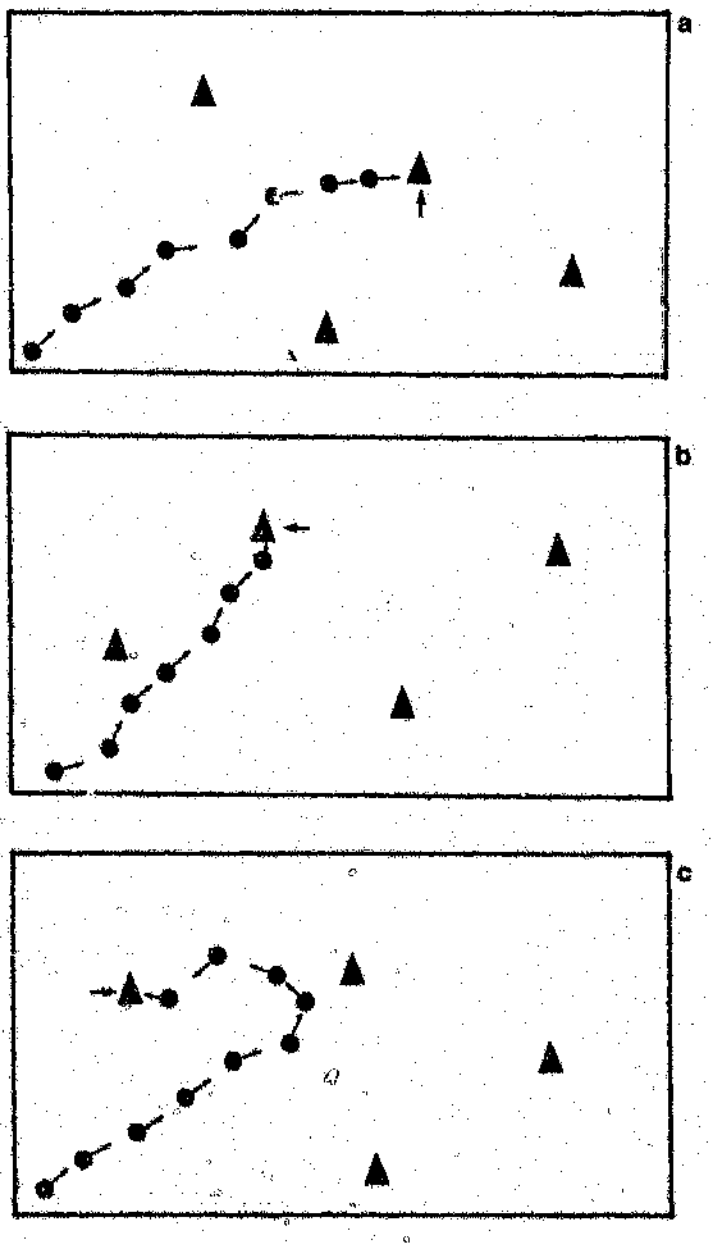



FIGURE 8.1 Examples of female approach paths through a chorus: (a) female approaching in a straight line path; (b) female bypassing a calling male while approaching in a straight line path; (c) female "visiting" a male who was not the eventually mated male.

▲ = calling males

→▲ = mated male

●_ = female approach path

## 8.4 DISCUSSION

The ability of this small anuran to localise a sound source with great precision is comparable to that found in other frog species (Feng et al., 1976; Gerhardt and Rheinlaender, 1980, 1982; Passmore et al., 1984; Rheinlaender et al., 1979). The interaural distance is small relative to the wavelength of the advertisement call (see Camhi, 1984). This, together with the results of other behavioural studies (Feng et. al., 1976; Gerhardt, 1987; Rheinlaender et al., 1979) implies that neither the pressure receiver mechanism, nor the interaural time difference mechanism are sufficient to explain the accuracy of sound localisation in anurans. These results suggest that the most likely mechanism of hearing is the pressure-gradient receiver system (Gerhardt, 1987).

Although the complexities characteristic of large natural choruses has been presumed to impair a female's ability to display the precision found in simplistic laboratory conditions (see Morris and Yoon, 1989; Robertson, 1986; Schwartz, 1986; and Telford and Dyson, 1988), there was no evidence of this in A. delicatus. The accuracy with which females localised individual calling males under complex sonic and physical environments was no different from that displayed under controlled, laboratory approaches. Additional sound sources, temporally overlapping stimuli and environmental complexity do not appear to influence the precision of female approaches. Females also do not localise larger or lower frequency males more accurately than others.

Female behaviour prior to amplexus indicated that females generally approached one of the nearest calling males irrespective of phenotype or behaviour. There was no evidence of successive sampling of males. Females rarely "visited" males without initiating amplexus and there was no significant difference between the rejected males and those that were accepted. Since females were free to choose among males, and there was no evidence of preferential attraction to any particular male trait examined, it is most likely that females either mated indiscriminately or were attracted to the most easily located or distinct call (which would most likely be produced by one of the nearest males). There is possibly a physiological threshold for female stimulation (Arak,

1988a) which could explain why females did not consistently mate with the closest male.

These results are consistent with the idea that females, when confronted with a chorus, select a target male and approach him in a relatively straight-line path while effectively ignoring other calling males. Females presumably "target in" on one of the nearest calling males irrespective of morphology, call characteristics or behaviour. Females may indiscriminately "lock-in" to a particular male while approaching the chorus, and other conspecific calls appear to have little effect on the approach.

# CHAPTER NINE

# CONCLUDING DISCUSSION

## 9.1 SEXUAL REPRODUCTION

If the advantage of sexual reproduction is that it increases the range of potential variation in a population, then the advantage refers to the population as a whole and not to any particular individual in it (Maynard Smith, 1975). Since natural selection operates at the level of the individual, there must be an individual advantage to sexual reproduction. This advantage lies in the increased variation of offspring produced by a single pair of biparental organisms under conditions of intense selection, i.e., under fluctuating conditions, the best adapted offspring is most likely to be a sexually produced one since all the asexual ones are identical (Williams, 1975).

In *A. delicatus* and other prolonged breeding anurans, sexual reproduction involves sexual advertisement, courtship, copulation and egg deposition. Males and females have coevolved to produce a complex and efficient set of behaviours and physical adaptations to ensure success at each of these stages. It is possible to recognize four kinds of selection pressures that may operate on the individual: (i) selection ensuring that an individual shall mate; (ii) selection ensuring that an individual shall mate with a conspecific partner of the opposite sex; (iii) selection ensuring that an individual shall mate with the fittest and most fertile mates and (iv) selection to increase the frequency with which an individual mates (Maynard Smith, 1975). These will be discussed hereunder.

In anurans, selection ensuring that an individual shall mate takes the form of both extrinsic and intrinsic factors. The extrinsic factors that trigger breeding include rainfall, light, temperature, daylength and food availability (Rabb and Rabb, 1963; Salthe and Mecham, 1974). In A. delicatus, rainfall seems to be the major factor influencing breeding activity and it probably initiates migration to the breeding area (chapter 5). Intrinsic factors are generally hormonal. The production of the mating call is controlled by the pituitary and testicular hormones (Schmidt, 1966). The mating call has further significance in terms of behavioural and physiological facilitation of breeding. Calling by active males stimulates calling behaviour by other individuals (Salthe and Mecham, 1974). It is also probable that chorusing triggers neuro-endocrinological changes in females that stimulate the mating response and may influence ovulation (Salthe and Mecham, 1974; Sughrue, 1969). The act of clasping may also play a role in bringing a female into a state of readiness for mating in some species (Bragg, 1941). In most species, peristaltic abdominal contractions in females occur during amplexus and may indicate ovulation that probably acts to stimulate the male to ejaculate (Salthe and Mecham, 1974).

Selection ensuring that an individual mates with a conspecific partner of the opposite sex is vitally important and is achieved through the SMRS. The SMRS of A. delicatus is species specific and facilitates efficient reproduction irrespective of other species presence. Stabilizing selection acts to keep the mate recognition system stable so as to ensure syngamy (Paterson, 1977, 1978, 1982, 1985). The SMRS is a coevolved signal-response chain which facilitates fertilisation. It operates during courtship and copulation. Courtship may be defined as a set of specialised behaviour patterns that form the normal preliminaries to mating (Manning, 1979). Sexual advertisement and the localisation of a mate constitute a large part of the courtship behaviour as well as the SMRS in anurans. Sexual advertisement to conspecific mates is facilitated by the trill call in A. delicatus (chapter 3). This signal is perceived by gravid females and acts as a releaser of the phonotactic response. Presumably the frequency structure of the call is precisely matched to the best excitatory frequency of the female's auditory system as in other species that have been investigated (Capranica, 1976). The biological sequence of events occurring during sound localisation is not fully understood, but most anurans,

including A. delicatus, are able to localise a sound source with extreme accuracy. Although the complexities characteristic of large natural choruses may be thought to impair a female's ability to display the precision of localisation found in simple laboratory conditions (chapter 8), there was no evidence of this in A. delicatus. The accuracy with which females located calling males under complex sonic and physical environments was no different from that displayed under controlled laboratory trials.

