

https://dspace.org/

Aspects of the reproductive biology of Breviceps

Minter, Leslie Rory

2014-09-18
http://hdl.handle.net/10539/15564

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

dark spots (Fig.32c) and, in one specimen, a slightly mottled mid-dorsal band. This sample thus has characteristics of both *verrucosus* and *tympanifer* patterns.

The variability of this character within the populations sampled strengthens the view that the subspecies *verrucosus* and *tympanifer* should no longer be recognised.

* *Abdomen uniform off-white, or with brown mottlings on a yellow-white background (verrucosus pattern),* **or** *abdomen usually immaculate off-white, rarely faintly speckled (tympanifer pattern).*
All populations show a yellow colouring on the throat which, in some specimens, extends backwards across the pectoral region to the anterior abdomen (Fig.4d). This is masked in darkly pigmented specimens in which the entire gular patch is black, and the yellow colouring is only apparent in the mottled pectoral region.

Mottling, where present, is concentrated in the anterior region of the abdomen. All populations exhibit varying degrees of mottling and speckling in the lateral and anterior regions of the abdomen (Fig 4b&d). However, most specimens from Harding are immaculate white below with only three showing slight mottling laterally.

These characters are therefore of no diagnostic value in distinguishing between *tympanifer* and *verrucosus*.

* *A light line present running from heel to heel over the vent, and nearly always joined by a light line running over the urostyle (tympanifer pattern).*
This character is present in the Seymour, Stutterheim, and Lydenberg samples and absent in the Harding, Eshowe and Graskop samples, ie. it is associated with the *tympannifer* pattern. However, it also occurs to a varying extent in other species such as *B. adspersus* and *B. mossambicus*, and is thus of little diagnostic value at the species level.

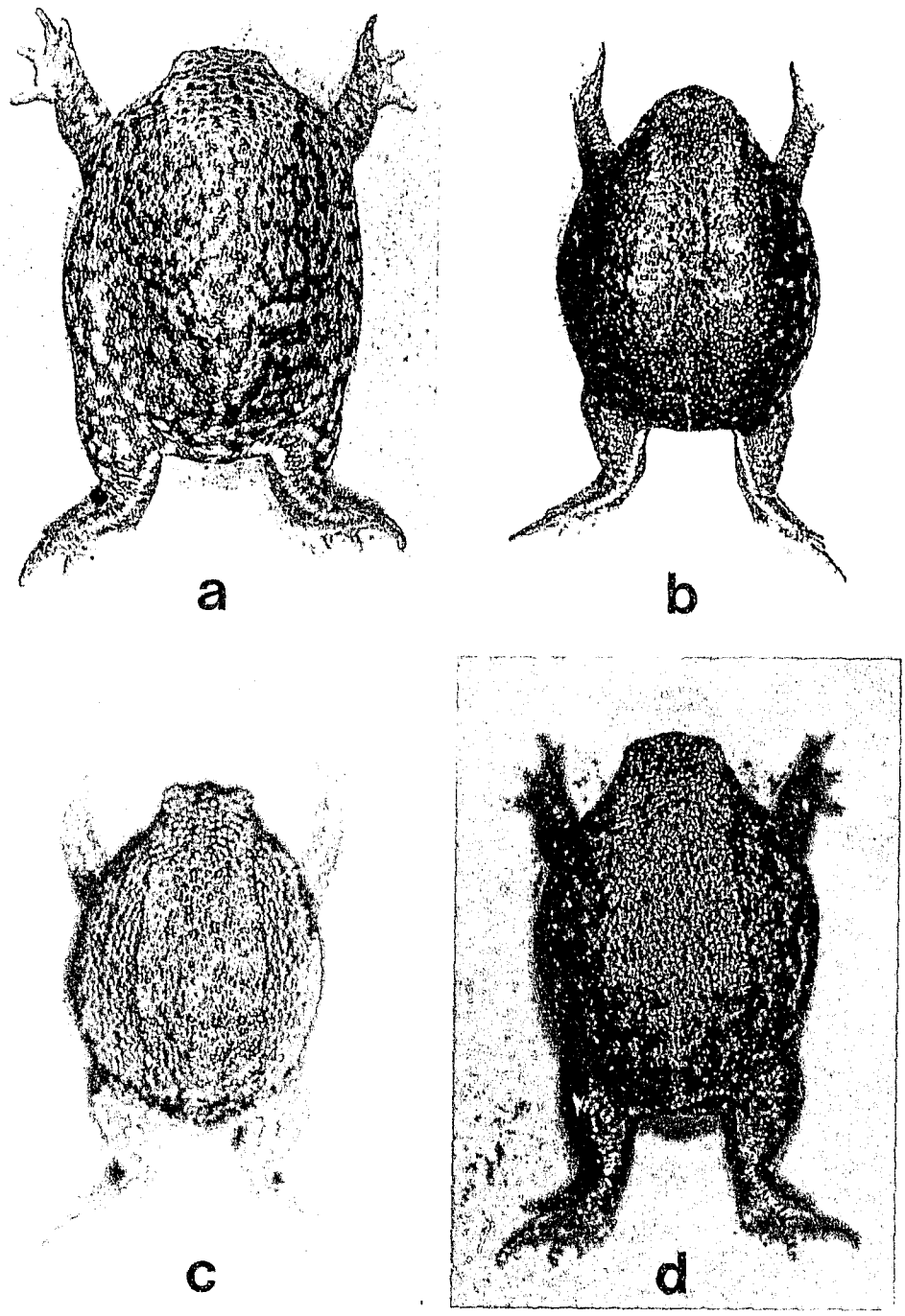


FIGURE 32. Variation in dorsal colouration of *B. verrucosus* males from: (a) Loc.45 (Seymour); (b) Loc.54 (Stutterheim); (c) Loc.6 (Eshowe); (d) Loc.27 (Lydenburg 1).

5. *Breviceps sylvestris* FitzSimons 1930

5.1 Material examined

Thirty males from two populations were examined. Both subspecies, viz: *B.s. sylvestris* and *B.s. taeniatus* are represented.

Loc. 15 (Houtbosdorp 2)	20 males	*sylvestris*
Loc. 24 (Louis Trichardt 1)	10 males	*taeniatus*

5.2 Diagnostic characters (Poynton, 1964 pp.75-76) (Fig.5a-b,)

Characters which differ in *taeniatus* are indicated in parentheses.

* *Tympanum hidden.*

The tympanum is indistinguishable in 11 specimens from both populations, ie. there are no surface features which allow one to distinguish it from the surrounding skin. All specimens bear tubercles on the tympanum, but in two *sylvestris* and two *taeniatus* specimens these tubercles are smaller and flatter than those surrounding the tympanum and the tympanic area is relatively distinct. In 15 specimens, although tubercles are present, the presence of the tympanum is indicated by a slightly raised anterior margin and smoother surface. However, this structure is certainly not as distinct as it is in *B. verrucosus*.

* *Outer toe only just reaching basal tubercle of fourth, falling far short of second (reaches as far as second in taeniatus).*

In nine *sylvestris* specimens the outer toe barely reaches the proximal subarticular tubercle of the fourth toe, while in 11 *sylvestris* and all 10 *taeniatus* specimens it reaches this tubercle but does not extend beyond it. Thus Poynton's observation that *taeniatus* has a relatively longer outer toe than *sylvestris* is not evident in these specimens.

* *Dorsal surface granular, with a pronounced ridge commencing behind each eye, converging with its opposite as far as the scapular region, then running parallel to its opposite at a distance subequal to the width of the mouth as far as the sacral region*

(glandular ridges do not converge markedly in taeniatus).
The granules are prominent with a deep central pit, similar to those of *B. verrucosus*. The texture of the skin between the glandular ridges is usually smoother than it is lateral to the ridges. Laterally, the skin is densely granular in 15 specimens and granular in 15. Between the ridges the skin is granular in 18 specimens and smooth in 12.

A pair of glandular ridges are present in all specimens (Fig.5a) but indistinct in two. Two pairs of ridges are present in three specimens: the inner pair are shorter and less prominent than the outer. In 14 *sylvestris* specimens the ridges converge markedly in the scapular region but in six specimens they converge only very slightly. In the *taeniatus* material the ridges run roughly parallel to one another in five specimens but converge slightly in five. This feature therefore has limited diagnostic value in distinguishing between the two subspecies.

* *Abdomen smooth to slightly granular (slightly granular in taeniatus).*
The surface of the abdomen is granular (23 specimens) to densely granular (five specimens), grading to smooth medially and posteriorly in 10 specimens. In two specimens the entire abdomen is smooth. No difference was apparent between *sylvestris* and *taeniatus* in respect of this character.

* *Dorsal pattern: median area between skin ridges sometimes with a few pairs of light paravertebral patches, or more generally lighter than the rest of the back, which is a uniform dark to light brown.Longitudinal glandular ridges coloured more darkly in younger specimens (in taeniatus, thick dark transverse lines lying in series down the back, pointing obliquely backwards and extending to the glandular ridges; anterior part of glandular ridge also with black markings).*
The area between the skin ridges is lighter than the rest of the dorsum in 16 *sylvestris* specimens and one *taeniatus* specimen. In all other specimens this area is neither lighter nor darker than the rest of the dorsum.

In 28 specimens light paravertebral and dorsolateral patches are present, which vary in size and conspicuousness. The light paravertebral patches alternate with darker

markings forming, in some cases, an irregular mottled pattern with only a faint suggestion of barring (Fig.5a). In other specimens the markings coalesce, forming more or less distinct light and dark transverse bars which point obliquely backwards (Fig.33a&b). This pattern is more obvious in the *taeniatus* specimens because the background colour is light brown in eight of the 10 specimens and the dark markings (black spots and blotches) contrast strongly against the light background(Fig.33a). In five *taeniatus* specimens the glandular ridge is darkened anteriorly.

In most of the *sylvestris* specimens the background colour is darker brown and the contrast is not as strong. However, the barred pattern is present to a varying degree in 16 of these specimens (Fig.33b) and is thus not restricted to *taeniatus*, although its frequency is higher in that taxon.

The degree of pigmentation varies considerably within the Woodbush population (Fig.33c&d). This population occupies closed canopy forest as well as the adjacent grassland, which may account for the great variation in markings and colouration.

* *Angle of jaw prominently light coloured.*
The broad, light margin of the down-turned mouth imparts a clown-like appearance to the face, and is a distinctive feature of this species (Fig.34). This character is well developed in 23 specimens and less distinct in seven. In three specimens which have a light gular patch, the lower margin of the "clowns mouth" is accentuated by a thin line of dark pigmentation.

* *Abdomen mottled brown on yellow-white (irregular brown markings on a cream background in taeniatus).*
It is assumed that "mottled brown"refers to confluent blotches of colour whereas "irregular brown markings"are more widely spaced. All the *taeniatus* and 11 of the *sylvestris* specimens are mottled while nine *sylvestris* specimens have more widely spaced, irregular brown blotches. The background colour of the abdomen is white in life and changes to cream or yellowish-cream after preservation.

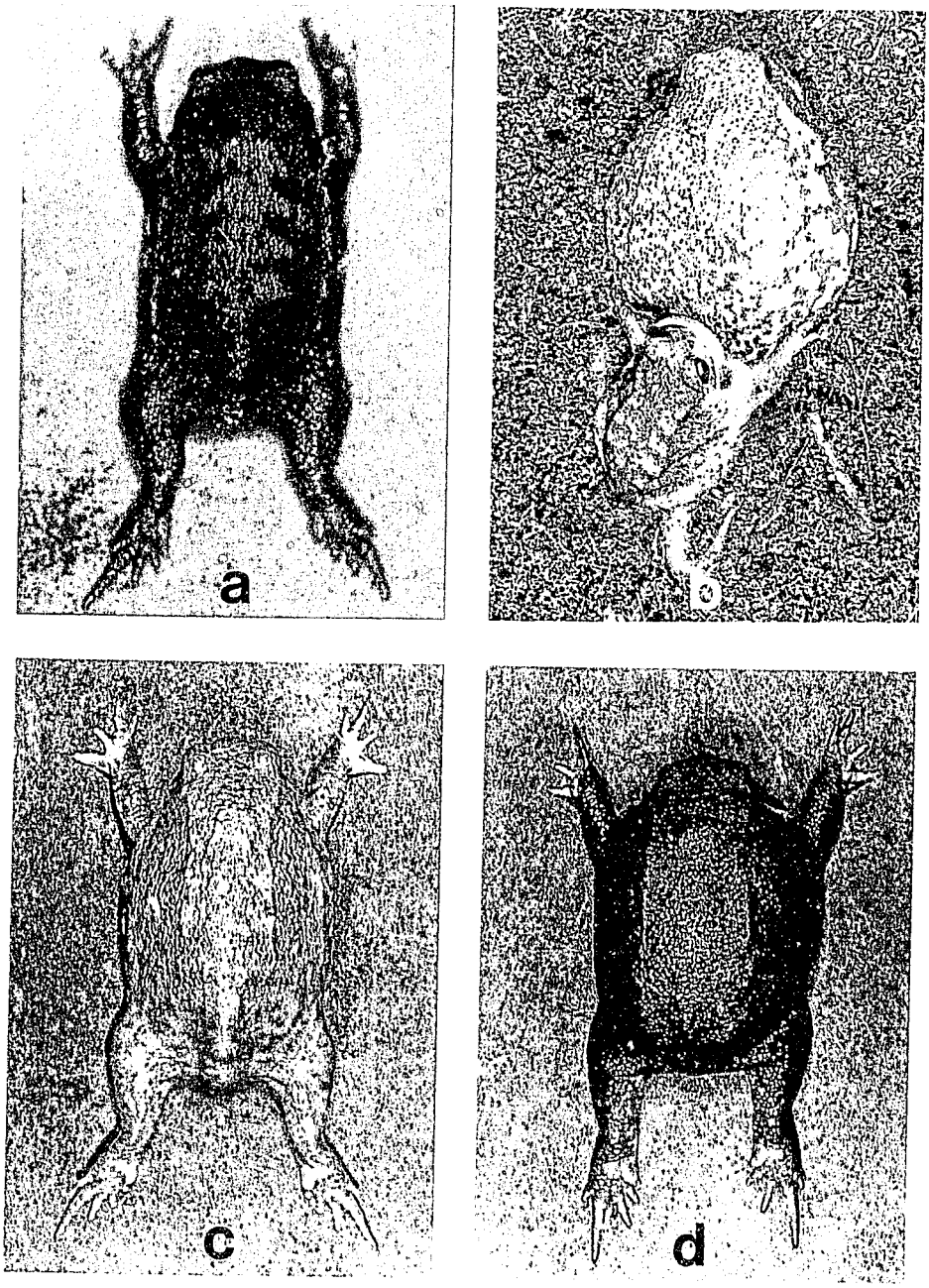


FIGURE 33. (a) Dorsal markings in a male *B.s. taeniatus* from Loc.24 (Louis Trichardt 1); (b) Dorsal markings in a male *B.s.sylvestris* of an amplexing pair from Loc.15 (Houtbosdorp 2); (c) Light pigmentation in a male *B.s. sylvestris* from Loc.15 (Houtbosdorp 2); (d) Dark pigmentation in a male *B.s. sylvestris* from Loc.15 (Houtbosdorp 2).



FIGURE 34. Distinctive light border to the mouth of a male *B.s.sylvestris* from Loc.15 (Houtbosdorp 2).

The diagnostic differences in abdominal markings and colour noted by Poynton are therefore not reflected in the material examined in this study. However, the mottled abdomen is of diagnostic value in distinguishing *sylvestris* and *verrucosus* from species that have an immaculate ventrum.

6. *Breviceps poweri* Parker 1934

6.1 Material examined

Forty males and one female specimen from Loc. 40 (Nampula) were examined.

6.2 Diagnostic characters (Poynton & Broadley, 1985 pp.525-526)(Fig.6a-b)

* *Outer finger not reaching to barely passing proximal subarticular tubercle of fourth finger.*

In all specimens the outer finger reaches or barely reaches the proximal subarticular tubercle of the fourth finger and never extends beyond it. The specimens therefore conform to this diagnostic character.

* *Inner and outer metatarsal tubercles fused to form a single continuous flange in most specimens, but more or less separated by a cleft in specimens from various parts of the range.*

The inner and outer metatarsal tubercles are united in 27 specimens, separated by a shallow groove in 12 and by a deep cleft in two. The specimens therefore conform to this diagnostic character.

* *A series of 3 to 6 dorsolateral patches present, which may be fused as an irregular light dorsolateral band.*

Well defined bright yellow or cream dorsolateral patches are present in 40 individuals, but indistinct in one very dark specimen. This appears to be a stable diagnostic character.

* *A light patch over urostylar tip, at intersection of a light heel-to-heel line and vertebral line which are usually present.*

A narrow, light vertebral line extends forward to reach the head in 31 specimens but is shorter in nine and absent in one. A light line running from heel-to-heel is present in 40 and absent in one individual. At the intersection of the vertebral and heel-to-heel lines, a light patch is clearly developed in 13 specimens, indistinct in 21 and absent in

seven. This character occurs at a lower frequency in other species, but even in *poweri* it is too variable to be of significant diagnostic value.

* *Gular region with a single uniformly darkened to marbled patch, which is separated from the dark infraorbital patch by a usually broad and uninterrupted light band from upper jaw to arm.*

The specimens conform to the first diagnostic character state in that the gular region is uniformly dark brown to black in all male specimens and mottled in the female. However, with regard to the second diagnostic character state, the dark gular and infraorbital patches are joined in 15 specimens and separated by a white stripe in 16. This stripe is broad in the female specimen and relatively narrow in males. Seven specimens show a combination of the preceding two character states.

7. ***Breviceps sp.***

7.1 **Material examined**

Eight males from Loc.51 (St Lucia 1), one from Loc.53 (St Lucia 3) and six males from Loc.22 (Komatipoort 2) were examined.

7.2 **Morphology** (Fig.25a-b)

A number of morphological characters are described below and their variability and potential diagnostic value is discussed.

* *Tympanum.*

The tympanum is not distinguishable.

* *Length of outer finger.*

The outer finger reaches the distal subarticular tubercle of the fourth finger in nine specimens and falls just short in one, while five specimens show a combination of these character states. This character distinguishes this species from *B. poweri* in which the outer finger is relatively short, but does not clearly separate it from *B. adspersus* or *B. mossambicus*.

* *Proximal subarticular tubercle of 4th finger.*

Not divided.

* *Inner and outer metatarsal tubercles.*

The inner and outer metatarsal tubercles are separated by a deep cleft in 10 specimens and by a shallow groove in four, while one specimen shows a combination of these character states. This character does not clearly separate this species from *B. adspersus* or *B. mossambicus.*

* *Length of outer toe.*

The outer toe is a stub which falls just short of the basal subarticular tubercle of the fourth toe. This character does not separate *B. sp.* from *adspersus*, *mossambicus* or *poweri*, and is therefore of no diagnostic value.

* *Light interocular bar.*

The bar is present but indistinct in 12 specimens and not distinguishable in three. This character does not distinguish this species from *adspersus* or southern populations of *mossambicus.*

* *Light paravertebral patches.*

These are present but indistinct in 13 specimens and absent in two. They are never clearly demarcated. This character state distinguishes this species from *B. adspersus*, in which these markings are usually very distinct and clearly demarcated, and from the northern Mozambique populations of *B. mossambicus* in which the markings are absent. However, this species could be confused with specimens from the southern populations of *B. mossambicus* in which the paravertebral and dorsolateral patches are indistinct.

* *Light dorsolateral patches.*

These are present but indistinct , and very faint in four specimens. The patches are fused in two specimens. The diagnostic value of these markings is the same as for the previous character.

* *Vertebral line.*

This is absent in 10 specimens, and present posteriorly, but indistinct, in five specimens from Komatipoort. Because of the variability of this character and and its presence in other species such as *adspersus* and *mossambicus*, it is of no diagnostic value.

* *Heel to heel line.*

This is absent in 11 specimens and present, but indistinct, in four. Because of its variability in this and several other species, such as *adspersus* and *mossambicus*, this character is of no diagnostic value.

* *Urostylar patch.*

Absent.

* *Gular region.*

This is uniformly dark in the nine specimens from KwaZulu/Natal. The Komatipoort sample is dark anteriorly and mottled posteriorly in four specimens, and entirely mottled in two. Because of its variability in this and several other species, such as *adspersus* and *mossambicus*, this character is of no diagnostic value.

* *Dark infraorbital patch.*

This is continuous with the gular patch in seven specimens and separated from it by a variable stripe in five. Three specimens show a combination of these character traits. This character shows a similar variability in other species, such as *adspersus* and *mossambicus*, and is therefore of no diagnostic value.

* *Abdomen.*

The ventrum is stippled or freckled laterally in nine specimens, while in four the markings form a band across the abdomen. In two specimens the abdomen is entirely stippled or freckled. While *B.a. adspersus* generally has an immaculate ventrum, speckling is present in *B.a. pentheri*. Some southern populations of *mossambicus*, eg. at Mtunzini and Eshowe, are also lightly speckled or freckled below. This character is

therefore of limited diagnostic value in separating *B. sp.* from *adspersus* and *mossambicus*.

* *Skin texture.*

The dorsum is densely covered in small granules, each bearing the opening of a gland at its apex; the ventrum is smooth. This character is of no diagnostic value in separating *B. sp.* from *adspersus* and the southern populations of *mossambicus*.

* *Colour and markings.*

The interocular bar, paravertebral patches and dorsolateral patches are light brown to cream. The dorsum medial to the dorsolateral patches varies from light golden brown to olive brown and greyish brown. Light pink patches in specimens from Komatipoort turned brown after preservation. Small dark speckles and spots are present and vary from very faint in three KwaZulu/Natal specimens, to distinct. Lateral (ventral) to the dorsolateral patches, the colour is light brown in 10 specimens and darker brown in five.

This species is very similar, in colour and markings, to certain specimens of *mossambicus* from coastal KwaZulu/Natal and the eastern escarpment.

DISCUSSION

1. The variability, function and differentiation of advertisement call and call bout characters in the *Breviceps* populations sampled.

1.1 Introduction.

The primary objective of this study is to describe the structure of advertisement calls collected from a number of natural populations of *Breviceps* and to use these data to delimit genetical species in accordance with the Recognition Concept of species.

