A STUDY OF THE *Pycnonotus* BULBUL SPECIES COMPLEX IN SOUTHERN AFRICA

THESIS

Submitted in Fulfilment of the
Requirements for the Degree of
MASTER OF SCIENCE
of Rhodes University

by

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January 1994

ABSTRACT

The three *Pycnonotus* bulbuls endemic to Africa, *P. barbatus*, *P. nigricans* and *P. capensis*, occupy mutually exclusive distributions in southern Africa. These species are closely related and appear to occupy very similar ecological niches, only in different regions. Using a multifaceted approach, this study attempts to explain the ecology of this species complex.

All three species show similar physiological responses to temperature extremes, and are therefore unlikely to be directly limited by environmental temperature. However, their distributions are highly correlated to a complex of environmental variables, particularly winter minimum temperatures, the coefficient of variation in mean annual rainfall, and the seasonality of rainfall. This combination of environmental parameters can be used to predict the distributions of at least one of the species, *P. nigricans*, accurately.

An analysis of the vocalizations and behaviour of the three species revealed that, whilst *P. capensis* has a number of recognizably different vocalizations, those of *P. barbatus* and *P. nigricans* are very similar. The three have nearly identical behaviours, particularly courtship and pre-copulatory behaviours. The mate recognition systems of the three are therefore extremely similar.

P. barbatus is territorial during the breeding season, and exhibits highly structured variation in male territorial song at the level of the local neighbourhood. The literature pertaining to song dialects is reviewed, and a new hypothesis is postulated to explain song-matching in terms of neighbour/stranger discrimination and the possible existence of cooperative territory defence.

A survey of the eastern Cape region, where all three species come into contact, showed that extensive hybridization is taking place between each species pair. Phenotypically, this hybridization is restricted to narrow hybrid zones, that are considered to be stable in both time and place. The evolutionary and ecological significance of these zones to the distributions of the species is discussed, and it is proposed that the zones are maintained by selection acting on differentially-adapted genomes along an environmental gradient.

A review of species concepts concluded that no current concept can adequately accommodate the three *Pycnonotus* taxa in its theoretical definition of a species. In a final analysis, the systematic status of the three taxa is re-assessed.

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ACKNOWLEDGEMENTS

I wish to extend my heartfelt thanks to the following people and organizations that assisted me in the completion of this project:

To my supervisors, Adrian Craig and Pat Hulley, for their provision of the funding and equipment for this project from their research grants, and for the free rein I was given in developing the project. Whilst we agreed to disagree on a number of theoretical points, their constructive criticism of the manuscript and our discussions proved invaluable in refining my arguments.

To Chris Brown, for his supervision of the work covered in Chapter 2 and his comments on that section of the manuscript.

To Anthony Davis and Neil Deacon, whose results from testing the physiological responses of the Blackeyed Bulbul and Redeyed Bulbul, respectively, at temperatures above 5°C, were used in Chapter 2.

To Tony Palmer at the Roodeplaat Grasslands Research Centre in Grahamstown, from whose databases I extracted the environmental variables necessary for the analyses in Chapter 3, and who produced the map for the predicted distribution of the Redeyed Bulbul.

To Martin Villet, for many fruitful discussions on species concepts and for patiently fielding a string of queries on statistical methods.

To Tania Olivieri, who, with painstaking attention to detail, formatted the entire manuscript for the final printing.

To Debbie Adamson, who kindly sacrificed many hours of potential leisure-time to help produce most of the figures in the manuscript.

To Di Tippler, for digitizing the map of the *Pyconontus barbatus/P. nigricans* hybrid zone (Figure 6.1), and Graeme Engelbrecht for digitizing Figures 5.2 and 5.8 on "ArcInfo".

To Martin Hill, Richard Chambers and Jaco Greeff for proof-reading various chapters of the manuscript and their constructive criticisms.

To Graham and Caryn Edwards of "Spuds" fruiterers, whose generous provision of their spoilt fruit ensured that the caged birds received first-class catering during their months in captivity.

To Terry Butterworth for assistance with technical matters, such as the building of cages to house the birds, and to Sarah Radloff for her advice on statistical methods.

To the Computing Centre for Water Research, Pietermaritzburg, for access to the XGRID data base used to extract environmental variables for the work covered in Chapter 3.

To the South African Bird Atlas Project for their provision of the quarter-degree distribution data for the three bulbul species.

The Foundation for Research and Development, a Rhodes University Masters Degree Scholarship and an Ian Mackenzie Scholarship for Environmental Studies provided the much-needed financial support for me to complete the project.

A special thanks to the many farmers in the eastern Cape who I had the pleasure of meeting, and who willingly granted me access to their properties; their friendliness and hospitality will long be remembered.

Finally, to my mother, Colleen Lloyd, who, under difficult circumstances, selflessly strove to provide three children with the very best education, and who instilled in me an independence of mind and the drive to excel. Such a gift of love can only be treasured.

CHAPTER ONE

GENERAL INTRODUCTION

Bulbuls belong to the family Pycnonotidae (Passeriformes, suborder Oscines), an Old World and largely tropical group of small to medium-sized birds. A total of 123 species in 15 genera is currently recognised (Campbell & Lack 1985; Keith 1992a). There are 52 African species, of which all but one are endemic (Keith 1992a). Most bulbuls inhabit forest, with a few occupying open country or scrub with trees. They eat fruit and insects, and occasionally nectar and pollen.

The genus *Pycnonotus* (Boie) is a recently expanding, speciating, derived genus comprising 36 species (Keith 1992a). *Pycnonotus* is a primarily Asian genus, the few African representatives being members of a widespread Asian superspecies which has recently invaded Africa via the Middle East (Hall & Moreau 1970). Whilst a few species are confined to forest, most inhabit open country with scattered trees and scrub, readily adapting to man-made habitats, especially gardens (Keith 1992a).

In Africa the genus is represented by three endemic species: the Blackeyed Bulbul *Pycnonotus barbatus* (Desfontaines), the Redeyed Bulbul *P. nigricans* (Vieillot), and the Cape Bulbul *P. capensis* (Linnaeus), which together form a species complex or 'superspecies' (Keith 1992a).

These three species are very closely related. They are extremely similar in voice, behaviour, habits and foraging and breeding ecology, and as such, can be regarded as ecological homologues. In southern Africa they differ mainly in the colour and size of the ring of bare skin around the eye: narrow and black in *P. barbatus*, wider and red in *P. nigricans*, broad and white in *P. capensis* (Figure 1.1). *P. barbatus* and *P. nigricans* resemble one another in plumage, whilst *P. capensis* differs in being a plain brown bird without the contrast between a darker head and pale belly of the other two.

The three species are parapatric and locally sympatric in distribution.

Figure 1.1 Photograph of the three *Pycnonotus* bulbuls, from left to right: *P. barbatus*, *P. nigricans* and *P.capensis*.

P. barbatus has been described by Keith (1992a) as "perhaps the most widespread and abundant bird in Africa". It occupies almost any wooded or bushy habitat, being absent only from large tracts of unbroken forest or woodland, open grassland with no bushes, and treeless desert. Having a predominantly frugivorous diet, it appears to require only a sufficient number of fruit-bearing shrubs or trees in its habitat. It therefore occupies clearings in tropical forest, macchia in North Africa, stands of papyrus mixed with *Miscanthidium*, and in the Sahara desert is found almost anywhere where there is water and a few trees. It is especially fond of riverine habitats, penetrating both forest and desert along streams. *P. barbatus* is sparse or absent in virgin stands of *Brachystegia*, *Baikiaea* and mopane woodland (where there would be few or no fruiting trees), but tolerates the more open areas where there are bushes and shrubs (and presumably more fruit) (Keith 1992a).

By all accounts then, *P. barbatus* is a common and successful habitat generalist that requires only access to drinking water and a sufficient number of fruit-bearing trees or shrubs within its habitat to satisfy its predominantly frugivorous diet.

It comes as some surprise, therefore, to find that in southern Africa, *P. barbatus* is replaced in the drier western regions by *P. nigricans* and in the fynbos (macchia) biome of the southern and south-western Cape Province of South Africa by *P. capensis* (Figure 1.2).

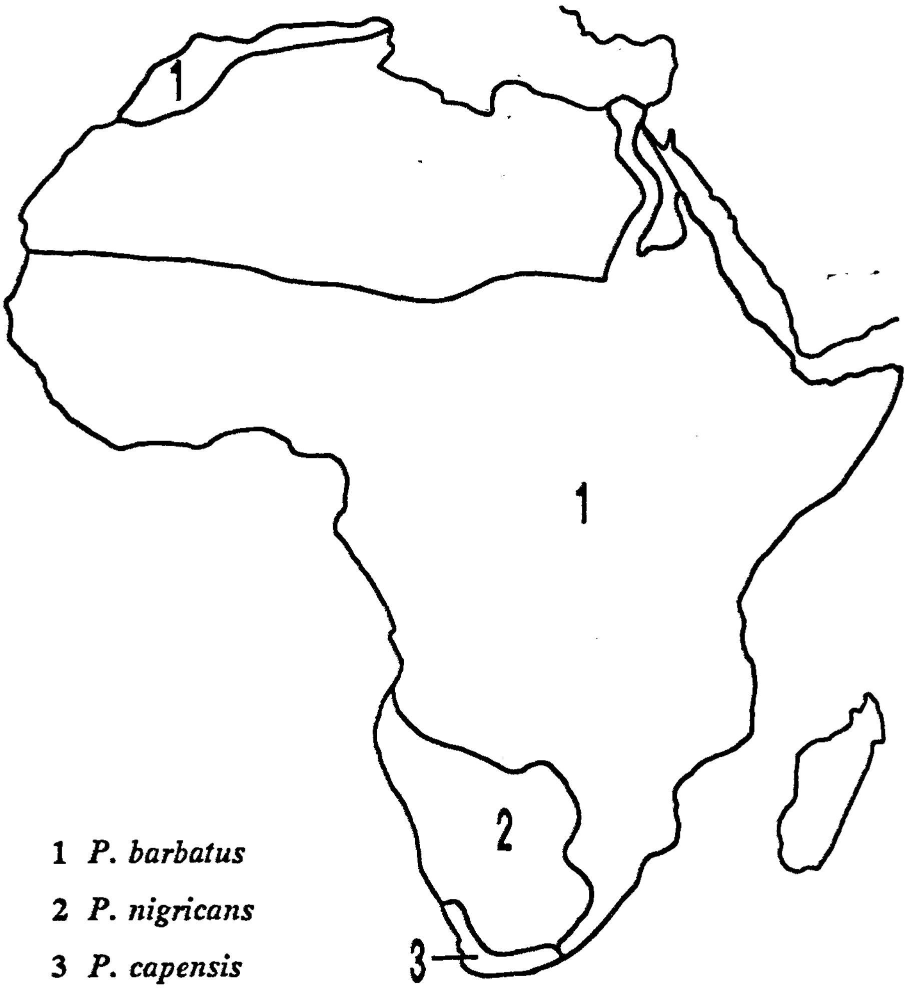


Figure 1.2 Distribution of the three endemic *Pycnonotus* bulbuls in Africa. Adapted from Keith (1992a) using August 1993 South African Bird Atlas Project (SABAP) data.

P. nigricans and *P. capensis* are equally common and successful within their ranges. Furthermore, *P. capensis* is to be found in habitats ranging from forest edges to the arid, semi-desert karoo. All three species are dependent upon water, and are common inhabitants of gardens around human settlements.

The question that naturally arises, is why three such closely related, common, and successful species, that each occupy a broad range of habitat types and share a catholic diet, should exhibit mutually exclusive distributions within southern Africa.

The absence of a species from a habitat may be due to:

a) historical factors,

b) unsuitable physical conditions,

c) lack of physical or biological requisites,

d) geographical isolation i.e. the species cannot reach the habitat, or

e) interspecific interactions (Debach 1966).

If some species are absent from certain zones or habitats which are potentially suitable to them, even though they may reach these habitats from time to time in suitable numbers, then their absence must involve some sort of biotic interaction.

The special type of interaction between species where one species brings about the extinction or displacement of another ecologically homologous species, or prevents a second such species from invading and successfully colonising all or part of its habitat (i.e. limits the range of distribution of that species), has become known as the competitive exclusion principle (Hardin 1960) or competitive displacement principle (Debach 1966). The theory that different species having identical ecological niches (that is, ecological homologues) cannot coexist for long in the same habitat on account of their competition for common resources or requisites was long regarded as a unifying principle that provides explanations for a plethora of observed ecological patterns. As stated by Hulley *et al.* (1988), "competition theory has dictated many of the ecological and evolutionary questions asked about animals, and thus the direction of much biological investigation and interpretation".

Whilst most ecologists consider interspecific competition to be of basic importance in ecology and evolution (see Debach 1966, Wiens 1977, Simberloff 1982 and Schoener 1983), its evolutionary importance in natural populations of animals has been disputed. Some investigators consider the magnitude and unpredictability of physical disturbances to be important factors controlling abundances, so that many populations seldom reach levels where competition is important (Andrewartha & Birch 1954; Wiens & Rotenberry 1981; Grossman *et al.* 1982). This has even lead others (summarized in Hulley *et al.* 1988) to criticize aspects of competition theory, considering competitive displacement in nature to be rare, of little importance, or overemphasized without due consideration of alternative explanations.

The situation becomes a little more complicated when the recognised species hybridise where they meet. Walter *et al.* (1984) pointed out that the species concept and current ideas on speciation are relevant to the debate on the significance of competition theory in community ecology. Using the framework of the Recognition Species Concept proposed by Paterson (1978, 1980, 1981, 1982, 1985), they argued that:

1. competition has a limited evolutionary role at speciation, and
2. once a new species comes under stabilising selection and expands, competition can produce only local and relatively minor adaptations.

Hybridization and the existence of stable hybrid zones between closely related species has been widely reported in the animal kingdom (see Moore 1977, Barton & Hewitt 1985, 1989, and Harrison 1990 for reviews). Hybridization can be viewed as generally occurring between taxa that have differentiated significantly but have not completed speciation.

Hybrid zones pose interesting questions for the taxonomist, for they contrast two views of the species; as a set of populations maintained in a particular stable equilibrium by selection and/or gene flow, and as a set of populations delimited by genetic barriers to gene exchange (Barton & Hewitt 1985). Empirical analyses of the genetic differences and the selective forces that separate the taxa involved may allow some inferences about the way these differences evolved and, by extrapolation, about the way fully isolated species diverge from each other (Barton & Hewitt 1985). Hybrid zones thus provide us with a window on the evolutionary process, and are regarded by some as unique and rigorous testing grounds of species concepts and evolutionary theory (Hewitt 1988). Furthermore, hybrid zones can be useful to studies of population biology, including everything from analyses of biogeographical factors to defining patterns of linkage disequilibria in local populations where differentiated genomes interact (Rand & Harrison 1989).

The designation of taxonomic rank to closely related hybridizing taxa is, in turn, of relevance to any discussion of competition between these taxa: the difference in the perceived evolutionary significance of inter- and intraspecific competition and territoriality is considerable.

A number of cases of hybridization between the *Pycnonotus* bulbuls of southern Africa have been recorded. White (1956), Irwin (1958) Clancey (1960), Markus (1963, 1966, 1967), and Liversidge (1985) documented cases of hybridization between *P. barbatus* and *P. nigricans*, whilst Lawson (1962) and Keith (1992b) reported presumed hybrids between *P. capensis* and each of *P. barbatus* and *P. nigricans* respectively.

The taxonomic status of the *Pycnonotus* bulbuls in southern Africa has long been a subject of debate. Lawson (1962) maintained that because hybridization has occurred between at least two of the three groups they should be considered as all belonging to a single species, *P. capensis*. However, on the basis that 1) there appears to be overlap without hybridization in some areas, 2) so few hybrids have been observed or collected in relation to the total number seen or collected, and 3) that the few cases of hybridization may have occurred where the habitat has been degraded by man (Liversidge 1985), most authors have recognised the different populations as belonging to three distinct species (White 1962; Hall & Moreau 1970; Clancey 1980; Liversidge 1985; Keith 1992a,b).

It was with these considerations in mind that this study into the ecology of the *Pycnonotus* bulbul species complex in southern Africa was undertaken. The primary objective of the study was to determine the factors responsible for the mutually exclusive distribution pattern of the three recognised species. Specific questions addressed were:

1. are the different populations specifically adapted to certain habitat types such that they are unable to colonise the habitat types occupied by another population? or
2. is the spread of any one population into the habitat occupied by another population limited by the presence of that second population i.e. are interspecific interactions such as competition limiting colonization?
3. to what extent is hybridization taking place between the species and what effect does it have on their distributional ecology? and
4. to what extent are the three species actually different?

In a final analysis, the taxonomic status of the different populations was re-assessed.

The study concentrated on the eastern Cape Province of South Africa, an area where all three species come into contact with one another.

CHAPTER TWO

TEMPERATURE AS A POSSIBLE FACTOR LIMITING THE DISTRIBUTION OF *Pycnonotus* BULBULS

2.1 INTRODUCTION

Two long-held hypotheses in ecology address the question of what shapes biogeographic patterns. One implicates biotic interactions, such as competition, as the main factors controlling these patterns (MacArthur 1958); the other postulates that abiotic factors, such as climate, are the primary forces shaping species' biogeographic ranges (Andrewartha & Birch 1954). Climate may influence a species' range directly through its impact on physiological processes, and/or indirectly (i.e. ecologically) through its influence on vegetation and food availability (Hayworth & Weathers 1984).

Whilst ecologists generally agree that abiotic and biotic factors interact to determine population abundances, it has been difficult to explain specific range boundaries (Repansky 1991). MacArthur (1972) commented that explanations for the distributions of individual species were to be found in terms of the particulars of the biology of each species rather than in a general framework. This did not deter Hall *et al.* (1992) from developing a synthetic theory arguing that observed patterns of distribution and abundance of species can be directly related to species-specific energy costs and gains (energy balances) in response to multiple environmental or resource gradients.

Krebs (1985) held the effect of temperature to be one of the "master limiting factors to the distribution of life on earth". A number of physiologists have broached the subject of factors limiting species' biogeographic patterns with "confidence that knowledge of the energetics of a species can help to explain its distribution and abundance" (Weathers 1979). Few studies have actually managed to link physiological stress from environmental extremes, such as cold ambient temperatures, directly with species' biogeographic patterns though.

Root (1988a) found that 60% of the bird species wintering in the United States and southern Canada have northern boundaries that coincide with isotherms of minimum daily January temperature. The passerine species within his data set were calculated to have metabolic rates at their northern limits that average 2.5 times basal metabolic rate, and Root (1988b, 1989) argued that the average is a ceiling on metabolic rate that constrains the northern distributions of species. These findings generated some debate, with Castro (1989) and Repansky (1991) criticizing Root's methodology and conclusions.

In a study of two closely related but allopatric magpie species (*Pica nuttalli* and *P. pica*), Hayworth and Weathers (1984) found that climate acted directly on at least one of the species to restrict its distribution, rather than indirectly through a secondary effect on food availability.

In southern Africa, there is an east to west decrease in annual rainfall (Tyson 1986) and thus an associated increase in aridity. The transition from the more mesic eastern seaboard habitats to the western inland semi-desert habitats is generally associated with a mountainous escarpment. The combination of these factors ensures that temperatures experienced in the arid western region are more extreme (in terms of seasonal maxima and minima) than those of the more mesic eastern region of the subcontinent (Table 2.1).

Table 2.1 Air temperatures recorded at sampling sites for the three *Pycnonotus* bulbul species (Weather Bureau 1986).

	Mean Max. Temp. of Hottest Month	**Mean Min. Temp. of Coldest Month**	**Highest Temp. Recorded**	**Lowest Temp. Recorded**
Grassridge (1921-1955) *P. nigricans*	38.2°C	-4.7°C	41.7°C	-8.6°C
Grahamstown (1923-1971) *P. barbatus*	36.6°C	-0.2°C	42.3°C	-4.0°C
Cape St Francis (1920-1984) *P. capensis*	29.5°C	9.7°C	42.8°C	0.8°C

A number of studies of southern African fauna have associated the biogeography of species with temperature. Stuckenberg (1969) showed that isotherms coincided closely with the distribution limits of southern African reptiles and amphibia. Geldenhuys (1981) found temperature, and in particular mean temperature of the coldest month, to be a reliable climatic indicator of the relationship between the distribution of the South African Shelduck *Tadorna cana* and environmental variables. Ward and Maclean (1989) also invoked temperature as a causal factor in the distribution of plovers (*Vanellus* spp.), and Rowan (1963), Craig (1985) and Craig and Hulley (1992) all found correlations between temperature and the distributions of various passerine bird species.

P.E. Hulley (*pers. comm.*), noted that the contact zones of both the Blackeyed Bulbul *Pycnonotus barbatus* and the Cape Bulbul *P. capensis* with the Redeyed Bulbul *P. nigricans* coincided closely with the -7°C minimum winter isotherm (Figure 2.1). *P. nigricans* inhabits the arid western interior of southern Africa that experiences the greatest range in ambient temperature.

Bearing in mind that animal distributions tend to be affected by extremes in the environment rather than by average conditions (Rowan 1963), I investigated the temperature tolerances of the three *Pycnonotus* bulbuls by measuring their metabolic responses to a range of temperatures from extreme minimum to extreme maximum. Using this method, I hoped to test directly whether *P. nigricans* is physiologically better adapted than the other two species to cope with the temperature extremes experienced in its habitat, and thus whether physiological tolerances to temperature limit the distributions of the three species.

2.2 METHODS

2.2.1 Experimental animals

All birds used in the study were captured with mistnets, at the following localities: Grahamstown (33°18'S 26°31'E: 33 *P. barbatus*), Rietvlei farm (32°17'S 26°01'E: 26 *P. nigricans*), Grassridge farm (31°47'S 25°29'E: 3 *P. nigricans*), and Cape St Francis (34°11'S 24°47'E: 7 *P. capensis*). Data on the seasonal temperature variations experienced at these localities are presented in Table 2.1.

After capture, the birds were colour ringed for individual identification and maintained in a single 5m x 3m x 2m outdoor aviary in Grahamstown, experiencing natural photoperiods and environmental temperatures, except when under test in the laboratory. The aviary was furnished with numerous perches and a wooden shelter.

KEY:

• = *P. barbatus*
♦ = *P. nigricans*
■ = *P. capensis*
○ = *P. barbatus & P. nigricans*
⌂ = *P. barbatus & P. capensis*
▲ = *P. nigricans & P. capensis*
/ = None at ≥25%
— = -7°C Isotherm

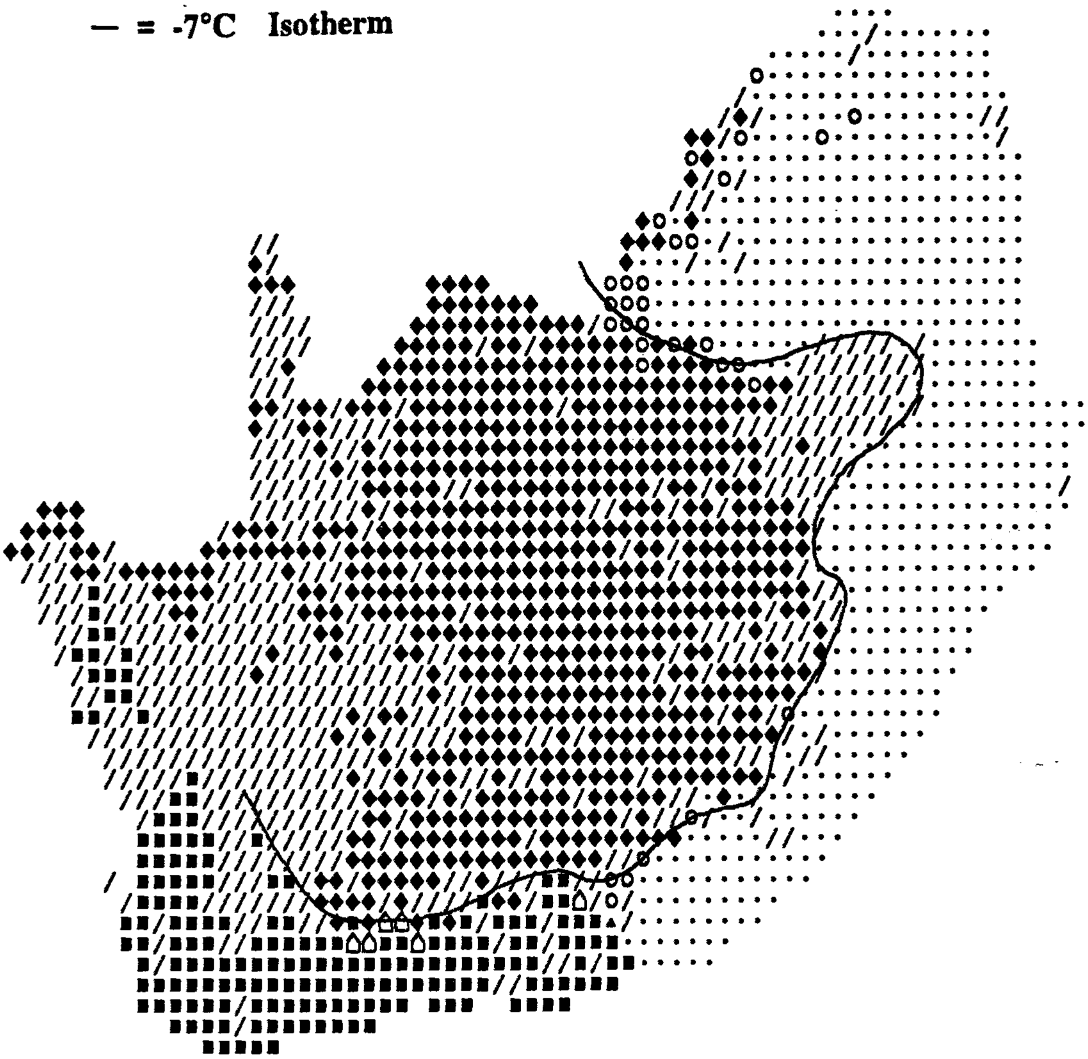


Figure 2.1 Distribution of the three *Pycnonotus* species in South Africa in relation to the -7°C minimum winter isotherm. Distribution data from SABAP (see Chapter 3). Isotherm determined from records in Weather Bureau (1986).

The birds were provided with fresh fruit, "Pronutro" cereal (calorific value 3.89 kcal/g), and water *ad libitum*. Mealworms occasionally supplemented this diet, and a "Calsup" calcium and mineral supplement was mixed with the Pronutro. Following an outbreak of Colibacillosis in 1991 which killed five birds, an antibiotic was administered daily with the food.