Selection ensuring that an individual will mate with the fittest and most fertile mate has been widely invoked as a means of explaining non-random mating in anurans (Ryan, 1982). Intersexual selection in a wild population is difficult to demonstrate since it is necessary to show that a female is selecting some kind of male in preference to all others and furthermore, in so doing, she is increasing the average number or quality of offspring she leaves (Arak, 1983a). A further complication is that intersexual selection can operate only if those males with the character which increases their mating success, are also fitter parents, but it is difficult to demonstrate such a correlation in a wild population (Maynard Smith, 1975). I found no evidence of such selection in the A. delicatus population and found that female behaviour prior to amplexus did not seem to indicate the selection of any particular class of males. Although there was variation in male mating success, it appeared to be independent of morphological or behavioural traits. On a nightly basis, males' probabilities of mating were equal.

Selection to increase the frequency with which an individual mates is widespread in anurans. There is obviously strong selection on each individual to increase its reproductive success by mating more frequently. Since anurans seem to be unable to judge the quality of their mates (chapter 6 and 8), there would be selection to increase the number of offspring left (Maynard Smith, 1975). Male-male competition for access to females is common in species where there is the potential for male multiple mating. In this study it was found that males can increase their probability of mating by calling regularly. Presumably there is an energetic constraint on the amount of time individual males can spend calling, although larger males were not found to call more regularly than smaller males in this species. In numerous birds (Gladstone, 1979; Stacey, 1982) as well as in A. delicatus, both males and females employ the strategy of multiple

mating. Although males benefit from multiple mating by increasing the number of offspring, this is not so in females. No proximal explanation for polyandrous behaviour in this species is evident. It is possible that the increased variation in offspring produced by polyandrous females is beneficial, but it is more likely that this behaviour has no adaptive value.

## 9.2 REPRODUCTIVE STRATEGY

A 'reproductive strategy' is a set of tactics that has been selected as the adaptations which have contributed, on average, the greatest number of offspring in recent generations (Wilbur, 1977). The reproductive strategy is determined by the collective behaviour of individuals' responses to, and compromises among,various selection pressures (Ducllman and Trueb, 1986). Ecological as well as social parameters impose limits on the range and type of behaviour that will be adaptive (Arak, 1983a; Emlen and Oring, 1976). There is often considerable flexibility in the mating system of a population and it may vary with differences in male density, synchronisation of female arrival and environmental fluctuations (see chapter 6; Arak, 1983a; Wells, 1977b).

One factor hindering the development of a sociobiological framework of the theory of reproductive strategy has been "a recurring tendency for fieldworkers to search for and discuss 'adaptiveness' in the context of the survival and well-being of the population or species. To understand mating systems, we must abandon species- or group-selection viewpoints and return to the evolutionary tenet of natural selection operating at the level of the individual" (Emlen and Oring, 1977).

### 9.2.1 Male Reproductive Strategy

Emlen and Oring (1977) proposed that intrasexual interactions associated with mating are basically competitive. Male competition for females is direct in explosive breeding anurans, but generally indirect in prolonged breeders (Wells, 1977b). Males compete amongst themselves for access to females. Variation in male mating success may depend entirely on the ability of some males to outcompete rivals (Dyson, 1986). Intrasexual

selection would promote the evolution of characters that confer an advantage on males in this way.

In **A. delicatus**, communal reproductive areas are used, thus increasing the complexity of the mating system. Chorusing enhances the attraction ability of individuals, but at the same time neccessitates the maintenance of social organisation. The female encounter rate would be high for those males that position themselves in the aggregations rather than singly since the enhanced stimulus effect of the chorus would preferentially attract females (Emlen and Oring, 1977). In **A. delicatus**, the chorus is distinctly divided into small groups of males that form independently of resource availability (chapter 5). Male clustering may be advantageous if polyandrous females returned to the same sites on subsequent nights (chapter 9).

**Afrixalus delicatus** displays normal prolonged breeding behaviour in which males call from stationary sites on eulittoral zone vegetation in permanent bodies of standing water. The male mating effort is spread more or less evenly throughout the breeding season since female arrival is, to a large extent, unpredictable. Males communicate their species, sex, reproductive state and location using vocalisations. In numerous bird songs there seem to be a segregation of information within a single vocalisation (Emlen, 1972; Jellis, 1977; Marler, 1960). Similarly, in most anurans, the advertisement call may simultaneously convey separate messages to both sexes (Narins and Capranica, 1976). However, **A. delicatus** has evolved a two-part call that is functionally partitioned in the context of male-male communication and female attraction (chapter 3). Males are capable of altering the relative proportion of call components in response to various social conditions, producing an increased number of female attracting notes when a female is present, and increasing the number of male-male communication notes when the chorus density is high. This facilitates an effective response by the receiver to the vocalisation and hence an increase in the efficiency of communication.

Most prolonged breeder male anurans maintain an inter- individual distance in the chorus that usually results in the regular distribution of calling males at the breeding site (Arak, 1983a). In **A. delicatus**, the individual distance is maintained using the zip call,

the encounter call and physical combat or the threat of combat (chapter 4). Although aggression is a significant feature of social behaviour (Test, 1954), fighting is expensive in terms of energy, time and risk of injury (Robertson, 1986); thus most disputes in **A. delicatus** are settled using the encounter call. The individual areas around males are non-resource based and males are therefore non-territorial (see Telford, 1982). The maintenance of an individual distance may be a means by which males can increase their reproductive success since spacing decreases the acoustic interference between near neighbours (Whitney and Krebs, 1975a) which results in an increase in a male's locatability and the distinctiveness of his call. Spacing also provides a clear pathway for female approach (Whitney and Krebs, 1975a) which prevents neighbouring males from intercepting an approaching female. Spacing in **A. delicatus** acts to reduce the number of potential competitors, but only under conditions of limited space. In most natural breeding conditions, the limitation of competition may not be facilitated since additional males would be accommodated on the periphery of the chorus.

Subtle variations in habitat suitability within chorus locations may make some calling sites better than others for attracting females (Arak, 1983a). In **A. delicatus**, particular calling sites are selected. Although individual males' call sites do not appear to increase their mating success, the sites used by this species as a whole may offer increased sound propagation properties (Fellers, 1979a) which would allow females to localise individuals easily.

Males that are unable to compete with rivals may employ an alternative mating tactic (Howard, 1984). Satellite males do not call and do not defend an individual distance; they either wait for a call site to become vacant after the resident male has achieved amplexus, or they intercept females as they approach calling males (Wells, 1977b). My observations of satellite behaviour in **A. delicatus** (chapter 6) are similar to those of many other authors (Arak, 1983a; Fellers, 1979a; Howard, 1984; Perrill et al., 1978; Wells, 1977b). Satellite males were smaller than callers and attended the chorus less regularly. The satellite tactic was found to be unsuccessful in terms of mate acquisition, and for this reason, it is thought that these males are "making the best of a bad job" (Maynard-Smith, 1975). This tactic may persist in the population because it is a low

cost/low reward behaviour. There are presumably constraints on the individuals adopting this tactic that prevent them from calling.

9.2.2 Female Reproductive Strategy

The coadaptation between the advertisement call and the female's auditory system forms the basis of the signal- response chain which promotes the meeting of the sexes (Narins and Capranica, 1976; Paterson, 1978, 1985). Anuran female arrival at the breeding site is generally asynchronous (Wells, 1977b), and in **A. delicatus**, arrival of gravid females occurs over a five month breeding period. Females locate calling males using the information obtained from the vocal signals (Wells, 1977b). In **A. delicatus**, the localisation of a sound source is extremely accurate and is unaffected by complexities in the sonic and physical environments. Amplexus is followed by egg deposition. Probably the most primitive female anuran reproductive strategy involves the deposition of a single, large clutch of eggs in open water where the eggs and larvae develop (Salthe and Mecham, 1974). In nearly all amphibian populations that have been studied, predation pressures on the egg and larval stages are high, and juvenile mortality fluctuates more than adult mortality (Duellman and Trueb, 1986). Modifications in reproductive strategy have allowed for the partial avoidance of predation on the early developmental stages and selection has favoured the production of multiple small clutches deposited at various places and at different times. This decreases the chance of a total reproductive failure for a given breeding season (Duellman and Trueb, 1986). Egg deposition in **A. delicatus** is partially terrestrial since eggs are laid in nests constructed on vegetation above water. The clutch size has been sacrificed for increased egg size. The deposition of terrestrial eggs may be viewed as an adaptation to avoid the uncertainty of the aquatic environment (i.e. water availability, predator density etc.), but may also be advantageous in that the tadpoles spend less time in the hazardous aquatic environment before metamorphosis (Duellman and Trueb, 1986).