The mate recognition function of the advertisement call is undisputed and it is generally accepted that frog calls are species specific. Numerous studies have confirmed that species differ in the selectivity of females with respect to particular acoustic properties, while there is also evidence that some call characters have little or no relevance in the context of mate recognition (Gerhardt 1988:478). In many instances it has been found that recognition involves a combination of several call characters and that the relative importance of these characters differs from one frog species to another (Introduction, 4.5). Therefore, one cannot be sure that one has successfully identified the characters of the SMRS, without conducting phonotaxis experiments, ie. "the call property or properties that are important cannot be determined unequivocally from field investigation alone" (Gerhardt, 1988:476).

Nevertheless, many cryptic species have been recognised and described primarily on the basis of differences in advertisement call structure (eg.Boycott, 1982; Channing, 1986; Passmore & Carruthers, 1975; Perret, 1985) without supporting evidence or verification by way of call discrimination experiments. Some of these species possess less obvious behavioural and/or morphological differences, which confirm their specific status. The number and extent of differences in the call, and the maintenance of these call differences in areas of sympatry with congeners are other factors which may indicate that a separate, stable SMRS has evolved.

An investigation of the mate recognition function of advertisement call characters of *Breviceps* by means of call discrimination experiments was not attempted in this study because amplexing pairs are seldom encountered. Also, receptive females in amplexus cannot be separated from the male without inflicting considerable trauma on both partners owing to the sticky secretion bonding them together. Unmated receptive females are difficult to find as they are silent and possess cryptic colouration and markings. It is likely that receptive females mate quite soon after approaching a group of calling males: eg. in *Hyperolius marmoratus* this period was estimated to be 15 minutes (Bishop, 1994).

Although it is not possible to identify with absolute certainty the call characters responsible for recognition in the *Breviceps spp.* studied, or to rank them in order of importance, several advertisement call and call bout characters exhibit a relatively high degree of stability within and between populations of the *Breviceps spp.* sampled. This is attributed to the co-adapted nature of the sender-receiver signalling system involved in mate recognition and supports the assertion that the SMRS plays a fundamental, cohesive role in genetical species. Other characters show greater variability and are therefore less likely to be important in mate recognition.

The call data reveal the presence of six groups which differ significantly in advertisement call structure. These groups are taken to represent genetical species, five of which are presently recognised, while one is an undescribed cryptic species, morphologically indistinguishable from certain of its congeners. The logical premises implicit in the Recognition Concept of species, and experimental evidence of the function of the advertisement call and its components in other frog species, support this interpretation of the call data. Four of the 62 populations sampled exhibit anomalous features which are taken to indicate the presence of hybrids.

The variability of the call bout and call characters, their relative importance in mate recognition and the differentiation of these characters among the *Breviceps spp.* sampled, is discussed below. Unless specified, figures and statistics quoted refer to unadjusted data.

1.2 Call bout characters.

1.2.1 Bout duration.

This character is highly variable and seems, from field observations, to be positively correlated with chorus intensity. However, since the latter was not measured, this correlation cannot be confirmed. It is considered unlikely that bout duration has a mate recognition function.

The call bouts of sympatric *B. mossambicus* and *B. poweri* in northern Mozambique are of similar duration and considerably shorter than those of Pietersburg *B. adspersus*. *B. verrucosus* produces, on average, markedly longer call bouts than *B. sylvestris*.

1.2.2 Call rate.

This character varies with air temperature ($r = 0.64$ for *B. adspersus*; $r = 0.60$ for *B. sylvestris*) and also appears to be positively correlated with chorus intensity (field observations). *B. adspersus, B. mossambicus* & *B. sylvestris* males were observed to increase their call rate when approached by females.

The relatively high coefficient of variation for call rate in *B. adspersus* & *B. mossambicus* may be partly due to the presence of both single and grouped calls in the call bouts of these species: since the call intervals between single calls, call groups and calls within a group differ significantly, the call rates of bouts will vary according to the percentage of grouped calls they contain. In *B. poweri*, on the other hand, almost all of the calls are grouped and the call groups are relatively large: this minimises the effect of the difference between the call interval between call groups and the interval between calls within the group. Thus the coefficient of variation for call rate in *poweri* is relatively small compared to that of *adspersus* and *mossambicus*.

In species which group their calls it is unlikely that the call rate for the bout as a whole has a mate recognition function. The call rate within call groups is a more stable character, as evidenced by the relatively low coefficient of variation of the call interval within groups (see 1.2.4 below). In the species which do not group their calls,

call rate is also relatively variable.

Although call (repetition) rate has not been implicated in mate recognition by means of call discrimination experiments (Introduction: 4.5.2), it may serve this function in some species. The present study shows that call repetition rate is the only call character which clearly separates *Breviceps verrucosus* from *B. sylvestris* (a difference in call duration is also present but there is an overlap in the range of this character in the two species). Thus, if these two allopatric taxa are indeed separate taxa, it is possible that call rate is implicated in mate recognition in these *Breviceps spp.*

Call rate appears to be fairly well differentiated among the species sampled. Allowing for the effect of temperature (mean air temperature in parentheses), it ranges from **22** min^{-1} (at 14.8 °C) in *B. verrucosus*, and **23** min^{-1} (at 19.3°C) in *B. sp.*, to **63** min^{-1} (at 15.7 °C) in *B. adspersus*, **69** min^{-1} (at 13.1 °C) in *B. sylvestris*, **106** min^{-1} (at 26.9 °C) in *B. mossambicus* and **175** min^{-1} (at 25.5 °C) in *B. poweri*.

1.2.3 The grouping of calls and the percentage of grouped calls.

Three species, all of which have calls of relatively short duration, viz: *B. adspersus*, *B. mossambicus* and *B. poweri*, group their calls within the call bout but differ in the percentage of calls grouped and in the size of the call groups (Fig. 35). While *adspersus* and *mossambicus* exhibit a fairly high degree of variation in the percentage of calls grouped, *B. poweri* males group 94-100% of their calls (Table 43). The grouping of calls also appears to be positively correlated with chorus intensity (field observation). Despite its variability, this character usually enables one to distinguish these species easily and accurately in the field. *B. verrucosus*, *B. sylvestris* and *B. sp.*, which produce calls of relatively long duration, never group their calls.

The variability of these characters suggests that they do not play an important role in mate recognition. However, it is possible that they form part of a suite of characters recognised by the female, or that they function in male-male interactions.

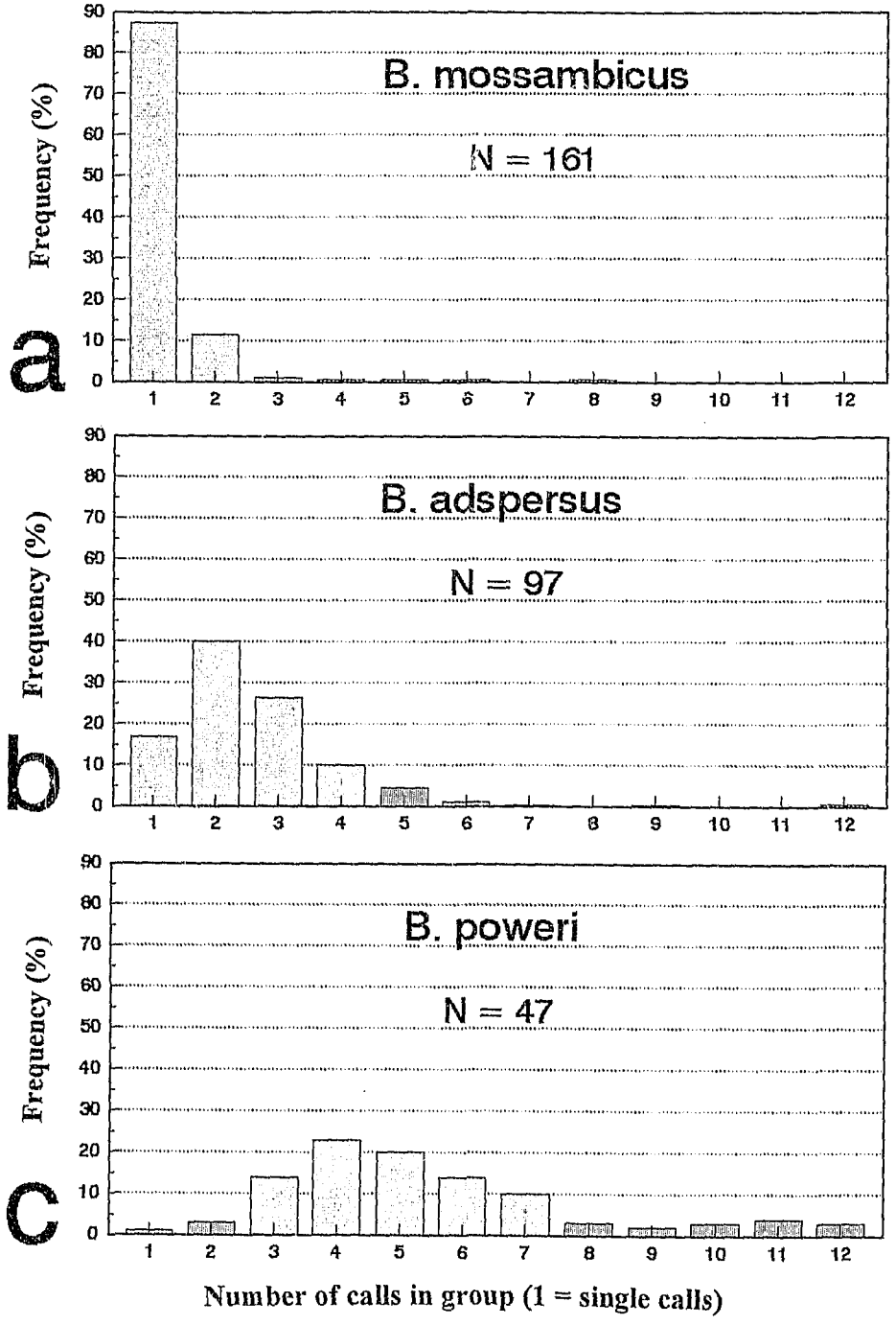


FIGURE 35. Histograms showing the relative frequency of single & grouped calls in the call bouts of: (a) *B. mossambicus*; (b) *B. adspersus*; and (c) *B. poweri*.

In spite of their variability within species, these call bout characters are fairly well differentiated among the species sampled. Perhaps the shortening and grouping of calls on the one hand, and the lengthening of ungrouped calls on the other, represent alternative strategies for increasing their attractiveness to females.

1.2.4 Call interval.

In the species which group their calls, the interval between single calls, call groups, and between calls within a call group differs considerably. Within each of these categories of call interval, variation is relatively low: in *B. poweri* the coefficient of variation in the call interval within call groups is 8.4 (Table 43), while in *adspersus* and *mossambicus* it is 20.7 and 23.1 respectively (Tables 1 & 13). Call interval varies to a similar extent in the species which do not group their calls: eg. the coefficient of variation is 12.8 in *B. verrucosus* (Table 39) and 20.7 in *B. sylvestris* (Table 42).

Call interval is negatively correlated with air temperature: eg. correction of the *adspersus* data results in a reduction of the coefficient of variation from 20.7 to 15.9 (Table 4).

While call interval has not been specifically linked to mate recognition in other frog species, the relative stability of this character in species such as *poweri, adspersus & verrucosus* suggests that it may be involved in mate recognition or in male-male interactions.

Among the species that group their calls, the mean call interval within groups is shortest in *poweri* (0.24s), longer in *mossambicus* (0.27s) and longest in *adspersus* (0.54s). Call interval is longer in the other species: 0.88s in *sylvestris* and 2.16s in *verrucosus*. Thus this character has also undergone considerable differentiation in some of the species sampled.

1.3 Advertisement call characters.

1.3.1 Dominant frequency.

Of all the call characters analysed in this study, dominant frequency has the lowest coefficient of variation: this is further reduced by correction of the data to a common body mass, due to the negative correlation which exists between these two variables. This character is also the least variable call character in *Acris crepitans*, and Ryan (1988) has suggested that spectral characters are more conservative than temporal characters because they are primarily under morphological (passive) control rather than behavioural or physiological (active) control.

In the *Breviceps spp.* sampled, the dominant frequency of the call falls within the range of the basilar papilla, ie. above 1.2kHz (Zakon & Wilczynski, 1988). Phonotaxis experiments involving several frog species in which the call falls within this frequency range, have shown that females prefer calls in which the frequency is closest to the population mean (Introduction, 4.5.3). In these species the receptors of this papilla are tuned to a narrow range of best frequencies which correspond to the minimum SPL required to elicit a response. However, as SPL rises, the receptors respond over an increasingly broader frequency range. Thus the species specificity of the frequency component of the advertisement call seems to be more important at a distance (low SPL) whereas at close quarters the female's preference is influenced to a greater extent by the relatively higher SPL.

On the basis of a variety of four-choice phonotaxis experiments, Bishop et al. (1995) suggest that in a small natural chorus, females of *Hyperolius marmoratus* are unable to identify the loudest male in the group, provided that the majority of males' calls fall within the normal inter-individual SPL range of 5-6dB. They conclude that the large-male mating advantage observed by Telford et al. (1989) in small choruses is based on the females' ability to perceive differences in dominant frequency, a character linked to body mass. In large choruses no large-male mating advantage has been observed. It is probable that at close quarters SPL overrides female preference based on frequency and a two-choice situation develops in which females are attracted to the louder

signal, which is usually the closer male. In this species, the only trait that predicts male mating success in the field is call rate (Passmore et al. 1992), and this is not linked to body size. Once the male becomes aware of the female's presence (visual cues) he may increase the attractiveness of his call by increasing the call rate.

It is therefore possible that in *Breviceps*, dominant frequency has an important mate recognition function at the periphery of the chorus but that as the female nears the males she is attracted to the louder and/or faster call. Females of *B. verrucosus*, *B. sylvestris* and *B. sp.* that sometimes call from elevated positions have two possible advantages over males calling from the surface: they may minimise the attenuation and degradation of their calls and maximise the range, and they might also notice approaching females earlier than males calling from the surface.

Little differentiation in respect of dominant frequency has taken place among the *Breviceps* species sampled, with the exception of *B. sp.* in which the mean frequency of 3237Hz (mean body mass: 2.02g), is 750Hz higher than that of the southern populations of *B. mossambicus* (2480Hz; mean body mass: 2.39g). The dominant frequency of southern *mossambicus* populations, when adjusted to the mean mass of the northern populations (8.14g) is very similar (1856Hz and 1835Hz respectively). These mean frequencies are not far removed from those of *adspersus* (1743Hz; 6.43g), *verrucosus* (1830Hz; 9.04g), *sylvestris* (1741Hz; 7.24g) and *poweri* (1728Hz; 6.89g), even when the differences in mean body mass are taken into consideration.

The absence of marked differentiation in dominant frequency among several of the *Breviceps* species does not preclude this character from forming part of the SMRS. The members of a suite of SMRS characters may differentiate at different rates: it is their combined effect which ultimately determines whether or not a speciation event has taken place. Ryan (1988) found that call characters in *Kassina* and *Smilisca* have undergone mosaic evolution, with characters changing at different rates.

1.3.2 Call duration.

This temporal call variable is negatively correlated with air temperature, a factor

which tends to obscure its relative stability. For example, in *B. adspersus*, the coefficient of variation for call duration is reduced from 17.97 to 13.53 when the data are adjusted to a common air temperature of 18°C. Allowing for the effect of temperature, the variability of this character is relatively low in all the other species. The high coefficient of variation (39.21) for call duration in the combined southern populations of *B. mossambicus* (Table 31) is probably due to the wide temperature range (7.4 - 29.5°C) over which the data were collected. Correction of these data to a common temperature would reduce the variability considerably: this was not possible because the samples of *B. mossambicus* (northern sample) and *B. verrucosus* did not yield significant correlation coefficients.

The relative stability of this character suggests that it too functions in mate recognition. However, most frog species investigated by means of phonotaxis experiments do not appear to discriminate between calls on the basis of their duration (Introduction: 4.5.2). In those species that do show a preference for normal calls, this preference is SPL dependent. A few species show a preference for longer calls. In *Bombina bombina*, *B. orientalis* and *Rana temporaria* the call must have a minimum duration in order to elicit a response, but beyond this, duration does not appear to affect recognition (Walkowiak, 1988).

In these *Breviceps* species, there is considerable differentiation in call duration: this is a useful aid to identification in the field. Calls increase in duration from *mossambicus*, through *poweri*, *adspersus*, *sylvestris*, and *verrucosus* to *B. sp.* The uncorrected call duration data of species with pulsed calls, and the ranges in air temperature are illustrated in Figs 36 & 37 respectively.

An analysis of the evolution of call characters in the genera *Kassina* and *Smilisca* (Ryan, 1988) suggests that temporal characters, which are under behavioural and physiological (active) control are less conservative than spectral characters, which are determined by morphology (passive control). Similarly, in *Breviceps*, greater divergence is observed in call duration and number of pulses than in dominant frequency. This connection, if it indeed exists, has not been satisfactorily explained.

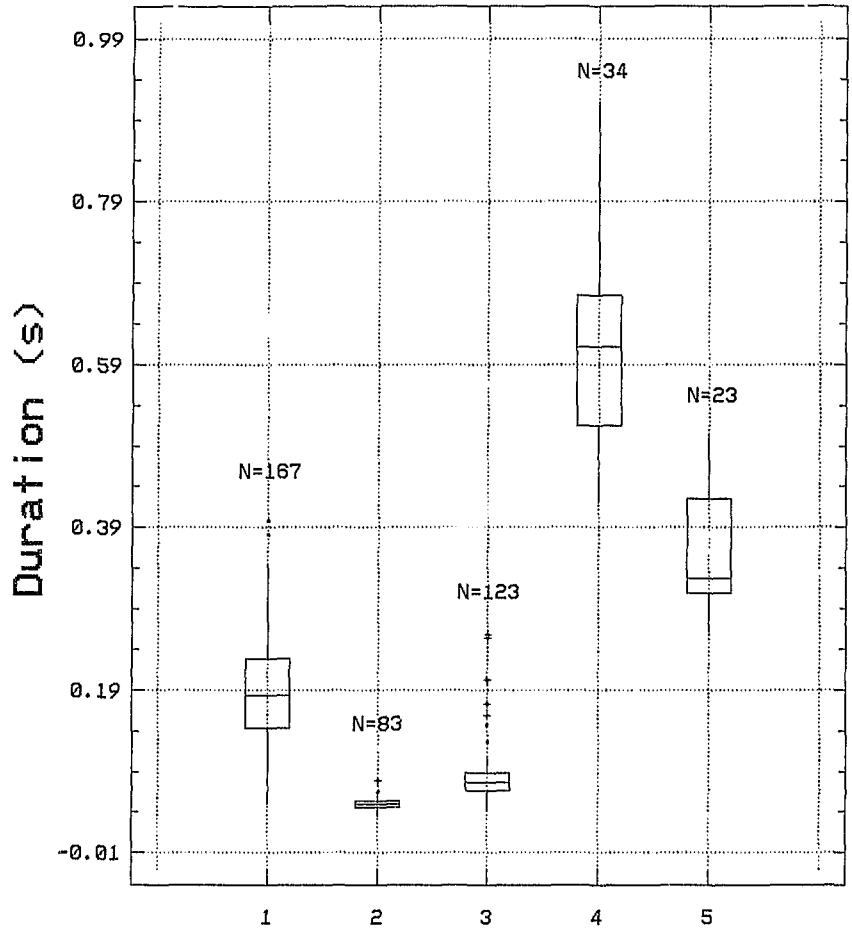


FIGURE 36. Box & whisker plots of unadjusted call duration in: 1. *B.a. adspersus*; 2. northern *B. mossambicus*; 3. southern *B. mossambicus*; 4. *B. verrucosus*; 5. *B. sylvestris*. The plot divides the data into four areas of equal frequency and the median is represented by the horizontal line in the box.

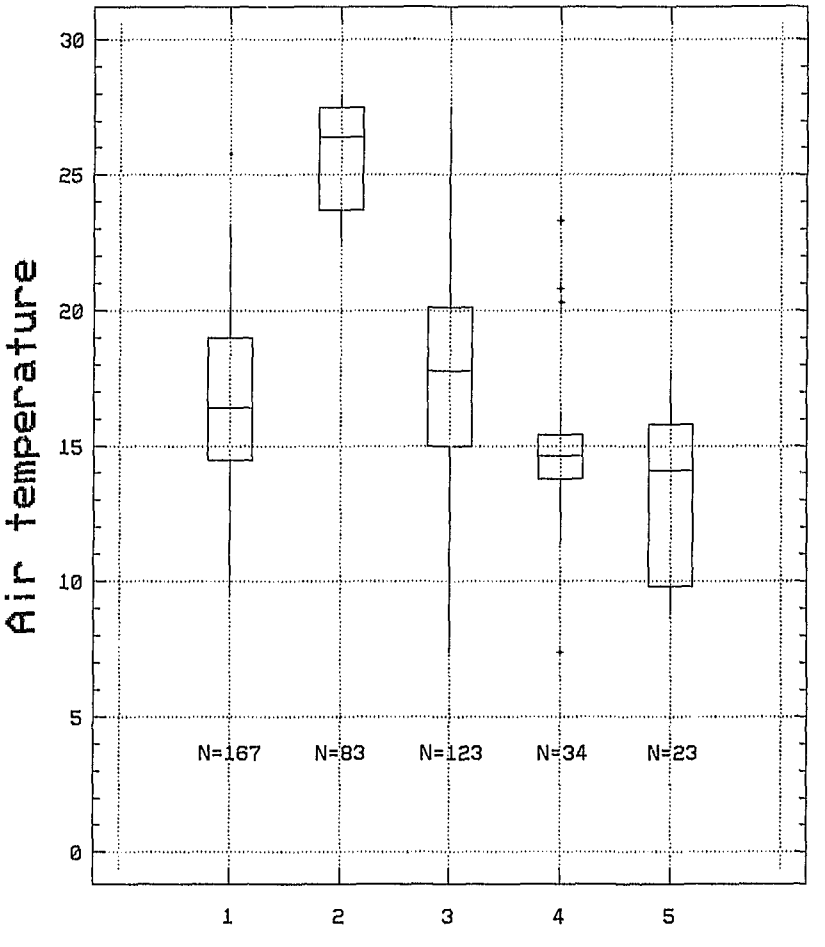


FIGURE 37. Box & whisker plots of air temperature for the samples 1 - 5 represented in Fig. 36.