2.2.2 Experimental regime

Following an acclimation period of at least one week in the aviary, metabolic rates, evaporative water losses and body temperatures of the birds were studied at constant ambient temperatures in the range -10°C to 43°C under controlled laboratory conditions. Oxygen consumption was used as a measure of metabolism in an open, flow-through respirometry system (Gessaman 1987).

Individual birds were first weighed and then placed on a wire mesh platform in an airtight perspex metabolism chamber (30cm x 30cm x 75cm). A layer of vegetable oil under the mesh ensured that excreta did not contribute to measurements of water loss. The chamber was then placed inside a darkened constant-temperature cabinet (precision ± 1°C). Chamber temperature was measured via a thermocouple inserted into the chamber through a rubber bung and positioned in the air space above the bird. For temperatures below 5°C, the metabolism chamber was placed into a large, darkened refrigerator.

Dry, carbon dioxide-free air was passed into the chamber under positive pressure. Tubes of Carbosorb and silica gel were used to absorb carbon dioxide and water vapour, respectively. The air flow rate was monitored with an Aalborg GFM 1700 mass flowmeter calibrated against a bubble flowmeter. Flow rate was set to maintain an oxygen concentration of at least 20.5% inside the chamber. Flow rates varied between 300 and 1 000 ml/min, depending on the chamber temperatures; high flow rates were used at low ambient temperatures to compensate for high oxygen consumption, and again at high ambient temperatures to compensate for increased chamber humidities, since high humidities influence thermoregulatory capability (Lasiewski *et al.* 1966).

Air exiting the chamber passed first through a pre-weighed tube of desiccated silica gel before entering an Applied Electrochemistry CD-3A carbon dioxide analyzer. The air was then passed through a tube of Carbosorb/silica gel tube, before entering an Applied Electrochemistry S-3A1 oxygen analyzer. Oxygen depletion and carbon dioxide enrichment values were recorded automatically every 20 seconds by a microcomputer using Datacan data acquisition software (Sable Systems Inc., Salt Lake City).

Rates of evaporative water loss were measured gravimetrically immediately downstream of the chamber, as described by Dawson and Fisher (1969). Freshly-dried silica gel was used for each run.

The birds remained in the chamber until their oxygen consumption had stabilised at the lowest level for a period of at least 20 minutes. Each run typically lasted 2 to 2.5 hrs.

Body temperature was measured immediately after the removal of the bird from the chamber, by inserting a 26 gauge thermocouple approximately one cm into the cloaca, and reading the temperature on a Sensortek BAT-12 digital thermometer.

The testing of the three species at subzero temperatures was conducted during the winter months to control for the effects of seasonal temperature acclimatization (Hart 1962; Chaffee & Roberts 1971; Swanson 1990; Clarke 1993).

Dry thermal conductance (C) in J/g/hr was calculated using the relation:

$$C = (H_m - H_e)/(T_b - T_a) \quad \text{(McNab 1980)}$$

where H_m = heat produced by metabolism in J/g/hr (1 ml O_2 being equivalent to 20.084 J),
H_e = heat lost through evaporation in J/g/hr (1 mg H_2O being equivalent to 2.427 J),
T_b = body temperature, and
T_a = ambient temperature.

Percentage heat lost by evaporative cooling ($\%H_{e/m}$) was calculated from the relation:

$$\%H_{e/m} = 100x(H_e/H_m)$$

Statistical analyses of the data were performed using STATGRAPHICS (Statistical Graphics Corporation, Inc.).

2.3 RESULTS

2.3.1 Metabolic rate (VO_2)

Metabolic rates of the three species are plotted on Figure 2.2. Table 2.2 summarises their observed and predicted physiological parameters. The three species had similar lower critical temperatures (T_{lc}: 30.1°C for *P. barbatus*; 33.9°C for *P. nigricans*; 32.5°C for *P. capensis*), that were substantially higher than predicted values (18.0°C, 18.6°C and 18.4°C respectively).

Although *P. nigricans* started to pant at temperatures above 42°C, this was not accompanied by any marked increase in metabolic rate, and in all three species, the thermoneutral zone (the temperature range over which metabolic rate remains roughly constant) extended from the T_{lc} to the highest temperatures tested (40°C for *P. barbatus*; 43°C for *P. nigricans*; 39°C for *P. capensis*).

Basal metabolic rate (BMR) within the thermoneutral zone for *P. barbatus*, *P. nigricans* and *P. capensis* were similar to predicted values (Table 2.2). There were no significant differences between the BMRs of the three species (one-way ANOVA: $F = 0.12$; d.f. = 2,32; $P = 0.89$). Below the T_{lc}, VO_2 increased with temperature, the relationships being described by the following equations:

$VO_2 = 5.364 - 0.074T_a$ ($r^2 = 0.68$) for *P. barbatus*,
$VO_2 = 5.499 - 0.069T_a$ ($r^2 = 0.62$) for *P. nigricans*, and
$VO_2 = 5.240 - 0.058T_a$ ($r^2 = 0.60$) for *P. capensis*.

There were no significant differences in either the slopes or intercepts of these regression equations (analysis of covariance: $F = 1.33$; d.f. = 4,176; $P = 0.26$). Using these equations, VO_2 at an ambient temperature of -10°C was calculated to be equivalent to twice the basal metabolic rate (Table 2.2).

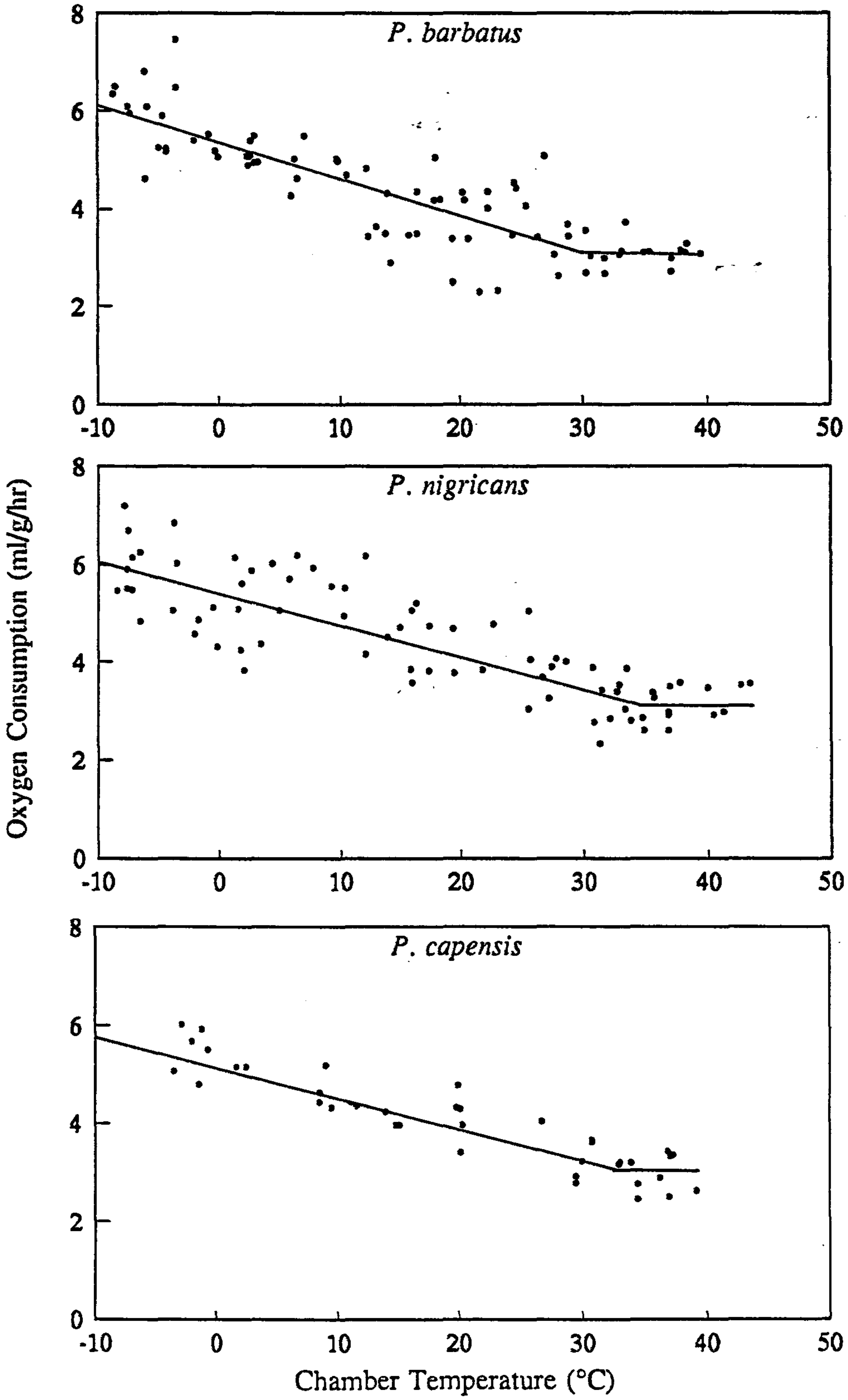


Figure 2.2 The relationship between metabolic rate (as ml O_2 consumed/g body weight/hr) and chamber temperature for the three *Pycnonotus* bulbuls.

Table 2.2 Daytime (active phase) standard metabolic measurements for the three *Pycnonotus* bulbul species.

	P.barbatus	*P.nigricans*	*P.capensis*
Mean Mass (g)	42.02 ± 3.54	38.84 ± 3.62	41.71 ± 3.33
Mean Body Temperature T_b (°C)	41.09 ± 1.62	41.40 ± 1.18	41.49 ± 0.72
Lower Critical Temperature T_{lc} (°C)	30.1	33.9	32.5
Predicted T_{lc} (°C) [(a)]	18.0	18.6	18.4
Basal Metabolic Rate BMR (ml O_2/g/hr)	3.14 ± 0.30 (n = 20 measurements on 11 individuals)	3.11 ± 0.40 (n = 27 measurements on 18 individuals)	3.06 ± 0.22 (n = 15 measurements on 6 individuals)
Predicted BMR (ml O_2/g/hr) [(b)]	3.13	3.20	3.13
Metabolic Rate VO_2 at -10°C (ml O_2/g/hr)	6.10 (1.9 x BMR)	6.14 (2.0 x BMR)	5.82 (1.9 x BMR)
Evaporative Water Loss EWL Critical Temperature (°C)	30.2	27.4	22.7
EWL at T_a< Critical Temperature (mg H_2O/g/hr)	3.84 ± 1.45 (n = 58)	4.13 ± 1.43 (n = 50)	5.33 ± 1.31 (n = 20)
Predicted EWL at 25°C [(c)] (mg H_2O/g/hr)	3.49	3.71	3.51
Conductance at T_a<T_{lc} (J/g/hr)	2.83 ± 0.84 (n = 54)	2.98 ± 0.84 (n = 53)	2.77 ± 0.51 (n = 26)
Predicted Conductance (J/g/hr) [(d)]	3.05	3.71	3.06

(a) Calculated from $T_{lc} = T_b - 11.5g^{0.187}$ from Hayworth & Weathers 1984.

(b) Calculated from kcal/day = $140.9kg^{0.704}$ from Hayworth & Weathers 1984.

(c) Calculated from g H_2O/day = $1.563g^{0.217}$ from Crawford & Lasiewski 1968.

(d) Calculated from ml O_2/g/hr = $0.857g^{-0.463}$ after Aschoff 1981.

2.3.2 Dry thermal conductance

Figure 2.3 illustrates the relationship between dry thermal conductance and ambient temperature for the three species. Conductances increased minimally from values of 2.0-2.4 J/g/hr at subzero temperatures to values of 3.4-4.0 J/g/hr at or just above the lower critical temperature (T_{lc}), where a critical point was reached. Thereafter, conductances increased markedly with increasing temperature, reaching values of 10-16 J/g/hr at 40°C. There was no significant difference in conductance at ambient temperatures below the T_{lc} between the three species (one-way ANOVA: $F = 0.79$; d.f. = 2,130; $P = 0.46$). Mean conductance values for these temperatures were slightly lower than the predicted values for each species (Table 2.2).

2.3.3 Evaporative water loss (EWL)

Figure 2.4 illustrates the relationship between EWL and ambient temperature for the three species, whilst Figure 2.5 illustrates the percentage of the total metabolic heat production that is lost through EWL.

A 2-phase regression analysis (Yaeger & Ultsch 1989) detected a critical point in the increase in EWL at 30.2, 27.4 and 22.7°C for *P. barbatus*, *P. nigricans* and *P. capensis* respectively. The regression equations describing EWL at ambient temperatures below and above these critical temperatures are:

$\mathrm{EWL} = 3.31 + 7.08\mathrm{x}10^{-2}T_a$ ($r^2 = 0.30$) : $\mathrm{EWL} = -24.55 + 0.99T_a$ ($r^2 = 0.94$) for *P. barbatus*,
$\mathrm{EWL} = 3.60 + 7.81\mathrm{x}10^{-2}T_a$ ($r^2 = 0.39$) : $\mathrm{EWL} = -19.77 + 0.93Ta$ ($r^2 = 0.92$) for *P. nigricans*, and
$\mathrm{EWL} = 4.20 + 0.14T_a$ ($r^2 = 0.59$) : $\mathrm{EWL} = -5.12 + 0.55T_a$ ($r^2 = 0.95$) for *P. capensis*.

Average EWL values below the critical temperatures were significantly different only in the case of *P. capensis* (one-way ANOVA: $F = 8.49$; d.f. = 2, 125; $P = 0.00$). These values are similar to predicted EWL at 25°C for *P. barbatus* and *P. nigricans*, but higher than that predicted for *P. capensis* (Table 2.2).

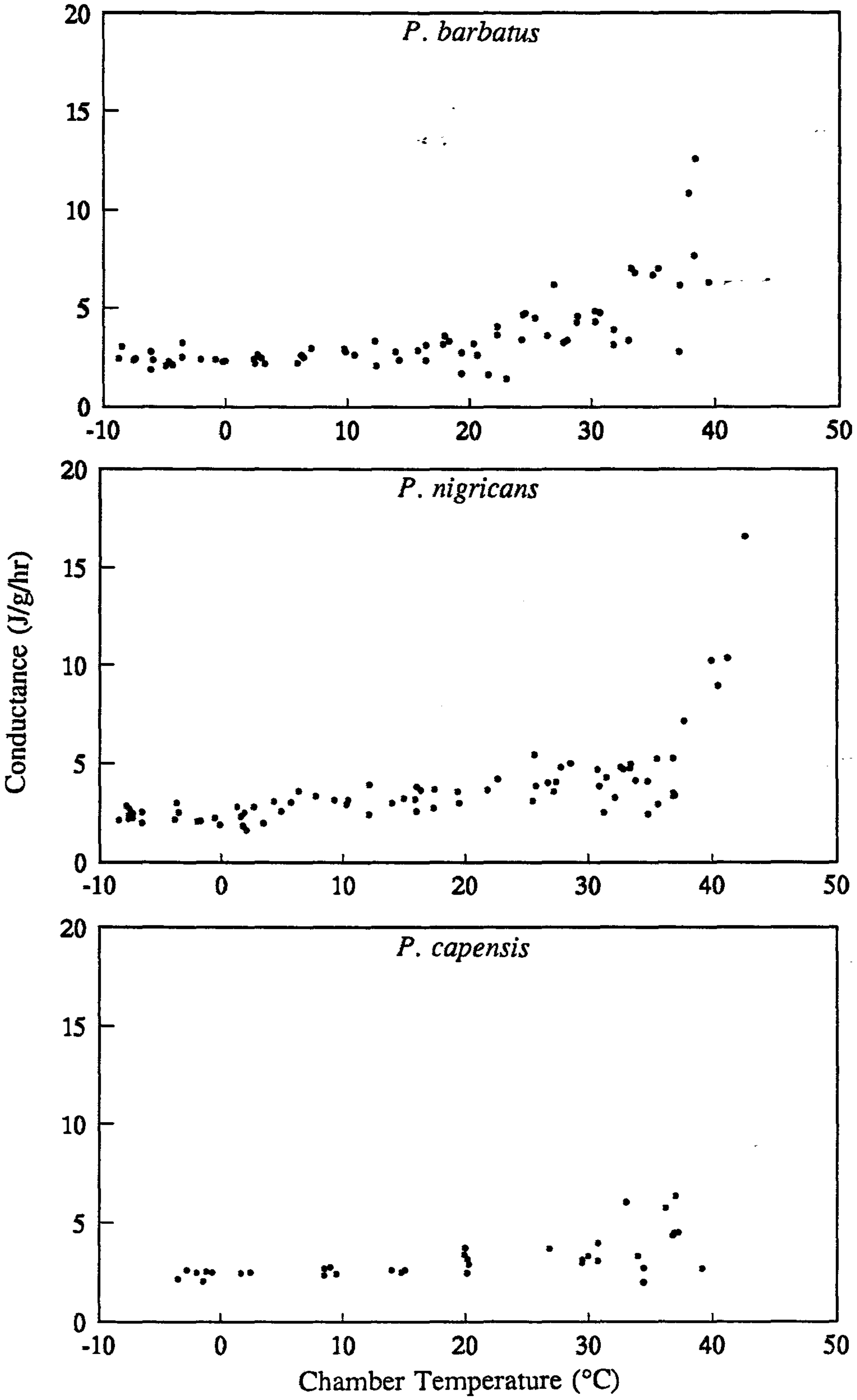


Figure 2.3 The relationship between dry thermal conductance and chamber temperature for the three *Pycnonotus* bulbuls.

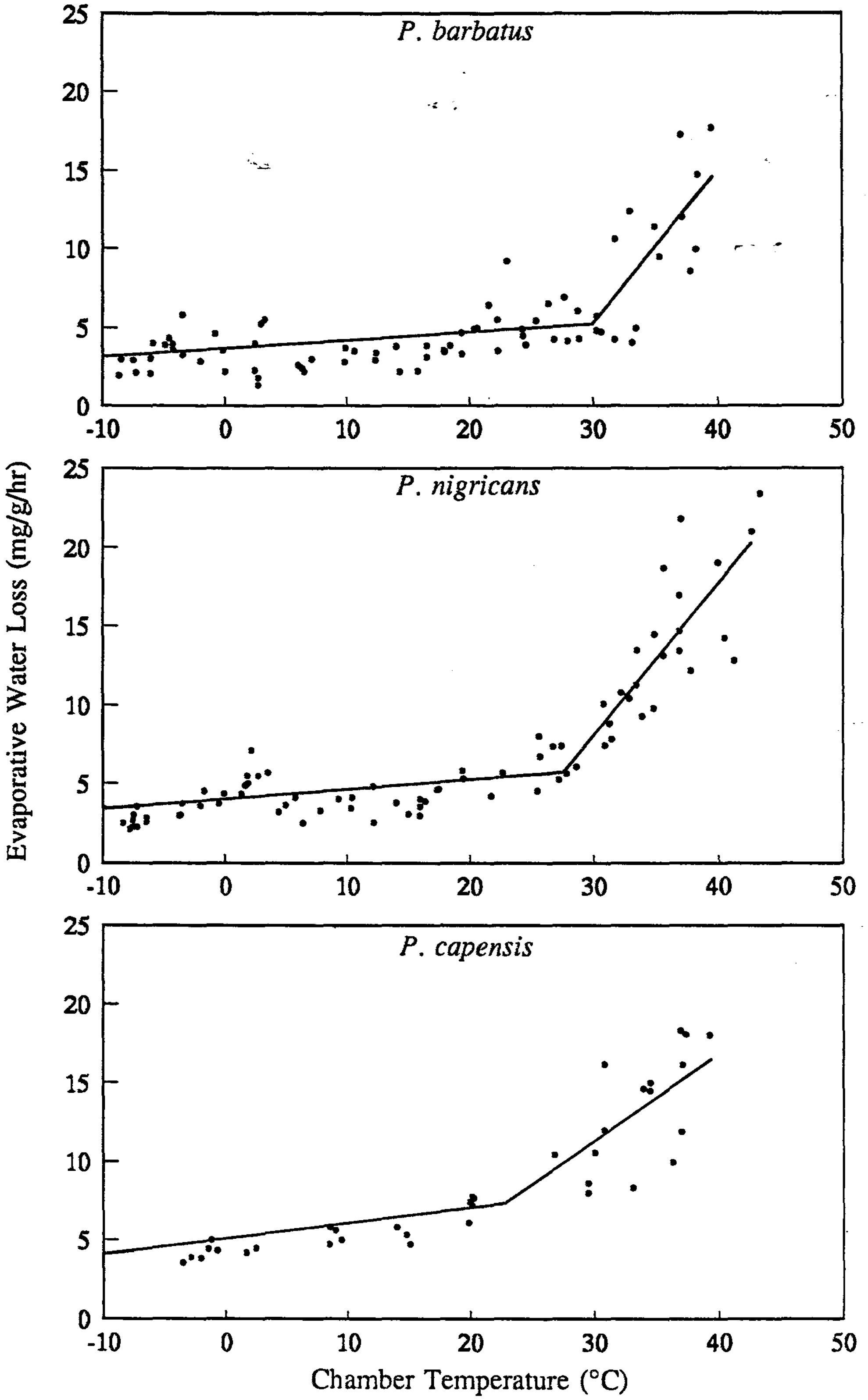


Figure 2.4 The relationship between evaporative water loss (EWL) and chamber temperature for the three *Pycnonotus* bulbul species.

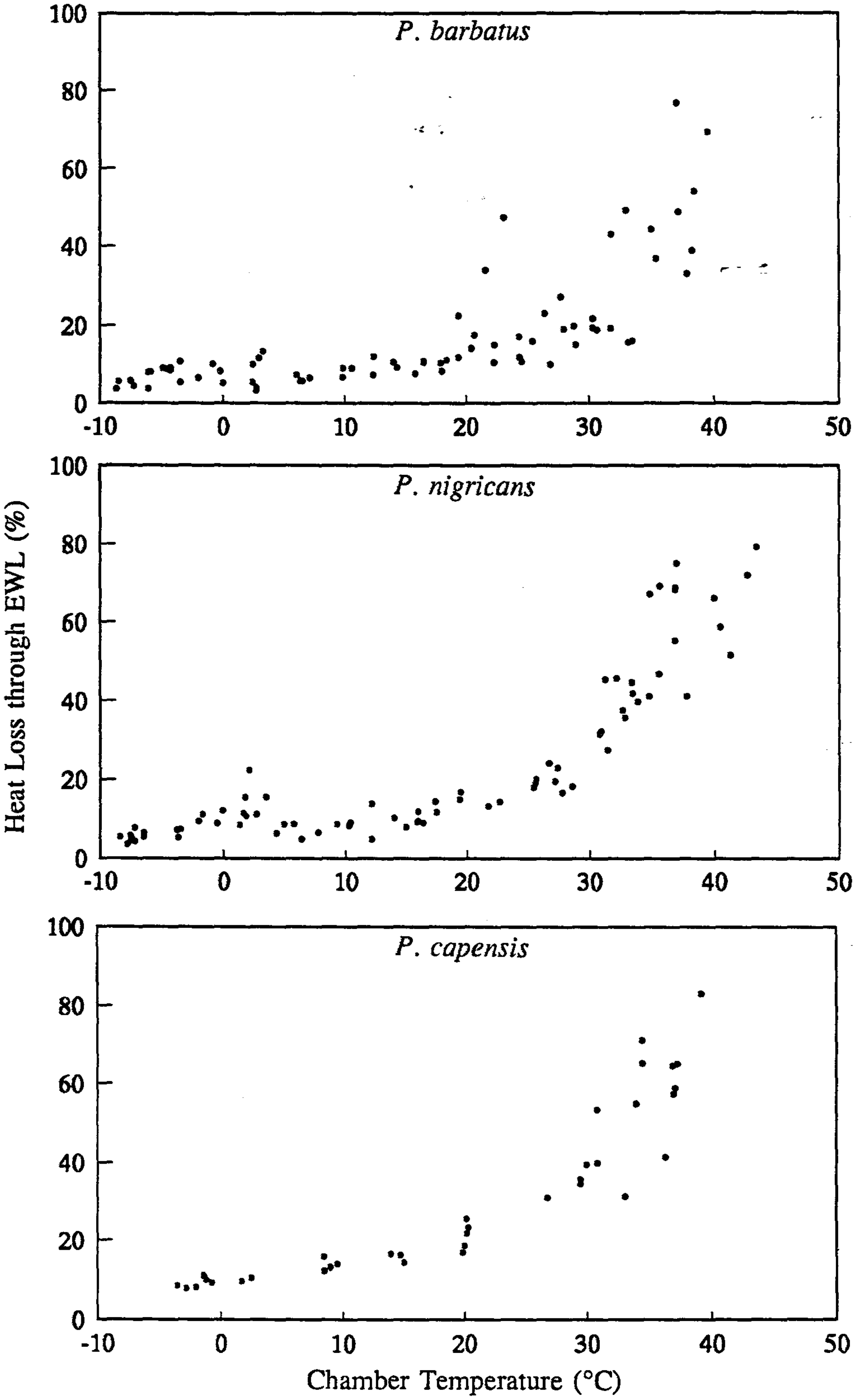


Figure 2.5 The relationship between heat loss through evaporative water loss (EWL) and chamber temperature for the three *Pycnonotus* bulbuls.

Using an exponential regression analysis the relationship between the percentage of metabolic heat dissipated evaporatively ($\%H_{e/m}$) and ambient temperature is described by the following equations:

$\%H_{e/m} = e^{1.90 + 0.042Ta}$ ($r^2 = 0.69$) for *P. barbatus*,
$\%H_{e/m} = e^{1.98 + 0.048Ta}$ ($r^2 = 0.82$) for *P. nigricans*, and
$\%H_{e/m} = e^{2.19 + 0.050Ta}$ ($r^2 = 0.94$) for *P. capensis*.

Using Kolmogorov-Smirnov two-sample tests, no significant differences were found between observed $\%H_{e/m}$ values and those predicted by the relation $\%H_{e/m} = 5 + 1.48e^{0.087Ta}$ (Calder & King 1974) for each of the three species ($P = 0.64$ for *P. barbatus*; $P = 0.31$ for *P. nigricans*; $P = 0.12$ for *P. capensis*).

All three species withstood the high temperatures tested with no visible signs of stress, but lost up to 3% of their body mass per hour through EWL. Panting was only observed at temperatures above 42°C, by *P. nigricans*, which was the only species tested at such high temperature. At these extreme temperatures, bulbuls could shed up to 80% of their metabolic heat through EWL.