The reproductive strategy of **A. delicatus** females is unusual in that it has allowed for rapid multiple clutch polyandry. Males have the opportunity to increase their reproductive success through multiple breeding in rapid succession. Although females

are unable to behaviourally control the number of offspring they leave, they may control the number of mates that fertilise their eggs (chapter 8).

### 9.2.3 Effects of Chorus Density on Reproductive Strategy

The reproductive strategy employed by the majority of individuals in a population may vary with varying ecological and social pressures (Arak, 1983a; Wells, 1977b). Chorus density has a profound effect on behaviour in many anurans (Dyson, 1989). Arak (1983a) proposed that, as the density of males changes at different times, individuals within the population may alter their reproductive strategies. "At low chorus densities, there is relatively little competition for the available females and all males will benefit from calling. As male density increases, some small males would do better by ceasing to call and attempting to intercept females approaching calling males. A further increase in density will favour the satellite strategy even more because satellites will be able to effectively patrol the periphery of the territories of several callers" (Arak, 1983a).

The density of calling males in the A. delicatus chorus affected the individual's social behaviour in four ways. First, an increase in chorus density led to an increase in the number of zip calls (male-male communication signals) and a decrease in the number of trill calls (female attraction signals) produced (chapter 3). Second, an increase in chorus density led to a decrease in the nearest neighbour distances (chapter 4). Third, the frequency of aggressive interactions, both vocal and physical, increased with an increase in the chorus density (chapter 4); and fourth, satellite behaviour was observed only when chorus density was high (chapter 6).

The chorus densities of approximately 2.0 males/m$^2$ and 3.2 males/m$^2$ (chorus sizes of 5 and 8 males respectively), appear to be the densities at which the male reproductive strategy is varied in response to social behaviour. At chorus densities lower than 2.0 males/m$^2$, males seem to be able to maximise the efficiency of their reproductive behaviour with relatively little social organisation. At densities of 2.0 - 3.2 males/m$^2$, males appear to regulate their behaviour in response to the presence of other males. Possibly social organisation is maximised at these densities and individual males

compromise between numerous selective pressures to facilitate adequate reproductive success. Chorus densities greate ⁻an 3.2 males/m$^2$ were extremely rare and this density appears to be the point at which further compromises become disadvantageous and males prevent additional callers from entering the chorus (see Figure 9.1).

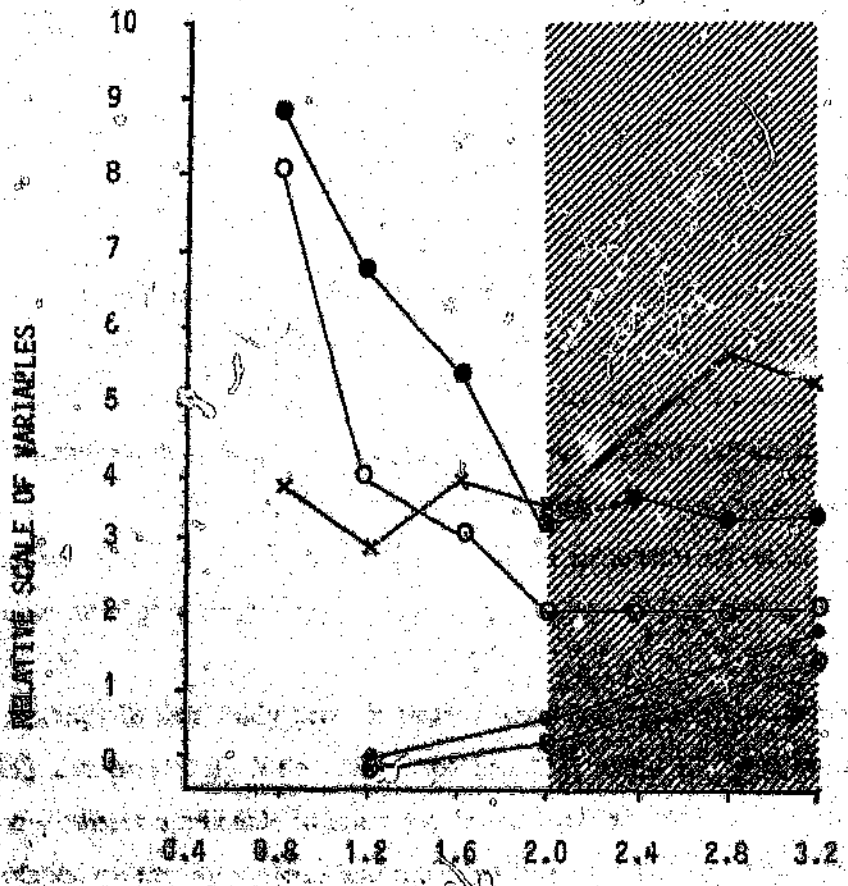



FIGURE 8.1 Density effects on the reproductive behaviour of A. dellenius males.

## 9.3 CONCLUSION

Anurans, as a group, have adopted a range of reproductive strategies that are contingent on environmental and social parameters. The reproductive strategies adopted by the studied population of **A. delicatus** are the result of adaptations in physiology, ecology and behaviour in response to various selection pressures acting on individuals. Factors such as the temporal pattern of rainfall, temperature, variation in predator pressure, population density and co-existence of competing species all probably affect the reproductive strategy employed. **A. delicatus** co-exists in a community with at least 19 other anurans species, most of which exibit specific preferences for particular microhabitats. The community structure is thus an incidental effect of the differing reproductive strategies employed by the component species (Littlejohn, 1977).

The findings in this study provide insight into the reproductive behaviour of an interesting and previously little-studied species. This study has generated numerous testable hypotheses applicable to other species. It has also added to the growing body of information on mating systems and their flexibility relative to social and ecological pressures. This is necessary if we are to understand anuran reproductive behaviour and its evolution.

# APPENDIX 1

## ANALYSIS OF MALE DISTRIBUTION PATTERNS IN ANURAN CHORUSES

The analysis of male distribution patterns in anuran choruses can be used to provide added insight into social behaviour as it determines whether or not the males are vocally interacting. There are four methods that have previously been used to analyse distribution patterns in anurans. I present, here, all four methods as applied to my data. I also present a concluding discussion relating my raw data to the analysis techniques.

### METHOD ONE: CLARKE AND EVANS' ANALYSIS OF SPATIAL DISTRIBUTION

In order to use Clark and Evans' (1954) analysis of spacing patterns, there are various conditions that must be met:

a) The nearest neighbour distances of the entire population as well as those of the sample selected for investigation must be normally distributed (Clark and Evans, 1954).

b) The correct density of the population must be known, since if an estimation of density is substituted for the true value, the rigor of the significance test is lost (Clark and Evans, 1954).

c) Very large sample sizes ( > 100) are required if there is variability in the nearest neighbour distances (Clark and Evans, 1954)

d) The derivation of the mean expected distances between nearest neighbours in a randomly distributed population is based on the assumption that the area occupied is

infinite although the measure is applied to finite populations occupying definite areas. Thus the area selected for investigation must lie well within the total area occupied by the population (Clark and Evans, 1954).

Even once these rigorous conditions are met, there are further complications in Clark and Evans' analysis:

a) The test is not sensitive enough to show non-randomness in all cases and a chi-square test is required for this (Clark and Evans, 1954).

b) The test cannot distinguish between clumped distributions and scattered pairs (Robertson, 1984).

c) The test is not designed for repeated samples. Thus, if the experiment is repeated, the value of N is the chorus size and not the number of observations.

d) When the sample size is small (< 100) the normal curve cannot be used and Pearsons' Type III curve should be substituted in order to determine the significance of the departure from randomness (Clark and Evans, 1954).

e) The test is not as sensitive as other tests (eg. Craig's test). Craig's (1953) mathematical techniques are of greater sophistication than Clark and Evans' and his test does not require that the exact density of the population be known (Blackith, 1958).

Application of Clark and Evan in anuran populations

Fellers (1979a) applied Clark and Evans' analysis to his data on nearest neighbour distances. However, the test was incorrectly applied and the expected values were too high. Consequently the values for R are incorrect (and one even falls outside the range of possible values of R). The t-test values therefore are also incorrect. He applied a Students-t test to the data instead of the standard variate. He did not use the full complement of nearest neighbour distances for each chorus, which may have influenced the calculation of rA and R.

Thiele and Bailey (1980) studied bush-crickets and applied Clark and Evans' analysis to the nearest neighbour data. The data met the requirements for the application of the test (the distances were normally distributed; the selected site was within the

population range; the site had distinct boundaries that allowed the correct density to be calculated and the experiment was not repeated so the correct value for N was used), but they still found that the value of R was underestimated due to patches within the study site which contained no males. The distribution was therefore found to be statistically random when, in practice, it was regularly distributed.

I conducted Clark and Evans' test on my data and found that males in all chorus sizes were randomly distributed (TABLE A1.1).