1.3.3 Number of pulses.

In the four species that modulate the amplitude of their calls, this temporal variable is not correlated with air temperature and is relatively stable. *B. adspersus, B. sylvestris* and the northern populations of *B. mossambicus* are less variable with respect to this character than are *B. verrucosus* and the southern populations of *B. mossambicus*. The masked amplitude modulation in the call of *B. poweri* (Results: Advertisement calls, 6.2.2; Fig. 24) is an interesting phenomenon which invites further investigation.

Several species of *Hyla* are able to differentiate between pulsed and unpulsed calls, and it has been shown that in this respect the basilar papilla is more sensitive than the amphibian papilla (Introduction, 4.5.2). There is therefore a strong possibility that amplitude modulation forms part of a suite of mate recognition characters in *Breviceps*.

While the effect of varying the number of pulses has not been investigated experimentally, shortening of the duration of the call while maintaining the pulse rate necessarily reduces the number of pulses. Such experiments therefore simultaneously test the effect of variation in duration and pulse number.

Ryan (1988) notes that frogs which use the basilar papilla encode species recognition in temporal characters rather than spectral characters. It is therefore interesting that the call of *B. sp.* contains no temporal parameters other than call duration, a rather variable character. In this species, dominant frequency may be the main call character facilitating mate recognition.

The species of *Breviceps* with amplitude modulated calls are well differentiated with respect to the number of pulses in the call (Figs 7&8).

1.3.4 Pulse rate.

This call character is also positively correlated with temperature. Correction of the data to a common temperature of 18°C reduces the coefficient of variation considerably (Figs 38 & 39). For example in *adspersus* it drops from 22.41 to 13.81, in southern

mossambicus from 28.71 to 18.86, in *verrucosus* from 12.51 to 10.19 and in *sylvestris* from 25.12 to 6.89.

The relative stability of this character suggests that it also forms part of the SMRS. Pulse rate has been implicated in mate recognition in a number of other frog species (Introduction, 4.5.2). Since *Breviceps* calls fall within the range of the basilar papilla, temporal characters are likely to be more important than spectral characters in encoding species recognition (Ryan 1988).

The species of *Breviceps* sampled in this study do not exhibit marked differentiation in respect of pulse rate, unlike many other genera, where pulse rate is highly differentiated and has an important mate recognition function. Although the calls of *Breviceps* species that occur in sympatry or parapatry, eg: southern *mossambicus* and *verrucosus*; southern *mossambicus* and *sylvestris*; and *adspersus* and *sylvestris*, do not differ significantly in pulse rate, they have differentiated in respect of duration and/or dominant frequency.

The absence of marked differentiation in pulse rate does not preclude this character from forming part of the SMRS: on the contrary, its stability suggests that this is the case.

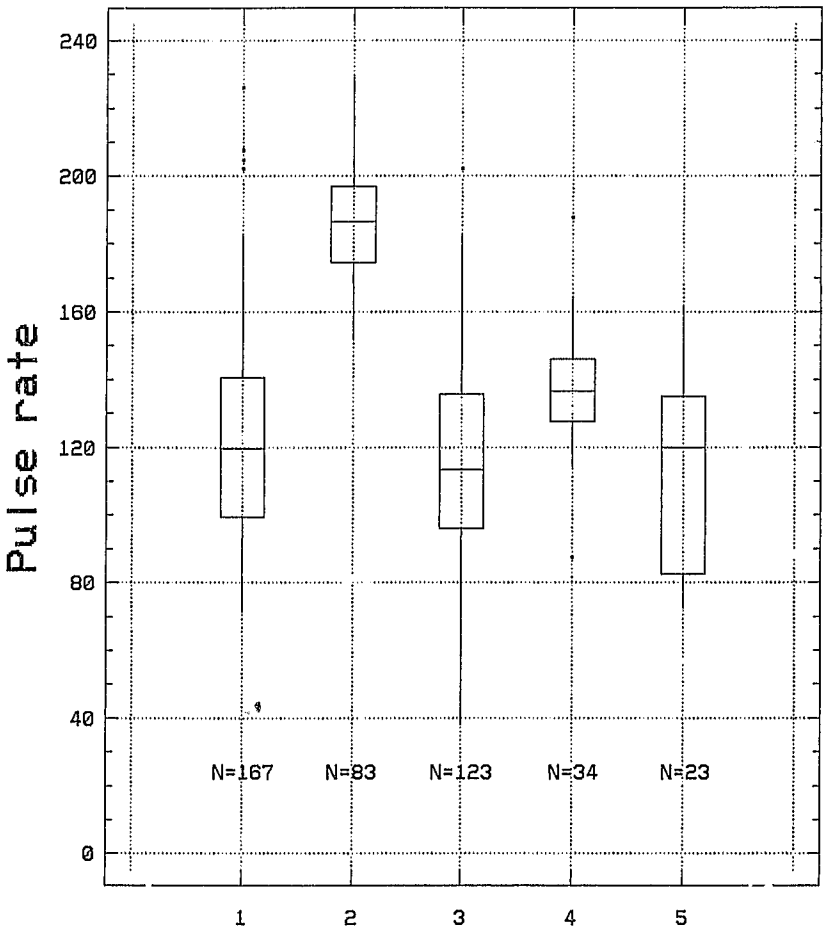


FIGURE 38. Box & whisker plots of unadjusted pulse rate in: 1. *B.a. adspersus*; 2. northern *B. mossambicus*; 3. southern *B. mossambicus*; 4. *B. verrucosus*; 5. *B. sylvestris*. The plot divides the data into four areas of equal frequency and the median is represented by the horizontal line in the box.

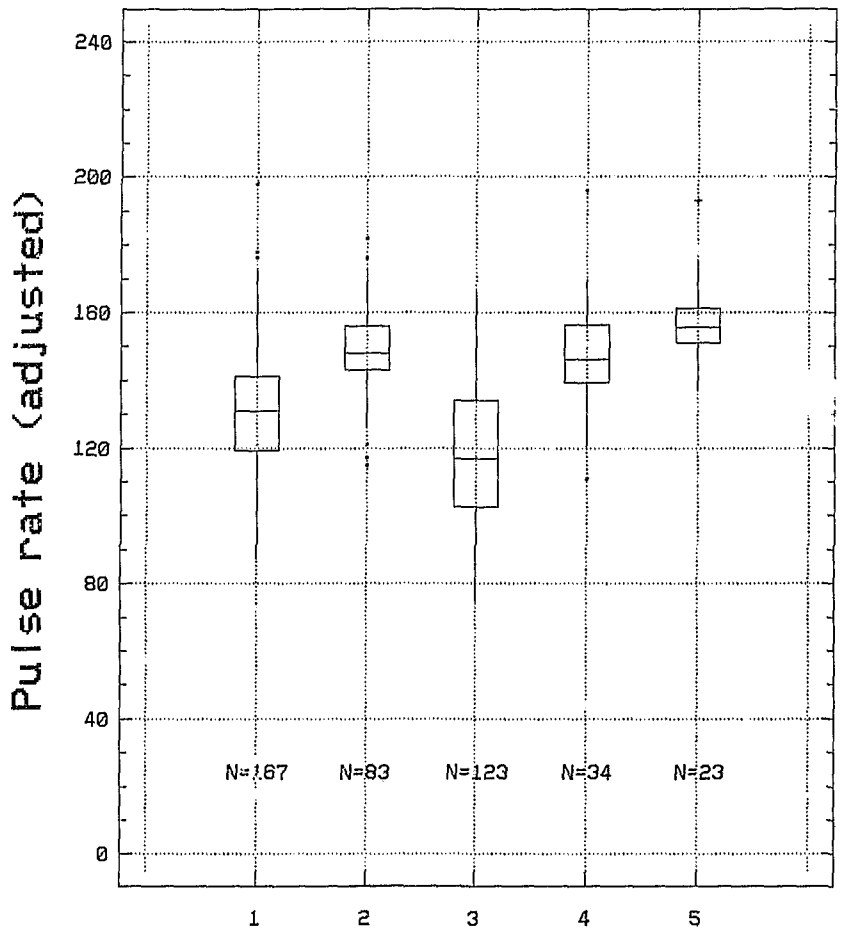


FIGURE 39. Box & whisker plots of pulse rate adjusted to 18°C in: 1. *B.a. adspersus*; 2. northern *B. mossambicus*; 3. southern *B. mossambicus*; 4. *B. verrucosus*; 5. *B. sylvestris*. The plot divides the data into four areas of equal frequency and the median is represented by the horizontal line in the box.

2. Taxonomic implications of the advertisement call data and morphology.

2.1 *Breviceps adspersus*

2.1.1 *B.a. adspersus*

Populations assigned to this taxon occupy semi-arid woodland habitats with sandy soils in the Northern Province and Mpumalanga. The assumption that these populations are conspecific is based on strong similarities in advertisement call structure and the absence of significant inter-population variation. Hybridization is suspected in three adjacent population samples in KwaZulu/Natal (Loc.16: Ingwavuma and Loc. 49&50: Sihangwane 4&5, see 3.1 below), in which the advertisement call structure is unusually variable, but all other population samples are comparatively homogeneous.

The advertisement calls of *B.a. adspersus* and *B. mossambicus* are similar in that they are both pulsed, grouped within the bout and have similar dominant frequencies and pulse rates. However, *B.a. adspersus* is clearly differentiated from the northern and southern populations of *B. mossambicus* with regard to call duration, the number of pulses in the advertisement call, the percentage of grouped calls and the size of call groups within the call bout. These differences are quite obvious in areas of parapatry along the eastern escarpment of South Africa and Swaziland. The advertisement call data therefore support the present taxonomic status of *B.a. adspersus*.

In morphology, *B. adspersus* can be distinguished from the northern Mozambique *mossambicus* populations by their light dorsal markings, but not from the southern coastal and escarpment populations. None of the other "diagnostic" morphological characters examined in this study, viz: the relative length of the outer finger, relationship between the inner and outer metatarsal tubercles, pigmentation of the gular patch, and presence or absence of continuity between the gular and interorbital patches, clearly distinguishes these two species from one another or from the *B. sp. nov.* Thus, at present, these species are separated solely on differences in advertisement call structure.

2.1.2 *B.a. pentheri*

The small sample of advertisement calls from populations in the Eastern Cape Province differs somewhat from the *B.a. adspersus* samples in having fewer pulses and a shorter duration, but the ranges of these variables overlap. There is therefore insufficient justification for recognising these populations as a separate species. The taxon *B.a. pentheri* is therefore retained but its distribution is restricted to the Eastern Cape Province.

It must also be noted that the advertisement call of *B.a. pentheri* is, in some respects, intermediate between *B.a. adspersus* and *B. mossambicus*. The relationship between *pentheri* and these other taxa therefore requires further investigation.

Populations from the eastern escarpment of KwaZulu/Natal, Swaziland and Mpumalanga which were previously referred to *B.a. pentheri* are, on the basis of advertisement call structure, referred to *B. mossambicus*.

B.a. pentheri differs morphologically from *B.a. adspersus* in having a more granular skin and a freckled chest and throat. Other characters examined proved to be of no diagnostic value in separating the two subspecies. However, none of these characters has significant diagnostic value in separating *pentheri* from the coastal and escarpment populations of *mossambicus*. A study of populations in the areas between the known ranges of *pentheri*, *adspersus*, and *mossambicus* is needed in order to shed more light on the relationships between these taxa.

2.2 *Breviceps mossambicus*

Northern populations of this species from the type locality (Mozambique Island) and the adjacent mainland have markedly similar advertisement calls and are clearly conspecific.

Similarly, southern populations from coastal KwaZulu/Natal and the eastern escarpment of South Africa and Swaziland are considered to be conspecific on the basis of

similarity in advertisement call structure, in spite of considerable variation in size, skin texture, colouration and markings (Figs 17, 29&30). The observed morphological differences are probably due to crypsis: i.e. they represent adaptations to the colour, texture, pattern and illumination of the substrates and surrounding topography of their various habitats.

Three populations in KwaZulu/Natal, viz: Jozini, Mkuze and Durban, have slightly different calls (see 3.2, below). However, in most respects these calls resemble those of *B. mossambicus*, and the populations are therefore assigned to this taxon.

This study also shows that, after correction of the call data to a common temperature and mass, the southern populations are indistinguishable from the northern populations with regard to advertisement call structure, and are therefore conspecific with northern *B. mossambicus*.

Since the southern populations of *mossambicus* possess lighter markings previously regarded as characteristic of *adspersus*, these morphological characters now have no diagnostic value. Other morphological characters regarded by Poynton & Broadley as diagnostic of *mossambicus* are shown, in this study, to be of little value in distinguishing between *mossambicus*, *adspersus* and *B. sp. nov.*

The southern populations of *B. mossambicus* may be sufficiently distinct from the northern populations, morphologically, to justify the erection of a subspecies. However, it is not presently known whether this morphological differentiation is the result of a geographical barrier such as, e.g. the Zambezi River, or whether the variation is clinal in nature. It is necessary to obtain samples from the intervening area before subspecific status can be assigned to the southern populations.

2.3 *Breviceps poweri*

In Nampula (Loc.40), this species occurs in sympatry with *B. mossambicus*. The calls of the two species are very different and little variability is present within each popu-

lation. Calls recorded from a population of *poweri* in Zambia, 1450km WNW of Nampula, by Prof. A. Channing, do not differ significantly from the Nampula sample.

The advertisement calls are characterised by being unpulsed and are emitted in relatively large groups within the call bout. The call data confirm that *B. poweri* is a valid genetical species with a wide distribution. No evidence of hybridization between *poweri* and *mossambicus*, *poweri* and *adspersus*, or *mossambicus* and *adspersus* was found in any of the call samples from northern Mozambique.

The relatively short outer finger and distinct dorsolateral patches are strong diagnostic characters which distinguish *poweri* from *adspersus* and *mossambicus*. The light urostylar patch is a less consistent character than indicated by the specimens at the disposal of Poynton & Broadley, and is therefore of less diagnostic value. Similarly, the presence of a single continuous flange formed by the fusion of the metatarsal tubercles will identify some, but not all, *poweri* individuals.

Morphological similarities, the grouping of the calls and the presence of masked pulses in the advertisement call of *poweri* (Results, 6.2.2; Fig.24) suggest that this species is closer, phylogenetically, to *adspersus* and *mossambicus* than to the other species dealt with in this study.

2.4 *Breviceps verrucosus*

This species is easily distinguished from the previous three species on the basis of its long, ungrouped advertisement call. On the other hand, the calls of *verrucosus* and *sylvestris* are quite similar, differing in call rate and duration, with some overlap in the ranges of the latter character.

Morphologically, *verrucosus* is characterised by a relatively longer outer toe than all of the other species studied, except *sylvestris*, where there is some overlap in the range of this character. The tympanum is more distinct in *verrucosus* than in *sylvestris*, and is, with very few exceptions, indistinguishable in individuals of the other species. The

presence of glandular, dorsal ridges also distinguishes *verrucosus* and *sylvestris* from the other species.

The variation in colouration and markings of different populations, which has resulted in the recognition of the subspecies *B.v. verrucosus* and *B.v. tympanifer*, is attributed to crypsis in the wide range of habitats occupied by this species, viz: coastal bush, closed canopy forest and montane grassland. There appears to be no justification for the recognition of these two subspecies.

The range of *B. verrucosus* is extended northwards as far as the Blyde River Canyon, south of the Olifants river.

2.5 *Breviceps sylvestris*

This species appears to be closely related to *B. verrucosus*, both in morphology and advertisement call structure. The advertisement calls of the two species differ in call rate and call duration although there is some overlap in their ranges with regard to the latter character. Since they were not found in sympatry it was not possible to confirm their specific status on this basis. In view of the relatively small differences in their advertisement calls, it could be argued that *B. sylvestris* is no more than a northern subspecies of *B. verrucosus*. Further investigation is therefore necessary in order to explore this possibility.

B. sylvestris is characterised by a slightly shorter toe than *B. verrucosus*, and a less distinct tympanum, but shares many of the characters which distinguish *verrucosus* from the other species. Among these are the glandular ridges on the dorsum, the deeply pitted granules, the mottled ventrum and the yellow pigmentation of the gular patch and pectoral region.

The advertisement calls of the subspecies *B.s. sylvestris* and *B.s. taeniatus* show no significant differences. Furthermore, the diagnostic morphological characters separating the two subspecies, viz: the presence in *taeniatus* of transverse dorsal bars, and

the alignment of the glandular ridges, are of limited value. The subspecies are retained in view of their allopatric distribution and slight morphological differentiation.

2.6 *Breviceps sp.*

This study reveals the existence of an undescribed cryptic species of *Breviceps*. The advertisement call differs markedly from those of all other species in the area sampled. It is characterised by a relatively high dominant frequency, long duration and is unusual in that it lacks temporal partitioning of the sound energy into pulses and call groups.

Morphologically, this species is indistinguishable from southern *B. mossambicus*, but can be separated from *B.a. adspersus* and *B. poweri* by the stippled or freckled ventrum. Also, *adspersus* and *poweri* have more distinct paravertebral and dorsolateral patches respectively.

This species occupies a variety of habitats, viz: coastal forest, sand, moist montane forest and dry, mixed woodland, and therefore it cannot be distinguished on the basis of habitat preferences.

3. Evidence of hybridization between the species sampled.

3.1 Localities 16 (Ingwavuma), 49 & 50 (Sihangwane 4 & 5).

These samples, assigned to *B.a. adspersus*, shows an unusually high coefficient of variation in call duration and the number of pulses. Some individuals give short, grouped calls similar in every respect to *B.a. adspersus*, while others give longer, ungrouped calls. Since hybrid advertisement calls are usually intermediate between those of the two parental populations, and assuming that one of the parental species is *B.a. adspersus*, it is possible that the individuals giving the longer, ungrouped calls are hybrids between *B.a. adspersus* and a species that has even longer, ungrouped calls. The only species that fits this description is *B. verrucosus*. Populations of *B. verrucosus* were not encountered in the immediate vicinity: the closest population of

verrucosus sampled in this study was at Eshowe, 200km south of these localities.

Morphologically, the specimens resemble *B.a. adspersus*, except that in 4 individuals, one iris is golden (as in *adspersus*), and the other, dark brown (as in *verrucosus*).

3.2 Localities 35 (Mkuze), 17 (Jozini 1) & 5 (Durban).

While these samples have a similar dominant frequency to the other coastal populations of *B. mossambicus*, the number of pulses and duration of the advertisement call are somewhat intermediate between that of *adspersus* and *mossambicus* (Fig.40). Also, the grouping of the calls within the call bout is intermediate between that of *adspersus* and *mossambicus* (Fig.41 cf. Fig.35a&b). It is interesting that although the body mass in the Mkuze sample is almost twice that of the Jozini sample, the mean dominant frequency of the former is actually higher (2383Hz) than that of the latter (2242Hz). This is not what one would expect considering the correlation which exists between body mass and call frequency. It is possible that these populations contain hybrids between *adspersus* and *mossambicus*.

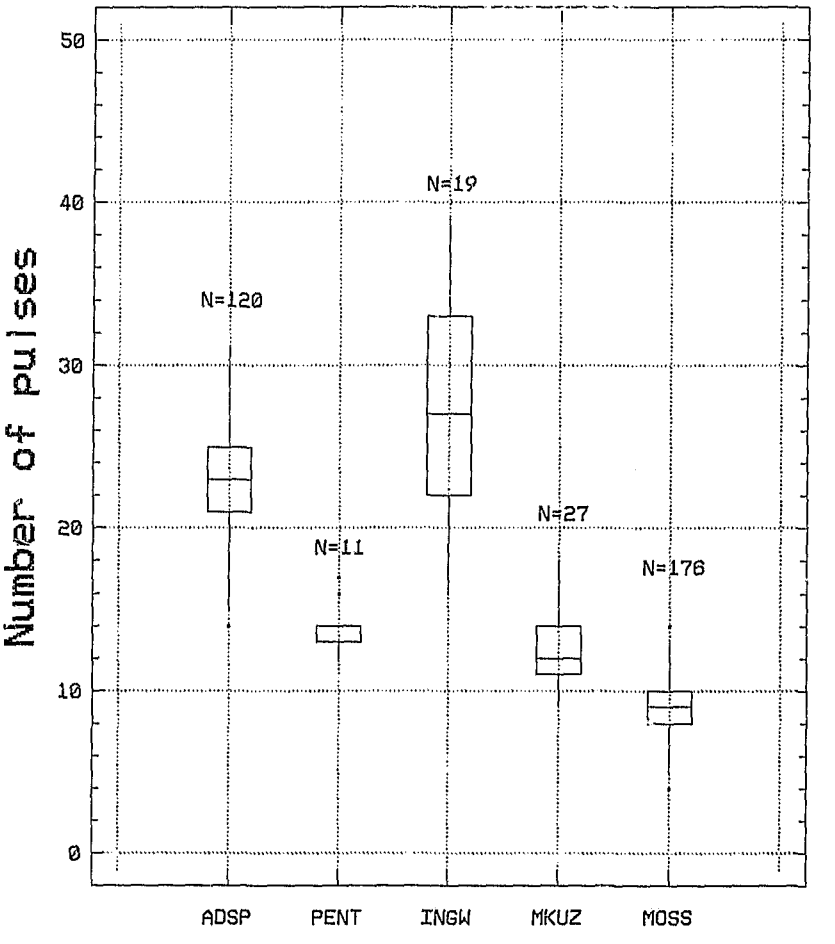


FIGURE 40. Box & whisker plot of the number of pulses in the calls of *B.a. adspersus* (ADSP), *B.a. pentheri* (PENT), the populations at Locality 16 (INGW), 35, 17 & 5 (MKUZ), and *B. mossambicus* (MOSS). The plot divides the data into four areas of equal frequency and the median is represented by the horizontal line in the box.