2.4 DISCUSSION

Physiological adaptations of birds to cold climatic conditions include reductions in thermal conductance, a reduction of the lower critical temperature and higher basal metabolic rates (BMRs) (Calder & King 1974; Schmidt-Nielsen 1983). Adaptations to hot climates and high thermal loads include high thermal conductance, decreased BMR, and, in desert-adapted species, reduced evaporative water loss (EWL) at higher temperatures (Dawson & Bennett 1973; Ellis 1980).

Pycnonotus bulbuls exhibited BMRs and thermal conductances more or less typical for passerines of equivalent mass, but higher than expected lower critical temperatures (Table 2.2). Although the upper critical temperature was not actually reached, it is certainly higher than that recorded for most birds, being matched only by some species adapted to hot climates (Dawson & Bennett 1973; Collins *et al.* 1980; Ellis 1980; Bucher 1981; Hayworth & Weathers 1984). This would tend to suggest that the three bulbul species are better adapted to hot, rather than cold climates.

The significant difference in EWL below the T_{lc} shown by *P. capensis* may be an artifact of slight variations in methodology between workers. Should this not be the case though, it is improbable that the higher EWL of this species plays any direct role in restricting its distribution, since it is recorded in habitat as arid as adjacent habitat occupied by *P. nigricans* (see Chapter 6), and experiences summer temperatures as extreme as those experienced by the other two species (see Table 2.1).

The exponential increase in the percentage of metabolic heat dissipated evaporatively is equivalent to that predicted by Calder and King (1974). The three species are very efficient at shedding heat by evaporative cooling, managing to lose up to 80% of the excess heat via this method at extreme temperatures. There is, however, a cost involved; at these extremes, the birds lose up to 3% of their body weight per hour. Clearly then, the birds are well adapted to hot climatic conditions in the sense that they can tolerate high thermal loading. On the other hand though, they are very dependent on water to achieve this.

Bulbuls were only observed to pant at temperatures above 42°C, yet EWL values began to increase markedly above a critical temperature between 23°C and 30°C, whereas metabolic rates (and presumably respiration rates) remained stable. Dawson (1982) reports that cutaneous evaporation by birds under heat loading can contribute substantially to evaporative cooling, particularly when there is considerable air movement over the body. The same would certainly appear to be true for bulbuls. It should be noted that air flow rates were increased at higher temperatures to compensate for increased humidities as a result of EWL. Arid-adapted birds, such as the Ostrich (*Struthio camelus*), have much reduced EWL through the skin (Schmidt-Nielsen *et al.* 1969). These results suggest that, although bulbuls might be adapted to hot climatic conditions, they are not particularly arid-adapted in the sense of exhibiting adaptations for water conservation. This correlates well with the known dependence on water of all three species.

The three species tolerated all temperatures tested down to -10°C with no ill effects. At this temperature, metabolic rates correlated to roughly 2 x BMR (Table 2.1), lower than the figure of 2.5 x BMR that Root (1988b, 1989) hypothesized as limiting the northern distribution limits of many American passerines. This result suggests that all three bulbul species can tolerate the lowest temperatures likely to be encountered anywhere in southern Africa.

It should be borne in mind, however, that this study has not tested the complicating effects of exposure and the wind-chill factor. A metabolic chamber is a sheltered environment, and as such, cannot replicate field conditions. A strong wind on a freezing-cold winter night can make a significant difference. Birds also thermoregulate behaviourally, and will roost in sheltered sites. The possibility that the three species exhibit different roosting behaviours that could affect their thermoregulatory ability, whilst remote, cannot be ignored.

In summary then, the three species of bulbul showed no significant inter-specific differences in any of the physiological parameters tested, except possibly EWL.

2.5 TEMPERATURE TOLERANCE AND DISTRIBUTION

The results of these physiological measurements lend no support to the hypothesis, suggested by their distribution patterns, that minimum winter temperatures in the region of -7°C limit the distributions of either *P. barbatus* or *P. capensis* through a direct physiological effect. Furthermore, since all three *Pycnonotus* species show similar tolerances to high temperatures, it would appear that temperature extremes have no direct limiting effect. Thus *P. nigricans* does not appear to be uniquely physiologically adapted to its arid habitat.

As a final footnote, however, it needs to be mentioned that these studies were completed before the existence of extensive hybridization between *P. barbatus* and *P. nigricans* was discovered (see Chapter 6). All *P. nigricans* used in this study were collected from the farm Rietvlei, at the edge of the hybrid zone between these two species. Whilst all birds collected for metabolic testing exhibited the phenotypic characteristics of typical *P. nigricans*, it is not known to what extent introgression of *P. barbatus* genes may have modified the physiological responses of these birds. I did subsequently collect phenotypic hybrids from Rietvlei.

CHAPTER THREE

CORRELATING THE DISTRIBUTION OF *Pycnonotus* BULBULS WITH ENVIRONMENTAL VARIABLES

3.1 INTRODUCTION

The distributions of both plants and animals are determined and/or affected by a wide variety of environmental and biotic factors (Krebs 1985). The distribution limits of a species might be in response to a single factor, such as the factor for which the organism has the narrowest range of adaptability or control (Liebig's law of the minimum), or in response to a complex interaction between multiple factors (Hall *et al.* 1992).

The previous chapter investigated the possible limiting effect of a single environmental factor, that of minimum winter temperatures in the region of -7°C. The results suggested that this factor, considered alone, is not directly responsible for limiting the distributions of the three *Pycnonotus* bulbul species. This does not preclude the possibility of temperature, as a variable, exerting an indirect influence on their distributions through its effect on, for example, vegetation, or as an integral component of a complex suite of environmental variables.

For terrestrial birds, vegetation, either in its floristic composition or spatial structure, has an important effect on species distributions, particularly at the local level. The problem with trying to relate species distributions directly to this factor, is the enormous effort required to quantify the structure and composition of vegetation (e.g. Cody 1968; Folse 1982), particularly when the species involved inhabit a wide variety of different vegetation types. This problem can be circumvented, to some extent, by obtaining indirect indices of vegetation through quantification of a variety of environmental factors that influence vegetation, such as temperature, rainfall and elevation.

Annual precipitation is an important vegetation determinant, particularly in semi-arid regions, with median annual rainfall providing a better index of aridity than the mean in direct gradient analysis (Palmer & van Staden 1992). Elevation is an indirect variable that influences plant growth through correlated changes in direct variables, and can be used as a location-specific surrogate for a complex set of environmental variables in gradient analysis (Austin *et al.* 1983). A combination of elevation and rainfall models has been useful in predicting the distribution of plant communities (Palmer 1991a,b; Palmer & van Staden 1992).

To examine the importance of environmental factors, large-scale studies are usually required, because the patterns caused by factors such as ambient temperature can easily be obscured or overlooked in a small-scale study (Root 1988a). Such studies require massive data sets. In this respect, we are fortunate in South Africa to have both a nationwide bird distribution database, that of the South African Bird Atlas Project (SABAP), and a number of digital databases modelling a variety of environmental variables (Dent *et al.* 1989; Palmer 1993).

The combination of these models provides the opportunity to relate the distribution of bird species to a complex of environmental variables, and ultimately to prepare a testable model of the relationship between a species' distribution and the environment.

3.2 METHODS

The latest available data (25 August 1993, Phase 3) from SABAP were used to plot the distributions of the three *Pycnonotus* bulbuls in South Africa. These atlas data were collected by professional and amateur ornithologists over a five-year period from 1986 to 1991. Bird lists on atlas cards at the geographic resolution of a quarter-degree square, were submitted monthly. This presence/absence data for individual species was then pooled to generate a value to serve as an index of abundance for each species in each quarter-degree square. Value categories were as follows:

9 : species recorded on 85-100% of cards
8 : species recorded on 75-84.9% of cards
7 : species recorded on 65-74.9% of cards
6 : species recorded on 55-64.9% of cards
5 : species recorded on 45-54.9% of cards
4 : species recorded on 35-44.9% of cards
3 : species recorded on 25-34.9% of cards

2 : species recorded on 15-24.9% of cards
1 : species recorded on 5-14.9% of cards
R : Rare - species recorded on 1-4.9% of cards
V : Vagrant - species recorded on <1% of cards
/ : cards returned, but species not recorded.

Pycnonotus bulbuls are lively, noisy and conspicuous birds that have adapted well to man-made habitats, especially gardens, where they are usually common residents. They thus have a high profile as far as ease of identification and visibility to birdwatchers is concerned. For this reason, their recorded absence from a locality or area is more likely to reflect their true absence/rarity rather than their being overlooked by the observer. To identify the regions of preferred, or "core", habitat, I reasoned that any quarter degree square that returned a value of less than 25% for a species' abundance represented a "marginal" area for the distribution of that species. I therefore modified the base SABAP data for each of the three species by changing the values 3-9 to "species present" and the values 2-V to "species absent". By overlaying the presence/absence data for each species, a single map plotting the "core" distributions of the three species at a quarter-degree resolution was produced.

Environmental variables for each quarter-degree square were then extracted from grid-based Geographical Information System (GIS) models which plot data for the entire South African land surface at a minimum resolution of a one-minute square. Variables used were:

1. Elevation (Dent *et al.* 1989),
2. Median annual rainfall (Dent *et al.* 1989),
3. Coefficient of variation in mean annual rainfall (Palmer 1993),
4. Mean January maximum temperatures (Palmer 1993),
5. Mean July minimum temperatures (Palmer 1993),
6. NOAA waveband 1: 0.55-0.68 um (visible light) scanned on 29 August 1985 (Palmer 1993), and
7. NOAA waveband 2: 0.725-1.10 um (near infra-red light) scanned on 29 August 1985 (Palmer 1993).

NOAA are a series of American weather satellites. The two waveband scans measure the spectral reflectance of the earth's surface. Waveband 1 is characterized by strong chlorophyll absorbtion of red wavelenghts; there is a strong relationship between spectral reflectance in this waveband and the amount of chlorophyll present. Waveband 2 is characterized by high levels of reflectance occurring in the absence of any absorptance; there is a strong relationship between spectral reflectance in this waveband and the amount of green vegetation biomass present (Tucker 1978).

Using these two waveband reflectance surfaces, a normalized difference green vegetation index (NDVI) surface was produced as: (waveband 2- waveband 1)/(waveband 2 + waveband 1). The NDVI is a sensitive indicator of green biomass, and increases as the vegetation becomes greener or more dense (Tucker 1979; Tucker *et al.* 1983; Tueller 1989).

For each quarter-degree square registering the presence of a *Pycnonotus* species, a random point was chosen, at which a value for each environmental variable was extracted. Those squares registering the presence of two species were simply recorded twice. A multivariate discriminant function analysis was then used to relate the distributions of the three species to the suite of six environmental variables (nos 1-5 above and the NDVI).

The standardized discriminant function coefficients for the first discriminant function were then used to generate a discriminant function values surface, using the relation:

$$Z = \lambda_1 X_1 + \lambda_2 X_2 + ... + \lambda_6 X_6$$

where λ = the standardized discriminant function coefficient, and X = the environmental variable value.

The quarter-degree Z-values were then ranked in ascending order and grouped into 50-member samples, from which the degree of confidence in predicting the presence of *P. nigricans* was determined. The approximate Z-values delimiting the confidence intervals: >95%, 80-95%, 70-79% and <70% were then determined. These values were finally used to categorise the Z-values surface generated for South Africa, and to plot the predicted distribution of *P. nigricans*, at the various confidence intervals within my 32°00'S 25°00'E to 34°00'S 27°00'E study area in the eastern Cape. This plot of the predicted distribution, at a one-minute square resolution, was then visually compared to my distribution plot for the study area at a five-minute square resolution.

The latter plot is the result of observations made on a number of surveys through the study area (see Chapter 6).

3.3 RESULTS

The August 1993 SABAP base data are illustrated in Figure 3.1. Figure 3.2 shows the modified SABAP data for the three *Pycnonotus* species.

The results of the discriminant analysis are presented in Tables 3.1 and 3.2.

Table 3.1 Discriminant function classification of *Pycnonotus* bulbul distributions using six environmental variables. BEB = *P. barbatus*; REB = *P. nigricans*; CB = *P. capensis*.

Actual Group	**Predicted Group (% of total)**			**Total no. of quarter-degree squares**
	BEB	**REB**	**CB**	
BEB	88	6	6	563
REB	6	92	2	702
CB	7	14	79	161

Table 3.2 Standardized canonical discriminant function coefficients and mean values for six environmental variables from the distributions of the three *Pycnonotus* bulbuls. BEB = *P. barbatus*; REB = *P. nigricans*; CB = *P. capensis*; * = percentage of total variance.

Environmental variable	**Discriminant Coefficients**		**Species means of variables**		
	Function 1 (72%)*	**Function 2 (28%)**	**BEB**	**REB**	**CB**
Elevation (m)	-0.11	-0.66	946	1267	503
Median annual rainfall (mm)	+0.23	-0.68	690	380	411
Coefficient of rainfall variation	-0.65	-0.02	24.3	41.2	32.9
January max. temperatures (°C)	-0.06	-0.36	28.1	30.9	29.0
July minimum temperaturs (°C)	+0.66	-0.26	5.1	1.0	5.1
NDVI	-0.08	+0.83	0.07	0.06	0.15

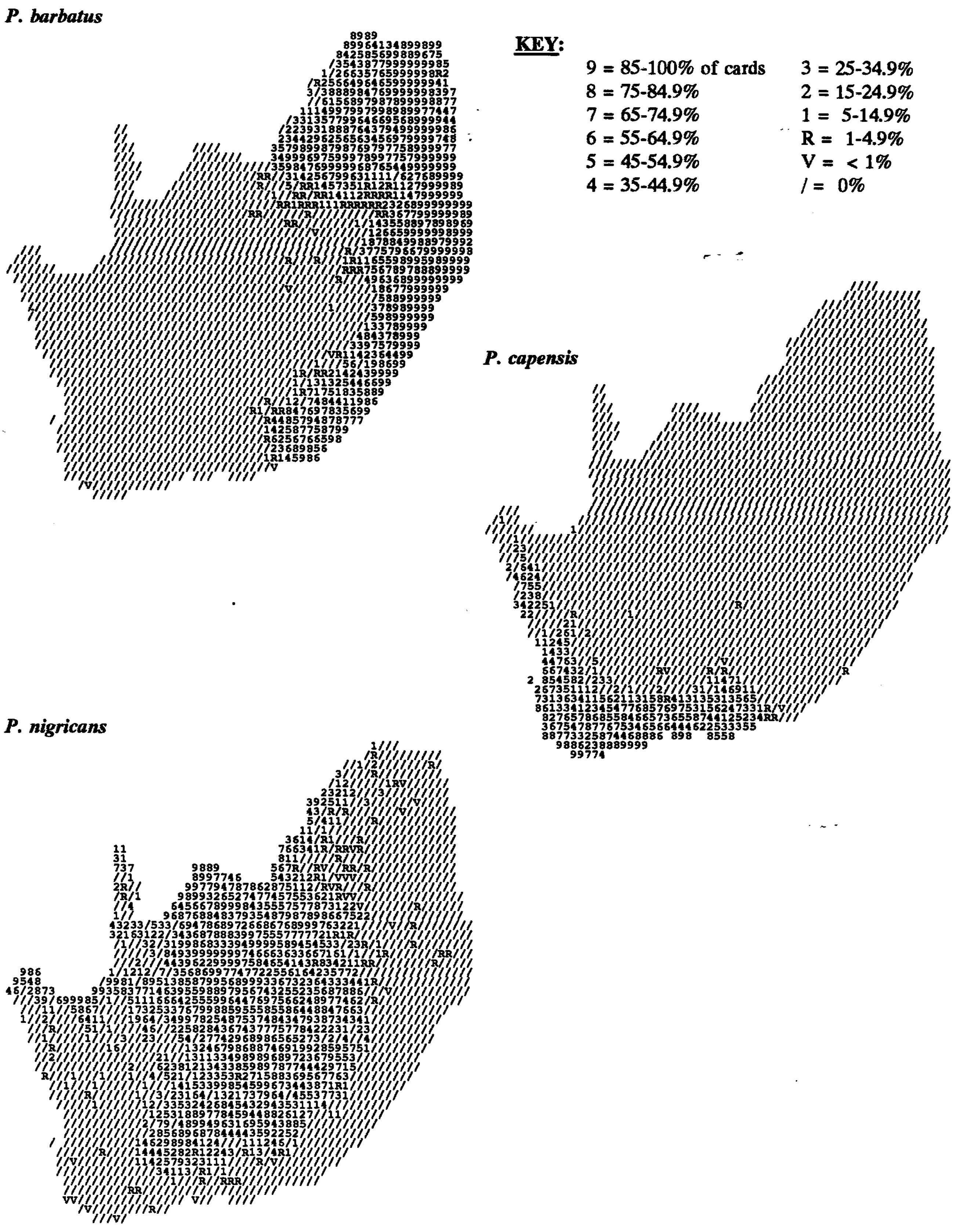


Figure 3.1 The quarter-degree square distributions and relative abundances of the three *Pycnonotus* bulbuls in South Africa. August 1993 SABAP data.

KEY:

• = *P. barbatus*
♦ = *P. nigricans*
■ = *P. capensis*
o = *P. barbatus & P. nigricans*
⌂ = *P. barbatus & P. capensis*
▴ = *P. nigricans & P. capensis*
/ = None at ≥25%

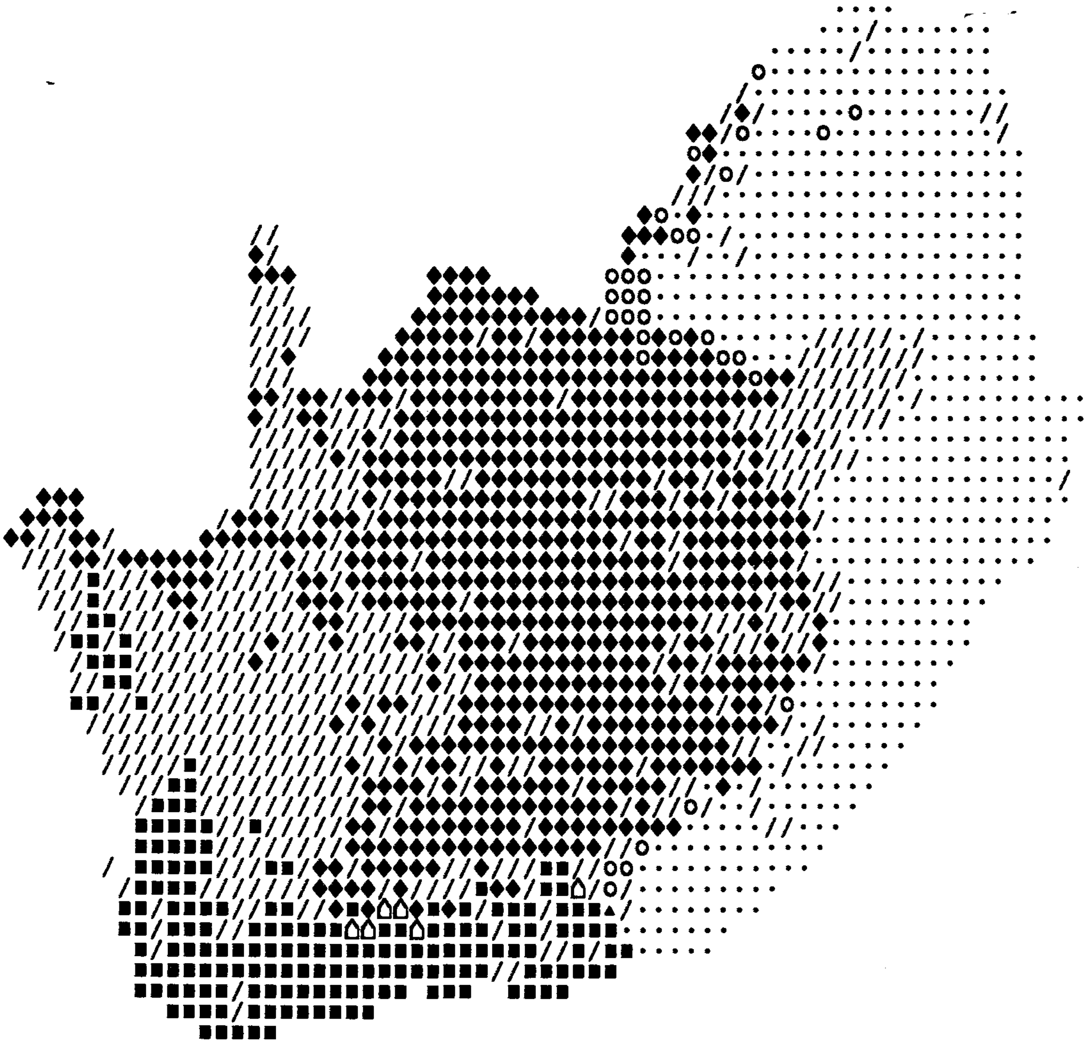


Figure 3.2 The "core" distributions of the three *Pycnonotus* bulbuls in South Africa. Modified SABAP data (see text).

This analysis correctly classified the distribution of the species for 89% of the 1426 quarter-degree squares analyzed (Table 3.1). Separation on the first function, which accounted for 76% of the total variance, was mainly by the coefficient of variation in mean annual rainfall and mean July minimum temperature. Figure 3.3, which plots the frequency distribution of Z-value classes of the first discriminant function for each of the three species, shows that the first discriminant function, alone, is successful in characterizing *P. nigricans*. Comparing the species' means (Table 3.2), it can be seen that this species occupies regions with a high coefficient of variation in annual rainfall and low July minimum temperatures.

Separation on the second function was mainly by the NDVI, with elevation and median annual rainfall playing a lesser role (Table 3.2). Since the satellite scan was conducted in August, towards the end of winter, those parts of the country that experience winter rains exhibit greener, actively growing vegetation, and therefore higher NDVI values. *P. capensis* distribution had a mean NDVI value of 0.15, more than double that of the other two species (Table 3.2). The second function thus serves to characterize *P. capensis*, whose distribution mirrors that of the Fynbos and Succulent Karoo biomes (Rutherford & Westfall 1986). These two biotic provinces receive most of their rainfall during the winter months (Tyson 1986).

The discriminant analysis correctly classified 87% of *P. barbatus*, 92% of *P. nigricans* and 82% of *P. capensis* quarter-degree distribution records (Table 3.1). This result shows that a model based on the six environmental variables chosen is very successful in classifying the distributions of the three species.The success with which the first discriminant function was able to characterize *P. nigricans* distribution lead to the decision to formulate a model to plot the predicted distribution of this species. This predicted distribution (derived from SABAP data) is illustrated in Figure 3.4, for comparison with the actual distribution of this species in the study area according to my own data (Figure 3.5).

To evaluate the model, the predicted distribution at the one-minute resolution was smoothed to a 5-minute resolution as follows: if any one-minute pixel predicting the presence of *P. nigricans* with 95% confidence fell within a 5-minute square, *P. nigricans* was recorded as "predicted present", otherwise as "predicted absent". The predicted distribution was then overlayed with the observed distribution, and the number of squares for which the predicted presence/absence matched the observed presence/absence were counted.

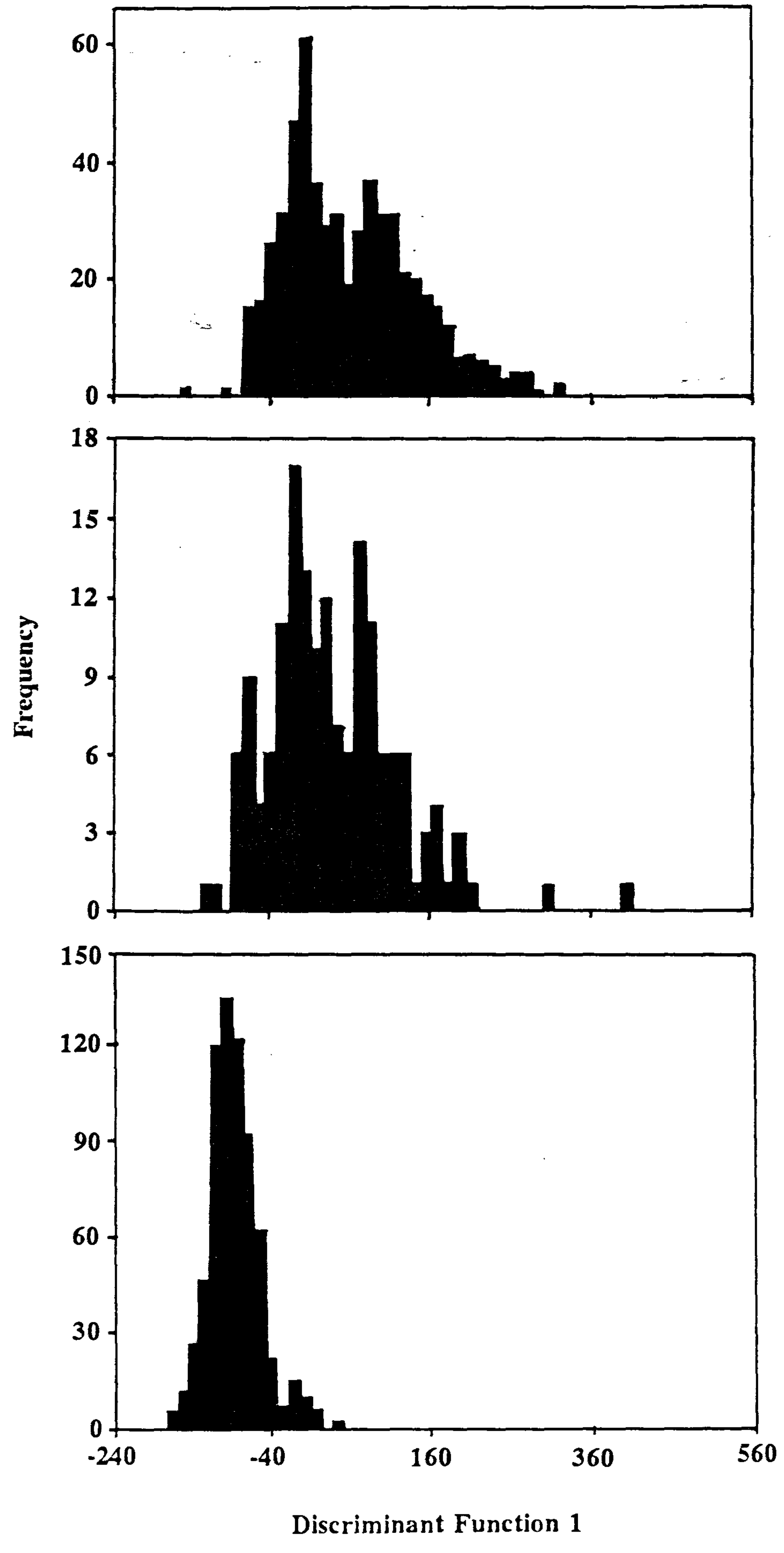


Figure 3.3 Frequency histograms of the first discriminant function values (Z-values) for the three *Pycnonotus* bulbuls.