METHOD TWO: CRAIG'S ANALYSIS OF SPATIAL DISTRIBUTION

Craig (1953) proposed a method of analysing distribution patterns which uses more sophisticated mathematical techniques than Clark and Evans' (1954) test. The major advantage of Craig's analysis technique is that the exact density of the population need not be known.

When using Craig's method, I found that all chorus sizes were randomly distributed (TABLE A1.2).

METHOD THREE: CHI-SQUARE TEST ON CLARK AND EVANS' AND CRAIG'S ANALYSES

The chi-square test takes into account the variability in nearest neighbour distances and is therefore a more sensitive analysis. When used in conjunction with Clark and Evans' test, I found that all chorus sizes were non-randomly distributed (TABLE A1.3); and when used in conjunction with Craigs' test, all chorus sizes were similarly non-randomly distributed (TABLE A1.4), i.e. either evenly spaced or clumped.

METHOD FOUR: PIELOU'S ANALYSIS OF SPATIAL DISTRIBUTION

Pielou (1962) provided an alternative method for analysing the distribution patterns in natural populations. Her method is able to detect regular distributions within clumps

and does not require the definition of the boundaries or densities of the populations (Robertson, 1984). Her method uses the squared nearest neighbour distances of a truncated sample and compares their distribution with a similarly truncated sample of an expected random population. A chi-square test is applied to the values at each class interval to detect discrepancies between the two populations. The mathematical statistics used in her analysis are extremely complicated and sophisticated.

On applying this method to my data, I found that choruses of 2 and 3 males were randomly spaced, and all larger choruses (4 - 8 males) were non-randomly spaced (aggregated) (Table A1.5).

CONCLUSIONS

The four tests used gave conflicting results. When considering my raw data in light of these opposing results, I propose that none of the methods gives an accurate account of the distribution patterns and I do not believe that they are suitable tests for anuran chorus distribution analysis. I believe that my raw data indicate that nearest neighbour distances are compressible to an extent (see Figure A1.1), as indicated by the initial decrease at choruses of 2 and 3 males. The graph then shows a gradual decrease in the extent to which the distance is compressible (i.e. the graph becomes more horizontal at higher chorus sizes). This may indicate that the males in these choruses are maintaining a minimum individual distance.

I propose that spacing is maximal at chorus sizes of 2, 3 and 4 and that the spacing patterns could be random since male-male interactions are uncommon at such low densities (see pp. 66). Spacing may be even (non-random) at chorus sizes of 5, 6, 7 and 8 males since a minimum individual distance would be maintained in these choruses (see pp. 68). I found that extra males were not accommodated in the A. delicatus chorus once the density was maximised (i.e., however many males were placed in the cage, only 8 would call). Therefore, I propose that spacing does not break down, but rather acts to reduce the number of potential competitors in the area.

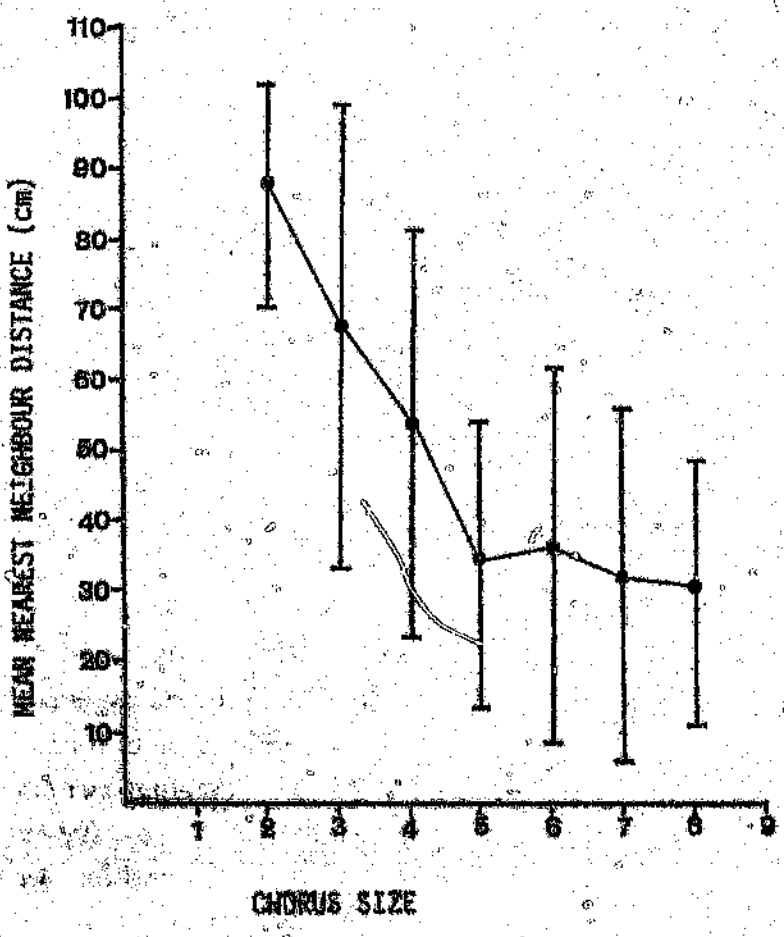



FIGURE A1.1 Nearest neighbour distances at different chorus sizes in A. delicatus

TABLE A1.1

Clarke and Evans' (1954) analysis of spacing patterns applied to A. delicatus data.

| CS | n | rA | q | rE | R | σE | c | P | pattern |
|---|---|---|---|---|---|---|---|---|---|
| 2 | 10 | 88.2 | 0.8 | 55.9 | 1.58 | 20.1 | 1.[illegible] | <0.05 | random |
| 3 | 15 | 67.7 | 1.2 | 45.6 | 1.48 | 13.8 | 1.60 | <0.05 | random |
| 4 | 20 | 52.8 | 1.6 | 39.5 | 1.34 | 10.[illegible] | .27 | <0.05 | random |
| 5 | 25 | 33.4 | 2.0 | 35.4 | 0.95 | 8.2 | -0.24 | <0.05 | random |
| 6 | 30 | 35.7 | 2.4 | 32.3 | 1.11 | 6.9 | 0.49 | <0.05 | random |
| 7 | 35 | 31.7 | 2.8 | 29.9 | 1.06 | 5.9 | 0.31 | <0.05 | random |
| 8 | 40 | 31.3 | 3.2 | 28.0 | 1.12 | 5.1 | 0.64 | <0.05 | random |

CS = chorus size
rA = observed mean NND
rE = expected mean NND
σE = standard error of E
q = chorus density
R = rA/rE
c = rA - rE/σq

TABLE A1.2

Craig's (1953) analysis of spacing patterns as applied to the A. delicatus data.

| CS | rA | q | rE | σE | ˌ | P | pattern |
|---|---|---|---|---|---|---|---|
| 2 | 141.1 | 0.8 | 88.2 | 32.67 | -1.62 | >0.05 | random |
| 3 | 87.8 | 1.2 | 67.7 | 20.10 | 1.00 | >0.05 | random |
| 4 | 59.8 | 1.6 | 52.8 | 13.76 | -0.49 | >0.05 | random |
| 5 | 34.0 | 2.0 | 33.4 | 7.87 | -0.08 | >0.05 | random |
| 6 | 32.6 | 2.4 | 35.7 | 7.55 | 0.41 | >0.05 | random |
| 7 | 27.0 | 2.8 | 31.7 | 6.25 | 0.75 | >0.05 | random |
| 8 | 24.7 | 3.2 | 31.3 | 5.73 | 1.15 | >0.05 | random |

TABLE A1.3

Chi-square , test for Clark and Evans' analysis of A. delicatus data.

| CS | $X^2$ | DF | P | pattern |
|---|---|---|---|---|
| 2 | 224.37 | 9 | <0.01 | non-random |
| 3 | 501.74 | 14 | <0.01 | non-random |
| 4 | 501.49 | 19 | <0.01 | non-random |
| 5 | 276.27 | 24 | <0.01 | non-random |
| 6 | 618.29 | 29 | <0.01 | non-random |
| 7 | 715.80 | 34 | <0.01 | non-random |
| 8 | 511.07 | 39 | <0.01 | non-random |

non-random = clumped or even/regular/uniform

TABLE A1.4

Chi-square test for Craig's analysis of A. delicatus data.

| CS | $X^2$ | DF | P | pattern |
|---|---|---|---|---|
| 2 | 213.28 | 9 | <0.001 | non-random |
| 3 | 245.68 | 14 | <0.001 | non-random |
| 4 | 268.68 | 19 | <0.001 | non-random |
| 5 | 254.88 | 24 | <0.001 | non-random |
| 6 | 606.87 | 29 | <0.001 | non-random |
| 7 | 814.37 | 34 | <0.001 | non-random |
| 8 | 632.26 | 39 | <0.001 | non-random |

TABLE A1.5

Pielou's analysis of spatial distribution applied to A. delicatus data.

| CS | N (truncated) | Z | P | pattern |
|---|---|---|---|---|
| 2 | 8 | 0.94 | >0.05 | random |
| 3 | 12 | 1.15 | >0.05 | random |
| 4 | 18 | 3.30 | <0.05 | non-random/aggregate |
| 5 | 25 | 5.00 | <0.05 | non-random/aggregate |
| 6 | 29 | 7.49 | <0.05 | non-random/aggregate |
| 7 | 34 | 8.35 | <0.05 | non-random/aggregate |
| 8 | 40 | 10.02 | <0.05 | non-random/aggregate |

## REFERENCES


**Alexander, R.D.** (1961) Aggressiveness, territoriality and sexual behaviour in field crickets (Orthoptera: Gryllidae). Behaviour 17(2,3) : 130-223.