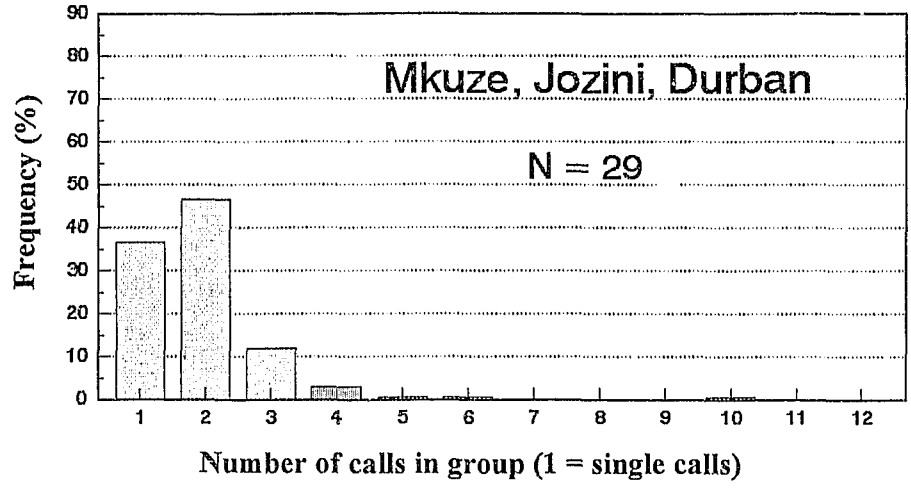


FIGURE 41. Histogram showing the relative frequency of single and grouped calls in the call bouts of samples from Loc.35 (Mkuze), Loc.17 (Jozini 1) and Loc.5 (Durban).

3.3 General remarks.

Apart from the examples cited above, all other populations are relatively homogeneous with regard to advertisement call structure and do not show signs of hybridisation. These data do not, therefore, support the hypothesis that extensive hybridisation occurs between *adspersus* and *mossambicus* in northern Zululand.

Geographic variation in other frog species has been attributed to habitat differences, environmental clines and geographical isolation (eg. Ryan & Wilczynski, 1991). Since most of the *Breviceps* species sampled in this study occupy a wide range of habitats, and are relatively non-vagile, a certain amount of geographical variation is to be expected, even in call structure. It is therefore possible that the geographical variation observed in some populations of *B. adspersus* and *B. mossambicus* may be due to genetic divergence rather than hybridization.

4. Synopsis.

This study advances our knowledge of the taxonomy and distribution of members of the genus *Breviceps* in the following ways:

* A detailed description of the structure of the advertisement calls of six *Breviceps spp.* is provided for the first time.
* An undescribed, cryptic species of *Breviceps* is discovered.
* *B. adspersus* and *B. mossambicus* are characterised on the basis of advertisement call structure: the data do not support the hypothesis (in litt.) that extensive hybridisation between these species occurs.
* The taxon *B.a. pentheri* is retained pending further investigation, but its distribution is restricted to the Eastern Cape Province.
* Island populations of *B. mossambicus* in northern Mozambique are shown to be conspecific with adjacent mainland populations.
* *Breviceps* populations in KwaZulu/Natal and along the eastern escarpment are shown to be conspecific with the northern *B. mossambicus* populations.
* The specific status of *B. poweri* is confirmed: it has a unique advertisement call and shows no signs of hybridisation with the sympatric *mossambicus* population.
* Several species are found to occupy a wide variety of habitats and to exhibit considerable variation in colouring and markings.
* The recognition of the subspecies *B.v. verrucosus* and *B.v. tympanifer* is not supported by the data.
* *B. verrucosus* and *B. sylvestris* are shown to be closely related, and possibly conspecific.
* The data indicate that a variety of call characters may be involved in mate recognition in these *Breviceps spp.*, and that during speciation some characters have diverged while others have remained relatively unchanged.

This study of the advertisement calls of *Breviceps* has added a behavioral perspective to the taxonomy which has previously been based almost entirely on morphology. The specific-mate recognition function of the call certainly makes it a good

taxonomic character at the species level but, in the absence of phonotaxis experiments, the variation in advertisement call structure between populations sometimes presents the taxonomist with the same kind of dilemma as does morphological variation - indecision as to what kind and degree of difference in the call indicates that a speciation event has taken place.

The advertisement calls in some *Breviceps* species are quite distinct while others seem not to have diverged very far from one another. Certain call characters are more stable than others, suggesting that they have a more important recognition function. These characters show the least variation within populations but some variation between populations was found.

In cases where the calls are clearly differentiated it is easy to justify the recognition of separate species but sometimes the situation is not as clear. Such instances require more extensive sampling, electrophoretic evidence and experimental work involving phonotaxis, before a clearer picture will emerge and an informed decision can be taken.

This study of advertisement call structure in a number of *Breviceps* populations illustrates the interplay of **chance** and **necessity** in biological systems. The element of chance, embodied in phenomena such as mutation and genetic recombination and tailored by natural selection, produces geographic variation in advertisement calls which may ultimately lead to a speciation event. At the same time, the stability of advertisement call characters at the population and species levels is a consequence of the necessity that mate recognition be facilitated by an efficient, co-adapted system.

APPENDIX A

POPULATION LOCALITIES:

Specimens, calls, or aural records referred to in the text of this thesis were collected at the localities listed below. In some instances, populations of more than one species were present at the same locality. Each locality description comprises: nearest town (distance and direction in parentheses) and/or place name; Province or, if outside South Africa, Country; specific site details; grid reference and altitude (taken from the South Africa 1:50 000 Topographical Map series); veld type of the region in general (Acocks, 1988), followed, in parentheses, by a structural description of the vegetation (following Edwards, 1983) at the site; and slope (gentle = 0 - 15°; moderate = 16 - 30°; and steep = > 30°).

1. **Addo Elephant Park**, Eastern Cape; in the vicinity of the boom at the main entrance to the Park; 33'S 25° 41'E; alt. 40m; Valley bushveld (low thicket); sandy soil; gentle slope.

2. **Belfast**, Mpumalanga; NW perimeter of town; 25° 41'S 30° 02'E; alt. 1850m; North-eastern sandy highveld (low closed grassland); sandy loam soil between scattered dolerite boulders; gentle slope.

3. **Burchenough Bridge** (30 Km W), Zimbabwe; roadside; 19° 55'S 32°E; alt. 750m; Mopani veld (grassy tall closed woodland); sandy soil in rocky terrain; gentle slope.

4. **Dullstroom** (18Km N), Mpumalanga; roadside at highest point on the Steenkampsberg; 25° 15'S 30° 07'E; alt. 2200m; North-eastern sandy highveld (low closed grassland); sandy loam; moderate slope.

5. **Durban**, KwaZulu/Natal; University of Natal campus; 29° 51'S 31°E; alt. 80m; Coastal forest and thornveld (cultivated lawns and gardens); sandy loam; gentle slope.

6. **Eshowe**, KwaZulu/Natal; residential gardens and parks; 28° 53'S 31° 28'E; alt. 530m; Ngongoni veld (cultivated lawns and gardens, and low closed grassland); sandy loam; no slope.

7. **Grahamstown**, Eastern Cape; rocky slopes on eastern perimeter and the botanical gardens; 33° 18'S 26° 32'E; alt. 550m; False macchia (short closed shrubland and short closed grassland); sandy loam; moderate slope.

8. **Graskop 1** (10KmN), Mpumalanga; Paradise Camp ; 24° 52'S 30° 52'E; alt. 1550m; North-eastern mountain sourveld (short closed grassland with patches of short forest); sandy loam soil; gentle slope.

9. **Graskop 2** (34Km N), Mpumalanga; Bourke's Luck Potholes; 24° 40'S 30° 48'E; alt. 1150m; North-eastern mountain sourveld (grassy tall open shrubland); sandy loam soil between scattered quartzite outcrops; gentle slope.

10. **Haenertsburg 1** (6KmNNE), Northern Province; farm Goedvertrouwen; 23° 53'S 29° 57'E; alt. 1480m; North-eastern mountain sourveld (tall moist forest and short closed grassland); clay loam soil; moderate slope.

11. **Haenertsburg 2** (13Km SE), Northern Province; Serala Wilderness Area; garden of forestry station on farm Klipdraai, and in Seralakop indigenous forest; 24° 03'S 30° 01'E; alt. 1520m; North-eastern mountain sourveld (short closed grassland and tall moist forest); clay loam soil; moderate slope.

12. **Harding**, (16Km W), KwaZulu/Natal; leaf litter on roadside and adjacent forest floor in Wesa Forest Reserve; 30° 32'S 29° 42'E; alt. 1200m; Ngogoni veld (tall moist forest); clay loam; steep slope.

13. **Hoedspruit** (28Km SW), Northern Province; farm Chester; 24° 29'S 31° 01'E; alt. 1100m; Arid lowveld (grassy short open woodland); sandy soil; gentle slope.

14. **Houtbosdorp 1**, Northern Province; lower NW slopes; 23°49'S 29°54'E; alt.1400m: Sourish mixed bushveld (grassy short closed woodland); sandy soil; gentle slope.

15. **Houtbosdorp 2** (6.5Km E), Northern Province; Dap Naude Dam; grassy and forested slopes at NW side of Dam; 23° 49'S 29° 58'E; alt. 1600m; North-eastern mountain sourveld (tall moist forest and short closed grassland); clay loam soil; moderate to steep slope.

16. **Ingwavuma** (12Km E), KwaZulu/Natal; at T-junction of tar road from Jozini with the road from Ingwavuma to Kosi Bay; 27° 07'S 32° 06'E; alt. 240m; Lowveld (grassy short openwoodland); sandy soil; no slope.

17. **Jozini 1**, KwaZulu/Natal; rocky undeveloped land in the town; 27° 26'S 32° 04'E; alt 250m; Zululand thornveld (grassy short closed woodland), sandy loam; gentle slope.

18. **Jozini 2** (5Km W), KwaZulu/Natal; western slopes of Lebombos; 27° 28'S 32° 01'E; alt. 350m; Tall moist forest; sandy loam; steep slope.

19. **Jozini 3** (23Km N), KwaZulu/Natal; eastern slopes of Lebombos; 27° 18'S 32° 05'E; alt. 200m; Zululand thornveld (grassy low open woodland); sandy loam; gentle slope.

20. **King William's Town** (10Km SW), Eastern Cape; disturbed agricultural land along the main road; 33°S 27° 15'E; alt. 500m; Valley bushveld (tall closed grassland); sandy loam; gentle slope.

21. **Komatipoort 1**, Mpumalanga; developing residential area on outskirts of town; 25°26'S 31° 57'E; alt. 150m; Lowveld (grassy short open woodland); sandy soil; gentle slope.

22. **Komatipoort 2**, (2Km S), Mpumalanga; copse of trees on side of road to Ressano Garcia, just before turnoff to Swaziland; 25° 27'S 31° 58'E; Lowveld (grassy short closed woodland - Acacia nigrescens); clay loam; gentle slope.

23. **Lake Kosi**, KwaZulu/Natal; 26° 57'S 32° 49'E; alt. 30m; Coastal forest and thorn-veld (grassy tall open woodland and short closed grassland); sandy soil; no slope.

24. **Louis Trichardt 1**, Northern Province; Hanglip Forestry Reserve on wetter S slopes of Soutpansberg; at picnic area in the forest, and in grassland outside the forest; 23°S 29° 53'E; alt.1300m; North-eastern mountain sourveld (high forest and short closed grassland); clay loam; gentle slope.

25. **Louis Trichardt 2** (10Km N), Northern Province; Ingwe Motel on N slopes of Soutpansberg; lawns and gardens; 22° 58'S 29° 56'E; alt. 1250m; North-eastern mountain sourveld (short dry forest); clay loam; gentle slope.

26. **Lumbo**, (20Km W), Mozambique; under trees on roadside 2Km W of turnoff to Mossuril; 14°59'S 40°30'E; alt. 100m; Lowveld (grassy short closed woodland); sandy soil; noslope.

27. **Lydenburg 1** (15KmESE), Mpumalanga; near monument at the top of Long Tom Pass; 25° 08'S 30° 36'E; alt. 2100m; North-eastern mountain sourveld (grassy short sparse shrubland); sandy loam; no slope.

28. **Lydenburg 2** (23Km NNW), Mpumalanga; roadside on steep rocky northern slopes near the bottom of Waterfall River Pass; 24° 54'S 30° 19'E; alt. 1250m; Sourish mixed bushveld (short closed woodland); sandy loam; steep slope.

29. **Manzini**, Swaziland; vacant residential land in suburbs; 26° 29'S 29° 56'E; alt. 620m; Lowveld sour bushveld (short closed grassland); sandy loam; no slope.

30. **Maputo**, Mozambique; garden bed of Natural History Museum in city centre; 25°57'S 32°35'E; alt. 50m; sandy loam; no slope.

31. **Mbabane 1** (7Km SW), Swaziland; Hilltop; 26° 23'S 31° 06'E; alt. 950m; North-eastern mountain Sourveld (short closed grassland); sandy loam; gentle slope.

32. **Mbabane 2** (14Km SSE), Swaziland; alongside steep section of main road between Mbabane and Manzini; 26° 21'S 31° 09'E; alt. 1050m; North-eastern mountain sourveld (disturbed short closed grassland); sandy loam; moderate slope.

33. **Mbabane 3** (20Km N), Swaziland; Malolotja Nature Reserve; 26° 08'S 31° 07'E; alt. 1380m; North-eastern mountain sourveld (short closed grassland); sandy loam; gentle to steep slopes.

34. **Mica**, Northern Province; farm Parsons; 24° 10'S 30° 55'E; alt.400m; Arid lowveld (grassy short closed woodland); sandy soil; no slope.

35. **Mkuze**, KwaZulu/Natal; undisturbed land on outskirts of town; 27° 37'S 32° 02'E; alt. 130m; Lowveld (grassy short closed woodland; sandy clay soil; no slope.

36. **Mozambique Island**, Mozambique; public park next to Fort on northern end of Island; 15°02'S 40°44'E; alt. 5m; sandy soil; no slope.

37. **Mtunzini**, KwaZulu/Natal; farm Twin Streams; newly planted canefields, open grassland and coastal bush; 28° 49'S 31° 42'E; alt. 60m; Coastal forest and thornveld (short closed grassland and short thicket); sandy soil; no slope.

38. **Mutare 1** (30 Km S), Zimbabwe; roadside; 19° 10'S 32° 35'E; alt. 1100m; Brachystegia speciformis veld - Zambezi lowland type (grassy short closed woodland); sandy soil; no slope.

39. **Mutare 2** (40Km SE), Zimbabwe; mountainside above Burma Valley ; 19° 10'S 32° 44'E; alt. 1700m; Montane Themeda/Loudetia grassland (tall closed grassland); sandy loam; moderate slope.

40. **Nampula** (2KmE), Mozambique; cashew plantation 1Km N of main road to coast; 15°06'S 39°20'E; alt. 450m; sandy soil; no slope.

41. **Paterson** (24Km W), Eastern Cape; roadside at intersection with road to Addo; 33° 26'S 25° 43'E; alt. 100m; Valley bushveld (short closed grassland); sandy soil; no slope.

42. **Pietersburg**, Northern Province; Dalmada; 23° 52'S 29° 32'E; alt. 1350m; Pietersburg plateau false grassveld (grassy short sparse woodland); sandy soil; gentle slope.

43. **Piet Retief** (8Km W), Mpumalanga; farm Welverdiend 148, next to main road, on banks of Assegaai River; 27° 03'S 30° 44'E; alt. 1100m; Highland sourveld and Dohne sourveld (low closed grassland); sandy loam; gentle slope.

44. **Pilgrim's Rest** (20Km W), Mpumalanga; Mount Sheba Nature Reserve; 24° 56'S 30° 37'E; alt. 1800m; North-eastern mountain sourveld (short closed grassland); sandy loam; gentle slope.

45. **Seymour** (15Km N), Eastern Cape;viewsite at top of Nico Malan Pass ; 32° 28'S 26° 46'E; alt. 1500m; Highland sourveld and Dohne sourveld (short closed grassland); loam soil; steep slope.

46. **Sihangwane 1**, KwaZulu/Natal; campsite at Tembe Elephant Reserve; 27° 03'S 32° 25'E; alt. 100m; Lowveld (grassy short closed woodland); sandy soil; no slope.

47. **Sihangwane 2** (6Km W), KwaZulu/Natal; on the western boundary of Tembe Elephant Reserve; 27° 03'S 32° 22'E; alt. 55m; Lowveld (grassy short closed woodland); sandy soil; noslope.

48. **Sihangwane 3** (8Km NW), KwaZulu/Natal; on the western boundary of Tembe Elephant Reserve; 26° 59'S 32° 23'E; alt. 75m; Lowveld (grassy short closed woodland); sandy soil; no slope.

49. **Sihangwane 4** (15Km W), KwaZulu/Natal; heavily wooded area along tar road; 27° 03'S 32° 17'E; alt. 50m; Lowveld (grassy tall closed woodland); sandy soil; no slope.

50. **Sihangwane 5** (17Km W), KwaZulu/Natal; on west bank of Pongolo River; 27° 03'S 32° 15'E; alt. 50m; Lowveld (grassy short closed woodland); sandy soil; no slope.

51. **St. Lucia 1**, KwaZulu/Natal; forest and lawns in Natal Parks Board grounds; 28° 22'S 32° 25'E; alt. 40m; Coastal forest and thornveld (tall moist forest and short closed grassland); sandy soil; no slope.

52. **St. Lucia 2** (Km N), KwaZulu/Natal; Mission Rocks; 28° 16'S 32° 30'E; alt. 50m; Coastal forest and thornveld (grassy short closed woodland); sandy soil; no slope.

53. **St. Lucia 3** (12Km W), KwaZulu/Natal; picnic area in Dukuduku Forest Reserve; 28° 23'S 32° 18'E; alt. 50m; Coastal forest and thornveld (tall moist forest); sandy soil; no slope.

54. **Stutterheim**, Eastern Cape; grassy field just south of forestry reserve; 32° 33'S 27° 22'E; alt. 880m; Highland sourveld and Dohne sourveld (low closed grassland); sandy loam; no slope.

55. **Trichardtsdal** (20KmE), Northern Province; entrance to Legalameetse Nature Reserve at the bottom of Orrie Baragwanath Pass ; 24° 09'S 30° 13'E; alt.1020m to 1340m; Lowveld sour bushveld to North-eastern mountain sourveld (short closed woodland, through tall moist forest to short closed grassland); sandy soil through clay loam tosandy loam.

56. **Wakkerstroom** (12Km ENE), Mpumalanga; farm Tafelkop; 27° 18'S 30° 16'E; alt. 1900m; Highland sourveld and Dohne sourveld (low closed grassland); sandy loam; steep slope.

57. **White River**, (10Km N), Mpumalanga; between granite outcrops next to main road; 25° 14'S 31° 01'E; alt. 1000m; Lowveld sour bushveld (grassy short sparse woodland); sandy soil; gentle slope.

APPENDIX B

DISTRIBUTION MAPS:

The positions of the localities at which samples of the various *Breviceps spp.* were collected are shown on the following distribution maps (Figs. 42-47).

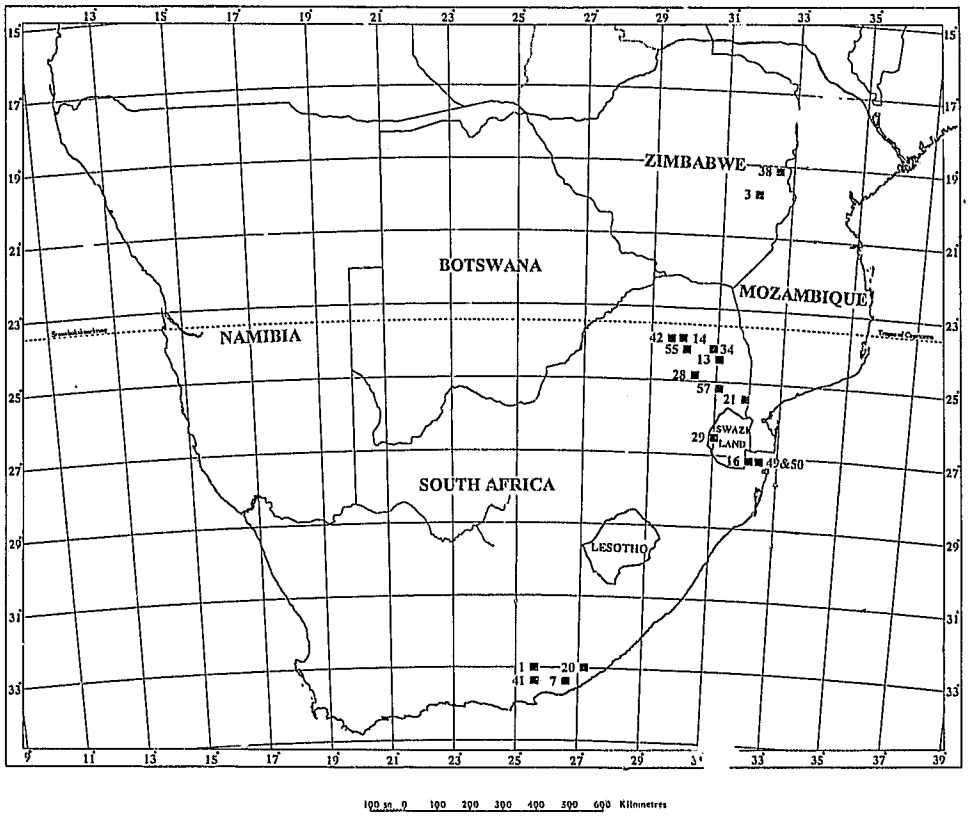


FIGURE 42. Location of populations assigned to *B. adspersus.*

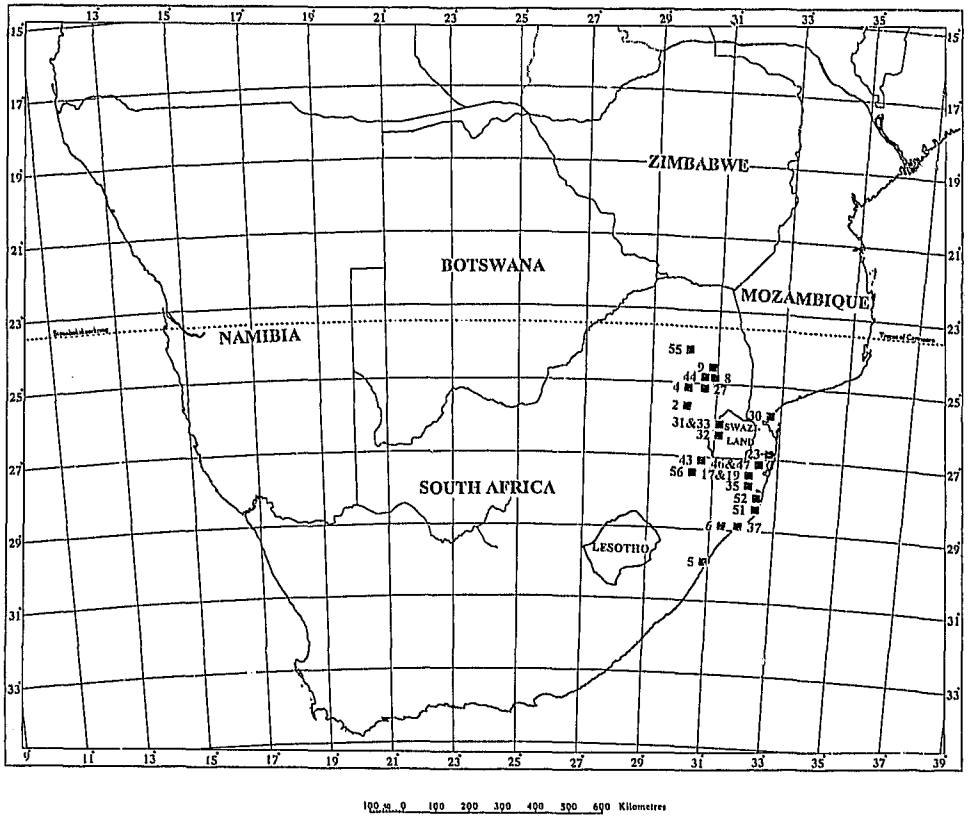


FIGURE 43. Location of southern populations assigned to *B. mossambicus*.