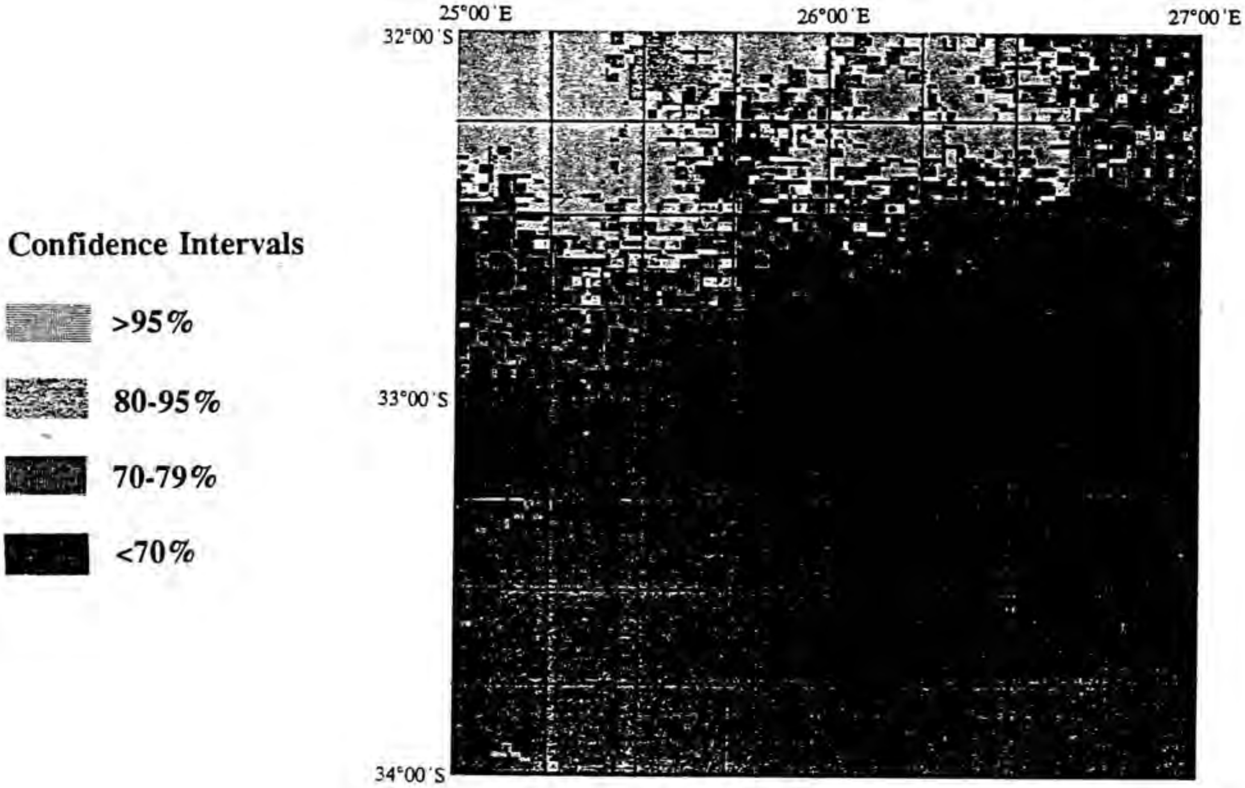
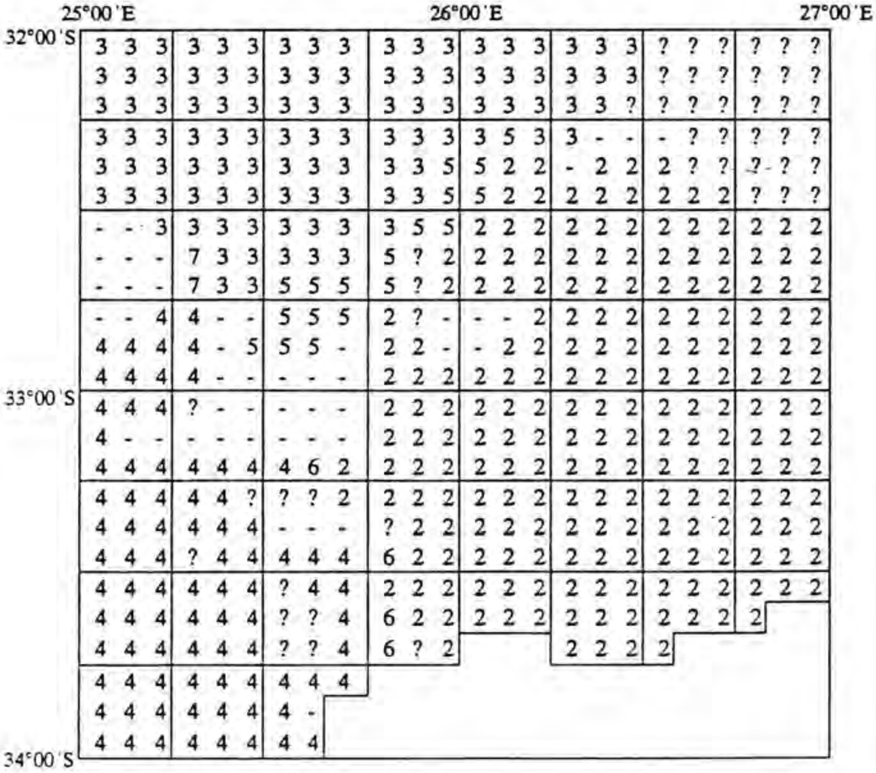


Figure 3.4 The predicted distribution (per one-minute square) of *P. nigricans* at the specified confidence intervals for the E Cape study area.

KEY

2 = *P. barbatus*
3 = *P. nigricans*
4 = *P. capensis*
5 = *P. barbatus* + *P. nigricans*
6 = *P. barbatus* + *P. capensis*
7 = *P. nigricans* + *P. capensis*
? = unknown
- = bulbuls mostly absent



3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	?	?	?	?	?	?
3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	?	?	?	?	?	?
3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	?	?	?	?	?	?	?
3	3	3	3	3	3	3	3	3	3	3	3	3	5	3	3	-	-	-	?	?	?	?	?
3	3	3	3	3	3	3	3	3	3	3	5	5	2	2	-	2	2	2	?	?	?	?	?
3	3	3	3	3	3	3	3	3	3	3	5	5	2	2	2	2	2	2	2	2	?	?	?
-	-	3	3	3	3	3	3	3	3	5	5	2	2	2	2	2	2	2	2	2	2	2	2
-	-	-	7	3	3	3	3	3	5	?	2	2	2	2	2	2	2	2	2	2	2	2	2
-	-	-	7	3	3	5	5	5	5	?	2	2	2	2	2	2	2	2	2	2	2	2	2
-	-	4	4	-	-	5	5	5	2	?	-	-	-	2	2	2	2	2	2	2	2	2	2
4	4	4	4	-	5	5	5	-	2	2	-	-	2	2	2	2	2	2	2	2	2	2	2
4	4	4	4	-	-	-	-	-	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	4	4	?	-	-	-	-	-	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	-	-	-	-	-	-	-	-	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	4	4	4	4	4	4	6	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	4	4	4	4	?	?	?	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	4	4	4	4	4	-	-	-	?	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	4	4	?	4	4	4	4	4	6	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	4	4	4	4	4	?	4	4	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
4	4	4	4	4	4	?	?	4	6	2	2	2	2	2	2	2	2	2	2	2	2		
4	4	4	4	4	4	?	?	4	6	?	2				2	2	2	2					
4	4	4	4	4	4	4	4	4															
4	4	4	4	4	4	4	-																
4	4	4	4	4	4	4	4																

Figure 3.5 The observed distribution (per 5-minute square) of the three *Pycnonotus* bulbuls in the E Cape study area (see Chapter 6 for details).

The results of this evaluation are presented in Table 3.3. The success of the model is demonstated by the high percentages of true predictions as opposed to false predictions.

Table 3.3 Evaluation of the model predicting the distribution of *P. nigricans* in the eastern Cape at a 5-minute square resolution.

	Predicted Presence	**Predicted Absence**
True	107 (88%)	335 (95%)
False	14 (12%)	18 (5%)
Total no. of squares	121	353

3.4 DISCUSSION

The plot of the "core" distributions of the three *Pycnonotus* species (Figure 3.2) shows that whilst the distributions abut one another closely, there is little overlap despite the coarseness of geographic resolution. See Chapter 6 for further evidence supporting this conclusion.

The results of the discriminant analysis (Table 3.1) suggest that the three species inhabit distinctly different habitats, as characterized by the complex of six environmental variables chosen. Certainly, this complex serves as an excellent index for predicting the species' distributions. The implications of this result for the evolutionary ecology of the species complex are dealt with in Chapter 6.

The predicted distribution of *P. nigricans* correlates very closely with its observed distribution in the study area (Figures 3.4 and 3.5; Table 3.3). This result provides some support for the initial decision to identify "marginal" areas of a species' distribution, at the resolution of a quarter-degree square, as those in which the species was recorded on less than 25% of atlas cards. This decision considerably reduced the number of squares in which overlap occurs (compare Figures 3.1 and 3.2), and probably gives a more accurate indication of the degree of geographic overlap and the sharpness of the transition zones between species. This conclusion will be further verified in Chapter 6.

CHAPTER FOUR

AN ANALYSIS OF THE SOCIAL BEHAVIOUR AND VOCALIZATIONS OF *Pycnonotus* BULBULS

4.1 INTRODUCTION

Communication is the pivot around which the social organization of any species revolves. In birds, the transfer of information between individuals is most commonly in the form of visual or vocal displays.

Bird vocalizations are of two kinds: calls and songs (Thorpe 1956). Calls are brief sounds with relatively simple acoustic structure, and rarely comprise more than five figures (notes). Calls are generally genetically determined and concerned with co-ordinating the behaviour of other members of the species in non-sexual, maintenance behaviour such as flocking, feeding and reactions to predators (Welty 1982).

Songs are more complex in rhythm and modulation than a series of call notes, and are more susceptible to modification by learning than are calls. Song commonly functions in territorial advertisement and defence, formation and maintenance of the pair bond, co-ordination of reproductive cycles within pairs and populations, individual recognition, and advertisement of motivation (Becker 1982).

In passerine birds, vocalizations are the primary form of communication, although associated behaviours may be equally important, particularly in the intersexual context. Most communication effort is directed towards conspecifics. As species-specific releasers, the signals must be easily recognizable to conspecifics if the message is to be received and responded to.

An enormous amount of research over the past 40 years has attempted to answer the apparently straightforward question "How do birds recognise their own species song?". In most studies, songs are first reproduced as sonograms for visual analysis. Various temporal and structural features are then quantified and analyzed using multivariate statistical techniques to gauge patterns of similarities and differences among populations (e.g. Lemon *et al.* 1985 and Wiens 1982). The songs are then often synthesized by computer to manipulate various features. The effects of these manipulations are finally tested in playback studies (e.g. Brooks & Falls 1975, Weary *et al.* 1986, 1990, and Horn *et al.* 1992).

Such analyses have led to the recognition of sympatric species best distinguished by voice rather than morphology, and a better understanding of various species complexes (reviewed in Payne 1986). Despite this extensive literature, the only generalizations that emerge are that "almost any song parameter can be used in song recognition", or "recognition usually depends on a constellation of features, all of which are necessary to evoke a full response" (Peters *et al.* 1980).

Most of the research effort has concentrated on the territorial songs of birds with an intrasexual function, with little work on intersexual signalling. Paterson (1978, 1980, 1985) refers to the set of characters involved in signalling between mating partners as the Specific Mate Recognition System, or SMRS.

When dealing with species complexes, particularly those that exhibit a potential for hybridization, it is important to understand the similarities and differences in both the intrasexual (territorial) and intersexual (SMRS) signalling systems among the species or populations. This study was thus undertaken to investigate the similarities and differences in the vocalizations and behaviour of the three southern African *Pycnonotus* species, and their bearing on the evolutionary ecology of the species complex as a whole.

4.2 METHODS

4.2.1 Multivariate analysis of territorial song

Territorial songs were recorded from bulbuls at localities across the southern African distribution of each of the three species. Localities included:

1. for *P. barbatus*: Harare (Zimbabwe), Giyani (E Transvaal), Maclear (NE Cape) and Grahamstown (E Cape);
2. for *P. nigricans*: Orkney (SE Transvaal), and Mountain Zebra National Park, Grassridge farm (31°47'S 25°29'E) and Rietvlei farm (32°17'S 26°01'E) (E Cape);

3. for *P. capensis*: Addo Elephant National Park (E Cape), George (S Cape) and three localities on the Cape Peninsula, namely Noordhoek, Fish Hoek and Clovelly.

The recordings were made using a Sennheiser ME 88 shotgun directional microphone attached to a Sony TC-D5M stereo cassette recorder. They were then reproduced as sonograms, using a Multigon Industries Uniscan II sonograph, from which various frequency and temporal features (following the terminology of Shiovitz 1975) were quantified as variables for statistical analysis (see also Figure 4.1):

1. HiF - highest frequency of each figure (kHz),
2. LoF - lowest frequency of each figure (kHz),
3. FRnge - frequency range of each figure (kHz),
4. StF - figure starting frequency (kHz),
5. EndF - figure ending frequency (kHz),
6. FSuc - frequency range between EndF and StF of successive figures in a phrase (kHz),
7. Int - pause between successive figures in a phrase (sec),
8. FigDur - figure duration (sec),
9. Fig/Int - ratio of FigDur to Int of the following pause,
10. ModR - segment modulation rate (segment frequency range ÷ segment duration kHz/sec), a segment being part of a figure consisting of roughly constant frequency modulation rate and direction,
11. FigNo - number of figures per phrase,
12. PhDur - phrase duration (sec), and
13. InfPt - number of inflection points per phrase, an inflection point being the locus of change between two segments.

A total of 42 *P. barbatus* phrases (comprising 209 figures), 31 *P. nigricans* phrases (comprising 144 figures) and 24 *P. capensis* phrases (comprising 120 figures) were analyzed in this manner. Statistical analyses of these data were performed using STATGRAPHICS (Statistical Graphics Corporation, Inc.).

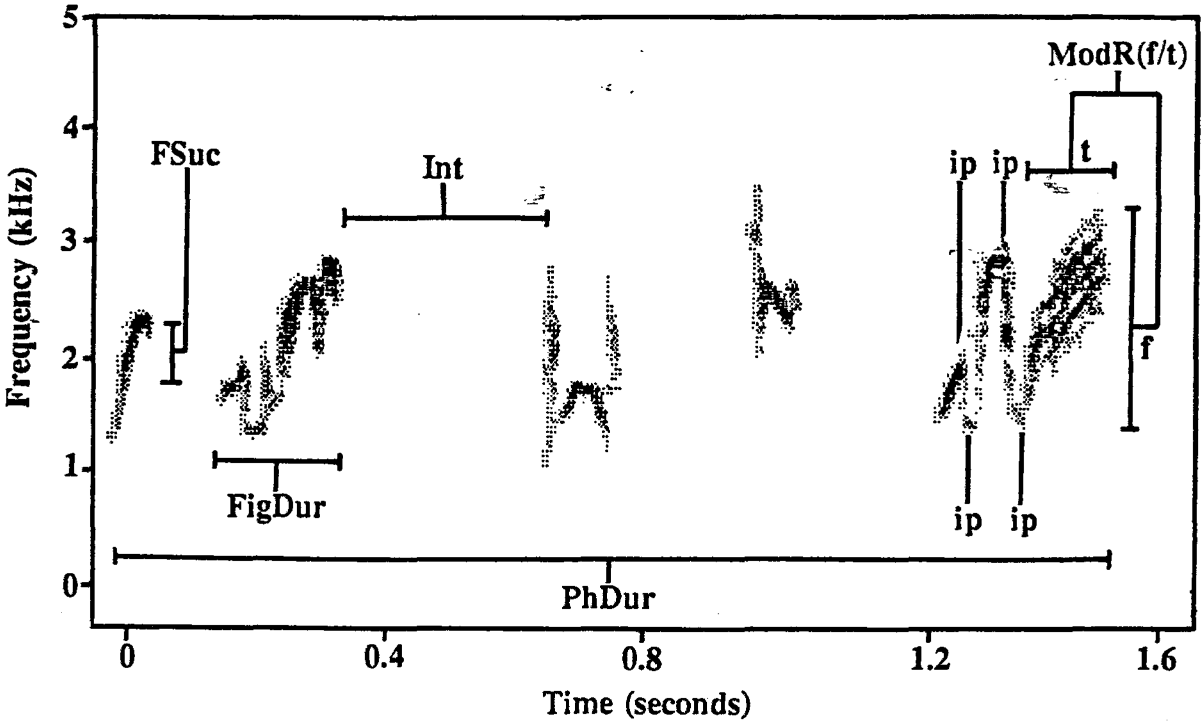


Figure 4.1 Explanation of some of the figure and phrase features quantified for comparative analysis of the songs of the three *Pycnonotus* bulbuls. FSuc = the frequency range between the ending frequency and the starting frequency of successive figures in a phrase; Int = pause between successive figures in a phrase; FigDur = figure duration; ip = inflection point; ModR = figure segment modulation rate (segment frequency range (f) ÷ segment duration (t)); Phdur = phrase duration.

4.2.2 Song playback experiment

A song playback experiment was conducted to test the response of territorial male Blackeyed Bulbuls (*P. barbatus*) to both conspecific song and heterospecific (*P. nigricans* and *P. capensis*) territorial songs. Stimulus songs from the following localities for each of the three species were used:

1. for *P. barbatus*: Harare (Zimbabwe), Zeerust (NW Transvaal) and Maclear (NE Cape);
2. for *P. nigricans*: Grassridge Farm, Cradock, and Rietvlei Farm (E Cape);
3. for *P. capensis*: Addo National Park (E Cape), George (S Cape) and Clovelly (Cape Peninsula).

The tests were conducted during the peak half-hour period of dawn announcement singing (see Chapter 5) in the months December 1992 to January 1993. During each playback run, a two minute recording of stimulus song was played from a Sony TCM-3 cassette recorder attached to an amplifier placed 20-30 m from the singing territorial male being tested. The response of the bird to playback was coded on a scale of 1 to 3, where:

1 = a strong response; the bird stops singing and approaches the speaker,
2 = a weak response; the bird stops singing and/or moves away from the speaker at some time during the two minute playback period, and
3 = no response; the bird continues to sing from its original perch throughout the two minute playback period, with no change in activity.

A total of 41 male Blackeyed Bulbuls occupying territories in suburban Grahamstown were tested. Eleven of these birds were tested with the song of all three species, with the rest tested against only one or two song types. In cases where a bird was tested more than once, the tests were spaced at least one week apart to minimize the possible effects of habituation. Since only a single two-minute length of song was played to a bird during each test, habituation was likely to be negligible. Each morning a different song stimulus was played to an average number of five males. Songs were used with approximately equal frequency in the experiment as a whole.

4.2.3 Other vocalizations and behaviours

Various vocalizations were recorded and the accompanying behaviours were observed in the field situation and simply described, with reference to the type of social interaction they were given in.

4.3 RESULTS

4.3.1 Multivariate analysis of territorial song

Appendix 4.1 provides the summary statistics for each of the song variables quantified. The Mann-Whitney U test and the Kruskal-Wallis One-way Analysis by Ranks procedure were used to test for significant differences between the three *Pycnonotus* species. The results of these statistical analyses are presented in Table 4.1.

Table 4.1 Statistical significance (*P*) values for pairwise *Pycnonotus* species comparisons (unpaired Mann-Whitney U tests) and between-species comparisons (Kruskal-Wallis test) for each of the song variables. * Denotes a statistically significant difference at $P<0.05$. See text for explanation of song variables. BEB = *P. barbatus*; REB = *P. nigricans*; CB = *P. capensis*.

	Song Variable												
	HiF	**LoF**	**FRnge**	**StF**	**EndF**	**FSuc**	**Int**	**FigDur**	**Fig/Int**	**ModR**	**FigNo**	**PhDur**	**InfPt**
BEB vs REB	<0.001*	0.950	<0.001*	0.679	0.111	0.310	0.764	<0.001*	0.004*	0.025*	0.159	0.841	0.915
BEB vs CB	0.000*	<0.001*	0.000*	0.135	0.000*	<0.001*	0.715	0.045*	0.557	0.000*	0.771	0.580	0.016*
REB vs CB	<0.001*	<0.001*	<0.001*	0.036*	<0.001*	<0.001*	0.640	0.060	0.053	0.000*	0.495	0.852	0.046*
Kruskal-Wallis	0.000*	<0.001*	<0.001*	0.127	0.000*	1.000	1.000	1.000	0.051	0.000*	0.406	0.877	0.043*

The Kruskal-Wallis tests showed *P. capensis* to be significantly different from the other two species for the song variables HiF, LoF, FRnge, EndF, ModR and InfPt. *P. capensis* had higher "figure highest frequencies" (mean of 3.45 kHz vs. 2.97 kHz for *P. nigricans* and 2.67 kHz for*P. barbatus*), higher "figure lowest frequencies" (1.75 vs. 1.53 and 1.53 kHz), larger "figure frequency ranges" (1.69 vs. 1.44 and 1.14 kHz), higher "figure ending frequencies" (2.96 vs. 2.42 and 2.31 kHz), higher "segment modulation rates" (41.81 vs. 30.27 and 26.31 kHz/sec), and larger "numbers of inflection points per phrase" (10.21 vs. 8.16 and 7.83). These differences correspond to those that are detectable to the human ear; *P. capensis* song is slightly higher pitched and less rich (more slurred) than that of the other two species.

P. nigricans was intermediate between *P. capensis* and *P. barbatus* for all of the above-mentioned song variable means, being significantly different from *P. barbatus* for only the HiF, FRnge and ModR variables. The songs of these two species are virtually indistinguishable to the human ear.

A multivariate discriminant analysis was performed using six figure variables, namely HiF, LoF, StF, EndF, FSuc, and FigDur. FRnge was excluded on account of it being significantly correlated with HiF, whilst the Int and Fig/Int variables were excluded since their values were not normally distributed. This analysis correctly separated only 69% of the 370 figures used in the comparisons (Table 4.2). Separation on the first function was mainly by highest frequency (HiF) and lowest frequency (LoF), whilst separation on the second function was mainly by ending frequency (EndF) (Table 4.3). The polygons including the data points show that *P. capensis* and *P. barbatus* overlap to a limited extent, whilst *P. nigricans* overlaps extensively with both *P. capensis* and *P. barbatus* (Figure 4.1).

The discriminant function analysis correctly classified 82% of the *P. capensis* figures and 75% of the *P. barbatus* figures, but only 49% of the *P. nigricans* figures (Table 4.2).

Table 4.2 Discriminant function classification of the three *Pycnonotus* bulbuls using six figure variables. BEB = *P. barbatus*; REB = *P. nigricans*; CB = *P. capensis*.

Actual Group	Predicted Group (% of Total)			Total no. of figures
	BEB	REB	CB	
BEB	75	20	5	161
REB	35	49	16	113
CB	5	13	82	96

Table 4.3 Standardized canonical discriminant function coefficients and mean values for six figure variables of the three *Pycnonotus* bulbuls. BEB = *P. barbatus*; REB = *P. nigricans*; CB = *P. capensis*; * = percentage of total variance.

Figure Variable	Discriminant Coefficients		Species means of variables		
	Function 1 (87%)*	Function 2 (13%)	BEB	REB	CB
HiF (kHz)	+0.67	-0.69	2.665	2.971	3.446
LoF (kHz)	+0.60	-0.21	1.527	1.530	1.753
StF (kHz)	-0.54	+0.22	2.060	2.095	1.941
EndF (kHz)	+0.02	+0.74	2.312	2.415	2.963
FSuc (kHz)	+0.29	-0.08	0.677	0.690	1.088
FigDur (sec)	-0.21	-0.69	0.107	0.129	0.149

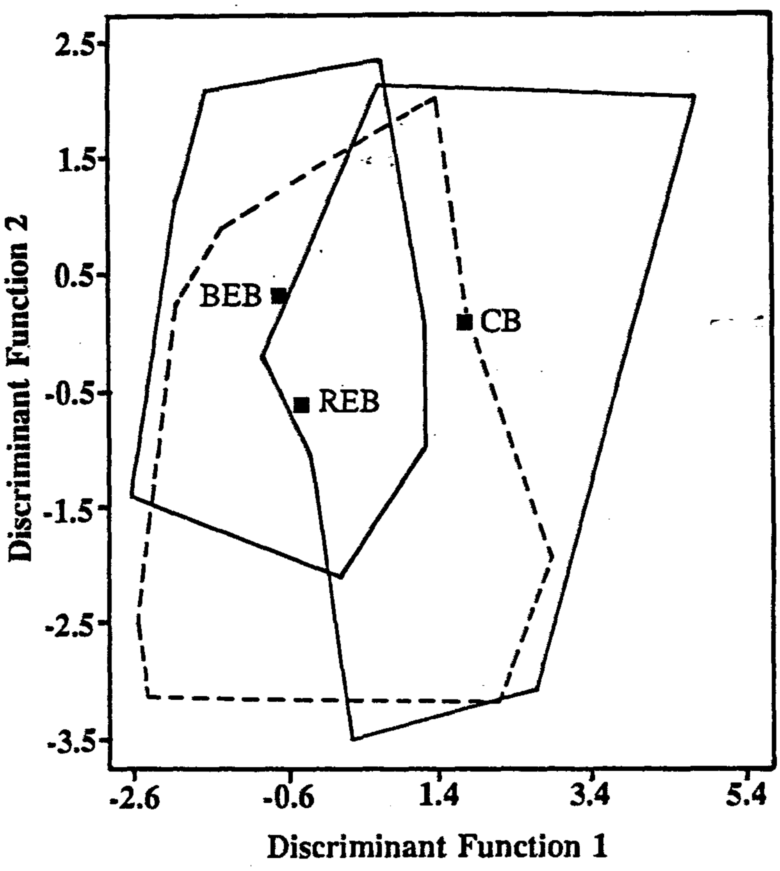


Figure 4.2 Discriminant function analysis of *Pycnonotus* bulbul songs. Polygons enclose the largest area among the points of individual species. ■ = group centroid; BEB = *P. barbatus*; REB = *P. nigricans* (dashed line polygon); CB = *P. capensis*.

4.3.2 Song playback experiment

The results of the song playback experiment are presented in Table 4.4.