**Alexander, R.D.** (1975) Natural selection and specialised chorusing behavior in acoustical insects. In : Insects, Science and Society. Pimental, D. (ed). Academic Press, New York. pp. 35-77.

**Allan, D.M.** (1973) Some relationships of vocalisations to behaviour in the Pacific treefrog Hyla regilla. Herpetologica 29: 366-371.

**Altig, R.** (1972) Defensive behaviour in Rana areolata and Hyla avivoca. Q. Jl. Fla. Acad. Sci. 35: 212-216. Cited in: Telford, S.R. (1982).

**Anderson, M.** (1982) Female choice selects for extreme tail length in a widow bird. Nature 229: 818-820.

**Arak, A.** (1983a) Male-male competition and mate choice in anuran amphibians. In: Mate Choice. Bateson, P. (ed). pp. 181-211. Cambridge University Press, Cambridge.

**Arak, A.** (1983b) Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, Philautus leucorhinus (Rhacophoridae). Anim. Behav. 31: 292-302.

**Arak, A.** (1983c) Callers and satellites in the natterjack toad: evolutionarily stable decision rules. Anim. Behav. 36: 416-423.

**Arak, A.** (1983d) Begging, feeding and sibling competition in the natterjack toad: active choice or passive submission? Behav. Ecol. Sociobiol. 22: 317-327.

Awbrey, F.T. (1978) Social interactions among chorusing Pacific treefrogs Hyla regilla. Copeia 1978: 208-214.

Beehler, B.B. and Forester, M.S. (1988) Hotshots, hotspots and female preference in the organisation of lek mating systems. Amer. Nat. 131(2): 203-219.

Bellis, E.D. (1957) The effect of temperature on salientian breeding calls. Copeia 1957: 85-89.

Bishop, P.J. (in prep.) Aspects of social organisation in anuran choruses. (PhD Thesis).

Blackith, R.E. (1958) Nearest neighbour distance measurements for the estimation of animal populations. Ecology 39(1): 147-150.

Bogert, C.M. (1960) The influence of sound on the behavior of amphibians and reptiles. In: Animal Sounds and Communication, Amer. Instit. Biol. Sci. Publ. 7: 137-320.

Bowker, R.G. and Bowker, M.H. (1972) Abundance and distribution of anurans in a Kenyan pond. Copeia: 278-285.

Bradbury, J.W. (1981) The evolution of leks. In: Natural Selection and Social Behaviour. Alexander, R.D. and Tinkle, D.W. (eds). Chiron Press, New York. Pages 138-169.

Bradbury, J.W. and Gibson, R. (1983) Leks and mate choice. In: Mate Choice. Bateson, P (ed). Cambridge University Press, Cambridge. Pages 109-138.

Bragg, A.N. (1941) Observations on the ecology and natural history of Anura. Turtox News. 19: 10-12.

Brattstrom, B.H. and Yarnell, R.M. (1968) Aggressive behavior in two species of leptodactylid frogs. Herpetologica 24: 222-228.

Broch, J.T. (1967) Acoustic Noise Measurements. Bruël and Kjaer, Denmark.

Brower, L.P. (1969) Ecological chemistry. Sci. Amer. 220(2): 22-29.

Brown, W.C. (1952) Amphibians of the Solomon Islands. Bull. Mus. Comp. Zool. 107: 3-64.

Brown, L.E. and Brown, J.R. (1977) Comparison of environmental and body temperatures as predictors of mating call parameters in spring peepers. Am. Midl. Nat. 97: 27-51.

Brush, J.S. and Narins, P.M. (1989) Chorus dynamics of a neotropical amphibian assemblage: comparison of computer simulation and natural behaviour. Anim. Behav. 37: 33-44.

Brzoska, J; Schneider, H and Nevo, E. (1982) Territorial behavior and vocal response in male Hyla arborea savignyi (Amphibia: anura). Israel. J. Zool. 31: 27-37.

Buck, J.B. (1988) Synchronous rhythmic flashing of fireflies. Q. Rev. Biol. 13(3): 301-314.

Bunnel, P. (1973) Vocalizations in the territorial behaviour of the frog, Dendrobates pumilio. Copeia 1973: 277-284.

Camhi, J.M. (1984) Neuroethology. Sinauer Associates Inc. Publishers, Massachusetts.

Capranica, R.R. (1965) The evoked vocal response of the bullfrog. Research Monograph No. 33. M.I.T. Press, Cambridge, Mass.

Capranica, R.R. (1976) The auditory system. In: Physiology of the Amphibia Vol. III, Lofts, B. (ed), pp. 448-466. Academic Press, New York.

Capranica, R.R. and Moffat, A.J.M. (1975) Selectivity of the peripheral auditory system of the spadefoot toads (Scaphiopus couchi) determined by middle ear characteristics. J. Comp. Physiol. 100: 231-249.

Clark, P.J. and Evans, F.C. (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445-453.

Craig, C.C. (1953) On a method of estimating biological populations in the field. Biometrika 40: 216-218.

Crook, J.H. (1973) The nature and function of territorial aggression. In : Man and Aggression. Ashley-Montage, M.F. (ed). Oxford University Press, New York. pp. 183-220.

Crump, M.L. (1972) Territoriality and mating behavior in Dendrobates granuliferus (Anura: Dendrobatidae). Herpetologica 28: 195-198.

Crump, M.L. (1974) Reproductive strategies in a tropical anuran community. Misc. Pub. Mus. Nat. Hist. Univ. Kansas 61:1-68.

Crump, M.L. and Kaplan, R.H. (1979) Clutch energy partitioning of tropical treefrogs (Hylidae). Copeia 1979: 626-635.

Davies, N.B. and Halliday, T.R. (1979) Competitive mate searching in male common toads, Bufo bufo. Anim. Behav. 27: 1253-1267.

Drewry, G. (1974) Ecology of Eleutherodactylus coqui (Thomas) in montane rain forests of eastern Puerto Rico. (abstracts) 5th Annual Conf. Am.Soc. of Ichthyol. Herpetol. pp.5. Cited in : Wells, K.D. (1977a).

Duellman, W.E. (1966) Aggressive behavior in dendrobatid frogs. Herpetologica 22: 217-221.

Duellman, W.E. and Trueb, L. (1986) Biology of the Amphibia. McGraw-Hill, Philadelphia.

Dunn, E.R. (1941) Notes on Diaglena cinereus. Copeia 1941: 88-93.

Dyson, M.L. (1986) Aspects of social behaviour and mate choice in a caged population of painted reed frogs, Hyperolius marmoratus. MSc Dissertation, University of the Witwatersrand, Johannesburg.

Dyson, M.L. (1989) Aspects of social behaviour and mate choice in a caged population of painted reed frogs, Hyperolius marmoratus. PhD Thesis, University of the Witwatersrand, Johannesburg.

Dyson, M.L. and Telford, S.R. (in press) The effect of chorus density on intermale spacing in the painted reed frog, Hyperolius marmoratus. Copeia.

Emlen, S.T. (1968) Territoriality in the bullfrog, Rana catesbeiana. Copeia 1968: 240-243.

Emlen, S.T. (1972) An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 42: 130-171.

Emlen, S.T. (1976) Lek organisation and mating strategies in the bullfrog. Behav. Ecol. Sociobiol. 1: 283-313.

Emlen, S.T. and Oring, L.W. (1977) Ecology, sexual selection and the evolution of mating systems. Science 197: 215-223.

Etges, W.J. (1987) Call site choice in male anurans. Copeia 1979: 910-923.

Fairchild, L. (1984) Male reproductive tactics in an explosive breeding toad population. Amer. Zool. 24: 407-418.

Fellers, G.M. (1979) Behavioral interactions in North American treefrogs (Hylidae). Chesapeake Sci. 16: 213-219.

Fellers, G.M. (1979a) Aggression, territoriality and mating behavior in North American treefrogs. Anim. Behav. 27: 107-119.

Fellers, G.M. (1979b) Mate selection in the gray treefrog, Hyla versicolor. Copeia 1979(2): 286-290.

Feng, A.S. (1981) Directional response characteristics of single neurons in the *torus semicircularis* of the leopard frog (Rana pipiens). J. Comp. Physiol. 144: 419-428.