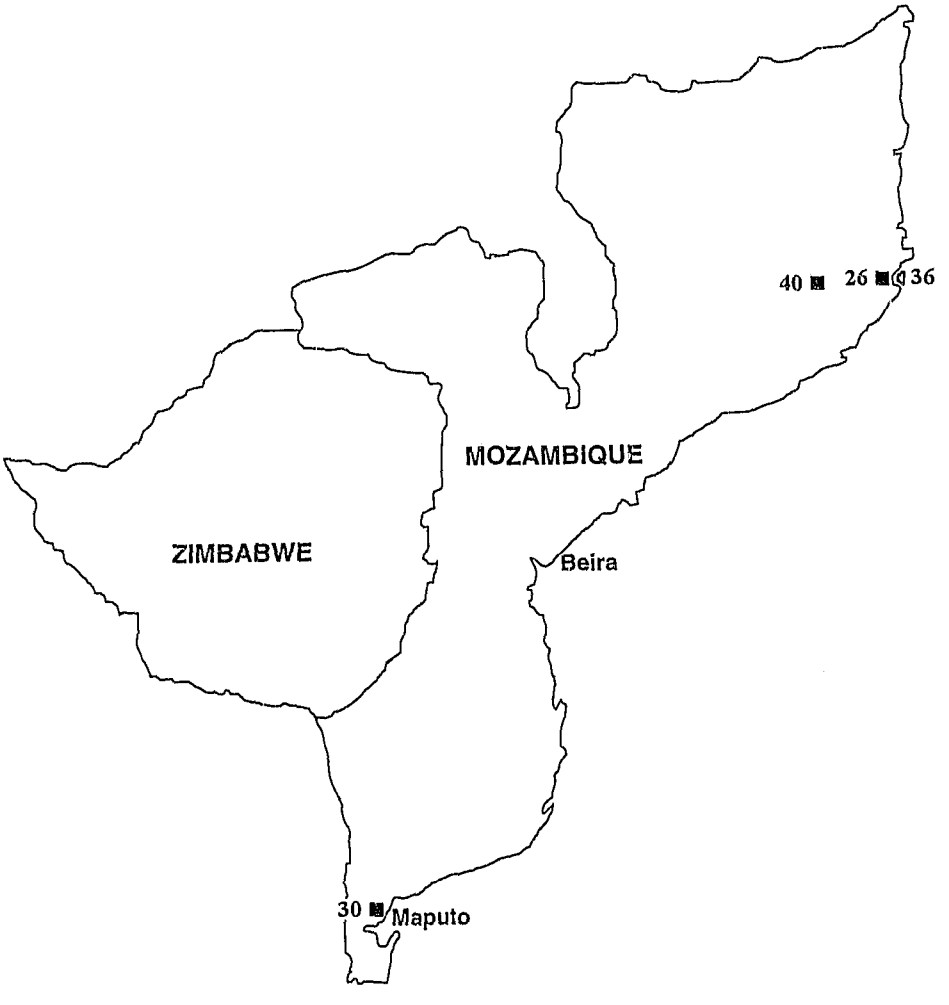


FIGURE 44. Location of the populations in Mozambique assigned to *B. mossambicus* and *B. poweri* (Loc.40).

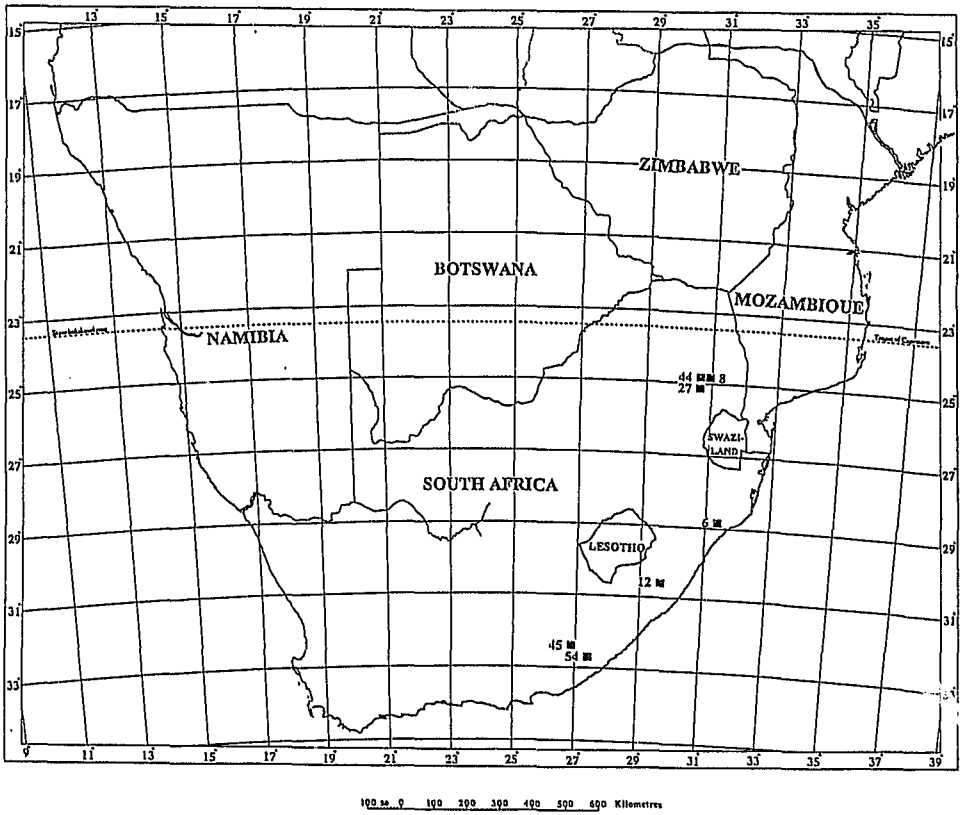


FIGURE 45. Location of populations assigned to *B. verrucosus.*

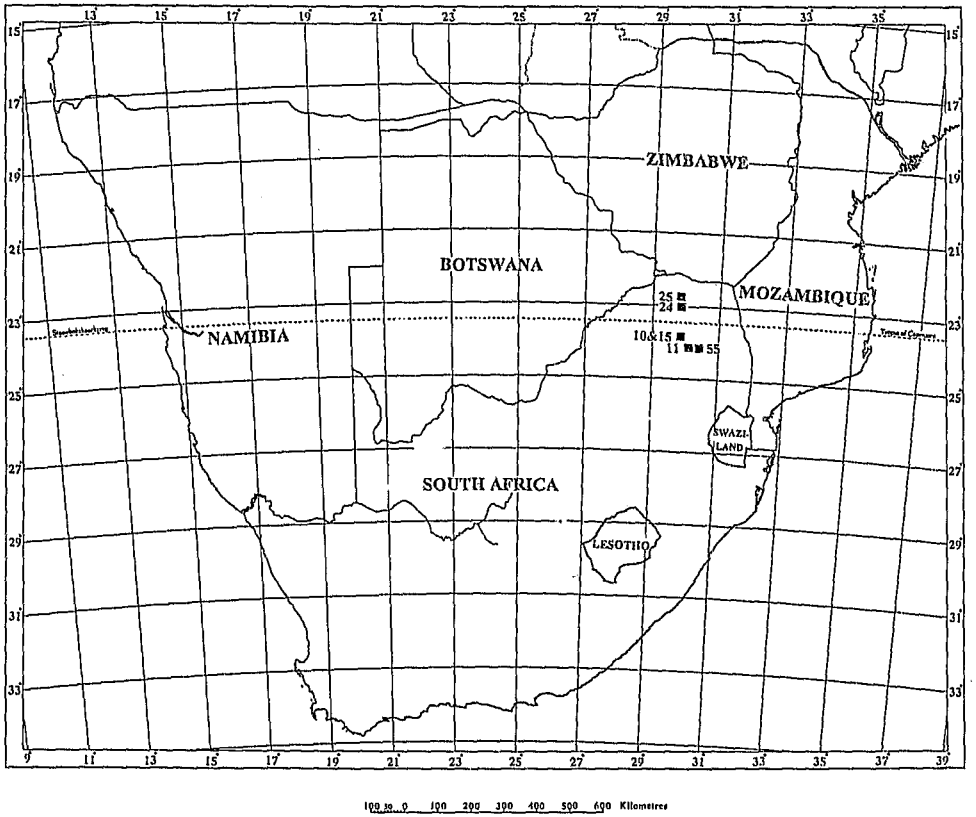


FIGURE 46. Location of populations assigned to *B. sylvestris*.

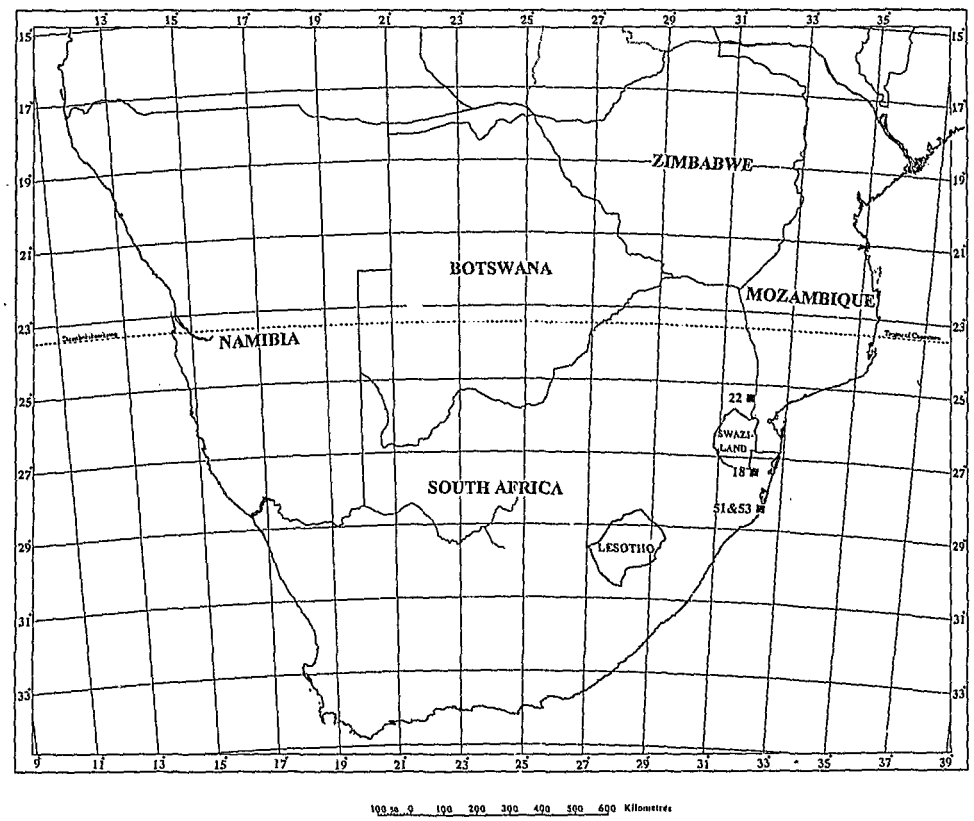


FIGURE 47. Location of populations assigned to *B. sp.* (Group 6).

APPENDIX C

OTHER DATA PERTAINING TO REPRODUCTIVE BIOLOGY:

During the course of the fieldwork various additional observations pertaining to behavioural and ecological aspects of the reproductive biology of the species studied, were made. While not extensive, these data are nevertheless recorded below in view of the paucity of such information in the literature.

1. *Breviceps adspersus*

1.1 Habitat.

The 19 populations sampled occur on sandy soils in grassy open, sparse or closed woodland, or, in the case of *adspersus pentheri*, in short closed shrubland, short closed grassland, and low thicket (Valley bushveld). In Pietersburg this species is common in the parks and suburban gardens: this may be due to the abundance of suitable nesting sites in the loose soil of flowerbeds. The soil surface at most localities is reddish brown, but yellowish brown to grey brown in some areas.

1.2 Breeding period and surface activity.

In the Pietersburg population, calling commenced in early to mid-October after moderate to heavy showers, but was discontinuous and a chorus did not develop. The first strong choruses were recorded in late October to early November. Most chorusing took place in November, while the latest chorus recorded during a breeding season at this locality was in mid-December. Isolated individuals were heard calling after rain in late December and early January.

In Pietersburg, the rainy season ends in about mid-March, but sporadic rainfall is experienced during the winter months. After these occasional showers, single juvenile or adult specimens were collected on the surface or found drowned in a swimming

pool, but no calling was heard. This restricted surface activity was recorded in all months between April and early October, excepting August. During the breeding season, groups of 4-12 males and females were seen feeding on alate termites emerging from the ground in the early morning and late afternoon.

In other areas, breeding activity was also linked to the rainfall patterns, commencing after the first heavy rains. In the lowveld, where the rainy season sometimes commences later than in Pietersburg, strong choruses were heard as late as the middle of March.

1.3 Response to rain and other environmental factors.

During the breeding season in Pietersburg, the response to rain was very rapid: the first calls were heard 15 to 30 minutes after rain began to fall, regardless of the time of day. Peak calling activity usually took place between 19:30 and 23:30 (N = 130 observations), after which time some individuals stopped calling while the remainder continued to call, at a lower intensity, until daybreak. If the day was overcast and warm, the intensity rose slightly and calling continued throughout the day. After a heavy rain (>30mm), however, high intensity choruses were maintained throughout the night and into the following day. In cloudless, hot weather the calling died away by mid-morning and started up again in the late-afternoon.

After heavy rain the calling continued for several consecutive nights, the longest recorded period being 11 nights following 36 mm of rain. Calling was inhibited by long periods of dry weather, wind and by a decrease in air temperature. In Pietersburg, calls were recorded at air temperatures ranging from 9.5° C to 20.3 °C (mean = 15.7 °C; mode = 14° C; N = 100), and in Zimbabwe, at a maximum of 23.1 °C.

Similar behaviour was observed in the other *adspersus* populations sampled.

1.4 Chorus structure and male-male interactions.

In Pietersburg, calling males formed discrete groups of 3 - 7 adjacent individuals (N = 8), which began and ended a bout of calling at approximately the same time. Call bouts were usually initiated by one member of the group but sometimes two individuals alternated as bout leaders. As the call intensity swelled within one group, the leader of an adjacent group began to call: thus the chorus spread from one group to the next and moved through the population in waves. While the calls of adjacent males alternated at first, this pattern was not maintained, and continuous antiphonal calling was never heard.

The distance between adjacent calling males varied from 0.6 to 19 m (mean = 6.25 m; mode = 5 m; N = 45). On three occasions silent males, which remained close (10-30 cm) to calling males for long periods of time, were encountered. Aggressive physical interactions between males were not observed.

1.5 Callsite, callsite fidelity, home range.

Of 161 calling Pietersburg males, 50% called from a shallow depressions; 40% from permanent positions on the surface (no depression); 9% called from the surface but moved between call bouts, and 1% called from deeper vertical burrows. The calls given from deeper burrows were abbreviated and appeared to be stifled by the confines of the burrow. These individuals soon emerged to call at the surface. During the day, males only called from well concealed, shallow depressions. The use of an elevated callsite, eg. on vegetation, was never observed.

The calling depression was often deep enough to accommodate most of the frog's body and was usually well concealed at the base of a grass tuft or small herbaceous plant and hidden by overhanging leaves (Fig.48a). When disturbed, the male crouched down in the depression so that his back was level with the soil surface; when calling, he raised himself, allowing the vocal sac to expand freely. Males which occupied a permanent callsite but had not constructed a depression were often prevented

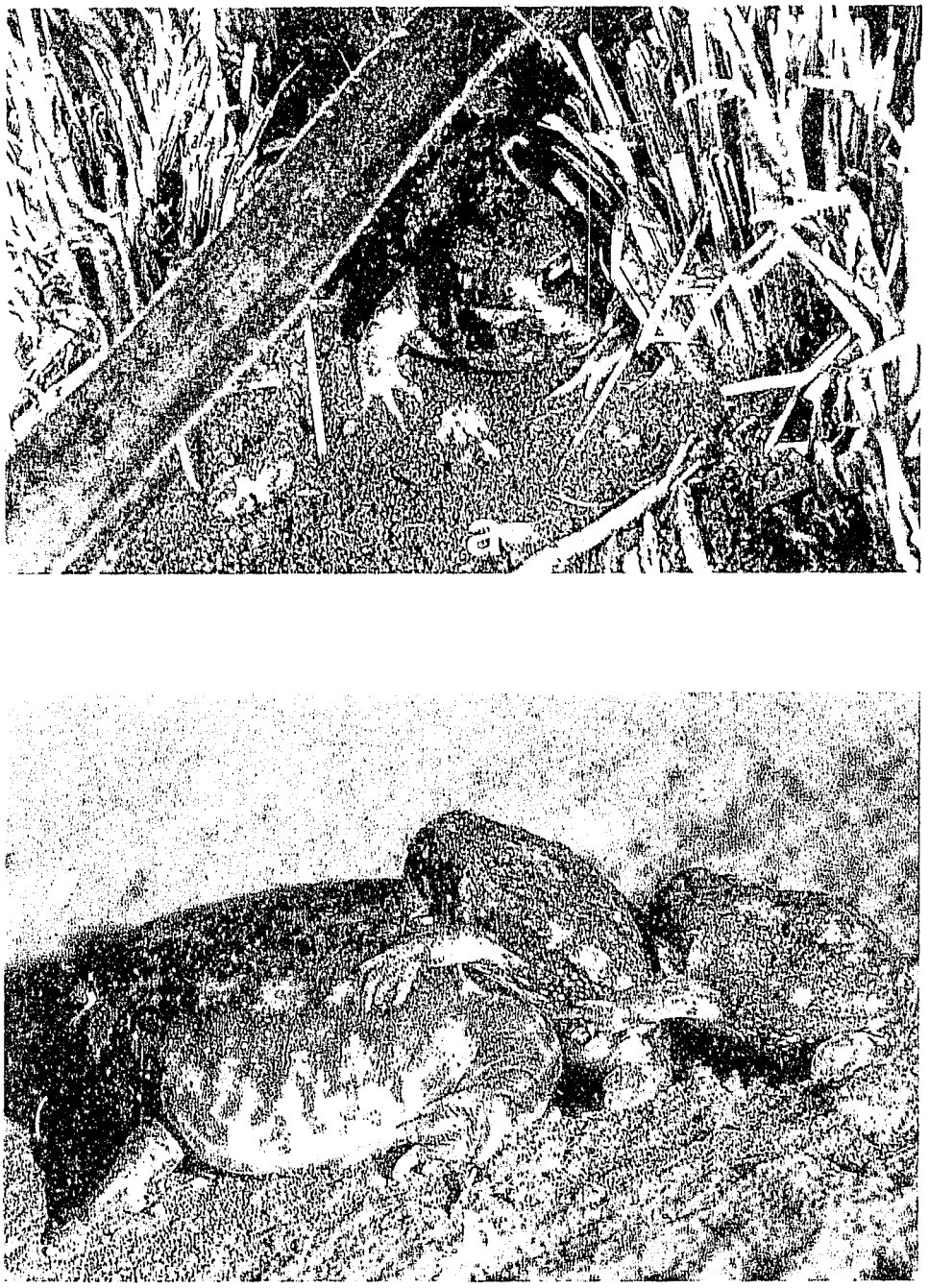


FIGURE 48. (a) *B.a. adspersus* calling from a shallow depression between grasstufts; (b) Amplexus involving an additional male, in *B.a. adspersus*.

from doing so by the absence of a suitable substrate, eg. those calling from the centre of a grass tuft or from stony ground. In such cases the substrate appeared to have been trampled, suggesting that the frog had attempted to create a depression. Some males seen calling at the surface, and moving between calls, later moved to shallow depressions, where they continued to call.

Some individuals used the same callsite more than once (seven observations), in one instance, for five consecutive nights. Males occupying a calling depression often remained there throughout the day if it was overcast and wet. However, if the day was hot and dry, they left the depressions to enter burrows nearby. On resumption of the chorus, males which had previously constructed a calling depression, emerged from their burrows and moved directly to their callsites, sometimes beginning to call before reaching them. Males which were disturbed while calling would sometimes leave the callsite and move directly to burrows 5 - 200 cm away (N = 11), entering them backwards. Three burrows were excavated, and found to consist of a single, vertical tunnel approximately 30 cm in length.

Of 11 males branded and released in November 1984 two were recaptured 16 days later within 60 m of their release point, and two were recaptured a year later within 50 m of their release point. In 1985, 27 males were marked and two recaptured 3 days later 50 - 100 m from their release point.

1.6 Amplexus, nest structure & development period.

A natural encounter between a male and female, leading to amplexus, was never observed, and on only two occasions were amplectant pairs encountered at the surface. On several occasions males and females confined together in a bucket or plastic box went into amplexus. Amplexus involves adhesion of the male to the back of the female by means of a sticky secretion. Some calling males collected during this study had sand adhering to their chests, suggesting that they had recently been in amplexus.