Table 4.4 Summary of the responses of *P. barbatus* territorial males to playback of conspecific and heterospecific song. Eighty-nine tests on 41 birds in Grahamstown.

Response	**Species stimulus song**		
	P. barbatus	***P. nigricans***	***P. capensis***
Approach (code 1)	18 (53%)	16 (47%)	0 (0%)
Silent/move away (code 2)	9 (18%)	2 (6%)	3 (14%)
No reaction (code 3)	7 (29%)	16 (47%)	18 (86%)
No. of tests	34	34	21

During a strong response (code 1), the male first flies from its song perch to a perch in the vicinity of the speaker, usually within 30 seconds of the start of playback. During the next 15 to 30 seconds, it slowly moves closer to the speaker, actively looking around to try to find the "intruder". On occasion, a bird was even observed to perch on the speaker itself, or on the ground immediately in front of it.

Roughly equal percentages of territorial *P. barbatus* males responded strongly and aggressively to conspecific (53%) as to *P. nigricans* (47%) song, whilst none of those tested showed a strong response to *P. capensis* song. Slightly more *P. barbatus* males exhibited a so-called "weak" response to conspecific song (18%) than to *P. nigricans* song (6%). Further work is required to establish the actual significance of this type of reaction though.

4.3.3 Vocalizations and behaviour

The following vocalizations and associated behaviours were recorded for one or more of the three species (interspecific comparisons are summarized in Table 4.5):

Territorial song

Loud and deliberate song uttered almost exclusively by the male of the species, and mainly during the breeding season (described in detail in Chapter 5). Figures 4.3 to 4.5 illustrate a representative sample of song phrases of each of the three species.

Subsong

A quiet, swizzling chatter given by a bird in a resting state, usually whilst hidden inside the foliage of a tree or shrub. Noted in *P. barbatus* and *P. nigricans.*

Contact calls

Figures 4.6 to 4.8 illustrate a representative sample of the contact calls of the three species. The contact calls of *P. barbatus* and *P. nigricans* are very variable, but all consist of a rapid jumble of 3-5 figures, the first generally high-pitched and the last with a low ending frequency. The calls of these two species are indistinguishable. *P. capensis* contact calls are recognisably different, consisting of two to five rapid repetitions of usually a single figure type.

Table 4.5 A comparison of the various vocalizations and behaviours described for each of the three *Pycnonotus* species. BEB = *P. barbatus*; REB = *P. nigricans*; CB = *P. capensis*; S = similar/identical; D = recognisably different; ? = uncertain/unknown.

Species compared	Territorial song	Subsong	Contact calls	Alarm calls	Flattened crest threat	Tail-flicking threat	Alert threat	Attack	Wing-flicking	Whiny wing-flutter	Soft greeting chatter	Allopreening
BEB vs REB	S	S	S	S	S	S	S	S	S	S	S	S
BEB vs CB	D	?	D	S	S	?	?	S	S	S	?	S
REB vs CB	D	?	D	S	S	?	?	S	S	S	?	S

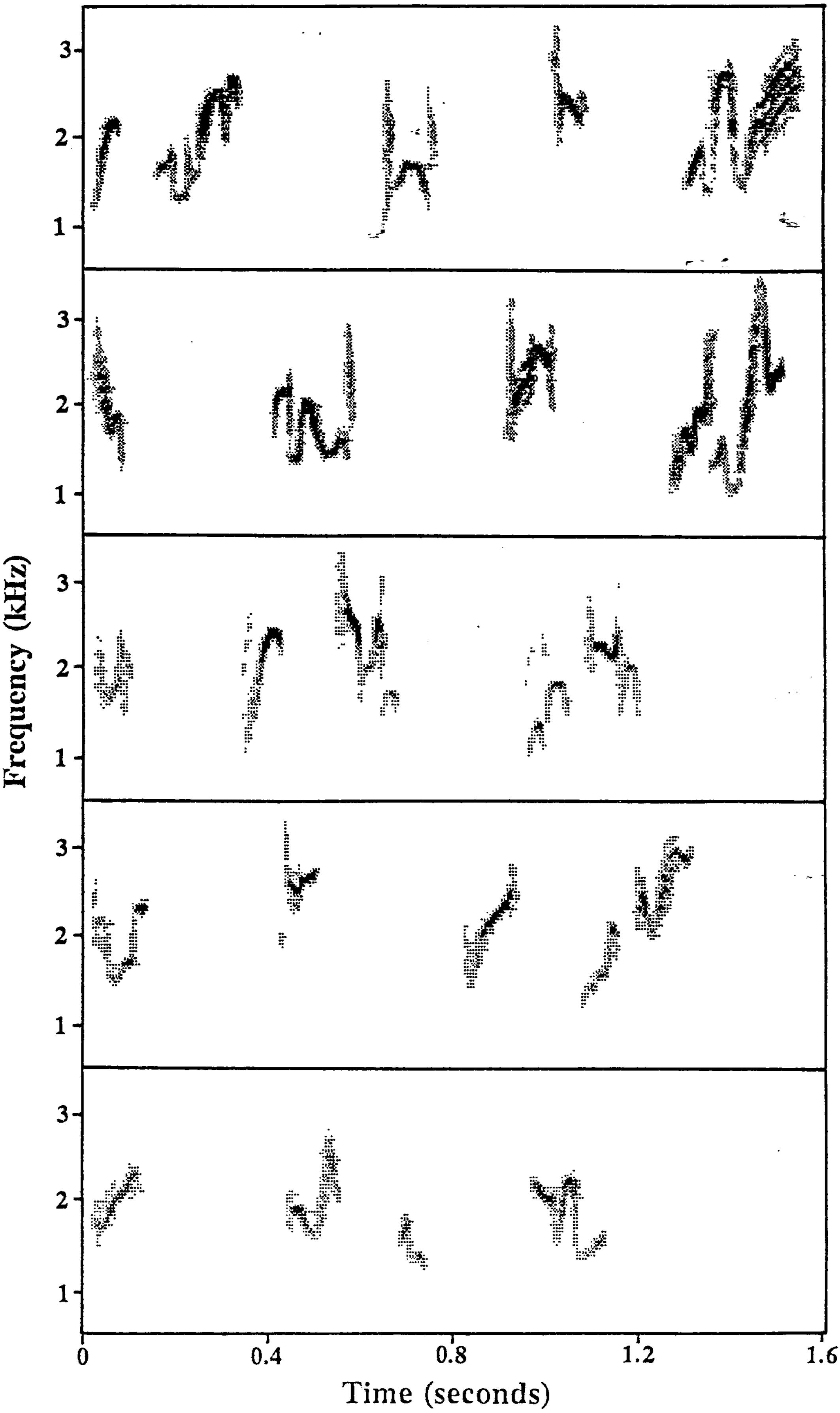


Figure 4.3 A representative sample of five *P. barbatus* song phrases.

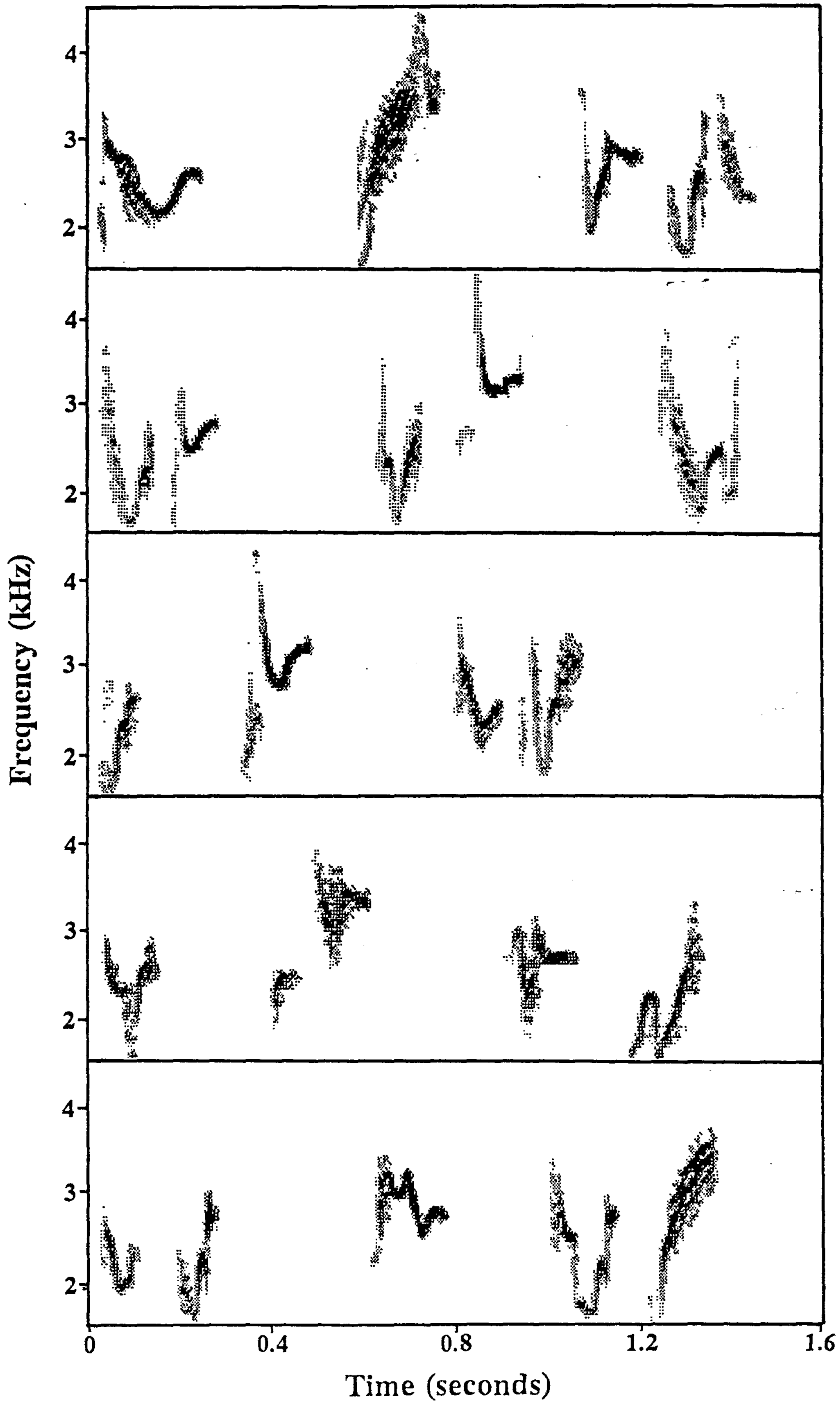


Figure 4.4 A representative sample of five *P. nigricans* song phrases.

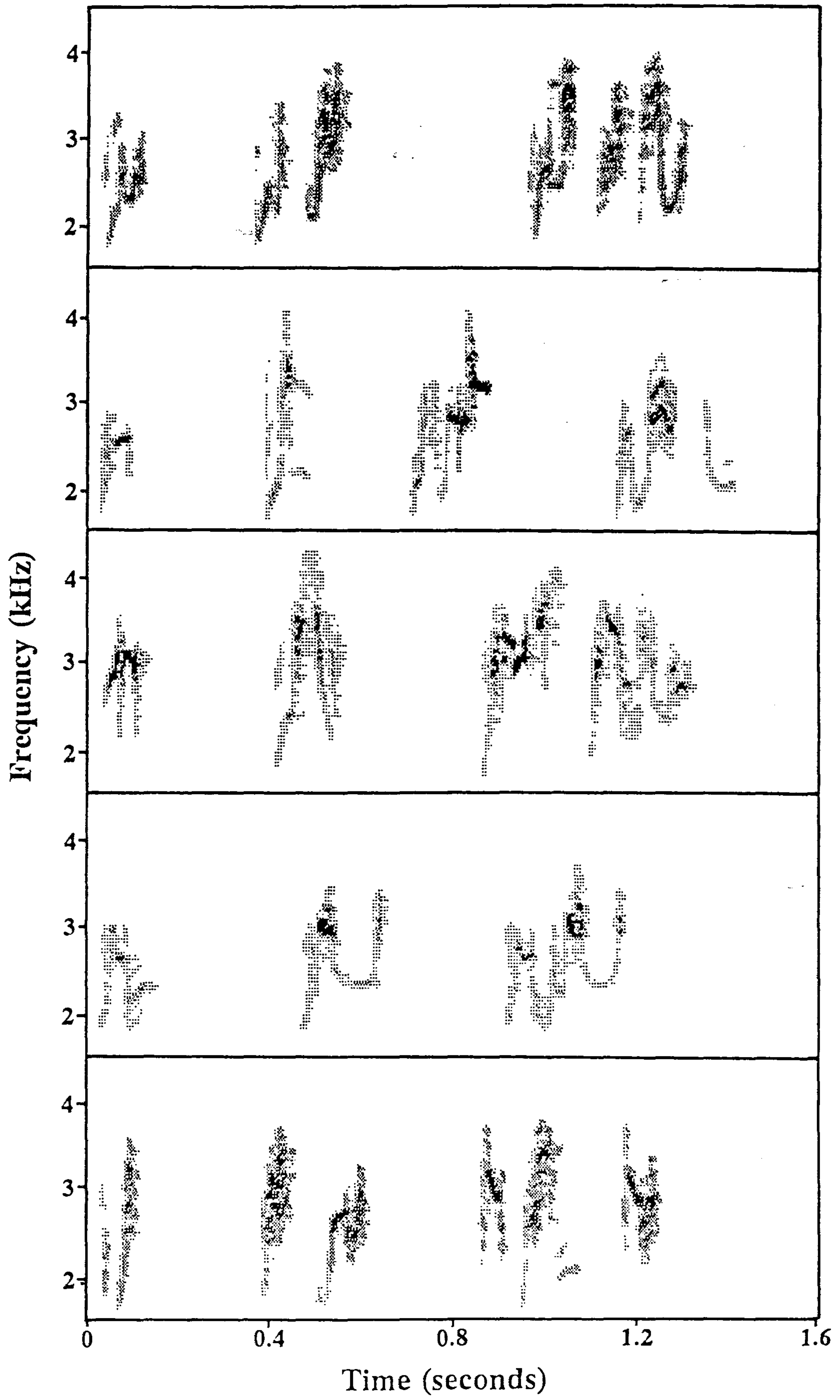


Figure 4.5 A representative sample of five *P. capensis* song phrases.

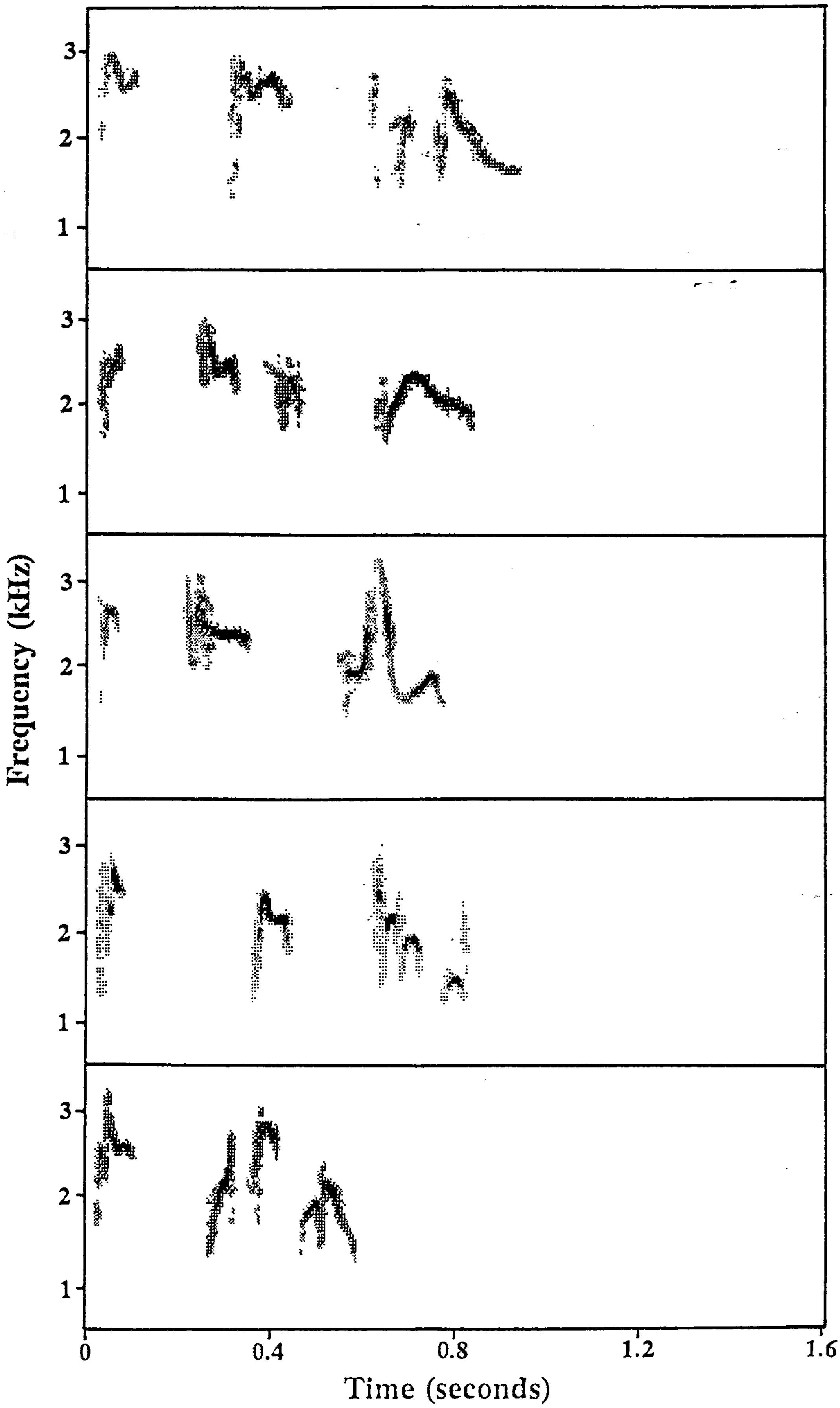


Figure 4.6 A representative sample of *P. barbatus* contact calls.

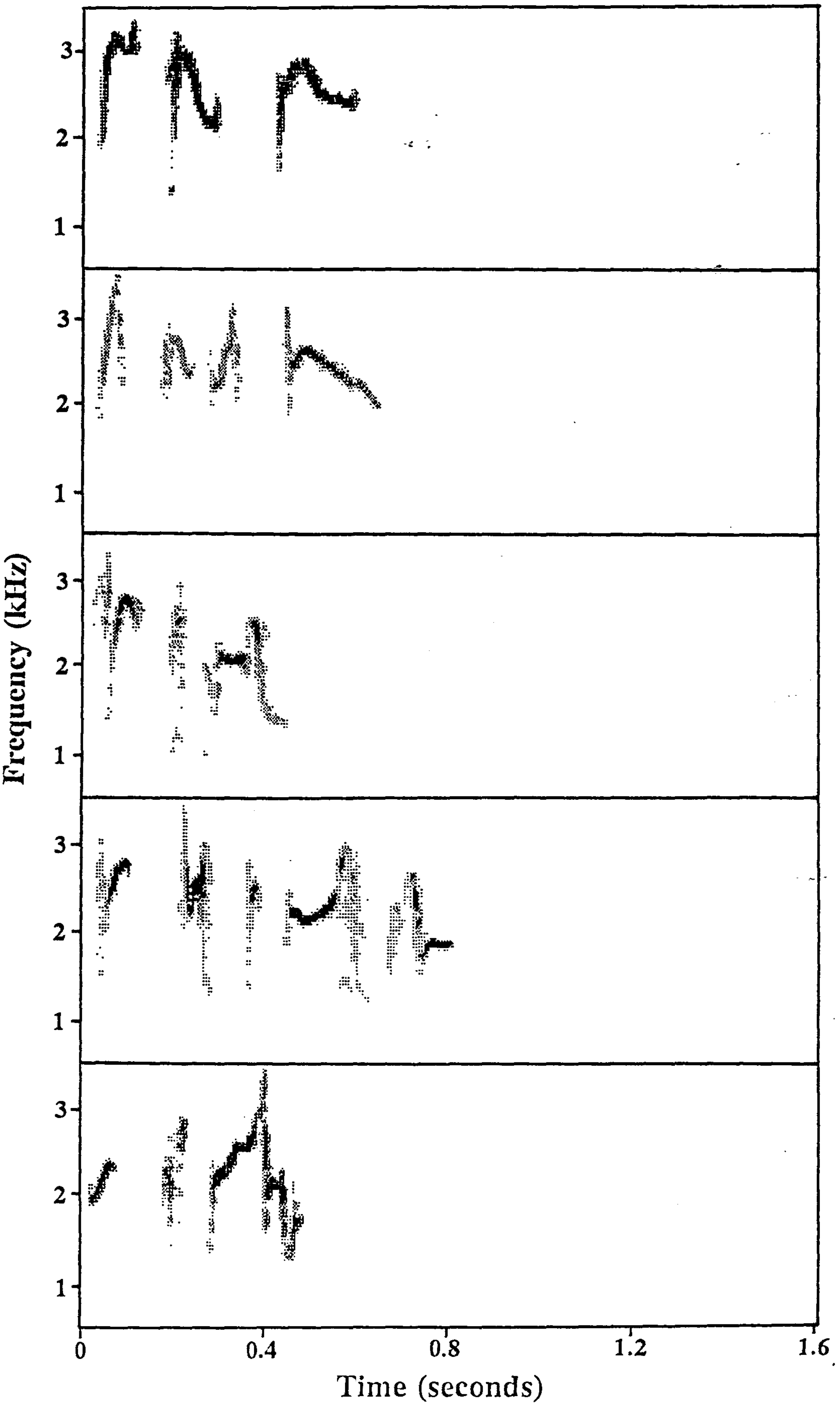


Figure 4.7 A representative sample of *P. nigricans* contact calls.

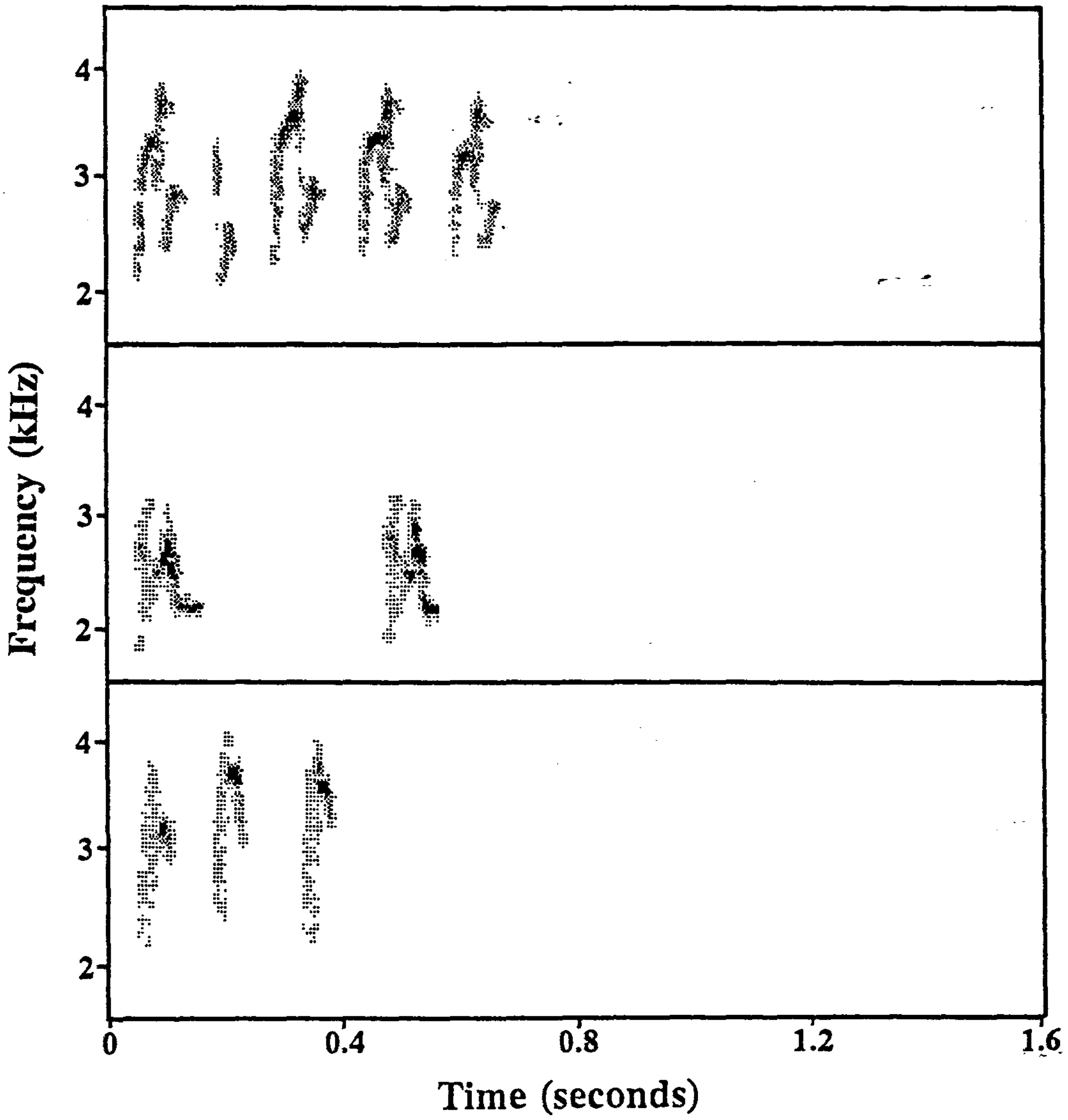


Figure 4.8 A representative sample of *P. capensis* contact calls.

During the breeding season, these calls are often uttered by a bird when separated from its mate. On several occasions, a bird calling in this manner for several minutes was observed to stop once the mate re-appeared. They do not function exclusively in signalling between members of the pair, however, since a member of the pair will often call, in the close presence of its mate, to other audible bulbuls.

Foraging flocks, which are particularly evident in the non-breeding season, are always noisy, with constant contact calling between members of the flock. Since such flocks often range about in search of food, and can be fairly dispersed, it may be important to maintain constant contact between members, or at least between paired individuals.

Alarm calls

At low intensity alarm, *P. barbatus* has a nasal *chirrik, chirrik* anxious call. At higher intensities, calling is transformed into a loud and rapid repetition of a single note, which I shall refer to as "machine-gun" alarm chatter (Figure 4.9). In high intensity bursts, the notes become louder and shriller, with more energy delivered at the higher frequencies. There is also a "crescendo" call, rather similar to the contact call, given at intervals during the "machine-gun" alarm on occasion. The alarm call of a bulbul rapidly attracts bulbuls and other bird species to the point of disturbance. *P. nigricans* has very similar alarm calls, but unfortunately, I obtained no acceptable recordings. *P. capensis* also has a similar "machine-gun" alarm call, but the timbre of the sound is slightly different.