Feng, A.S.; Gerhardt, H.C. and Capranica, R.R. (1976) Sound localization behavior of the green treefrog (Hyla cinerea) and the barking treefrog (Hyla gratiosa). J. Comp. Physiol. 107: 241-252.

Gerhardt, H.C. (1973) Reproductive interactions between Hyla crucifer and Pseudacris ornata (Anura: Hylidae). Am. Midl. Nat. 89: 81-88.

Gerhardt, H.C. (1974) The vocalizations of some hybrid treefrogs : Acoustic and behavioural analyses. Behaviour 49: 130-151.

Gerhardt, H.C. (1975) Sound pressure levels and radiation patterns of the vocalisations of some North American frogs and toads. J. Comp. Phys. 102: 1-12.

Gerhardt, H.C. (1982) Sound pattern recognition in some North American treefrogs (Anura: Hylidae) : implications for mate recognition. Amer. Zool. 22: 581-595.

Gerhardt, H.C. (1987) Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog, Hyla cinerea. Anim. Behav. 35: 1479-1489.

Gerhardt, H.C. and Rheinlaender, J. (1980) Accuracy of sound localization in a miniature dendrobatid frog. Naturwissenschaften 67: 362-363.

Gerhardt, H.C. and Rheinlaender, J. (1982) Localisation of an elevated sound source by the green treefrog. Science 217: 663-664.

Gerhardt, H.C.; Daniel, R.E.; Perrill, S.A. and Schramm, S. (1987) Mating behavior and mating success in the green treefrog. Anim. Behav. 35: 1490-1503.

Given, F. (1987) Vocalizations and acoustic interactions in the carpenter frog, Rana virgatipes. Herpetologica 43: 467-481.

Gladstone, D.E. (1979) Promiscuity in monogamous colonial birds. Am. Nat. 114(4): 545-557.

Greer, B.J. and Wells, K.D. (1980) Territorial and reproductive behavior of the tropical American frog Centrolenella fleischmanni. Herpetologica 36: 318-326.

Halliday, T.R. (1983) Do frogs and toads choose their mates? Nature 306: 226-227.

Harrison, P.A. and Littlejohn, M.J. (1985) Diphasy in the advertisement call of Geocrina laevis (Anura: Leptodactylidae): vocal responses of males during field playback experiments. Behav. Ecol. Sociobiol. 18: 67-73.

Heintzmann, V. (1970) Untersuchugen zuv bio-acoustik und "okologie der geburstskelerkrote". Oecologica 5: 19-55. Citad in: Wells, K.D. (1977a).

Howard, R.D. (1978a) The evolution of mating strategies in bullfrogs, Rana catesbeiana. Evolution 32: 850-871.

Howard, R.D. (1981) Male age-size distribution and male mating success in bullfrogs. In: Natural selection and social behavior pp. 61-77. Alexander, R.D. and Tinkle, D.W. (eds). Chiron Press, NY.

Howard, R.D. (1984) Alternative mating behaviors of young male bullfrogs. Amer. Zool. 24: 397-406.

Howard, R.D. (1988) Sexual selection on male body size and mating behavior in American toads, Bufo americanus. Anim. Behav. 36: 1796-1808.

Howard, R.D. and Young, A.M. (1988) Precopulatory mechanisms of sexual selection in wood frogs. Evolution 42: 568-572.

Inger, R.F. (1966) Comments on the definition of genera. Evolution. 19: 370-384.

Jacobson, S.K. (1985) Mate selection and parental care in glass frogs (Centrolenidae). Herpetologica 41: 396-404.

Janzen, D.H. (1977) A note on optimal mate selection by plants. Am. Nat. (111): 365-371.

Jaslov, A.P. (1979) Vocalization and aggression in Atelopus chiriquiensis (Amphibia, Anura, Bufonidae). J. Herpetol. 13: 141-145.

Jellis, R. (1977) Bird Sounds and Their Meanings. British Broadcasting Co. Gr. Britain.

Jenssen, T.A. and Preston, W.B. (1968) Behavioral responses of the male green frog, Rana clamitans, to its recorded call. Herpetologica 24: 181-182.

Klump, G.M. and Gerhardt, H.C. (1987) Use of non-arbitrary acoustic criteria in mate choice by female gray treefrogs. Nature (Lond.) 326: 286-288.

Lambiris, A.J. (1988) A preliminary survey of the amphibians of Natal/Kwazulu. MSc Dissertation, University of Natal, Durban.

Lemon, R.E. and Struger, J. (1980) Acoustic entertainment to randomly generated calls by the frog, Hyla crucifer. J. Acoust. Soc. Amer. 67: 2096-2098.

Littlejohn, M.J. (1977) The Litoria ewingi complex in south eastern Australia. IV: Variations in mating call structure across a narrow hybrid zone. Aust. J. Zool. 24: 283-293.

Littlejohn, M.J. (1977) Long-range acoustic communication in anurans: an integrated and evolutionary approach. In: The Reproductive Biology of Amphibians. Taylor, D.H. and Guttman, S.I. (eds). pp. 263-294. Plenum Publishing Co.

Littlejohn, M.J. and Harrison, P.A. (1985) The functional significance of the diphasic advertisement call of Geocrinea victoriana (Anura: Leptodactylidae). Behav. Ecol. Sociobiol. 16: 363-373.

Littlejohn, M.J. and Martin A.A. (1969) Acoustic interaction between two species of Leptodactylid frogs. Anim. Behav. (17): 785-791.

Loftus Hills, J.J (1973) Comparative aspects of auditory function in Australian anurans. Aust. J. Zool. 21: 353-367.

Loftus Hills, J.J. and Littlejohn, M.J. (1971) Mating call sound intensities of anuran amphibians. J. Acoustic Soc. Amer. 9; 1327-1329.

Loveridge, A. (1957) Checklist of the reptiles and amphibians of East Africa. Bull. Mus. Comp. Zool. Harv. 117: 152-362.

Lutz, B. (1948) Ontogenetic evolution in frogs. Evolution 2: 29-39.

Lutz, B. (1960) Fighting and an incipient notion of territoriality in male treefrogs. Copeia 1960: 61-63.

Manning, A. (1979) An Introduction to Animal Behaviour. Edward Arnold Publishers (Ltd), U.K.

Marler, P. (1960) Bird song and mate selection. In : Lanyon, W.E. and Tavolga, W. (eds). Animal Sounds and Communication. A.I.B.S. Washington DC. pp. 648-667.

Martin, A.A. (1967) Australian anuran life histories: some evolutionary and ecological aspects. In : Australian Inland Waters and Their Fauna. Whetherley, A.H. (ed). Aust. Nat. University Press, Canberra.

Maynard-Smith, J. (1978) The theory of Evolution. Nichalls and Co., Great Britain.

Maynard-Smith, J. (1978) Optimization theory in evolution. Ann. Rev. Ecol. Syst. 9: 31-56.

McDiarmid, R.W. (1978) Evolution of parental care in frogs. In : The Development of Behavior : Comparative and Evolutionary Aspects. Burghardt, G.M. and Bekoff. M. (eds). Garland STPM Press, New York.

McDiarmid, R.W. and Adler, K. (1974) Notes on territorial and vocal behavior of neotropical frogs of the genus Centrolenella. Herpetologica 30: 75-78.

McVey, M.E.; Zahary, R.G.; Perry, D. and McDougal, J. (1981) Territoriality and homing behavior in the poison dart frog (Dendrobates pumilio). Copeia 1981(1): 1-8.

Michaud, T.C. (1964) Vocal variations in two species of chorus frogs : Pseudacris nigrita and P. clarki. Evolution 18: 489-506.

Morris, M.R. and Yoon, S.I. (1988) A mechanism for female choice of large males in the treefrog Hyla chrysoscelis. Behav. Ecol. Sociobiol. 23: 65-71.

Morris, M.R. (1989) Female choice of large males in the treefrog Hyla chrysoscelis: the importance of identifying the scale of choice. Behav. Ecol. Sociobiol. 25: 175-281.

Hughes, E.B. and Capranica, R.R. (1976) Sexual differences in the auditory system of the treefrog Eleutherodactylus coqui. Science [illegible]

Hughes, E.B. and Capranica, R.R. (1978) Communicative significance of the [illegible] of the treefrog Eleutherodactylus coqui. J. Comp. Physiol. 127: 1-9.

Narins, P.M. and Capranica, R.R. (1976) The relationship between call intensity and frequency in the treefrog Eleutherodactylus coqui. Herpetologica 32(3): 357-368.

Cummings, U. (1979) (illegible) Young readers library, Time-Life International, Nederland.

Otte, D. (1972) Simple versus elaborate behaviours in grasshoppers : an analysis of communication in the genus Syrbula. Behaviour 42(3,4): 291-322.

Pallett, J.R. and Passmore, N.I. (1988) The significance of multi-note advertisement calls in a reed frog, (Hyperolius marmoratus). Bioacoustics 1: 13-23.