The male is attached to the female by the skin of his thorax and anterior abdomen, as well as the dorsal surface of his forelimbs (Fig 1a). It seems that the adhesive secretion

is only produced in the area of contact between the partners: in the amplexing female, the exposed area of the dorsum shows no evidence of a sticky secretion (such as adhering sand or organic detritus). If care is taken, it is possible to separate an amplectant pair without causing obvious damage to the skin of either partner.

Jurgens (1978) reported that a male *B. adspersus* became glued to the back of a *Tomopterna delalandi* while they were confined together in a plastic bag. This observation confirms that the male produces a sticky secretion during amplexus. On one occasion during the present study, the excavation of a trench revealed a trio consisting of an amplectant pair with a second male adhering to the back of the first (Fig.48b).

Both males and females exude a milky, sticky secretion over the entire dorsal surface when alarmed or injured (Fig 1b), presumably as a means of defense. This also occurs when the animals have been killed in urethane and are transferred to 70% alcohol. However, the glands on the ventral surface of males apparently only release their secretion during amplexus, as this was never observed at any other time.

Batches of eggs were found on three occasions:

1. In December 1985 a female and egg mass was exposed while digging a trench. The egg chamber was 30 cm below the surface, and the female was located in the soil about 5 cm above the egg chamber. No further information was recorded.

2. In early December 1992 a male and female went into amplexus when placed together in a plastic box. The following evening, the pair was released in an enclosed area of well-turned soil and by dawn they had disappeared below the surface. Seven days later, after 25mm of rain, the male was seen on the surface. The nest was excavated the next day and the female was found 12 cm below the surface and 7 cm above the roof of the egg chamber. The roof of the chamber was 12mm above the egg mass, and its floor was located 23.5 cm below the surface. The female was surrounded by loose sand but the eggmass was lying in a well-formed cavity (oval in vertical section) with hardened walls. The chamber was 45 mm high and 53 mm wide. About 45 egg cap-

sules containing creamy yc ; were located below a smaller cap of about 40-50 transparent egg capsules which lacked yolk (Fig 1c). The cloacal temperature of the female was 28.2° C, while the temperature of the soil surrounding the female was 27.7° C, and of the soil around the eggs was 25.9° C. The egg mass was removed to a box of damp soil, but did not develop.

3. In late-December 1993 an amplexing pair was released at night in an enclosed area of well-turned soil and by dawn had disappeared below the surface. The male, female and a chamber containing three tadpoles was excavated 32 days later. The male was found 20 cm below the surface, some distance from the female and nest, in damp soil at a temperature of 27.1° C.. The female was found 20.5 cm below the surface and 5 cm above the roof of the egg chamber. The temperature of the soil around the female was 27° C and of the chamber was 26.5° C. The chamber (Fig.49a) was 40 mm high, 65 mm wide, and there was a gap of 20 mm between the tadpoles and the roof. The walls of the chamber were considerably harder than the surrounding soil. The remains of the eggmass consisted of a number of dehydrated, undeveloped eggs which formed a hard but moist plate on the floor of the chamber. The surface of the plate was soiled, and three, almost fully metamorphosed tadpoles were moving around on it (Fig.49b). The dorsum of each of the two older tadpoles was grey with black speckles, while the younger specimen was grey medially and cream along the sides of the body. Their tails were transparent with blood lacunae at the tips. The ventral body wall was transparent. The nostrils were visible but not functional, and the eyes were not fully developed. The fore and hind limbs were fully functional. The following measurements were taken: body length (tip of snout to base of tail): 10.2, 9.0, 8.3 mm; tail length: 4.1, 7.7, 13.0 mm; interocular distance: 2.8, 2.5, 2.3 mm respectively.

The emergence of a large number of juveniles, presumably from a nest, was observed in early January and single juvenile specimens were collected on several other occasions during January and early February.

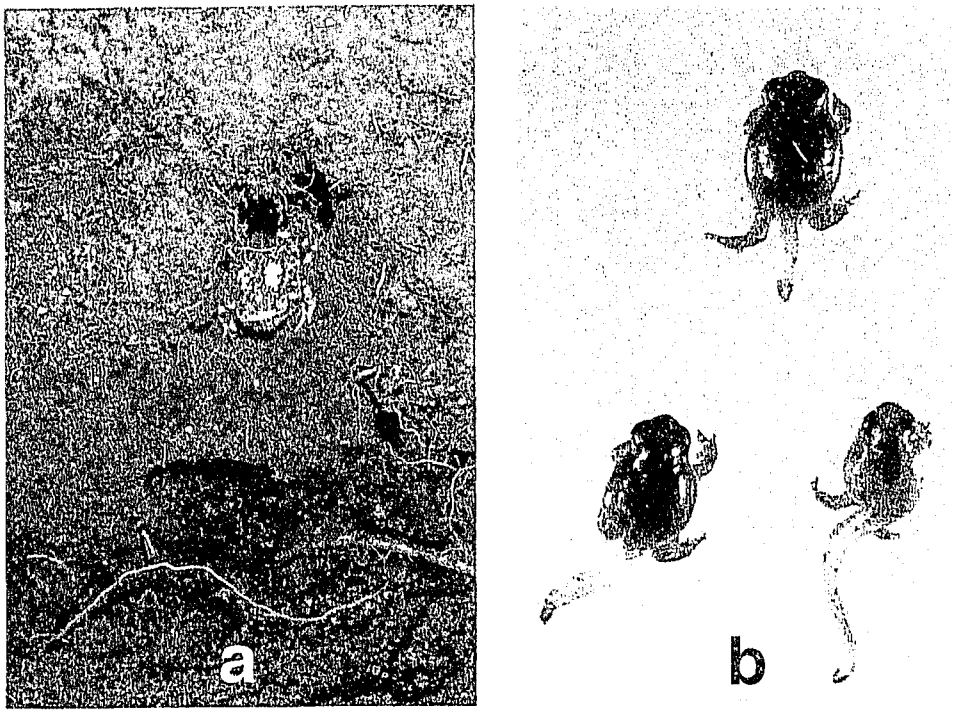


FIGURE 49. (a) Female of *B.a. adspersus* in the soil above her egg chamber; (b) Tadpoles from the egg chamber.

2. *Breviceps mossambicus*

2.1 Habitat

In northern Mozambique and on the coastal plain of KwaZulu/Natal, this species inhabits well drained sandy and sandy-loam soils in short, closed grassland and grassy, open or closed woodland. It is common in gardens and parks in heavily populated areas such as Mozambique Island, Maputo and Nampula.

It also occurs inland, where it is restricted to wetter areas on the crest and slopes of the eastern escarpment in KwaZulu/Natal, Swaziland, Mpumalanga and the Northern Province.

2.2 Breeding period and surface activity

Choruses developed after the first spring rains. The earliest chorus recorded at Graskop was on 7th September and at Nampula in northern Mozambique, on 28th November. Breeding activity was most intense for 6-8 weeks after the first spring rains but then tailed off.

Large numbers of males and females were observed feeding on worker termites in the early morning on Mozambique Island: in one instance 20 individuals were clustered around a termite emergence hole, with one even sitting on the back of another! Feeding individuals adopted a hunched posture over the termite emergence hole and caught the termites as they appeared at the surface (Fig.50b). The longest toe was held slightly above the surface, and toe-twitching was observed on numerous occasions (N=9). No calling was heard at this time.

Similarly, at Sihangwana, numerous males and females were seen feeding on alate termites which had emerged in the late afternoon. At such times the frogs are relatively conspicuous and large numbers can be collected.

2.3 Response to rain and other environmental factors

Once breeding had commenced,choruses developed rapidly in response to rain, regardless of the time of day. After the rain stopped, chorusing continued as long as the weather remained overcast or misty, sometimes for several days. Calling was inhibited by sun, wind and low temperatures. Along the coast, calls were recorded at air temperatures ranging between 13.9° C and 29.5° C, while on the escarpment, samples were collected between 7.4° C and 26.0° C.

On one occasion, males at Loc.11 (Haenertsburg 2) were heard calling at an air temperature of 31° C, from deep vertical burrows exposed to full sunlight at 10:00.

2.4 Chorus structure and male-male interactions

Individuals which initiated bouts of calling prompted adjacent males to call, and the chorus spread through the population in waves, as in *adspersus*. Two individuals sometimes alternated as bout leaders. Antiphonal calling was not heard. The distance between calling males varied between 5cm and 5m (mean = 1.58m ;N=29). Two non-calling males (possibly satellites) were seen near a calling male on Mozambique Island.

Following rain on Mozambique Island, a great deal of surface activity was observed, prior to the establishment of a strong chorus. This included feeding on termites, and aggressive interactions between males. In two instances, males stood upright on their legs and pushed against each other with their chests and arms (Fig.50a). This continued until one broke away and moved off, pursued for a few centimetres by the other male. In another case, a calling male turned to face an approaching male and increased his call rate. The second male stopped about 5cm from the first and then moved away. Another male intercepted a passing snail shell occupied by a hermit crab.

2.5 Callsite.

Of 187 males ranging across the entire area sampled, 27% were calling from permanent callsites in the form of shallow depressions, 71% were calling from the surface and 2% were calling from elevated positions.

2.6 Amplexus, nest structure & development period

Amplexus was not observed. A male, which was disturbed in the branches of a shrub at Mtunzini,emitted a long, loud squeal and produced a sticky secretion dorsally. Nests & tadpoles from the Wakkerstroom district have been described in the literature under the names *B. parvus* (de Villiers, 1929; FitzSimons & van Dam, 1929) and *B. adspersus pentheri* (Swanepoel, 1970).



FIGURE 50. *B. mossambicus* from Mozambique Island (Loc.36): (a) aggressive interaction between males; (b) feeding on worker termites.

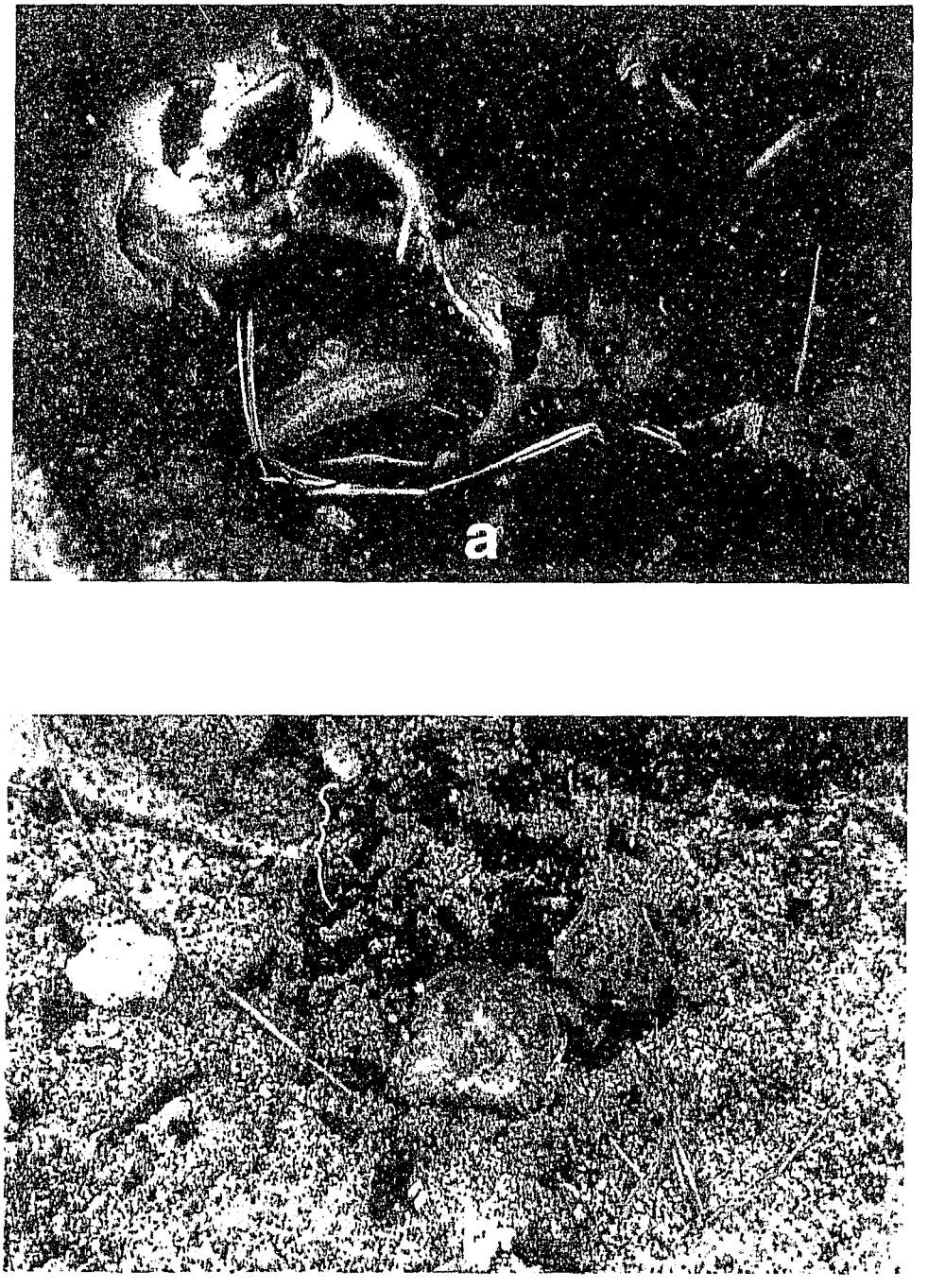


FIGURE 50. *B. mossambicus* from Mozambique Island (Loc.36): (a) aggressive interaction between males; (b) feeding on worker termites.

3. *Breviceps verrucosus*

The six populations sampled in this study were visited nine times and 36 specimens were recorded and/or collected. This species was also encountered at several other localities, viz: Kloof, Pennington and Port Edward in KwaZulu/Natal, and Swadini (Blyde River Canyon) and Mariepskop in Mpumalanga, but no specimens were collected nor recordings made of advertisement calls at these localities.

3.1 Habitat

Over its extensive range, *B. verrucosus* occupies a wide variety of habitats. In the Eastern Cape it occupies high altitude grassland (Nico Malan Pass) and grassland on the fringe of forest at lower altitudes (Stutterheim). In KwaZulu/Natal it was found at moderate altitudes in tall, moist forest and thornveld (Wesa and Eshowe) and in coastal forest and thornveld, venturing as close as 5m from the high-tide mark (Pennington and Port Edward). In Mpumalanga *verrucosus* inhabits forest and the forest fringe at Graskop, God's Window, Mount Sheba and Mariepskop, closed woodland at Swadini and the North-eastern Mountain Sourveld (grassland) at Long Tom Pass near Lydenburg. The soils at these localities vary from clay loam to sandy loam. At Eshowe, specimens were collected and recorded in suburban gardens.

3.2 Breeding period and surface activity

This species starts to breed after rain in early spring: advertisement calls were recorded between 8th September and 4th November, and very large choruses were heard in the forests of the Mpumalanga escarpment during September and early October.

3.3 Response to rain and other environmental factors

B. verrucosus choruses develop rapidly after rain and, during conditions of more or less continuous rain, drizzle and mist, continue unabated for several days and nights. Half of the calls in this sample were recorded during the day. Calls were recorded at

temperatures ranging from 7.4° C - 23.3° C.

Calling was inhibited by a drop in temperature and by wind. Specimens at Eshowe and Mariepskop were prompted to call by a human imitation of the call, even though no other individuals were calling at the time, and a hand-held specimen from Nico Malan Pass also called in response to a whistle.

3.4 Chorus structure and male-male interactions

Males are prompted to call by the calls of their immediate neighbours and the chorus spreads through the population in waves, as in *adspersus*. Within a group of calling males one individual usually initiates the bout of calling, which is immediately taken up by the surrounding males. Sustained antiphonal calling was not heard.

3.5 Callsite.

Of 34 males, 21 were calling from well concealed shallow depressions under grass or leaf litter, seven were calling from an elevated position on grass tufts (only at night), and six were calling from fairly exposed positions on the surface. Deeper vertical burrows were found near four of the males calling from shallow depressions, and one burrow was excavated for about three metres until it disappeared under a large rock.

3.6 Amplexus

Amplexus was not observed, but a sticky, white secretion was discharged from the skin when recently killed specimens were placed in 70% ethanol.

4. *Breviceps sylvestris*

The following notes are based on the seven populations sampled in this study, which were visited 17 times in total, as well as a number of isolated observations made at other localities where this species occurs.

4.1 Habitat

B. sylvestris was found along the crest, slopes and foothills of the Transvaal Drakensberg and the Wolkberg and Soutpansberg ranges in the Northern Province, in tall, moist forest as well as the adjacent short, closed grassland. These areas receive a higher rainfall than the surrounding bushveld and arid lowveld habitats. The soil varies from sandy loam to clay loam, covered by dense matted grass and herbaceous vegetation in the grassland habitat or by a thick carpet of leaf litter in the forests. Calling males were also found in disturbed habitats such as plantations of exotic trees, and in suburban parks and gardens.

4.2 Breeding period and surface activity

During the dry winter months specimens were occasionally encountered under logs and rocks in the forests, but no calling was heard. Breeding activity was strongly linked to rainfall and the first choruses developed after early spring rains. The earliest chorus recorded in this study was on 25th September, while the last was heard on 8th December.

4.3 Response to rain and other environmental factors

Choruses developed rapidly in response to rain, and when this was followed by light drizzle or heavy mist, chorusing usually continued unchecked, sometimes for several consecutive days and nights. Calling was inhibited by a drop in temperature and by wind. Normal choruses were recorded at temperatures ranging from 8.8° C - 17.7° C.

4.4 Chorus structure and male-male interactions

Males were prompted to call by the calls of their immediate neighbours so that the chorus spread through the population in waves, as in *adspersus* and *verrucosus*. Within a group of calling males one individual usually initiated the bout of calling, which was immediately taken up by the surrounding males. Sometimes two males alternated as bout leaders. Sustained antiphonal calling was not heard.

The distance between calling males varied between 2-5m (N=9). Aggressive physical interactions between males were not observed.

4.5 Callsite.

Males collected at night were calling from the surface (N=13), sometimes moving between calls, from elevated positions on grasstufts or herbaceous plants (N=4), or from shallow depressions, concealed by leaf litter or grass (N=3). During the day males only called from well concealed, shallow depressions (N=7). Deeper vertical burrows were sometimes found near calling males.

4.6 Amplexus and nest structure

A male and female went into amplexus while confined in a box. An adhesive substance was secreted as in other *Breviceps* species. Nests and eggs were not found but have been described by Wager (1965, pp.120-121).

5. *Breviceps poweri*

One population was sampled at Nampula, Mozambique, on 28-29 November 1994, following heavy showers. This locality is a cashew nut plantation in open woodland with a light brown, sandy soil. Both *poweri* and *mossambicus* share this breeding site, calling within centimeters of each other. The *poweri* chorus developed before sunset

on both days, whereas *mossambicus* only began calling after dark. Both species continued to call until just before dawn.

Most (38) *poweri* males called from the surface, while three occupied shallow depressions, partly concealed by vegetation or leaf litter. One amplexing pair was found, with the partners glued together by a sticky secretion, as in *adspersus*.

6. ***Breviceps sp.***

This species occurs in closed canopy coastal and low altitude forest at St Lucia and along the Lebombo range, respectively, as well as the relatively dry thornveld (grassy, short, closed woodland) at Hluhluwe, Mlawula and Komatipoort.

Calling activity was observed on eight separate occasions during the day and at night. Breeding takes place in spring and early summer: the earliest observation was on 20th October and the latest on 29th November. Calling took place during light to heavy rain and, unless this was followed by a heavy mist or drizzle, ceased immediately afterwards. This behaviour is similar to that of *verrucosus* and *sylvestris* but contrasts with *mossambicus* and *adspersus* which may continue to call for several days following heavy rain.

Of 23 males, eight called from elevated positions on fallen branches or small herbaceous plants, 5-30cm above the surface, while the remainder called from the surface of leaf litter under trees, sometimes amongst dense undergrowth. None of the males had constructed a shallow depression at the callsite, a phenomenon commonly observed in the other species. Amplexus was not seen.

APPENDIX D

COLLECTING DATES FOR THE SPECIMENS USED IN THIS STUDY:

The list below gives the dates (year/month/day or days) on which specimens and/or calls were collected for this study. Locality details are given in Appendix A above. All specimens have been fully labelled and are deposited in the collections of the Transvaal Museum, Pretoria.

Species	Locality	Date
B.a. adspersus	Burchenough Bridge	90/11/28
	Hoedspruit	89/11/12
	Ingwavuma	88/10/12-14
	Komatipoort 1	91/15/11
	Lydenburg 2	89/10/30
	Manzini	89/11/20
	Mbabane 2	89/11/20
	Mica	87/10/16 - 87/11/04
	Mutare 1	90/11/28
	Mutare 2	90/11/28-29
	Pietersburg	84/11/04-16
	"	85/10/24 - 85/11/13
	"	86/10/20 - 86/12/01
	"	87/11/30 - 87/12/06
	"	90/11/21-25
	Sihangwane 4	88/10/22
	Sihangwane 5	88/10/23
	White River	90/10/27
B.a. pentheri	Addo Elephant Park	86/10/10
	Grahamstown	89/10/12
	"	90/10/29-30
	King William's Town	90/11/01
	Paterson	90/10/30

Species	Locality	Date
B. mossambicus	Belfast	89/10/26 - 89/11/04
	Dullstroom	89/10/26
	Durban	88/10/18
	Eshowe	88/10/19
	"	89/10/16-20
	Graskop 1	87/09/07-9
	"	87/10/27-29
	"	89/10/31
	Jozini 1	88/10/15
	Jozini 3	88/10/20
	Lake Kosi	88/09/24-29
	"	88/10/14
	Lumbo	94/12/01
	Lydenburg 1	89/11/01
	Maputo	94/11/22
	Mbabane 1	89/11/19
	Mbabane 2	89/11/17-20
	Mbabane 3	89/11/20
	Mkuze	87/10/14
	"	88/10/12-20
	Mozambique Island	94/11/30 - 94/12/07
	Mtunzini	87/10/09-14
	"	88/10/18
	Nampula	94/11/28-29
	Piet Retief	88/11/17
	Pilgrims Rest	86/11/20
	Sihangwane 1	88/10/22
	Sihangwane 2	88/10/21-22
	"	89/12/02
	Sihangwane 3	88/10/22
	St Lucia 1	89/10/24-25

Species	Locality	Date
B. mossambicus	St Lucia 2	89/10/22
	Wakkerstroom	88/11/16
B. poweri	Nampula	94/11/28-29
B.s. sylvestris	Haenertsburg 2	85/11/20 - 85/12/08
	Haenertsburg 1	86/11/18
	Houtbosd.	87/09/26 - 87/11/10
B.s. taeniatus	Louis Trichardt 1	89/11/06-8
	Louis Trichardt 2	84/11/18
B. verrucosus	Eshowe	88/09/19
	"	89/10/16
	Graskop 1	87/09/08
	Harding	90/11/04
	Lydenburg 1	89/11/01
	Pilgrims Rest	86/11/20
	Seymour	89/10/07
	"	90/10/28
	Stutterheim	90/11/02
B. sp. nov.	Jozini 2	88/10/20
	Komatipoort 2	91/11/15
	St Lucia 1	89/10/23
	"	89/11/27-29
	St Lucia 3	90/11/06

REFERENCES

Acocks, J.P.H. 1988. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa, No.57., Botanical Research Institute, Dept. of Agriculture & Water Supply, South Africa.