Display

The display behaviour and vocalizations of *P. barbatus* and *P. nigricans* have not been described. I made a number of observations on these two species, which will be compared to those described for *P. capensis* (Liversidge 1970), and two Asian species, *P. cafer* and *P. leucogenys* (Short 1964). *P. barbatus* and *P. nigricans* were found to have identical display behaviours, and very similar vocalizations, and are therefore treated together in the descriptions that follow.

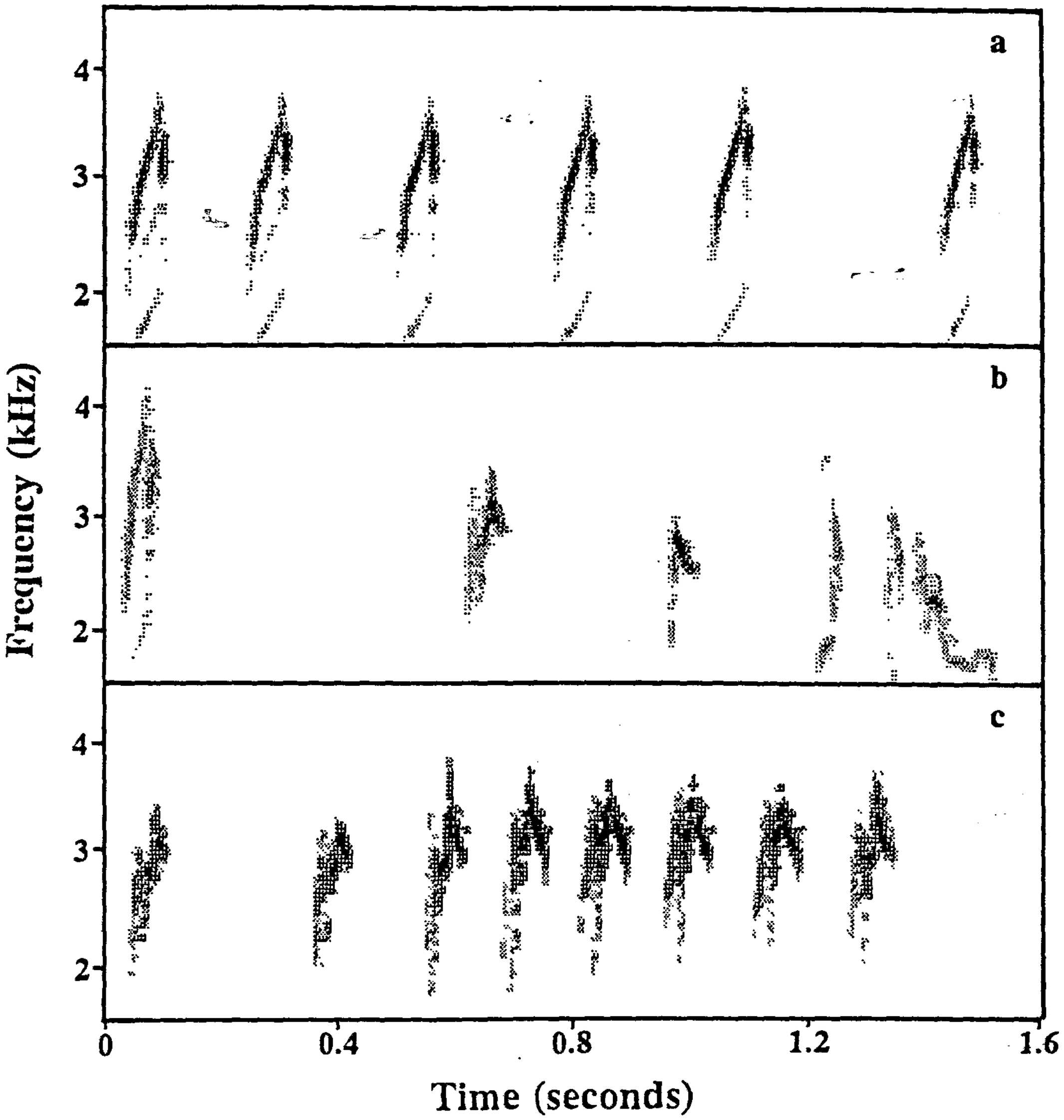


Figure 4.9 The alarm calls of *P. barbatus*. a = "machine-gun" alarm; b = "crescendo" call given at intervals during "machine-gun" alarm; c = a burst of high-intensity alarm.

Threat

A number of threat behaviours were observed:

a) **Head forward threat**:- the crest is flattened and the head lowered so that the crown and back form a straight line. The wings are slightly lifted out and the tail spread slightly. Such behaviour is identical to that described for *P. capensis.*

b) **Tail flicking**:- the bird perches a little more upright, and the widely-fanned tail is flicked quickly upwards, with a slower drooping back to the normal position. Also described for the Asian species, but not *P. capensis.*

c) **Alert threat**:- exhibited when the bird is more aroused and preparing for an attack on an intruder. The crest is raised, with the bird giving quick flicks of the wings and tail as it edges closer to its rival. Not previously described.

Attack

During an attack, a bird flies at its rival, the two usually grappling in the air and fluttering down towards the ground together. Birds will also chase one another.

Wing flicking

This display accompanies a loud chattering trill (Figures 4.10 and 4.11) uttered with the bird in a fairly upright stance, the tail often widely fanned, and the wings rapidly flicking. Liversidge (1970) states that the wings are flicked rapidly up to a vertical position above the body and then snapped down to the side of the body, the action being repeated so quickly that it is not possible to see the details of the movement. That may certainly be true, but I was only able to discern a rapid fluttering of the wings. This chatter consists of the rapid repetition of a discrete "unit" of a number of short figures (Figures 4.10 and 4.11), and can continue for 2-3 seconds. The wing-flicking chatter of the three species is indistinguishable to the human ear, and too varied to distinguish through a cursory examination of the sonograms.

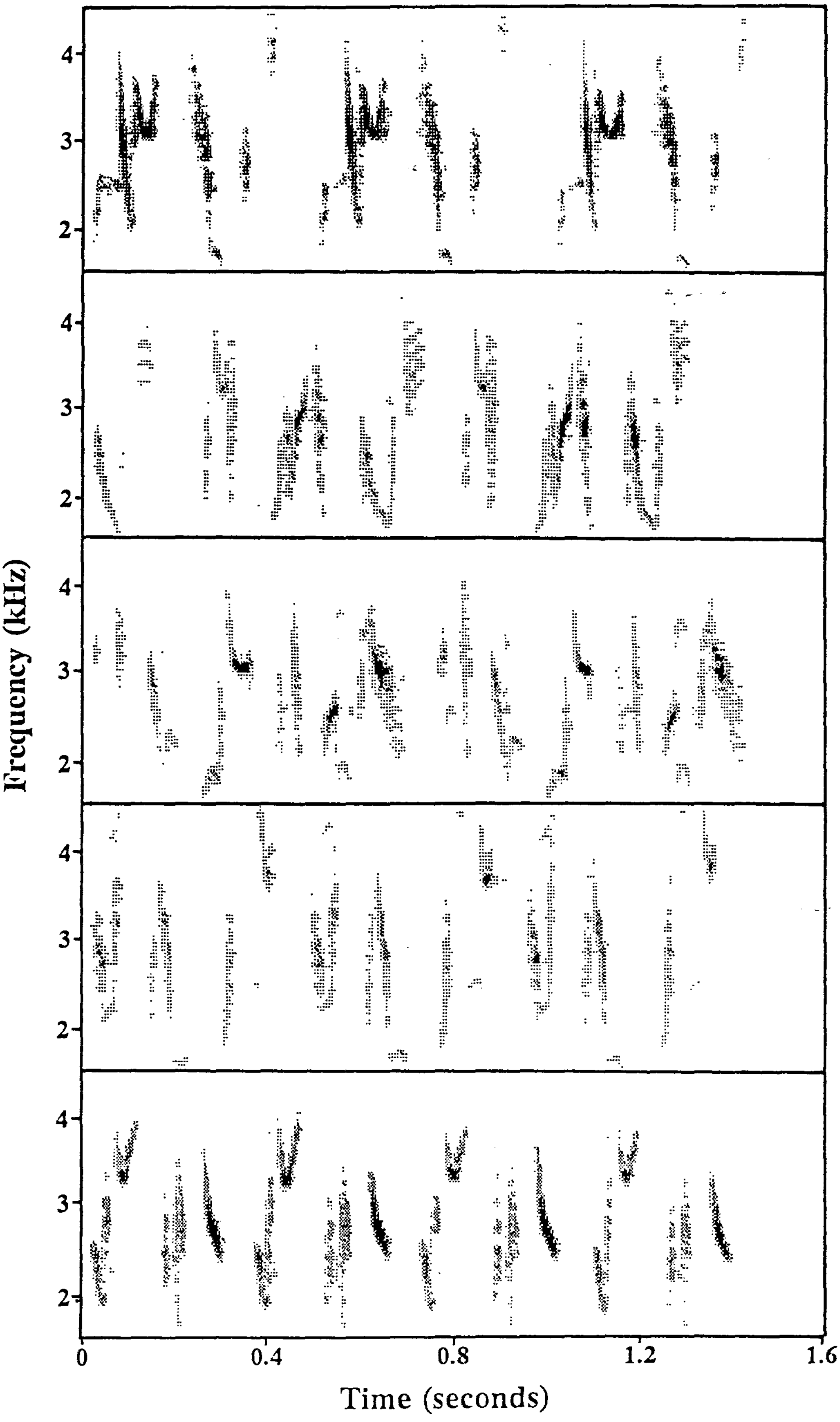


Figure 4.10 A representative sample of *P. barbatus* wing-flicking chatter.

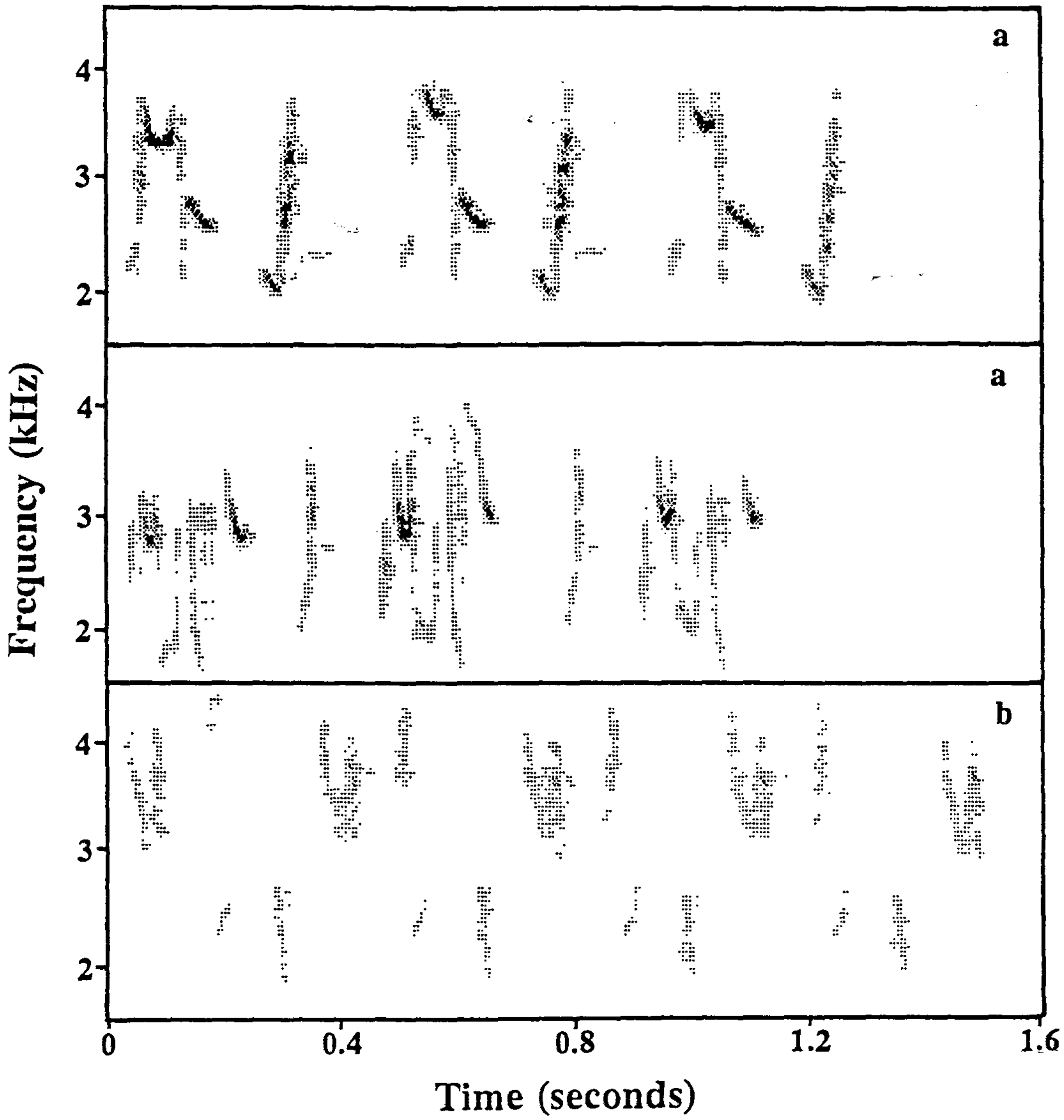


Figure 4.11 Wing-flicking chatter of *P. nigricans* (a) and *P. capensis* (b).

In *P. barbatus* and *P. nigricans*, I have seen this display and chatter given by males in two different contexts. The first is during conflict situations with another male in a territorial dispute, and as such, can be regarded as a threat display. In the second context, the display is given as a greeting or courtship call by the male when it lands next to the female, or when the female flies in and lands next to the male. This display is identical to that described for other *Pycnonotus* species. Short (1964) regarded it as a threat display in the two Asian species. Liversidge (1970) reports that whilst it may be used as a threat display in *P. capensis*, a female coming off the nest during incubation normally greets its mate with this display. I recorded this display in a conflict situation between two pairs of Cape Bulbuls on a single occasion.

Whiny wing-flutter

Whiny wing-flutter is a courtship display by the male, or a pre-copulatory display by both mating partners. This display is identical to that described for other *Pycnonotus* species. The head is bent forward and down, the body horizontal or the back sloping forward. The wings are lifted slightly out, with spread primaries, and fluttered gently and continuously. The tail is spread widely so that the outer tail feathers are close to the primaries. In the pre-copulatory display, the tail is often bent vertically down. The rump and lower-back feathers are fluffed up to look like a puff-ball. The bird then sways back and forth, sometimes swivelling through 360°, and sometimes displaying with its back to its partner. A very soft, almost inaudible, whiny vocalization is uttered throughout this display.

The female is usually attracted by such a display, hopping closer and around the displaying male. In cases where copulation took place, the female was also seen to give this display in close proximity to the displaying male.

Soft greeting chatter

When members of a pair landed next to their mate, one or both would often give a short burst of soft chatter.

Allopreening

Members of a pair can often be seen perched in close contact and preening one another, usually around the head area. Such behaviour must help to maintain the strong pair bond that is apparently maintained between adult birds throughout their lives (Liversidge 1970; *pers. obs.*).

4.4 DISCUSSION

Statistical analyses of the song features chosen for quantification showed the territorial song of *P. capensis* to be significantly different from that of the other two species for six of the 13 variables. Furthermore, the discriminant function analysis of six figure variables was able to classify 82% of *P. capensis* figures correctly. This suggests that there is probably sufficient information encoded in the songs of *P. capensis* to render them distinguishable from the songs of *P. barbatus* and *P. nigricans*. This suggestion is supported by the results of the playback experiment, which showed that *P. barbatus* does not confuse *P. capensis* song with conspecific song.

Whilst there are significant differences between *P. barbatus* and *P. nigricans* song for the variables HiF, FRnge and ModR (Kruskal-Wallis tests), and FigDur and Fig/Int (Mann-Whitney U tests), the ability of the birds themselves to discriminate between the two is questionable in the light of the results of the song playback experiment; roughly equal percentages of *P. barbatus* males responded strongly and aggressively to conspecific song as to *P. nigricans* song, suggesting that the birds were unable to discriminate between the two.

Further studies could:

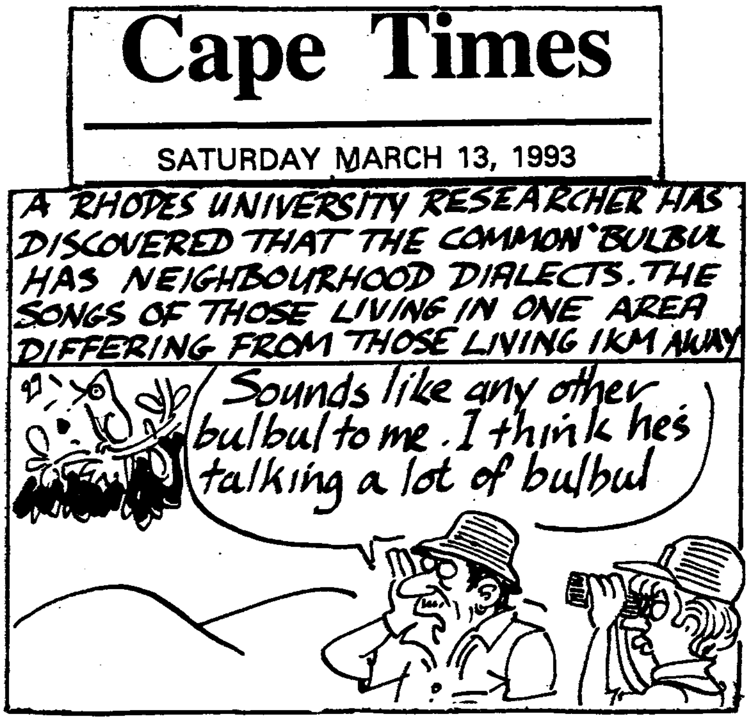
1. test the responses of the other two species to heterospecific song, and
2. test whether the responses in transition zones between any two species are modified by the presence of a second species.

Catchpole (1978) and Catchpole and Leisler (1986) found that male *Acrocephalus* warblers responded aggressively to heterospecific song in areas of sympatry, but not in areas of allopatry. Reed (1982) found a similar differential response between two unrelated species, the Chaffinch *Fringilla coelebs* and the Great Tit *Parus major*. These investigators interpreted their results as evidence of learning to exclude competitors. It would be interesting to know whether bulbuls also exhibit this type of differential response.

As far as the other vocalizations and behaviours are concerned, *P. capensis* is different from the other two species only in contact calls (Table 4.5). *P. barbatus* and *P. nigricans* are indistinguishable for all of the features described. Of particular interest is the near-identical courtship and pre-copulatory whiney wing-flutter display of the three species. Such a display must form an integral part of their specific mate recognition systems (SMRSs). If the SMRSs of the species are very similar, the potential for mistaken identity leading to heterospecific pairings and interbreeding exists. This point will be discussed further in Chapter 6.

CHAPTER FIVE

THE TERRITORIAL SONG OF THE BLACKEYED BULBUL *Pycnonotus barbatus*



Cape Times

SATURDAY MARCH 13, 1993

A RHODES UNIVERSITY RESEARCHER HAS DISCOVERED THAT THE COMMON BULBUL HAS NEIGHBOURHOOD DIALECTS. THE SONGS OF THOSE LIVING IN ONE AREA DIFFERING FROM THOSE LIVING 1KM AWAY

5.1 INTRODUCTION

Bird song, defined as a loud, sustained and complex vocalization normally uttered by the male of a species (Nottebohm 1972), is generally assumed to have two main functions, namely territorial defence and/or the attraction of mates (Catchpole 1982). Some species, such as the White-crowned Sparrow, *Zonotrichia leucophrys,* sing a single stereotyped song phrase that is repeated continuously. In at least three quarters of all songbird species though, each male sings more than one variant of the species-characteristic song (Krebs & Kroodsma 1980). This collection of song types, which can vary in number from two to several thousands, is referred to as the song repertoire.

Vocal development in songbirds involves memorization of an auditory model and subsequent motor practice, or "matching to memory" (Marler & Tamura 1964; Nottebohm 1969). For many bird species, song clearly qualifies as a culturally transmitted tradition (Mundinger 1980; Kroodsma & Baylis 1982). Behavioural biologists and population geneticists have long been interested in the possible relationships between cultural and biological evolution (Baker & Cunningham 1985).

The songs of many bird species vary geographically. This variation may involve changes in the occurrence, structure or sequencing of song elements, in the song types used by individuals, or in the composition of the song repertoire of individuals, and may be expressed within local populations, between populations, or over large geographical areas (Wiens 1982). Patterns in this variation have been loosely called "dialects", defined in terms of discrete boundaries separating groups of individuals singing different songs (Nottebohm 1975; Kroodsma *et al.* 1985), or simply in terms of song-sharing among neighbours (Jenkins 1977; Payne 1978, 1982).

Studies of song dialects have provided much information on the behavioural ecology of the species involved. The biological significance of song dialects has been variously considered in terms of the possible adaptive significance of learned song patterns as an indicator of:

1. past movements and founder effects of local populations (Baker 1975; Baptista 1975; Mundinger 1975; Slater & Ince 1979; Wiens 1982; Baker & Thompson 1985),
2. local adaptations to the acoustic properties of the habitat (Morton 1975; Nottebohm 1975; Wiley & Richards 1978, 1982; Bowman 1979; Wasserman 1979; Gish & Morton 1981; Date & Lemon 1993),
3. adaptive features that enhance local genetic specialization by reducing gene flow between populations experiencing different selective pressures (Marler & Tamura 1962; Nottebohm 1969, 1975; Marler 1970; Nottebohm & Selander 1972; Baker 1975; Handford & Nottebohm 1976; Baker & Mewaldt 1978, 1981; King *et al.* 1980; Baker *et al.* 1982; Fleischer & Rothstein 1988), and
4. social adaptations of local immigrant recruits which act in male-male competition (Weeden and Falls 1959; Payne 1978, 1981a, 1982, 1983; Kroodsma 1981) or in mate selection that may promote assortative mating (Jenkins 1977; Baker & Mewaldt 1978; Bateson 1978, 1980; Baker *et al.* 1981; Kroodsma *et al.* 1985).

In the course of collecting recordings for the work described in Chapter 4, it was noticed that immense variation in the territorial song of the Blackeyed Bulbul was in fact highly structured on a microgeographic scale. A study of the observed pattern of song variation was then undertaken in an effort to further an understanding of the behavioural ecology of this species, and the possible significance of this to interspecific relations with the other two species.

5.2 METHODS

5.2.1 Study site

The study was conducted in the suburban confines of the town of Grahamstown, eastern Cape Province, South Africa (33°19'S 26°32'E). The area covered was approximately 4.7 km^2. The habitat occupied by the bulbuls consisted of garden trees and shrubs in residential areas.

5.2.2 Sampling procedure

Songs were recorded during a peak half-hour period of dawn singing each morning from the first week of December to the first week of March 1991-1993. The breeding season, which generally lasts from September to April (Maclean 1984; Keith 1992a) was therefore well under way. In the 1991/'92 season, 51 males were recorded, representing virtually the entire singing population within the study area. In the 1992/'93 season, 19 males on a 3.2 km east-west transect across the study area were sampled more intensively.

Recordings were made using a Sennheiser ME 88 shotgun directional microphone attached to a Sony TC-D5M stereo cassette recorder. These recordings were reproduced as sonograms with a Multigon Industries Uniscan II sonograph. The sonograms of the different song phrases were distinct enough to be characterised and matched by eye.

5.3 RESULTS

5.3.1 Behaviour

Black-eyed Bulbuls are normally seen in pairs or, towards the end of the breeding season, in family groups of 3-4 birds. During the non-breeding season these pairs often aggregate into loose flocks that move around feeding together. These flocks range in size from just a few pairs to, in one case, a group of well over a hundred birds.

At the start of the breeding season, these flocks break up and the males establish breeding territories that are actively defended against intruders. It is now that the male begins to sing sustained advertisement song. The sexes are identical in appearance, so the singing bird was presumed to be male since:

1. only one bird in the pair really ever sang,
2. the second bird (presumed the female) was normally silent; it was rarely recorded uttering song phrases - these phrases matched those of the paired male, but were very different in frequency and temporal characteristics, being higher pitched and rapid,
3. it was only the singing bird that was observed to enter into aggressive encounters with an intruder, and
4. in the vast majority of oscines, it is the male that sings to maintain its territory and/or attract a mate (Welty 1982).

The advertisement song is further presumed to function in male-male and not male-female interactions since:

1. territorial males responded quickly and aggressively in pilot playback studies,
2. the female either perches in a nearby bush or moves off out of sight, and
3. the two sexes normally ignore one another during singing bouts.

Song is given almost every morning through the breeding season for a half-hour period starting 30-45 minutes before sunrise, during the "dawn chorus". At sunrise, singing activity usually ceases as the birds begin to preen and forage. Singing bouts of variable duration then occur irregularly through the day, with a slight increase in singing activity in the late afternoon.

The song is normally uttered whilst perched in an exposed position at a height of 5-10 m. The bulbuls are birds of habit, singing the dawn song from the same perch positions throughout the breeding season, and indeed most birds used the same perches over the two seasons studied. Most birds sang from only a single perch each morning, whilst a few alternated between two or more adjacent positions. One particular bird used four to five different perches 20-40 m apart, spending no more than half a minute singing at each. This behaviour was observed in a few other birds following the recent intrusion of another bird into the territory, but this particular bird exhibited it on every occasion it was observed in two breeding seasons, and this was evidently an individual peculiarity.