Passmore, N.I. (1977) Mating calls and other vocalisations of five species of Ptychadena (Anura: Ranidae). S. Afr. J. Sci. 73: 212-214.

Passmore, N.I. (1981) The relevance of the Specific-Mate Recognition Concept to anuran reproductive biology. Italian J. Zool. 6: 93-108.

Passmore, N.I. and Carruthers, V.C. (1979) South African Frogs. Witwatersrand University Press, Johannesburg.

Passmore, N.I. and Telford, S.R. (1983) Random mating by size and age in the painted reed frog, Hyperolius marmoratus. S. Afr. J. Sci. 79: 353-355.

Passmore, N.I.; Capranica, R.R.; Telford, S.R. and Bishop, P.J. (1984) Phonotaxis in the painted reed frog (Hyperolius marmoratus): the localisation of an elevated sound source. J. Comp. Physiol. 154: 189-197.

Paterson, H.E.H. (1977) The Isolating Mechanism as a canaliser of evolutionary change. Unpublished manuscript.

Paterson, H.E.H. (1978) More evidence against speciation by reinforcement. S. Afr. J. Sci. 74: 369-371.

Paterson, H.E.H. (1982) A plea for the recognition of the unknown and unknowable. Proceedings of Conference on Biological Interpretation. S. Afr. J. Sci. 78: 113-114.

Paterson, H.E.H. (1985) Recognition or speciation by Reinforcement. S. Afr. J. Sci. 79: 52-57.

Paterson, H.E.H. (1985) The recognition concept of species. In: Species and Speciation Verba, E.S. (ed). Tvl. Mus. Pretoria, S.A.

Pengilly, R.K. (1971) Calling and associated behaviour of some species of Pseudophryne (Anura: Leptodactylidae). J. Zool. Lond. 163: 73-92.

Perrill, S.A. (1984) Male mating behavior in Hyla regilla. Copeia 1979: 727-732.

Perrill, S.A.; Gerhardt, H.C. and Daniel, R. (1978) Sexual parasitism in the green treefrog (Hyla cinerea). Science 200: 1179-1180.

Pickersgill, M. (1984) Three new Afrixalus (Anura: Hyperolidae) from South Eastern Africa. Durban Mus. Novitates 13(17): 203-220.

Pickersgill, M. (in prep.) A taxonomic evaluation of continental East African dwarf Afrixalus.

Pielou, E.C. (1962) The use of plant-to-neighbour distances for the detection of competition. J. Ecol. (50): 357-367.

Poynton, J.C. (1964) The amphibians of South Africa. A faunal study. Ann. Natal Mus. 17: 1-334.

Rabb, G.B. and Rabb, M.S. (1963) On the behaviour and breeding biology of the American gliid frog, Hymenochirus boettgeri. Z. Tierpsychol. 20: 215-241.

Rand, A.S. and Ryan, M.J. (1981) The adaptive significance of a complex vocal repertoire in a neotropical frog. Z. Tierpsychol. 57: 209-214.

Rhainds, M.; Gerhardt, H.C.; Waldman, B.; Doherty, J.D. and Carpenter, R.E. (1979) Accuracy of phonotaxis in the green treefrog (Hyla cinerea). J. Comp. Physiol. 133: 247-255.

Robertson, J.G.M. (1984) Acoustic spacing by breeding males of Uperoleia rugosa (Anura: Leptodactylidae). Z. Tierpsychol. 64: 288-297.

Robertson, J.G.M. (1986) Male territoriality, fighting and assessment of fighting ability in the Australian frog, Uperoleia rugosa . Anim. Behav. 34: 763-772.

Roble, S.M. (1985) Observations on satellite males in Hyla chrysoscelis, Hyla picta and Pseudacris triseriata. J. Herpetology 9: 1087-1089.

Rosen, M and Lemon, R.E. (1974) The vocal behaviour of spring peepers, Hyla crucifer. Copeia 1974: 940-950.

Ryan, M (1980) Female mate choice in a neotropical frog. Science 209: 523-525.

Ryan, M.J. (1982) Sexual selection and communication in a neotropical frog, Physalaemus pustulosus. Evolution 37: 261-272.

Ryan, M. (1983) Sexual selection and communication in a neotropical frog, Physalaemus pustulosus. Evolution 37: 261-272.

Ryan, M. and Rand, A.S. (1990) The sensory basis of a sexual selection for complex calls in the Tungara frog, Physalaemus pustulosis. Evolution 44(2): 305-314.

Schlie, S.M. and Moulton, J.S. (1974) Reproductive and courtship patterns. In: Physiology of the Amphibia, Vol. II. Lofts, B. (ed). pp. 310-378. Academic Press, New York.

Schiotz, A. (1963) The amphibians of Nigeria. Vidensk. Meddr. dansk. naturh. Foren. 125: 1-92.

Schiotz, A. (1974) Revision of the genus Africalus (Anura) in Easter. Africa. Vidensk. Meddr. dansk. naturh. Foren. 137: 9-18.

Schmidt, R.S. (1966) Hormonal mechanisms of frog mating calling. Copeia 1966: 637-644.

Schneider, D. (1963) Insect olfaction: deciphering system for chemical messages. Science 163: 1031-1037.

Schneider, H. (1977) Acoustic behaviour and physiology of vocalisations in the European treefrog, Hyla arborea (L). In: The Reproductive Biology of the Amphibians. Taylor, D.H. and Guttman, S.I. (eds). Plenum Publishers, pp. 295.335.

Schroeder, E.E. (1968) Aggressive behavior in Rana clamitans. Herpetologica 1: 95-106.

Schwartz, J.J (1986) Male calling behavior and female choice in the neotropical frog, Hyla microcephala. Ethology 73:116-127.

Schwartz, J.J. and Wells, K.D. (1985) Intra- and interspecific vocal behavior of the neotropical frog, Hyla microcephala. Copeia 1: 27-38.

Seymour, R.S. (1973) Energy metabolism of dormant spadefoot toads (Scaphiopus) Copeia 1973: 435-445.

Silverstone, P.A. (1973) Observations on the behavior and ecology of a Columbian poison-arrow frog, the Kokoe-pa (Dendrobates histrionicus, Berthold). Herpetologica 29: 295-301.

Silverstone, P.A. (1976) A revision of the poison-arrow frogs from the genus Phyllobates Bibron in Sagra (Family: Dendrobatidae). Nat. His. Mus., Los Angeles County Sci. Bull. 27: 1053 Cited in: Wells, K.D. (1977a).

Simon, M.P. (1983) The ecology of parental care in a terrestrial breeding frog from New Guinea. Behav. Ecol. Sociobiol. 14: 61-67.

Strayer, T.B. (1983) Female promiscuity and male reproductive success in social birds and mammals. Am. Nat. 120(1): 51-64.

Stewart, M.M. (1967) The Amphibians of Malawi. State University of New York Press, Albany, New York.

Sughrue, M. (1969) Underwater acrobatics. Brookfield Bandarlog 37: 6-10.

Sullivan, B.K. (1982) Male mating behaviour in the great plains toad, Bufo cognatus. Anim. Behav. 30: 939-940.

Sullivan, B.K. (1983) Sexual selection in Woodhouse's toad (Bufo woodhousei) II. Female choice. Anim. Behav. 31: 1011-1017.

Telford, S.R. (1982) Aspects of mate recognition and social behaviour in a sub-tropical frog community. PhD Thesis. University of the Witwatersrand, Johannesburg.

Telford, S.R. (1985) Mechanisms and evolution of intermale spacing in the the painted reed frog, Hyperolius marmoratus. Anim. Behav. 33: 1353-1361.

Telford, S.R. and Dyson, M.L. (1983) Sexual selection and the evolution of the mating system in a painted reed frog, Hyperolius marmoratus. Behav. 106: 265-278.

Telford, S.R. and Passmore, N.I. (in prep). Frequency preferences of female Hyperolius marmoratus: active choice or passive attraction?

Telford, S.R., Dyson, M.L. and Passmore, N.I. (in press) Mate choice occurs only in small choruses of the painted reed frog, Hyperolius marmoratus. Copeia.

Test, F.H. (1954) Social aggressiveness in an amphibian. Science 19: [illegible]

Thiele, R. and Bailey, W.J. (1980) The function of sound in mate spacing behaviour of the bush crickets (Tettigoniidae; Orthoptera). Aust. J. Zool. 5: 875-886.

Tihen, J.A. (1960) Comments on the origin of the amniote egg. Evolution 14: 513-516.

Townsend, D.S., Stewart, M.M. and Pough, F.H. (1984) Male parental care and its adaptive significance in a neotropical frog. Anim. Behav. 32: 421-431.

Trivers, R.L. (1972) Parental investment and sexual selection. In: Sexual Selection and the Descent of Man. Campbell, B.G. (ed). Aldine Press, Chicago, pp. 136-179.

Tuttle, M.D. and Ryan, M.J. (1982) The role of synchronized calling, ambient light and ambient noise in anti-bat predator behaviour of a treefrog. Behav. Ecol. Sociobiol. 11: 125-131.