Alexander, R.D. 1962. Evolutionary change in cricket acoustical communication. Evol. 16: 443-467.

Arak, A. 1983a. Male-male competition and mate choice in anuran amphibians. In: Bateson, P., ed. Mate choice. Cambridge University Press, Cambridge.

Arak, A. 1983b. Sexual selection by male-male competition in natterjack toad choruses. Nature Lond. 306: 261-262.

Avise, J.C. 1976. Genetic differentiation during speciation from molecular evolution. In: Ayala, F.J., ed. Molecular evolution. Sinnauer Associates, Sunderland, Massachusetts.

Awbrey, F.T. 1965. An experimental investigation of the effectiveness of anuran mating calls as isolating mechanisms. Unpublished Ph.D. Thesis, Univ. Texas, Austin.

Ayala, F.J., Tracey, M.L. & Richmond, R.C. 1974. Genetic differentiation during the speciation process in *Drosophila*. Evol. 28: 576-592.

Ayala, F.J. 1975. Genetic differentiation during the speciation process. Evol. Biol. 8: 1-78.

Backwell, P.R.Y. 1988. Functional partitioning in the two-part call of the leaf-folding frog, *Afrixalus brachycnemis*. Herpetologica 44: 1-7.

Backwell, P.R.Y. & Jennions, M.D. 1993. Mate choice in the Neotropical frog, *Hyla ebraccata*: sexual selection, mate recognition and signal selection. Anim. Behav. 45: 1248-1250.

Barbour, T. & Loveridge, A. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. Memoirs Museum Comp. Zool. 50: 87-261.

Bishop, P.J. 1994. Aspects of social organization in anuran choruses. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg, South Africa.

Bishop, P.J., Jennions, M.D. & Passmore, N.I. 1995. Chorus size and call intensity: female choice in the painted reed frog, *Hyperolius marmoratus*. Behaviour 132 (9-10): 721-731.

Blair, W.F. 1955. Mating call and stage of speciation in the *Microhyla olivacea - M. carolinensis* complex. Evol. 9: 469-480.

Blair, W.F. 1958. Mating call in the speciation of anuran amphibians. Am. Nat. 92: 27-51.

Blair, W.F. 1963. Acoustic behavior of Amphibia. In: Busnel, R.G., ed. Acoustic behavior of animals. Elsevier Publ. Co., Amsterdam.

Blair, W.F. 1964. Evolution at populational and intrapopulational levels: isolating mechanisms and interspecies interactions in anuran amphibians. Quart. Rev. Biol. 39: 333-344.

Blair, W.F. & Littlejohn, M.J. 1959. Stage of speciation of two allopatric populations of chorus frog (*Pseudacris*). Evol. 14: 82-87.

Blake, D.K. 1965. The fourth Umtali Museum expedition to Mozambique: November-December, 1964. J. Herp. Assoc. Rhodesia 23/24: 31-46.

Bogert, C.M. 1960. The influence of sound on the behavior of amphibians and reptiles. In: Lanyon, W.E. & Tavolga, W.N., eds. Animal sounds and communication. Amer. Inst. Biol. Sci. Publ., 7: 137-320.

Botma, J. du P. 1971. Food of *Canis mesomelas* in South Africa. Zool. Afr. 6: 195-203.

Boulenger, G.A. 1907. Description of a new Engystomatid frog of the genus *Breviceps* from Namaqualand. Ann. Mag. nat. Hist. (S.7) 20: 46-47.

Boulenger, G.A. 1910. A revised list of the South African reptiles and batrachians, with synoptic tables, with special reference to the specimens in the South African Museum, and descriptions of new species. Ann. S. Afr. Mus. 5: 455-538.

Boycott, R. 1982. On the taxonomic status of *Heleophryne regis* Hewitt, 1909 (Anura: Leptodactylidae). Ann. Cape Prov. Mus. (Nat. Hist) 14: 89-108.

Broadley, D.G. 1966. An Umtali Museum expedition to the Gona-re-Zhou, December 1966. J. Herp. Assoc. Afr. 3: 14-18.

Broadley, D.G. 1971. The reptiles and amphibians of Zambia. Puku 6: 1-143.

Bush, G.L. 1974. The mechanism of sympatric host race formation in the true fruit flies (Tephritidae). In: White, M.J.D., ed. Genetic mechanism of speciation in insects. Australia and New Zealand Book Co., Sydney.

Bush, G.L. 1975. Modes of animal speciation. Ann. Rev. Ecol & Syst. 6: 339-364.

Butlin, R.K. 1987. Species, speciation and reinforcement. Am. Nat. 130: 461-464.

Camhi, J.M. 1984. Neuroethology: Chapter 6, Auditory worlds. Sinauer Associates Inc. Publ., Sunderland, Massachusetts.

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

Capranica, R.R. 1977. Auditory processing of vocal signals in anurans. In: Taylor, D.H. & Guttman, S.I., eds. The reproductive biology of amphibians. Plenum Press, New York.

Capranica, R.R., Frishkopf, L.S. & Nevo, E. 1973. Encoding of geographic dialects in the auditory system of the cricket frog. Science 182: 1272-1275.

Capranica, R.R. & Moffat, A.J.M. 1983. Neurobehavioral correlates of sound communication in anurans. In. Ewert, J.P., Capranica, R.R. & Ingle, D.J., eds. Advances in Vertebrate neuroethology. NATO ASI Series A, 56: 701-730. Plenum Press, New York.

Capranica, R.R. & Rose, G. 1983. Frequency and temporal processing in the auditory system of amphibians. In. Huber, F. & Markl, H., eds. Neuroethology and behavioral physiology. Springer-Verlag, Berlin.

Carson, H.L. 1957. The species as a field for gene recombination. In: Mayr, E., ed. The species problem. American Association for the Advancement of Science Publication No.50. Washington, D.C.

Carson, H.L. 1987. The contribution of sexual behavior to Darwinian fitness. Behavioral Genetics 17: 597-611.

Chandler, C.R. & Gromko, M.H. 1989. On the relationship between species concepts and speciation processes. Syst. Zool. 38(2): 116-125.

Channing, A., du Preez, L. & Passmore, N.I. 1994. Status, vocalization and breeding biology of two species of African bullfrogs (Ranidae: *Pyxicephalus*). J. Zool. Lond. 234: 141-148.

Channing, A. & Griffin, M. 1993. An annotated checklist of the frogs of Namibia. Madoqua 18(2): 101-116.

Channing, A. & van Dijk, D.E. 1976. A guide to the frogs of South West Africa. Univ Durban-Westville Monogr. Ser. 2: 1-49.

Channing, A. & van Wyk, A. 1987. Life history: *Breviceps macrops*: Distribution and ecology. J. Herp. Assoc. Afr. 33: 33.

Coyne, J.A., Orr, H.A. & Futuyma, D.J. 1988. Do we need a new species concept? Syst. Zool. 37: 190-200.

de Villiers, A. L. 1988. In: Branch, W.R. (ed.), South African Red Data Book - Reptiles & Amphibians. South African National Scientific Programmes Report No. 151. Pretoria, Foundation for Research Development.

de Villiers, C. 1929. Some features of the early development of *Breviceps*. Ann. Transvaal Mus. 13: 142-151.

Dobzhansky, T. 1935. A critique of the species concept in biology. Philosophy of Science. 2: 344-355.

Dobzhansky, T. 1937. Genetics and the origin of species (1st edition). Columbia University Press, New York.

Dobzhansky, T. 1951. Genetics and the origin of species (3rd edition). Columbia University Press, New York.

Dobzhansky, T. 1970. Genetics of the evolutionary process. Columbia University Press, New York.

Dobzhansky, T. 1972. Species of *Drosophila*. Science 177: 664-669.

Dobzhansky, T. 1976. Organismic and molecular aspects of species formation. Inala, F.J., ed. Molecular evolution. Sinnauer Associates, Sunderland, Massachusetts.

Doherty, J.A. & Gerhardt, H.C. 1983. Hybrid tree frogs: vocalizations of males and selective phonotaxus of females. Science 220: 1078-1080.

Doherty, J.A. & Gerhardt, H.C. 1984. Evolutionary and neurobiological implications of selective phonotaxis in the spring peeper (*Hyla crucifer*). Anim. Behav. 32: 875-881.

Donoghue, M.J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. The Bryologist 88(3): 172-181.

Donoghue, M.J. 1987. South African perspectives on species: an evaluation of the recognition concept. Cladistics 2: 285-294.

Duellman, W.E. & Trueb, L. 1985. Biology of Amphibians. McGraw-Hill Book Co., New York.

Dyson, M.L. 1985. The effect of call sound pressure level on the selective phonotaxis of female *Hyperolius marmoratus*. S. Afr. J. Sci. 81: 209.

Dyson, M.L. 1989. Aspects of social behavior and mate choice in a caged population of painted reed frogs, *Hyperolius marmoratus*. Unpublished Ph.D. Thesis, Univ. of the Witwatersrand, Johannesburg.

Dyson, M.L. & Passmore, N.I. 1988. Two-choice phonotaxis in *Hyperolius marmoratus* (Anura: Hyperoliidae): the effect of temporal variation in presented stimuli. Anim. Behav. 36: 648-652.

Edwards, D. 1983. A broad-scale structural classification of vegetation for practical purposes. Bothalia 14(3&4): 705-712.

Eldredge, N. 1985. Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, New York.

Eldredge, N. & Gould, S.J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M., ed. Models in paleobiology. Freeman, Cooper & Co., San Francisco.

Ehrlich, P.R. & Raven, P.H. 1969. Differentiation of populations. Science 165: 1228-1232.

Fairchild, L. 1981. Mate selection and behavioral thermoregulation in Fowler's toads. Science 212: 950-951.

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

Feng, A.S., Narins, P.M. & Capranica, R.R. 1975. Three populations of primary auditory fibers in the bullfrog (*Rana catesbiana*): Their peripheral origins and frequency sensitivities. J. Comp. Zool. 100: 221-229.

Fitzsimons, V.F.M. 1930. Descriptions of new South African reptiles and batrachia, with distribution records of allied species in the Transvaal Museum collection. Ann. Transvaal Mus. 14: 20-48.

Fitzsimons, V.F.M. 1935. Scientific results of the Vernay-Lang Kalahari Expedition, March to September, 1930. Reptilia and Amphibia. Ann. Transvaal Mus. 16: 295-397.

Fitzsimons, V.F.M. 1939. An account of the reptiles and amphibians collected on an expedition to south-eastern Rhodesia during December 1937 and January 1938. Ann. Transvaal Mus. 20: 17-49.

Fitzsimons, V.F.M. 1946. An account of the reptiles and amphibians collected on an expedition to the Cape Province, October to December, 1940. Ann. Transvaal Mus. 20: 351-377.

Fitzsimons, V.F.M. 1947. Descriptions of new species and subspecies of reptiles and amphibians from Natal, together with notes on some other little known species. Ann. Natal Mus. 11: 111-137.

Fitzsimons, V.F.M. 1950. Notes on a collection of reptiles and amphibians from the west coast of southern Africa. Ann. Transvaal Mus. 21: 253-259.

Fitzsimons, V.F.M. 1958. On a small collection of reptiles and amphibians from the Inyanga district, S. Rhodesia. Occ. Pap. Nat. Mus. S. Rhod. 22(b): 204-214.

Fitzsimons, V.F.M. & van Dam, G. 1929. Some observations on the breeding habits of *Breviceps*. Ann. Transvaal Mus. 13: 152-153.

Forester, D.C. 1973. Mating call as a reproductive isolating mechanism between *Scaphiopus bombifrons* and *S. hammondii*. Copeia 1973: 60-67.

Forester, D.C. & Czarnowsky, R. 1985. Sexual selection in the spring peeper, *Hyla crucifer* (Amphibia: Anura): role of the advertisement call. Behaviour 92: 112-128.

Fouquette, M.J. Jr. 1975. Speciation in chorus frogs. I. Reproductive character displacement in the *Pseudacris nigrita* complex. Syst. Zool. 24: 16-23.

Frishkopf, L.S., Capranica, R.R. & Goldstein, M.M. 1968. Neural encoding in the bullfrog's auditory system - a teleological approach. Proc. IEEE 56: 969-980.

Fuzessery, Z.M. 1988. Frequency tuning in the anuran central auditory system. In: Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E., and Walkowiak, W., eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

Gayou, D.C. 1984. Effects of temperature on the mating calls of *Hyla versicolor*. Copeia 1984: 733-738.

Gerhardt, H.C. 1974. Significance of some spectral features in mating call recognition in the green treefrog (*Hyla cinerea*). J. Exp. Biol. 61: 229-241.

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

Gerhardt, H.C. 1978a. Mating call recognition in the green treefrog (*Hyla cinerea*): the significance of some fine-temporal properties. J. exp. Biol. 74: 59-73.

Gerhardt, H.C. 1978b. Temperature coupling in the vocal communication system of the gray treefrog, *Hyla versicolor*. Science 199: 992-994.

Gerhardt, H.C. 1981. Mating call recognition in the barking treefrog (*Hyla gratiosa*): responses to synthetic mating calls and comparisons with the green treefrog (*Hyla cinerea*). J. Comp. Physiol. A 144: 17-25.

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

Gerhardt, H.C. 1983. Acoustic communication in treefrogs. Verh. Dtsch. Zool. Ges. 1983: 25-35.

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. 1988. Acoustic properties used in call recognition by frogs and toads. In: Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E., and Walkowiak, W., eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

Gerhardt, H.C. 1989. Acoustic pattern recognition in anuran amphibians. In: Dooling, R.J. & Hulse, S.H., eds., The comparative psychology of audition: perceiving complex sounds. Lawrence Erlbaum Associates, Hillsdale.

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

Gerhardt, H.C. & Doherty, J.A. 1988. Acoustic communication in the gray treefrog, *Hyla versicolor*: evolutionary and neurobiological implications. J. Comp. Physiol. 162: 261-278.

Gerhardt, H.C. & Mundry, K.M. 1980. Temperature effects of frequency preferences and mating call frequencies in the green treefrog, *Hyla cinerea* (Anura: Hylidae). J. Comp. Physiol. 137: 1-6.

Ghiselin, M.T. 1966. On psychologism in the logic of taxonomic controversies. Syst. Zool. 15: 206-215.

Ghiselin, M.T. 1969. The triumph of the Darwinian method. University of Chicago Press, Chicago.

Gow, C. E. 1962. Some collecting techniques and general notes. J. Herp. Assoc. Rhodesia 19: 13-14.

Henderson, N.R. & Lambert, D.M. 1982. No significant deviation from random mating of worldwide populations of *Drosophila melanogaster*. Nature 300: 437-440.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Illinois.

Hewitt, J. 1911. A key to the species of the South African Batrachia together with some notes on the specific characters and a synopsis of the known facts of their distribution. Rec. Albany Mus. 2: 189-228.

Hewitt, J. 1925. Descriptions of three new toads belonging to the genus *Breviceps* Merrem. Ann. Natal Mus. 5: 189-194.

Hewitt, J. 1932. Some new species and subspecies of South African batrachians and lizards. Ann. Natal Mus. 7: 105-128.

Hewitt, J. 1937. A guide to the vertebrate fauna of the eastern Eastern Cape Province, South Africa. Part II. Albany Museum, Grahamstown.

Hewitt, J. & Power, J.H. 1913. A list of South African Lacertilia, Ophidia and Batrachia in the McGregor Museum, Kimberley: with field notes on various species. Trans. R. Soc. S. Afr. 3: 147-176.

Hillery, C.M. & Narins, P.M. 1984. Neurophysiological evidence for a travelling wave in the amphibian inner ear. Science 225: 1037-1039.

Hoffman, A.C. 1940. Three new species of frog from Greytown, Natal. Söol. Navors. nas. Mus. Bloemfontein 1: 97-101.

Hoffman, A.C. 1944. Frogs from Chitiala, Nyasaland, together with descriptions of new species. Söol. Navors. nas. Mus. Bloemfontein 1: 173-182.

Hoy, R.R., Hahn, J. & Paul, R.C. 1977. Hybrid cricket behaviour: evidence for genetic coupling in animal communication. Science 195: 82-84.

Hubl, L. & Schneider, H. 1979. Temperature and auditory thresholds: Bioacoustic studies of the frogs *Rana r. ridibunda, Hyla a. arborea* and *Hyla a. savignyi* (Anura, Amphibia). J. Comp. Physiol. A 130: 17-27.

Hull, D.L. 1965. The effect of essentialism on taxonomy - two thousand years of stasis (I). British J. of the Philosophy of Sci. 15: 314-326.

Hull, D.L. 1976. Are species really individuals? Syst. Zool. 25: 174-191.

Hull, D.L. 1980. Individuality and selection. Ann. Rev. of Ecol. & Syst. 11: 311-332.

Hull, D.L. 1988. Science as a process. University of Chicago Press, Chicago.

Hulley, P.E., Walter, G.H. & Craig, A.J.F.K. 1988. Interspecific competition and community structure, II: The recognition concept of species. Rev. Biol. 81: 261-283.

Inger, R.F. 1959. Amphibia. In: Hanström, B., Brink, P. & Rudebeck, G. eds., South African Animal Life, Vol. 6, Chap. 10, pp. 510-553.

Jacobsen, N.H.G. 1989. A herpetological survey of the Transvaal. Unpublished PhD Thesis, University of Natal, South Africa.

Jurgens, J.D. 1978. Amplexus in *Breviceps adspersus* - who's the sticky partner? J. Herp. Assoc. Afr. 18: 6.

Konishi, M. 1970. Evolution of design features in the coding of species specificity. Am. Zool. 10: 67-72.

Lambert, D.M. & Henderson, N.R. 1986. The stability of the specific-mate recognition system of *Drosophila melanogaster*. Behavior Genetics. 16:(3) 369-373.

Lambert, D.M. & Paterson, H.E.H. 1984. On 'Bridging the gap between race and species': The isolation concept and an alternative. Proc. Linn. Soc. N. South Wales. 107: 501-514.

Lambiris, A.J.L. 1989a. A review of the amphibians of Natal. Lammergeyer 39: 1-210.

Lambiris, A.J.L. 1989b. The frogs of Zimbabwe. Monografie X, Torino, Museo Regionale di Scienze Naturali.

Lewis, E.R. & Leverenz, E.L. 1983. Morphological basis for tonotopy in the anuran amphibian papilla. Scanning Electron Microscopy 1983: 189-200.

Lewis, E.R., Leverenz, E.L. & Koyama, H. 1982. The tonotopic organization of the bullfrog amphibian papilla, an auditory organ lacking a basilar membrane. J. Comp. Physiol. 145: 437-445.

Lewis, E.R. & Narins, P.M. 1985. Do frogs communicate with seismic signals? Science 227: 187-189.

Lewontin, R.C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York.

Linnaeus, C. 1758. Systema Naturae, Tomus I, 10th Edition., Facsimile B.M.Nat.Hist.(1956).

Littlejohn, M.J. 1959. Call differentiation in a complex of seven species of *Crinia*. Evol. 13: 452-468.

Littlejohn, M.J. 1960. Call discrimination and potential reproductive isolation in *Pseudacris triseriata* females from Oklahoma. Copeia 1960: 370-371.

Littlejohn, M.J. 1965. Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). Evol. 19: 234-243.

Littlejohn, M.J. 1968. Frog calls and the species problem. Australian Zoologist 14(3): 259-264.

Littlejohn, M.J. 1969. The systematic significance of isolating mechanisms. In. Systematic Biology. National Academy of Sciences, Washington, D.C., Publ. 1692: 459-482.

Littlejohn, M.J. 1976. The *Littoria ewingi* complex (Anura: Hylidae) in south-eastern Australia. IV. Variation in mating-call structure across a narrow hybrid zone between *L. ewingi* and *L. paraewingi*. Aust. J. Zool. 24: 283-293.

Littlejohn, M.J. 1977. Long range acoustic communication in anurans: an integ rated and evolutionary approach. In: Taylor, D.H. & Guttman, S.I., eds. The reproductive biology of amphibians. Plenum Press, New York.

Littlejohn, M.J. 1981. Reproductive isolation: a critical review. In: Atchley, W.R. & Woodruff, D.S., eds. Evolution and Speciation. Cambridge University Press, Cambridge.

Littlejohn, M.J., Fouquette, M.J. & Johnson, G. 1960. Call discrimination by female frogs of the *Hyla versicolor* complex. Copeia 1960: 47-49.

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

Littlejohn, M.J. & Loftus-Hills, J.J. 1968. A experimental evaluation of premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). Evol. 22: 659-663.

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

Littlejohn, M.J. & Michaud, T.C. 1959. Mating call discrimination by females of Strecker's chorus frog (*Pseudacris streckeri*). Texas J. Sci. 11: 86-92.

Littlejohn, M.J. & Watson, G.F. 1973. Mating-call variation across a narrow hybrid zone between *Crinia laevis* and *C. victoriana* (Anura: Leptodactylidae). Aust. J. Zool. 21: 277-284.