5.3.2 Description of song

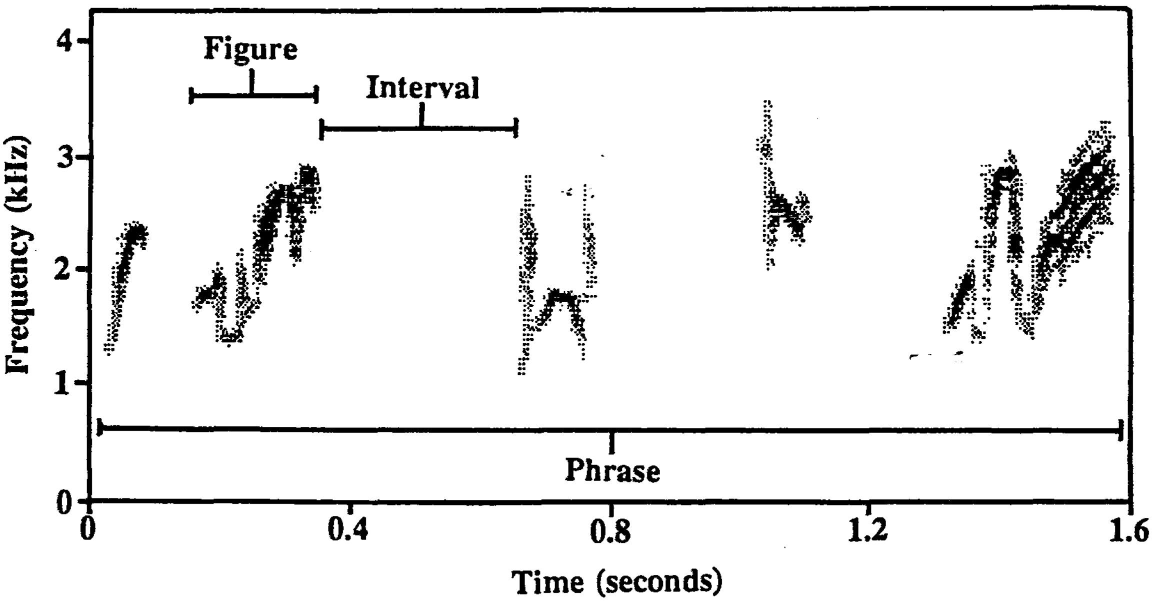
The song consists of sequentially repeated phrases (Figure 5.1). Phrases consist of 3-7 figures (following the terminology of Shiovitz 1975) with a duration of 0.8 to 2 seconds. The intervals between the individual figures of any particular phrase are irregular and in the order of 0.03-0.40 sec. Intervals between phrases range from 1-10 sec, but are generally in the order of 3-6 sec.

From the song population of 51 birds sampled in the 1991/'92 season (Figure 5.2), 64 different phrases were identified (Appendix 5.1). The repertoire size of individuals ranged from 2-9 (average 5.5) when all phrases were considered. Phrases were not used with equal frequency in the song of any individual. When rare phrases (those occurring at a frequency of less than 5% in the song) were excluded, repertoire size averaged 4.8 (range 2-8). By far the most common all-phrase repertoire size was 5 (Figure 5.3). Figures 5.4 and 5.5 illustrate the complete repertoires of two individuals 1.6 km apart, as an example of inter-individual repertoire variability. Song phrases are presented in irregular sequences of immediate variety (e.g. ABCABAABC...).

The distribution of any particular phrase in the song population was certainly not random (see Figure 5.6). Birds sharing a phrase tended to be neighbours or at least found fairly close to one another. Although territory boundaries were not determined in this study, it is safe to say that phrase sharing birds were never separated by more than two territories occupied by non-sharers.

Individual phrases tended to be distributed independently of one another, forming an overlapping mosaic of phrase clusters across the song population (Figure 5.6).

Figure 5.7 illustrates the song compositions of males along the 3.2 km transect (Figure 5.8) sampled in the 1992/'93 season. Following McGregor and Krebs (1982) and Catchpole and Rowell (1993), the proportion of phrases shared between any two males along this transect was calculated as $2Ns/(R1+R2)$, where Ns = the number of shared phrases, and $R1$ and $R2$ are the repertoire sizes of the two birds. This gives a song sharing index which expresses the proportion of song phrases shared between any two males. Although all birds were found to share phrase types with other individuals, no pairs shared all phrases in their repertoires. Taking the distance between any two males as the measured distance between the primary song posts within each territory, Figure 5.9 shows the relationship between song sharing and distance between birds



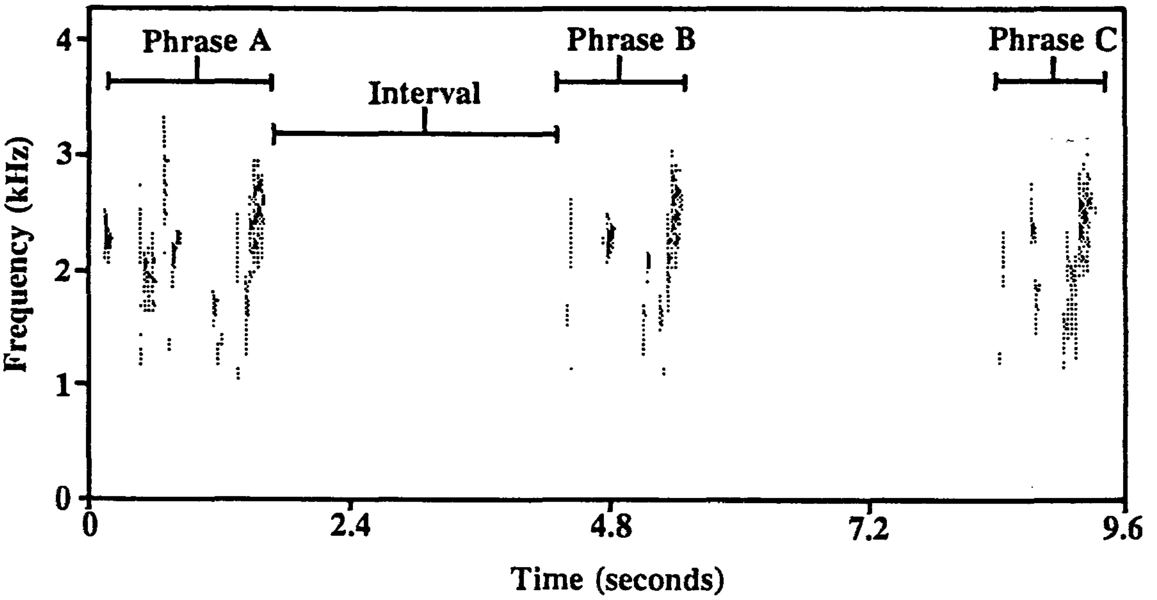


Figure 5.1 The organisation of a phrase (top) and a sequence of phrases (bottom) in the song of the Blackeyed Bulbul.

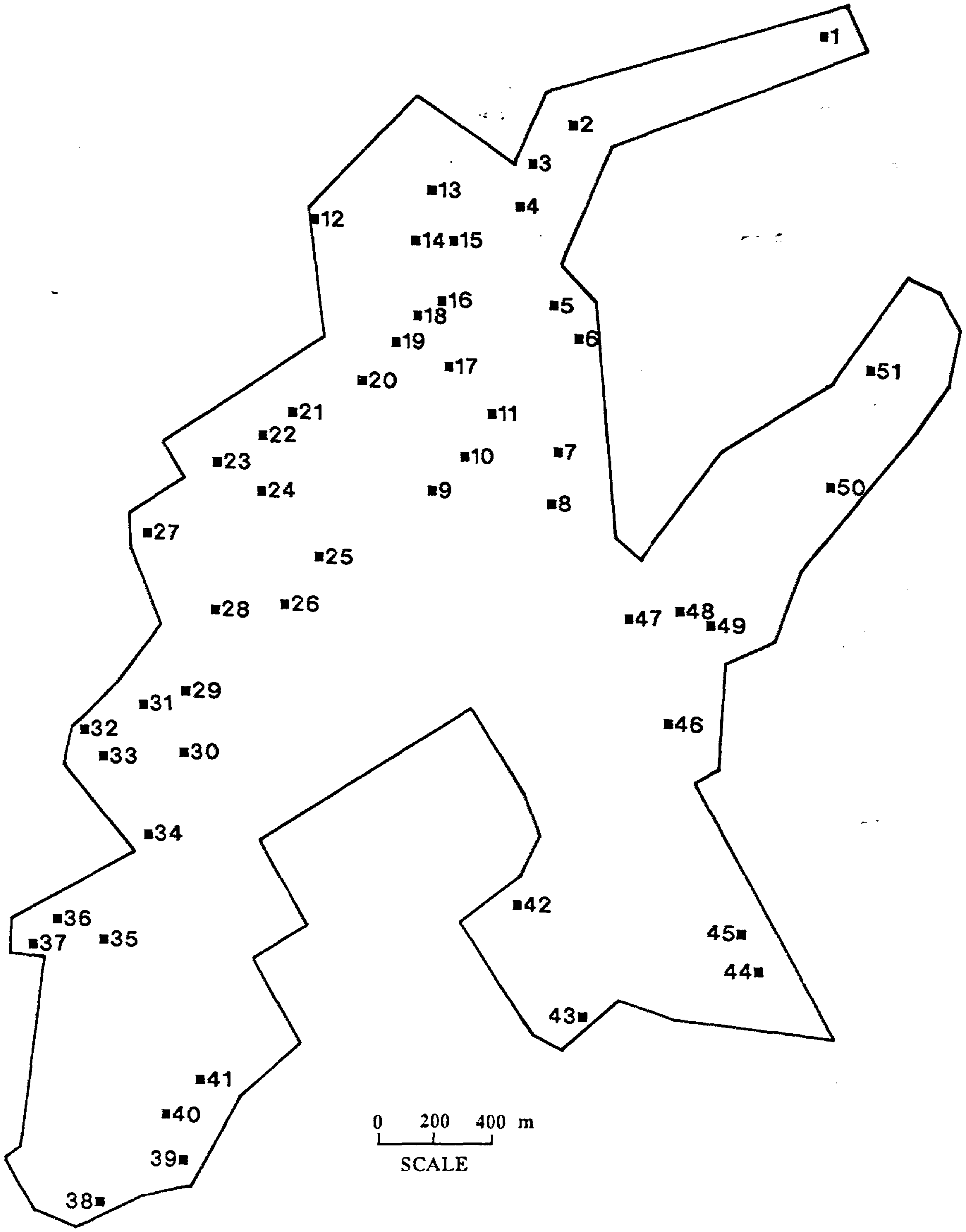


Figure 5.2 Positions of the 51 territorial male Blackeyed Bulbuls recorded in the 1991/'92 breeding season in suburban Grahamstown. ■ = position of primary song perch, with territory number.

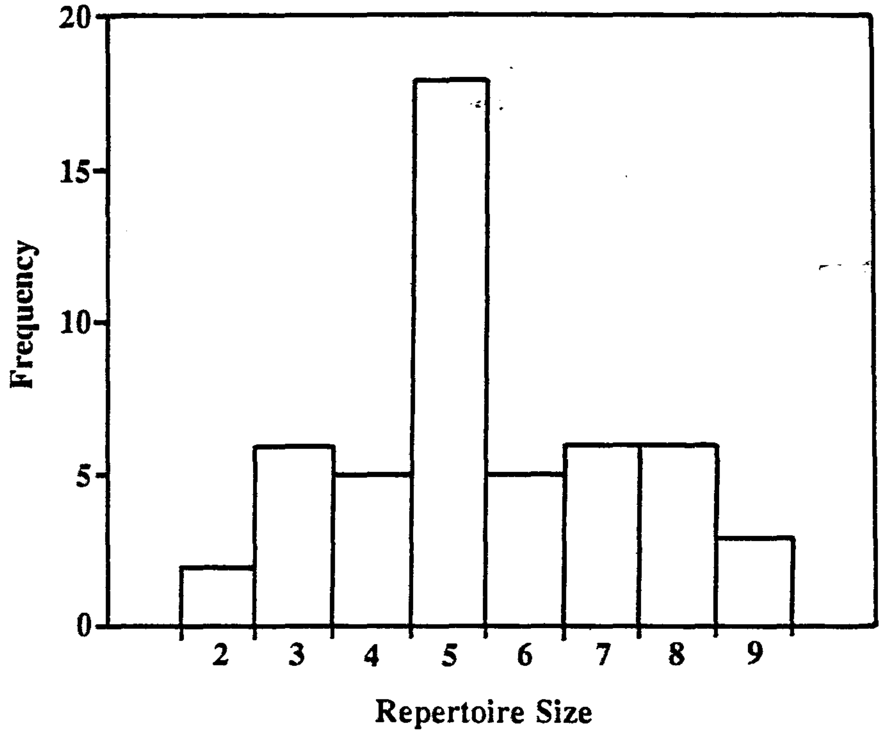


Figure 5.3 Frequency of different sized repertoires in the 1991/'92 season population of 51 males.

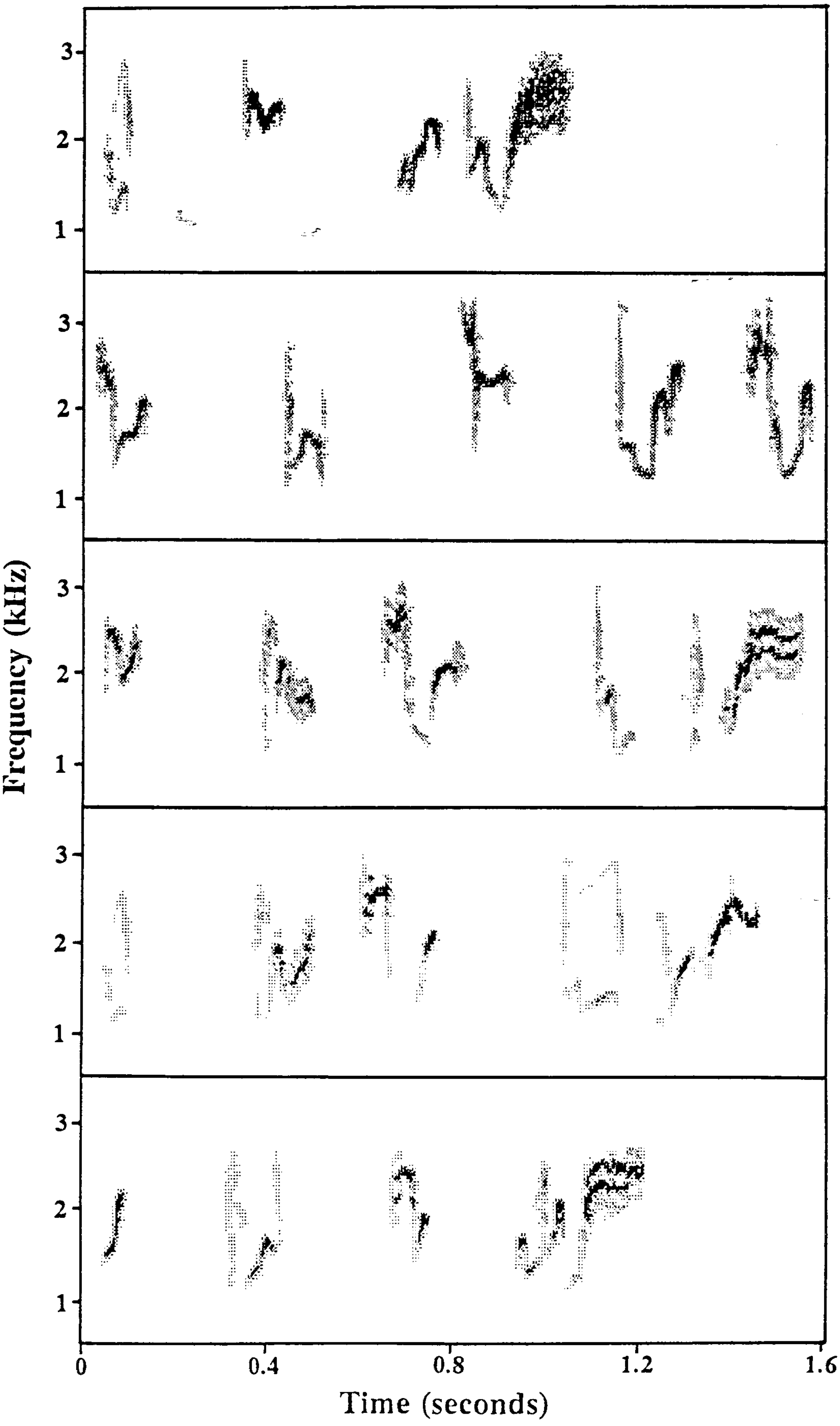


Figure 5.4 Five-phrase repertoire of the bird on territory no. 16 (1991/'92 season).

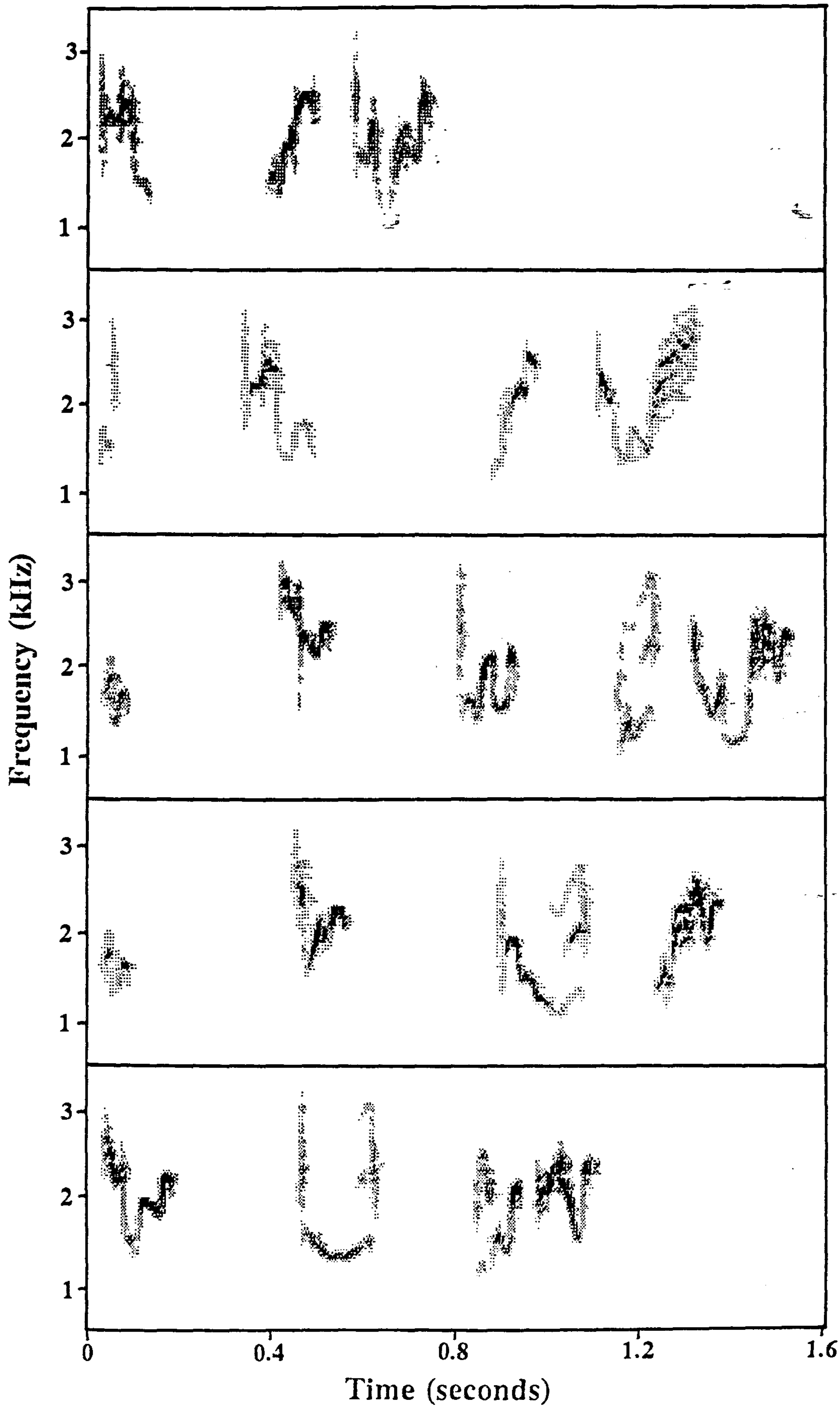


Figure 5.5 Five-phrase repertoire of the bird on territory no. 29 (1991/'92 season).

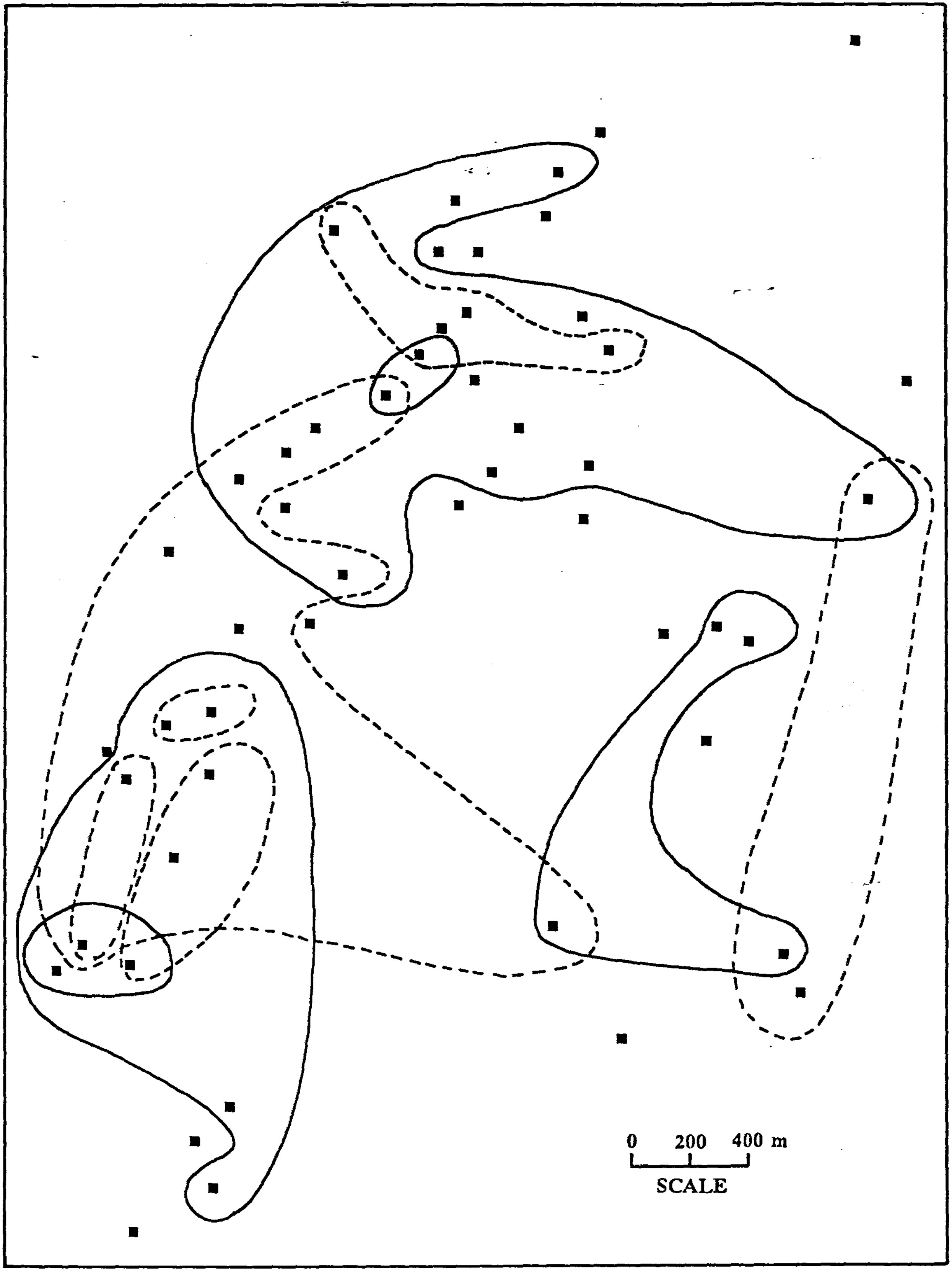


Figure 5.6 Distribution of 11 selected isoglosses in the 1991/'92 season song population. An isogloss is a line delimiting the distribution of a particular phrase type (after Mundinger 1982). Two line types used for clarity only.

Phrase Number	4	5	16	18	19	20	21	22	24	27	52	28	29	30	34	35	53	40	39
23																			12
14																			6
26																		19	17
32																		17	13
31																17	9	20	19
15															13	8	7		
28														5	20	24	16	10	16
13													3	17	30	26	14	22	16
25														2	9	16	23	6	
24														14		1			
22														13	6			1	
21										25	21	16	8	5					
12										28	21	11	10	4					
20						12	8	3	4	16	15	11	41	6	1	3	22	6	
19					17	6	12	32	32	30	26	48	27	33	23	5	9		1
18						2	8	25	20										
17							1	1	1										
16						9						11							
34						3													
10		1		12	34	15	34	16	22		18	2	7						
11			33		10														
9				1	3	14	12		1										
8				6															
7	54	27	30	19	26	36	24	22	17										
4	38	46	11	20		14	1												
1	7	25	26	39															

Bird Number

Figure 5.7 Song compositions (as percentage of song output made up by different phrases) of the 19 male Blackeyed Bulbuls recorded in the 1992/'93 breeding season along a 3.2 km transect across suburban Grahamstown. Bird number corresponds to territory number.