Van Dijk, D.E. (1971) Anuran ecology in relation particularly to oviposition and development out of water. Zoologica Africana 6(1): 119-132.

Van Gelder, J.J. and Hoedemaekers, H.C.M. (1971) Sound activity and migration during the breeding period of Rana temporaria, Rana arvalis, Pelobates fuscus and Rana esculenta. J. Anim. Ecol. 40: 559-568.

Veloso, A.M. (1977) Aggressive behaviour and the generic relationships of Caudoverbera caudoverbera (Amphibia: Leptodactylidae). Herpetologica 33: 434-442.

Vehrencamp, S.L. and Bradbury, J.W. (1984) Mating systems and ecology. In: Behavioural Ecology: an Evolutionary Approach (2nd ed) Krebs, J.R. and Davies, N.B. (eds). Blackwell Scientific Publications, Oxford.

Wager, V.A. (1966) The spiny reed frogs. Afr. Wildlife 10: 319-323.

Wager, V.A. (1965) The Frogs of South Africa. Purnell and Sons, Cape Town.

Wells, K.D. (1976) Territorial behavior of the green frog (Rana clamitans). PhD Thesis, Cornell University. Cited in: Wells, K.D. (1977b).

Wells, K.D. (1977a) The courtship of frogs. In: The Reproductive Biology of the Amphibians. Taylor, D.H. and Guttman, S.I. (eds). pp. 233-261. Plenum Publishing Corporation.

Wells, K.D. (1977b) The social behaviour of anuran amphibians. Anim Behav. 25: 666-693.

Wells, K.D. (1978) Territoriality in the green frog (Rana clamitans): Vocalisations and agonistic behaviour. Anim. Behav. 26: 1051-1063.

Wells, K.D. (1980) Behavioral ecology and social organisation of a dendrobatid frog (Colostethus inguinalis). Behav. Ecol. Sociobiol. 6: 199-209.

Wells, K.D. (1981) Parental behavior of male and female frogs. In: Natural Selection and Social Behavior. Alexander, R.D. and Tinkle, D.W. (eds). Chiron Press, New York.

Wells, K.D. and Bard, K.M. (1987) Vocal communication in a neotropical treefrog, Hyla ebraccata: responses of females to advertisment and aggressive calls. Behavior 101: 200-210.

Wells, K.D. and Greer, B.J. (1981) Vocal responses to conspecific calls in a neotropical hylid frog, Hyla ebraccata. Copeia 1981(3): 615-624.

Wells, K.D. and Schwartz, J.J. (1984) Vocal communication in a neotropical treefrog, Hyla ebraccata : advertisement calls. Anim. Behav. 32: 405-420.

Whitney, C.L. (1980) The role of the encounter call in spacing of Pacific treefrogs, Hyla regilla. Can. J. Zool. 58: 75-79.

Whitney, C.L. and Krebs, J.R. (1975a) Spacing and calling in Pacific treefrogs, Hyla regilla. Can. J. Zool. 53: 1519-1527.

Whitney, C.L. and Krebs, J.R. (1975b) Mate selection in Pacific treefrogs, Hyla regilla. Can. J. Zool. 53: 1519-1527.

[illegible]lbur, H.M. (1977) Density dependent aspects of metamorphosis in Ambystoma and Rana sylvatica. Ecology 57: 1291-1296.

Wilbur, H.M.; Rubenstein, D.I. and Fairchild, L. (1978) Sexual selection in toads. The role of female choice and male body size. Evolution 32: 264-270.

Williams, G.C. (1975) Sex and Evolution Princeton University Press, New York.

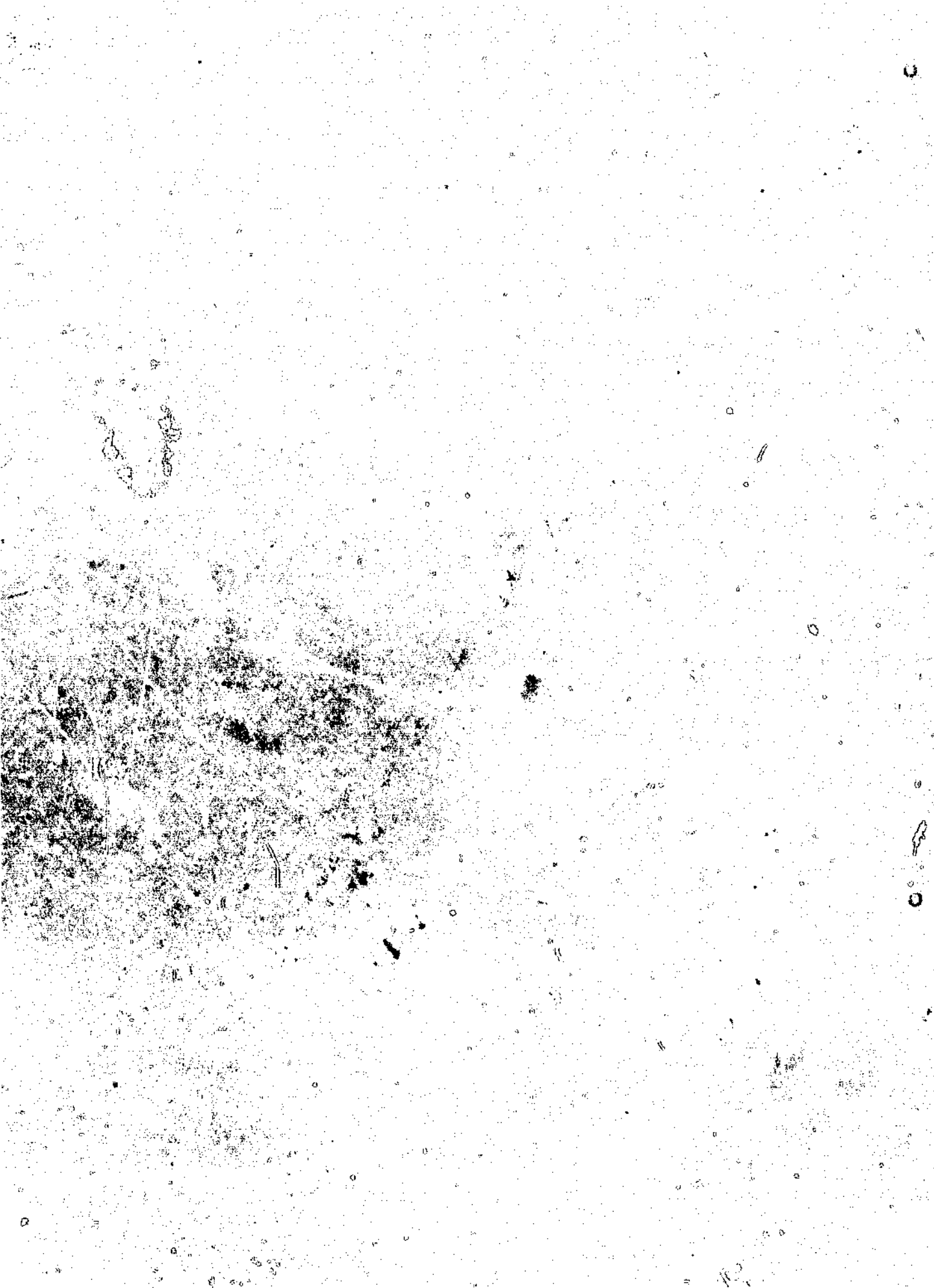
Wilson, E.O. (1975) Sociobiology Belknap Press, Harvard, London.

Woodward, B.D. (1982) Sexual selection and non-random mating patterns in desert anurans (Bufo woodhousii, Scaphiopus couchi, S. multiplicatus a .. s. bombifrons). Copeia 1982: 351-355.

Woodward, B.D. (1984) Arrival to and location of Bufo woodhousii in the breeding pond: effect on the operational sex ratio. Oecologica 62: 240-244.

Zweifel, R.G. (1968) Effects of temperature, body size and hybridization on mating calls of toads, Bufo americanus and Bufo fowleri. Copeia 1968: 269-285.





**Author: Backwell Patricia Ruth Yvonne.**
**Name of thesis: Aspects Of Reproduction In The Leaf-folding Frog, Afrixalus Delicatus.**

***PUBLISHER:***
**University of the Witwatersrand, Johannesburg**
**©2015**

***LEGALNOTICES:***

**Copyright Notice:** All materials on the University of the Witwatersrand, Johannesburg Library website are protected by South African copyright law and may not be distributed, transmitted, displayed or otherwise published in any format, without the prior written permission of the copyright owner.

**Disclaimer and Terms of Use:** Provided that you maintain all copyright and other notices contained therein, you may download material (one machine readable copy and one print copy per page)for your personal and/or educational non-commercial use only.

The University of the Witwatersrand, Johannesburg, is not responsible for any errors or omissions and excludes any and all liability for any errors in or omissions from the information on the Library website.