Littlejohn, M.J. & Watson, G.F. 1976a. Mating-call structure in a hybrid population of the *Geocrinia laevis* complex (Anura: Leptodactylidae) over a seven-year period. Evol. 30: 848-850.

Littlejohn, M.J. & Watson, G.F. 1976b. Effectiveness of a hybrid mating call in eliciting phonotaxis by females of the *Geocrinia laevis* complex (Anura: Leptodactylidae). Copeia 1976: 76-79.

Littlejohn, M.J. & Watson, G.F. 1985. Hybrid zones and homogamy in Australian frogs. Ann. Rev. Ecol. Syst. 16: 85-112.

Littlejohn, M.J., Watson, G.F. & Loftus-Hills, J.J. 1971. Contact hybridization in the *Crinia laevis* complex (Anura: Leptodactylidae). Aust. J Zool. 19: 85-100.

Loftus-Hills, J.J. 1973. Comparative aspects of auditory function in Australian anurans. Aust. J. Zool. 21: 353-376.

Loftus-Hills, J.J. 1975. The evidence for reproductive character displacement between the toads *Bufo americanus* and *B. woodhousei fowleri*. Evol. 29: 368-369

Loftus-Hills, J.J. & Littlejohn, M.J. 1971a. Pulse repetition rate as the basis for mating call discrimination by two sympatric species of *Hyla*. Copeia 1971: 154-156.

Loftus-Hills, J.J. & Littlejohn, M.J. 1971b. Mating call sound intensities of anuran amphibians. J. Acoust. Soc. Amer. 9: 1327-1329.

Loftus-Hills, J.J. & Littlejohn, M.J. 1992. Reinforcement and reproductive character displacement in *Gastrophryne carolinensis* and *G. olivacea* (Anura: Microhylidae): a reexamination. Evol. 46(4): 896-906.

Lopez, P.T. & Narins, P.M. 1991. Mate choice in the neotropical frog, *Eleutherodactylus coqui*. Anim. Behav. 41:757-772.

Löve, A. 1964. The biological species concept and its evolutionary structure. Taxon 8(2): 33-45.

Loveridge, A. 1925. Notes on East African batrachians, collected 1920-1923, with the description of four new species. Proc. Zool. Soc. London 25(1): 763-791.

Loveridge, A. 1953. Zoological results of a fifth Expedition to East Africa. IV. Amphibians from Nyasaland and Tete. Bull. Mus. Comp. Zool. 110: 325-406.

Macnamara, M. & Paterson, H.E.H. 1984. The recognition concept of species. S. Afr. J. of Sci. 80: 312-318.

Masters, J.C., Rayner, R.J., McKay, I.J., Potts, A.D., Nails, D., Ferguson, J.W., Weissenbacher, B.K., Allsopp, M., & Anderson, M.L. 1987. The concept of species: recognition versus isolation. S. Afr. J. Sci. 83: 534-537.

Masters J.C. & Spencer, H.G. 1989. Why we need a new genetic species concept. Syst Zool. 38(3): 270-279.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York.

Mayr, E. 1949. Speciation and systematics. In: Jepsen, G.L., Mayr, E. & Simpson, G.G., eds. Genetics, Paleontology and Evolution. Princeton University Press, Princeton, New Jersey.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Company, New York.

Mayr, E. 1970. Populations, species and evolution. Harvard University Press, Cambridge, Massachusetts.

Mayr, E. 1976. Evolution and the diversity of life. Harvard University Press, Cambridge, Massachusetts.

Mayr, E. 1991. Introduction: an overview of current evolutionary biology. In: Warren, L. & Koprowski, H., eds. New perspectives on evolution. Wiley-Liss Inc., Philadelphia, Pennsylvania.

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

McEvey, S.F. 1988. Courtship and hybridization in the *Drosophila nasuta* subgroup. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg, South Africa.

McKitrick, M.C. & Zink, R.M. 1988. Species concepts in ornithology. The Condor. 90(1): 1-14.

Merrem, B. 1820. Tentamen Systematis Amphibiorem. J. Krieger, Marburg.

Milstein, P. le S. 1967. Hibernation of the rain frog. Afr. Wildlife 21(2): 167-168.

Minter, L.R. 1997. Advertisement call structure and morphology of *Breviceps mossambicus* Peters and *B. poweri* Parker (Anura, Microhylidae) from northern Mozambique. Ann. Natal Mus. 38: 5-19.

Moffat, A.J.M. & Capranica, R.R. 1976. Effects of temperature on the response properties of auditory nerve fibers in the American toad (*Bufo americanus*). J. Acoust. Soc. Am. 60, Suppl.1, 80.

Mohneke, T. & Schneider, H. 1979. Effect of temperature upon auditory thresholds in two anuran species, *Bombina v. variegata* and *Alytes o. obstetricans* (Amphibia, Discoglossidae). J. Comp. Physiol. A 130: 9-16.

Monod, J. 1970. Chance and necessity. William Collins Sons & Co. Ltd., Glascow.

Moore, J.A. 1957. An embryologists view of the species concept. In: Mayr, E., ed. The species problem. American Association for the Advancement of Science Publication No.20. Washington, D.C.

Morton, E.S. 1975. Ecological sources of selection on avian sounds. Am. Nat. 109: 17-34.

Narins, P.M. & Capranica, R.R. 1976. Sexual differences in the auditory system of the treefrog *Eleutherodactylus coqui*. Science 192: 378-380.

Narins, P.M. & Capranica, R.R. 1977. An automated technique for analysis of temporal features in animal vocalisations. Anim. Behav. 25: 615-621.

Narins, P.M. & Hillery, C.M. 1983. Frequency coding in the inner ear of anuran amphibians. In: Klinke, R. & Hartman, R., eds. Hearing - Physiological Bases and Psychophysics. Springer-Verlag, Heidelberg., 70-76.

Nevo, E. & Capranica, R.R. 1985. Evolutionary origin of ethological reproductive isolation in cricket frogs, *Acris*. In. Hecht, M.K., Wallace, B. & Prance, G.T., eds. Evolutionary biology. Plenum Publishing Corporation.

Oatley, T.B. 1970. Observations on the food and feeding habits of some African robins (Aves: Turdidae). Ann. Natal Mus. 20: 293-327.

Oldham, R.S. & Gerhardt, H.C. 1975. Behavioral isolation of the treefrogs *Hyla cinerea* and *Hyla gratiosa*. Copeia 1975: 223-231.

Palmer, N.G. 1982. The bushpig and the rainfrog. Afr. Wildlife 36: 113.

Parker, H.W. 1934. A monograph of the frogs of the family Microhylidae. British Museum, London.

Passmore, N.I. 1977. Mating calls and other vocalizations 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. Monitore Zoologico Italiano Suppl.(15): 93-108.

Passmore, N.I. 1985. Sibling species, the acoustic environment and the anuran specific-mate recognition system. In: Vrba, E.S., ed., Species and Speciation, pp.125-127. Transvaal Museum Monograph No.4 Transvaal Museum, Pretoria.

Passmore, N.I., Bishop, P.J. & Caithness, N. 1992. Calling behaviour influences mating success in male painted reed frogs, *Hyperolius marmoratus*. Ethology 92: 227-241.

Passmore, N.I. & Carruthers, V.C. 1975. A new species of *Tomopterna* (Anura: Ranidae) from the Kruger National Park, with notes on related species. Koedoe 18: 31-50.

Passmore, N.I. & Carruthers, V.C. 1995. South African Frogs: a complete guide. Revised edition, Witwatersrand University Press, Johannesburg.

Passmore, N.I. & Malherbe, M. 1985. High nocturnal body temperature in the painted reed frog (*Hyperolius marmoratus*). Herpetologica 41(2): 212-215.

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

Paterson, H.E.H. 1973. Animal species studies. J. R. Soc. W. Aust. 56: 31-36.

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

Paterson, H.E.H. 1980. A comment on 'Mate Recognition Systems'. Evol. 34: 330-331.

Paterson, H.E.H. 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. S. Afr. J. Sci. 77: 113-119.

Paterson, H.E.H. 1982a. Perspectives on speciation by reinforcement. S. Afr. J. Sci. 78: 53-57.

Paterson, H.E.H. 1982b. Darwin and the origin of species. S. Afr. J. Sci. 78: 272-275.

Paterson, H.E.H. 1985. The recognition concept of species. In: Vrba, E.S., ed., Species and Speciation, pp.21-29. Transvaal Museum Monograph No.4 Transvaal Museum, Pretoria.

Paterson, H.E.H. 1986. Environment and species. S. Afr. J. Sci. 82: 62-65.

Paterson, H.E.H. 1993a. Variation and the specific-mate recognition system. In: Bateson, P.P.G. et al., eds., Perspectives in Ethology, Vol.10, Chap.8: Behavior and Evolution. Plenum Press, New York.

Paterson, H.E.H. 1993b. Animal species and sexual selection. In: Lees, D.R. & Edwards, D., eds. Evolutionary patterns and processes. Academic Press, London.

Perret, J. 1985. Description of *Kassina arboricola* n. sp. (Amphibia, Hyperoliidae) from the Ivory Coast and Ghana. S. Afr. J. Sci. 82: 196-199.

Peters, W. 1854. Ubersicht der auf seine Reise gesammelten Amphibien. Monatsb. königl. Akad. Wiss. 1854: 614-629.

Peters, W. 1882. Naturwissenschaftliche Reise nach Mossambique, auf Befehl seiner Majestät des Königs Friedrich Wilhelm IV. In den Jahren 1842 bis 1848 ausgeführt. Zoologie. III Amphibien. G. Riemer, Berlin.

Pickersgill, M. 1975. Some surprises in the ecology of *Breviceps v. verrucosus* Rapp. J. Herp. Assoc. Afr. 14: 23-27.

Pienaar, U. de V. 1963. The zoogeography and systematic list of Amphibia in the Kruger National Park. Koedoe 6: 76-82.

Pienaar, U. de V., Passmore, N.I. & Carruthers, V.C. 1976. The frogs of the Kruger National Park. National Parks Board of South Africa, Pretoria.

Polakow, D.A., Backwell, P.R.Y., Caithness, N. & Jennions, M.D. 1995. Stabilising or directional selection in signalling systems: Investigations in a population of painted reed frogs, *Hyperolius marmoratus*. S. Afr. J. Sci. 91: 270-272.

Power, H.J. 1926. A monographic revision of the genus *Breviceps*, with distribution records and descriptions of new species. Ann. S. Afr. Mus. 20: 451-471.

Poynton, J.C. 1963. Descriptions of southern African amphibians. Ann. Natal Mus. 15: 319-332.

Poynton, J.C. 1964. The amphibia of southern Africa: a faunal study. Ann. Natal Mus. 17: 1-334.

Poynton, J.C. 1980. The amphibia of Maputaland. In: Bruton, M.N. & Cooper, K.H., eds., Studies on the ecology of Maputaland. Chap. 21: 245-250. Rhodes University and the Natal Branch of the Wildlife Society of Southern Africa.

Poynton, J.C. 1982. On species pairs among southern African amphibians. S. Afr. J. Zool. 17: 67-74.

Poynton, J.C. & Broadley, D.G. 1985. Amphibia Zambeziaca 1. Scolecomorphidae, Pipidae, Microhylidae, Hemisidae, Arthroleptidae. Ann. Natal Mus. 26: 503-553.

Poynton, J.C. & Pritchard, S. 1976. Notes on the biology of *Breviceps* (Anura: Microhylidae). Zool. Africana 11(2): 313-318.

Ralin, D.B. 1968. Ecological and reproductive differentiation in the cryptic species of the *Hyla versicolor* complex (Hylidae). Southwest Nat. 13: 283-299.

Ralin, D.B. 1977. Evolutionary aspects of mating call variation in a diploid-tetraploid species complex of treefrogs (Anura). Evol. 31: 721-736.

Ramer, J.D., Jenssen, T.A., & Hurst, C.J. 1983. Size related variation in the advertisement call of *Rana clamitans* (Anura: Ranidae), and its effect on conspecific males. Copeia 1983: 141-155.

Rand, A.S. 1988. An overview of anuran communication. In: Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E., and Walkowiak, W., eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

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

Rapp, W. 1842. Neue Batrachier. Arch. f. Naturgesch. 8: 289-291.

Raubenheimer, D. & Crowe, T.M. 1987. The recognition species concept: is it really an alternative? S. Afr. J. Sci. 83: 530-534.

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

Rose, G. & Capranica, R.R. 1983. Temporal selectivity in the central auditory system of the leopard frog. Science 219: 1087-1089.

Rose, G.J. & Capranica, R.R. 1985. Sensitivity to amplitude modulated sounds in the anuran auditory nervous system. J. Neurophysiol. 53: 446-465.

Rose, W. 1962. The reptiles and amphibians of southern Africa. Maskew Miller Ltd., Cape Town.

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

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

Ryan, M.J. 1983b. Frequency modulated calls and species recognition in a neotropical frog. J. Comp. Physiol. 150: 217-221.

Ryan, M.J. 1985. The Tungara frog: a study in sexual selection and communication. University of Chicago Press, Chicago.

Ryan, M.J. 1988. Constraints and patterns in the evolution of anuran communication. In: Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E., and Walkowiak, W., eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

Ryan, M.J. 1990. Signals, species and sexual [illegible]n. Am. Sci. 78: 46-52.

Ryan, M.J., Cocroft, R.B. & Wilczynski, W. 1990. The role of environmental selection in intraspecific divergence of mate recognition signals in the cricket frog, *Acris crepitans*. Evol. 44(7): 1869-1872.

Ryan, M.J., Perrill, S.A. & Wilczynski, W. 1992. Auditory tuning and call frequency predict population-based mating preferences in the cricket frog, *Acris crepitans*. Am. Nat. 139(6): 1370-1383.

Ryan, M.J. & Wilczynski, W. 1988. Coevolution of sender and receiver: effect on local mate preference in cricket frogs. Science (Washington, D.C.) 240: 1786-1788.

Ryan, M.J. & Wilczynski, W. 1991. Evolution of intraspecific variation in the advertisement call of a cricket frog (*Acris crepitans*, Hylidae). Biol. J. Linn. Soc. 44: 249-271.

Schiøtz, A. 1973. Evolution of anuran mating calls. Ecological aspects. In. Vial, J.L., ed. Evolutionary biology of the anurans: contemporary research on major problems. Columbia University, Missouri Press.

Schleidt, W.M. 1974. How 'fixed' is a fixed action pattern? Z. Tierpsychol. 36: 184-211.

Schneider, H. 1974. Structure of the mating calls and relationships of the European tree frogs (Hylidae, Anura). Oecologica (Berl.) 14: 99-110.

Schwartz, J.J. 1986. Male call behavior and female choice in a neotropical treefrog. Ethology 73: 116-127.

Schwartz, J.J. 1987. Spectral and temporal properties in species and call recognition in a neotropical treefrog with a complex vocal repertoire. Anim. Behav. 35: 340-347.

Scoble, M.J. 1985. The species in systematics. In: Vrba, E.S., ed., Species and Speciation pp 31-34. Transvaal Museum Monograph No.4 Transvaal Museum, Pretoria.

Seba, 735. Locu pletissimi rerum naturaleum thesauri accurata descriptio et iconibus. Amstaedami.

Simpson, G.G. 1961. Principles of animal taxonomy. Columbia University Press, New York.

Skolimowski, H. 1974. Problems of rationality in biology. In: Ayala, F.J. & Dobzhansky, T., eds. Studies in the philosophy of biology. Macmillan, London.

Sokal, R.R. 1973. The species problem reconsidered. Syst. Zool. 22: 360-374.

Sokal, R.R. & Sneath, P.H.A. 1963. Principles of numerical taxonomy. W.H. Freeman & Co., San Francisco.

Stewart, M. M. 1967. Amphibians of Malawi. State University of New York Press.

Stewart, M. M. & Bishop, P.J. 1994. Effects of increased sound level of advertisement calls on calling male frogs, *Eleutherodactylus coqui*. J. Herpetol. 28(1): 46-53.

Stiebler, I. & Narins, P.M. 1990. Temperature-dependence of auditory nerve response properties in the frog. Hear. Res. 46: 63-82.

Straughan, I.R. 1966. An analysis of the mechanism of sex and species recognition and species isolation in certain Queensland frogs. Unpublished Ph. D. Dissertation, University of Overland, Brisbane, Australia.

Straughan, I.R. 1967. Reproductive isolation in selected Anura. Supplement to The Frogs of Queensland. An analysis of biospecies and their evolution. Unpublished PhD thesis, Univ. Southern California, Los Angeles.

Straughan, I.R. 1973. Evolution of anuran mating calls: bioacoustical aspects. In: Vial, J.L., ed. Evolutionary biology of the anurans: contemporary research on major problems. Univ. of Missouri Press, Colombia.

Straughan, I.R. 1975. An analysis of mechanisms of mating call discrimination in the frogs *Hyla regilla* and *Hyla cadaverina*. Copeia 1975: 415-424.

Sullivan, B.K. 1982. Significance of size, temperature and call attributes to sexual selection in *Bufo woodhousei australis*. J. Herpet. 16: 103-106.

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

Swanepoel, J.H. 1970. The ontogenesis of the chondrocranium and of the nasal sac of the microhylid frog *Breviceps adspersus pentheri* Werner. Ann. Univ. Stellenbosch 45: Series A, No. 1.

Taigen, T.L. & Wells, K.D. 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). J. Comp. Physiol. B 155: 163-170.

Telford, S.R., Dyson, M.L. & Passmore, N.I. 1989. Mate choice occurs only in small choruses of painted reed frogs *Hyperolius marmoratus*. Bioacoustics 2: 47-53.

Templeton, A.R. 1987. Review of Species & Speciation. Evol. 41(1): 233-235.

van Bergeijk, W.A. & Witschi, E. 1957. The basilar papilla of the anuran ear. Acta Anat. 30: 81-91.

van Dijk, D.E. 1971. The zoocartographic approach to Anuran ecology. Zool. Africana 6: 85-117.

van Dijk, D.E. 1977. Habitats and dispersal of southern African Anura. Zool. Africana 12: 169-181.

van Dijk, D.E. 1982. Anuran distribution, rainfall and soils in southern Africa. S. Afr. J. Sci. 78: 401-406.

van Dijk, P., Lewis, E.R. & Wit, H.P. 1990. Temperature effects on auditory nerve fiber response in the American bullfrog. Hear. Res. 44: 231-240.

Viljoen, S. & Davis, D.H.S. 1973. Notes on the stomach content analysis of various carnivores in southern Africa (Mammalia: Carnivora). Ann. Transv. Mus. 28: 353-367.

Visser, J. 1979. Calling and spawning dates of South Western Cape Amphibians. J. Herp. Assoc. Afr. 21: 21-28.

Visser, J., Cei. J.M. & Gutierrez. L.S. 1982. The histology of dermal glands of mating *Breviceps* with comments on their possible functional value in microhylids (Amphibia:Anura). S. Afr. J. Zool. 17: 24-27.

Vrba, E.S. 1985. Introductory comments on species and speciation. In. Vrba, E.S., ed., Species and Speciation, pp. ix-xviii. Transvaal Museum Monograph No.4 Transvaal Museum, Pretoria.

Wager, V.A. 1957. "Hardy," our Glossy Ibis. Afr. Wild Life 11(2): 151-154.

Wager, V.A. 1960. The blaasop or rainfrog (*Breviceps adspersus*). Afr. Wildlife 14(3): 235-240.

Wager, V.A. 1965. The Frogs of South Africa. Purnell, Cape Town.

Walkowiak, W. 1988. Central temporal encoding. In: Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E., and Walkowiak, W., eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

Walkowiak, W. & Brzoska, J. 1982. Significance of spectral and temporal call parameters in the auditory communication of male grass frogs. Behav. Ecol. Sociobiol. 11: 125-131

Walter, G.H. 1988. Competitive exclusion, coexistence and community structure. Acta Biotheretica. 37: 281-313.

Walter, G.H., Hulley, P.E. & Craig, A.J.F.K. 1984. Speciation, adaptation and interspecific competition. Oikos 43: 246-248.

Wasserman, A.O. 1957. Factors affecting interbreeding in sympatric species of spadefoots (Genus *Scaphiopus*). Evol. 11: 320-338.

Watson, G.F. 1972. The *Littoria ewingi* complex (Anura: Hylidae) in south-eastern Australia. II. Genetic incompatibility and delimitation of a narrow hybrid zone between *L. ewingi* and *L. paraewingi*. Aust. J. Zool. 20: 423-433.

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

Wells, K.D. 1977b. The courtship of frogs. In: Taylor, D.H. & Guttman, S.I., eds. The reproductive biology of amphibians. Plenum Press, New York.

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

Wells, K.D. 1980. Social behavior and communication of a dendrobatid frog, *Colostethus trinitatus*. Amer. Zool. 20: 189-199.

Wells, K.D. 1988. The effect of social interactions on anural vocal behavior. In: Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E., and Walkowiak, W., eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

Werner, F. 1899. Beschriebung einiger neuer Schlangen und Batrachier. Zool. Anz. 22: 114-117.

Werner, F. 1903. Abh. bayer. Akad. Wiss. 22: 383: S. W. Africa.

White, M.J.D. 1978. Modes of speciation. W.H. Freeman, San Francisco.

Wilczynski, W., Zakon, H.H. & Brenowitz, E.A. 1984. Acoustic communication in spring peepers: Call characteristics and neurophysiological aspects. J. Comp. Physiol. 155: 577-584.

Wiley, E.O. 1978. The evolutionary species concept reconsidered. Syst. Zool. 27: 17-26.

Wiley, R.H. & Richards, D.G. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3: 69-94.

Williams, G.C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey.

Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. In: Proceedings of the Sixth International Congress of Genetics. Ithaca, New York.

Zakon, H.H. & Wilczynski, W. 1988. The physiology of the anuran eighth nerve. In: Fritzsch, B., Ryan, M.J., Wilczynski, W., Hetherington, T.E., and Walkowiak, W., eds., The evolution of the amphibian auditory system. John Wiley & Sons, New York.

Zweifel, R.G. 1968. Effects of temperature, body size and hybridization on the mating calls of toads, *Bufo a. americanus* and *B. woodhouseii fowleri*. Copeia 1968: 269-284.

Author Minter, Leslie Rory.
Name of thesis Aspects of the reproductive biology of Breviceps / Leslie Rory Minter. 1999

PUBLISHER:
University of the Witwatersrand, Johannesburg
©2013

LEGAL NOTICES:

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.