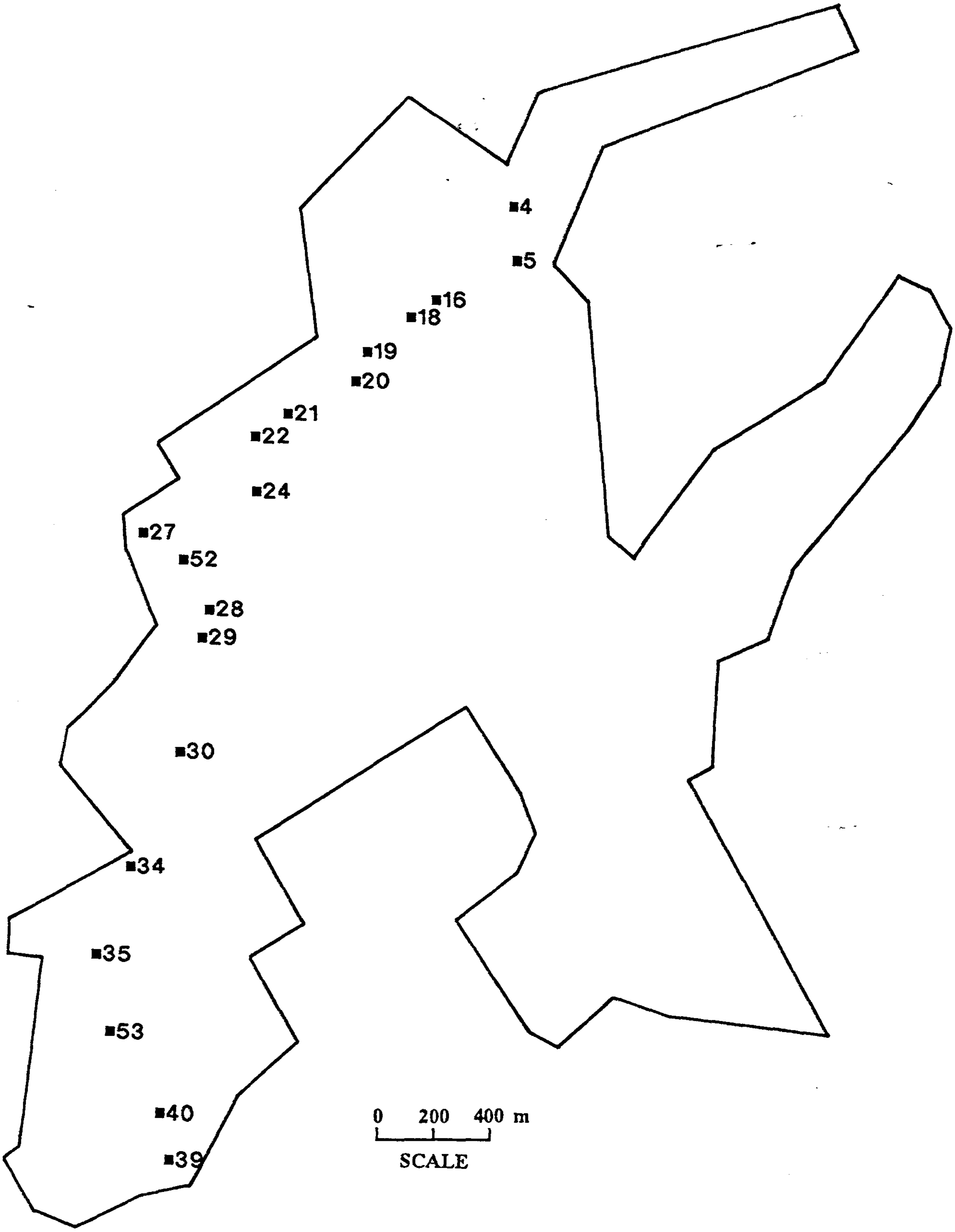


Figure 5.8 Positions of the 19 territorial male Blackeyed Bulbuls recorded along a 3.2 km transect in the 1992/'93 breeding season. ■ = postion of primary song perch, with territory number.

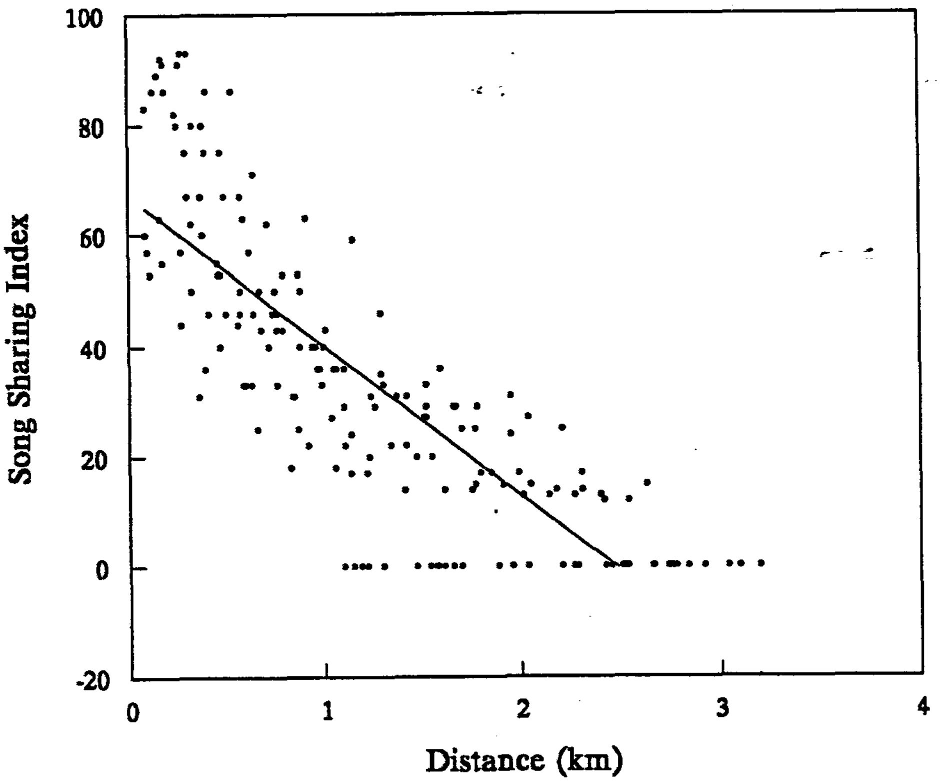


Figure 5.9 The relationship between song sharing and distance between males on the 1992/'93 season transect. Regression equation: $y = -27.14x + 67.22$ ($r^2 = 0.68$, $P = 0$, $n = 171$ distances between 19 males).

along the 1992/'93 transect. There was a strong and highly significant inverse correlation between song sharing and distance ($r^2 = 0.68, P = 0$). Maximum song sharing values of just over 90% were recorded at inter-male distances 100-300 m. Males as little as one km apart sang completely different sets of phrase types, and birds over 2.6 km apart exhibited no phrase type sharing.

Whilst neighbours (in terms of song perch locations) often had nearly identical songs, a birds song was not necessarily more similar to that of its closest neighbour than to other neighbours or even more distant individuals.

I hesitate to call these patterns dialects as such, since most dialect definitions refer to boundaries separating groups of song-conforming individuals.

Careful analysis of the sonograms revealed that:

1. few birds shared exact copies of song phrases; individuals usually possessed characteristic differences in the fine structure of at least one note, representing errors in copying (see Figure 5.10);
2. although repeated renditions of the same phrase by an individual were usually identical, variations did occur, with some birds even consistently singing several identifiable variations of the same song type;
3. phrases were often sung incompletely, with any number of notes omitted; a bird would often sing only the first few notes before breaking off;
4. hybrid phrases consisting of the first few notes of one phrase followed by the last few notes of another were quite common. Since these were generally not copied by neighbours, they were not treated as new song types for the purposes of this study. Certain birds could be characterised by their hybrid song phrases, though.

Although the rate of phrase singing does vary within individuals, certain birds could be individually characterised by a consistently slow or rapid singing tempo. Despite being unbanded, males were reliably distinguished from one another by means of their characteristic song "signatures", i.e. peculiarities in figure fine structure or sequencing. These identifications were usually supported by various individual peculiarities in song perch location and singing behaviour.

Table 5.1 lists the known fate of 27 territories followed over the two breeding seasons studied.

Table 5.1 The fate of the territories for which there is sufficient information over the two breeding seasons studied.

Territories reoccupied by the same male	15
Territories reoccupied by a different male	8
New territories added in the 2nd season	2
Territories in the 1st season not occupied in the 2nd season	2
TOTAL	27

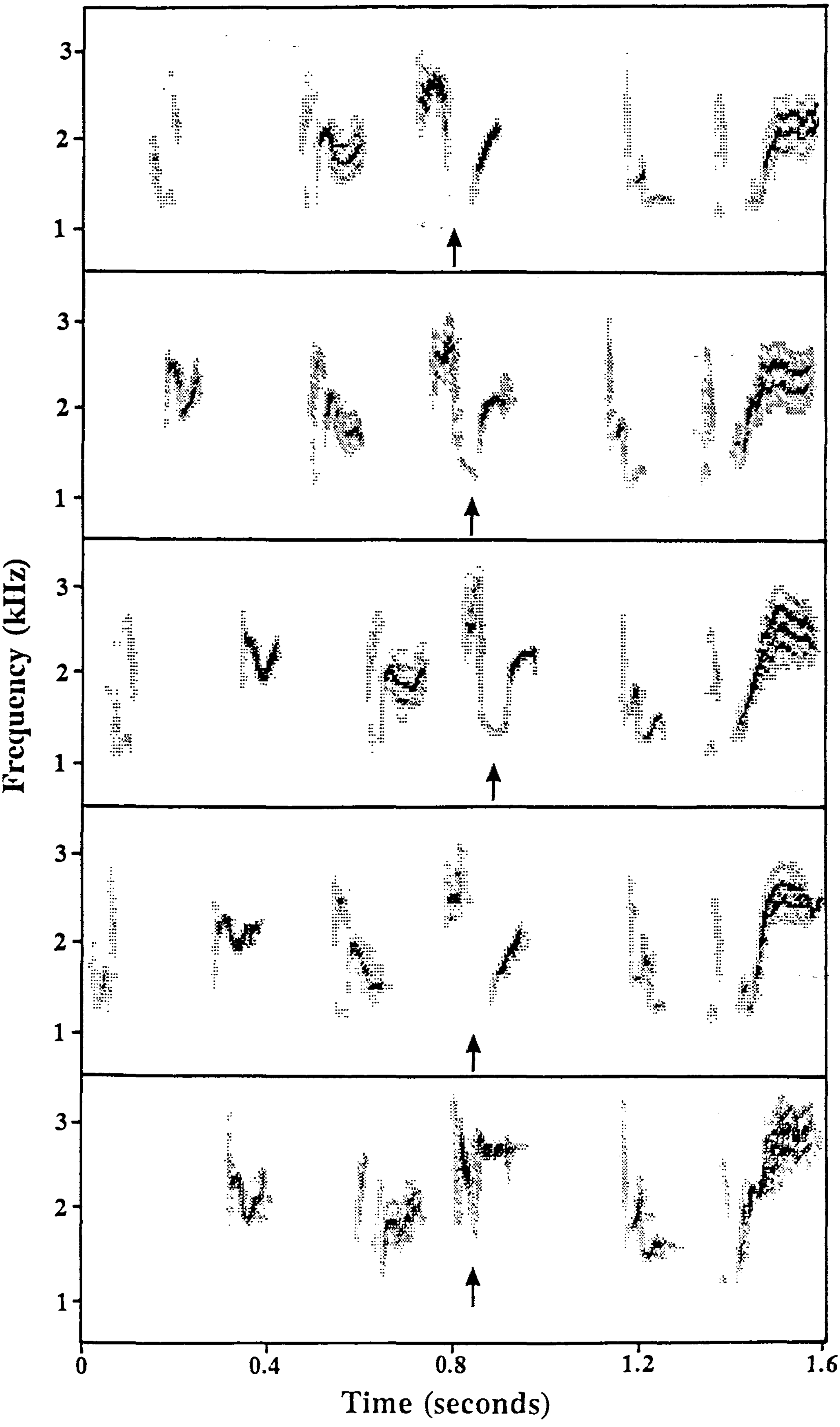


Figure 5.10 Variations of phrase no. 7 sung by five different Blackeyed Bulbuls. Arrows mark one of the figures that exhibit fine structural differences ("signatures") between individuals.

Of the 25 males occupying territories in the first season (1991/'92), 15 (60%) are judged to have returned in the second season (1992/'93), using the song signature criteria for individual identification. With the exception of one bird which shifted 100 m into a vacant area adjacent to its previous years territory, all returning birds reoccupied their original territories. With the further exception of a male that moved just 30 m towards a vacated territory to a new song perch position, all returners reoccupied their original song perches. Due to the rather limited nature of the study area, it was not possible to determine whether any of the ten non-returners had moved to a territory some distance from the original territory. In four of the eight territories reoccupied by new males, the new birds used the same song perch positions as the previous season's occupant.

Table 5.2 lists the song compositions of birds on 23 territories over the two seasons studied. Ten of the 15 returners showed virtually no change in repertoire composition, and indeed little change in the frequency of use of each phrase type. The remaining five had changed their repertoires slightly, through the addition or deletion of formerly rarely sung phrases.

The songs of newcomers were usually quite similar to those of the previous territory holders. The only exception occurred on territory 40 (Table 5.2), where the 1991/'92 occupant had a repertoire of completely alien phrase types. The 1992/'93 replacement male copied none of these phrases, conforming closely to the songs of its neighbours instead. The new males occupying the two new territories (52 and 53 in Figure 5.8) in the 1992/'93 season also conformed closely to the songs sung by their neighbours.

The bird occupying territory 26 provided some interesting data. In its repertoire of eight phrases, six were alien to the study area, whilst the remaining two (phrases 1 and 2 in Table 5.2) were the two phrases sung most frequently by its neighbours. In the 1991/'92 season, these latter two phrases together constituted only 27% of the song. In the 1992/'93 season, their contribution had increased to 50%.

Table 5.2 Summary of the song compositions (as percentage of song output made up by different phrases) of males occupying the 23 territories for which there was sufficient information over the two seasons studied.

Territory No.	Season	Phrase Number												
		1	2	3	4	5	6	7	8	9	10	11	12	13
		Returning male - no repertoire changes												
30	1991/2	27	14	11	9	9	9	7	7	5				
	1992/3	17	6	33	14	13	5	5	2	4				
26	1991/2	18	9	26	20	10	6	5	5					
	1992/3	23	27	11	11	12	5	8	5					
21	1991/2	28	17	15	14	14	8	3	1					
	1992/3	34	24	12	12	8	8	1	1					
36	1991/2	21	18	18	15	12	6	6	3					
	1992/3	15	20	7	14	17	11	7	8					
39	1991/2	21	18	15	14	14	12	5	1					
	1992/3	19	16	17	16	12	13	6	1					
25	1991/2	39	25	21	5	5	3	2						
	1992/3	17	30	19	8	7	10	8						
18	1991/2	32	21	15	14	12	6							
	1992/3	19	12	1	20	39	6							
27	1991/2	37	23	22	17									
	1992/3	30	28	25	16									
		Returning male - slight repertoire changes												
20	1991/2	48	12	12	9	8	3	2	1					
	1992/3	26	15	2	14		3	14	12	9				
35	1991/2	26	19	16	12	12	8	7						
	1992/3	24	26	17	16	5		8	3	1				
13	1991/2	31	21	21	5	5	3	2						
	1992/3	38	10	6	8	7	10	8						
17	1991/2	30	26	26	16	12								
	1992/3	37	34	1	10	5	3							
22	1991/2	39	23	19	19									
	1992/3	25	32	22	16	3	1							
5	1991/2	44	26	26	3	1								
	1992/3	46	27	25		1								
4	1991/2	50	50	1										
	1992/3	54	38		7									

Table 5.2 continued

Territory No.	Season	Phrase Number												
		1	2	3	4	5	6	7	8	9	10	11	12	13
		Different male - same song perch position(s)												
24	1991/2	58	26	15										
	1992/3	22	32	17	20	4	1	1	1					
28	1991/2	44	21	19	6	6	2	1	1					
	1992/3	48	11	11	16			11						
38	1991/2	57	33	9										
	1992/3	17	13		25	20	10	10	5					
16	1991/2	48	29	12	6	5								
	1992/3	11	30	26			33							
		Different male - different song perch position(s)												
40	1991/2	40	27	13	10	10								
	1992/3						22	20	19	17	10	6	6	1
34	1991/2	20	20	19	13	11	7	7	3					
	1992/3	6	1	20		30	22		9	13				
29	1991/2	34	24	23	15	4								
	1992/3	41	3	27	8	10	7	3	1					
19	1991/2	44	16	14	13	7	6							
	1992/3	36	34		3			17	10					

5.4 DISCUSSION

The principal findings of this study can be summarized as follows:

1. Blackeyed Bulbuls exhibit substantial microgeographic variation in song phrase types within a highly structured song population;

2. Neighbours show a strong tendency to share phrase types and even whole repertoires, and repertoire similarity decreases rapidly with increasing distance between individuals being compared;

3. Individual phrase types are shared independently by discrete clusters of birds;

4. Population song structure is temporally stable.

5.4.1 Song sharing as an epiphenomenon

The first question to be addressed is whether such highly structured song variation is a mere incidental by-product of the song learning process, as first proposed by Andrew (1962), or whether the capacity for such "dialects" has some biological function. Imitation of adult songs appears to play an important role in the development of song in most species of songbird studied so far (Krebs & Kroodsma 1980). Clearly then, if a young bird remains in the vicinity of its song tutor(s) after the maturation of its song, and new phrase types arise with sufficient frequency (by means of copying errors, improvisations or immigrant phrase types), it may be possible to arrive at the structuring evident in bulbul song populations.

The principal weakness of the epiphenomenon idea, however, is its failure to explain why a genetically controlled song strategy should have been abandoned during evolution for a learned strategy if the capacity for learning has no adaptive significance (Jenkins 1977); the capacity for song learning, and subsequent emergence of dialects, is presumably gene encoded and therefore subject to natural selection.

The search for a functional framework to explain these dialects has led to the emergence of a plethora of functional hypotheses relating to a variety of aspects of bird song biology. I shall now discuss Blackeyed Bulbul song variation in relation to some of these hypotheses, to arrive at a tentative functional hypothesis for the structuring revealed by this study.

5.4.2 Song ontogeny

The question as to whether a young bird learns its song before or after dispersal from its natal territory is crucial to most hypotheses of dialect formation and maintenance. The timing of vocal learning is known for very few species though, and even within this set, differences in all conceivable details of methodology, the difficulty of relating laboratory studies to the real world, and the fact that the outcome of behavioural experiments may depend on conditions which the experimenter knowingly or unwittingly varies, render comparisons difficult (Bateson 1979).

I have only one possible observation of a juvenile Blackeyed Bulbul learning to sing. One morning towards the end of the breeding season, I found two birds in a small tree not far from a singing adult male. The one was presumably the female paired to the singing male, and the other could well have been a juvenile male. The latter was singing a rather quiet and very croaky version of the adult male's song. Unfortunately, this observation is not at all illuminating, and I shall have to discuss song ontogeny in this species on the basis of the observed song-sharing patterns.

In most well-studied northern hemisphere oscines, learning appears restricted to the first few months of life, usually before juvenile dispersal (Marler & Tamura 1964; Mulligan 1966; Immelmann 1969; Marler 1970; Kroodsma 1974, 1982; Mundinger 1975; Cunningham & Baker 1983; Baker & Cunningham 1985; Kroodsma *et al.* 1985; but see Petrinovich *et al.* 1981, Baptista & Petrinovich 1984, 1986, Petrinovich 1985, and Baptista & Morton 1988 for conflicting evidence).

If young bulbuls learn their adult songs from their father or neighbours before natal dispersal, then they should not disperse further than two territories distance from their natal territory to produce the pattern of song variation that is exhibited. Whilst most passerines studied are philopatric, with median natal dispersal distances usually less than ten territories from their birth site (Baker & Mewaldt 1978; Greenwood *et al.* 1979; Greenwood & Harvey 1982; Drilling & Thompson 1988; Arcese 1989; Zack 1990), only cooperatively breeding birds typically show dispersal distances as short as two territories from the natal territory (Zack 1990; Russell & Rowley 1993).

Bulbuls are not cooperative breeders. Furthermore, the fact that they often range around in flocks during the winter months suggests that the juveniles are likely to disperse greater distances than just a few hundred metres.

A number of species have been shown to learn all or most of their songs from neighbours when they establish a territory for the first time after natal dispersal (Thorpe 1958a,b; Dittus & Lemon 1969; Jenkins 1977; Payne & Payne 1977; Baptista & Morton 1988). In some, song learning begins during the first autumn and terminates the following spring (Thorpe 1958a,b; Dittus & Lemon 1969), whilst others are capable of learning new song types from other adults in new dialect areas should they disperse again as older birds (Jenkins 1977; Payne & Payne 1977).

I believe that the only reasonable explanation for the high degree of microgeographic song-sharing by neighbouring territory-holding Blackeyed Bulbuls lies with an hypothesis of song learning from neighbours at the time a young male establishes a territory for the first time after natal dispersal.

Once a bulbul's adult song has been learned, it appears to remain relatively static, although adults can apparently learn new phrase types from neighbours. Thus, the repertoires of a number of birds remained unchanged over the two seasons studied, whilst other birds added a phrase type. These "new" phrases (assuming no sampling errors) were sung with low frequency. I used rather conservative criteria for identifying individuals by their songs, so some of the territory holders I judged to be different individuals over the two seasons may have been the same birds if they are capable of altering their songs appreciably. For the purposes of this study though, I shall have to assume that the "signature" songs are a reliable indicator of individual identity.

Given the reasonable assumption that bird 26 is a foreigner, with a repertoire of foreign phrases, that entered the Grahamstown population as an adult after learning its repertoire at a locality some distance away, it is clear that an adult can accurately copy phrase types from new neighbours. This bird provides clear evidence of song learning after the initial sensitive phase.

The fact that bird 26 copied the two phrases most frequently sung by its two closest neighbours suggests that a bird might copy the phrases it hears with the greatest frequency. The song learning process is unlikely to be this simple though; this hypothesis fails to explain the bewildering array of different song types. A number of studies have shown that a young bird learns more effectively from a tutor with which it interacts socially, especially in aggressive physical encounters normally associated with territory formation and defence (Price 1979; Payne 1981a, 1982; Baptista & Petrinovich 1984, 1986).

5.4.3 Maintenance of dialect patterns

Jenkins (1977) regarded the epiphenomenon idea of dialects as untenable in Saddlebacks *Philesturnus carunculatus* because of the extensive evidence for active maintenance of the conformity to the dialect pattern by birds that shifted. This appears, to a certain extent, to hold true for bulbuls too, as evidenced by bird 26. This individual copied two phrases present in the repertoires of its two closest neighbours in an apparent attempt to conform to the neighbourhood song-sharing complex. This conformity was, however, not very accurate since this bird did not drop any of the original "foreign" phrases from its repertoire, but it is revealing that (1) the phrases acquired were the two phrases most frequently sung by the two neighbours, and (2) bird 26 increased its frequency of singing these two phrases from 27% to 50% over the two seasons.

A puzzling feature of the phrase groups is the failure of a bird to copy particular phrase types of its neighbour. At a given point in all the phrase type distributions, a particular song phrase was not imitated by the next bird, and consequently the phrase groups retained their compactness and small size. The very existence of such discrete, small song groups argues against this pattern of song variation being an epiphenomenon of song learning. This finding replicates that of Jenkins (1977) who suggested that without this inexplicable discontinuity, the phrase group system would have disappeared and all patterns would have become general.

5.4.4 Origin of new phrase types

Errors in the song-copying process certainly do occur (see Figure 5.10), but whether cultural drift due to the accumulation of minor changes in figure type and sequence of figures (Payne *et al.* 1981) can give rise to new phrases in bulbuls is less clear. A number of birds sang hybrid phrases though, recombining figures from different phrases to effectively form a new phrase type. This may be construed as either an error in the copying process, or an innovation. Either way, it could explain why rather different song phrases can share individual figures or figure combinations.

This study was unable to determine whether the rare "signature" phrase types characterizing many individuals (see Appendix 5.1) arose through innovation on the part of the bird, or are phrase types whose origin falls outside the narrow confines of the study area. Undoubtedly the latter situation exists, but given the incredible diversity of song phrases (64 identified from 51 birds), a degree of innovation probably also takes place.

5.4.5 Stability of dialect patterns

McGregor & Krebs (1984) have argued that since annual adult mortality in many passerines is in excess of 50%, the proportion of models (old birds) available as song tutors is no higher than the proportion of mimics - a situation in which accurate cultural transmission of dialect patterns is unlikely to be effective. My study suggests that a minimum of 60% of bulbul territories were reoccupied by the same male in the second season. This return rate is equivalent to, or higher than, adult survival figures available for a number of species (Lack 1966; Payne & Payne 1977, 1990; Payne 1991). The figure for bulbuls may thus approximate the level of annual adult mortality, unless males shifted their breeding territory to a location outside of the rather limited confines of the study area. The fact that bulbuls exhibit a high degree of philopatry to their breeding territories suggests that such an effect is likely to be minimal.

Ringing recoveries have found a number of bulbuls still alive after 10 years (Hanmer 1985; Oatley 1986), and a captive bird even lived to the grand old age of 26 years (Dryden 1981). The relatively low adult mortality rates, together with the high degree of philopatry suggest that the opportunity for effective song mimicry does exist in bulbuls. Certainly, newcomers to the study area in the second breeding season conformed very closely to their local song-sharing neighbourhoods.

5.4.6 Song sharing amongst neighbours

This brings us to the question of whether the capacity for copying the songs of neighbours has any adaptive value. Studies on a wide variety of species have demonstrated song sharing or matching among neighbours, and the existence of microgeographic structure in song populations such that local dialect clusters of up to 20 males share song types or have similar song structures (Snow 1968; Payne 1978, 1981a, 1983; Mundinger 1975; Jenkins 1977; Falls *et al.* 1982; McGregor & Krebs 1982, 1984; Wiens 1982; Lemon *et al.* 1985; Cunningham *et al.* 1987; Shackell *et al.* 1988; Catchpole & Rowell 1993). Whilst some authors have interpreted such patterns as merely a result of vocal learning between neighbours (Slater *et al.* 1981; Wiens 1982), most regard it as adaptive (Jenkins 1977; Payne 1982, 1983; Wiley & Richards 1982; Baker & Cunningham 1985; Baker & Thompson 1985).

5.4.7 Deceptive mimicry

Payne (1982) hypothesized that the mechanisms through which song matching enhances biological success involve deceptive mimicry directed towards the other males that compete for breeding space in the same neighbourhood. Two versions of this hypothesis exist, only one of which is applicable to the Blackeyed Bulbul.

In this social adaptation hypothesis, Payne (1982) proposed that a young male may give the deceptive impression of being an established male by copying the songs of older neighbours and thus conforming to the local dialect group. Before discussing this hypothesis with respect to bulbuls, we need to first investigate the possible reasons for, or adaptive value of, conforming to a local dialect group.

5.4.8 Neighbour/stranger discrimination

Numerous studies have shown that territorial residents generally respond more intensely to an intrusion (usually simulated by song playback) by a stranger than by a known neighbour (reviewed in: Krebs & Kroodsma 1980; Falls 1982; Mundinger 1982; Ydenberg *et al.* 1988; Stoddard *et al.* 1990).

Two main functional hypotheses have been proposed to explain the functional significance of this neighbour/stranger discrimination (Ydenberg *et al.* 1988):

1. discrimination minimises the considerable time and energy spent in aggressive encounters associated with the formation of territories (Weeden & Falls 1959); and
2. discrimination may prevent escalated contests between neighbours.

Both these hypotheses argue that once boundaries have been set, established neighbours pose little threat to one another (i.e. are "dear enemies") and should avoid repeated, expensive conflicts along the boundaries (Ydenberg *et al.* 1988). The establishment of dear enemy relationships is assumed to involve a cost in time, energy and increased susceptibility to predation. The appearance of a singing stranger, on the other hand, can pose a serious threat of usurpation of an entire territory, or portions of several territories, since the stranger is presumably signalling its intention of establishing a territory in an area that may already be fully occupied.

This is where Payne's (1982) deceptive mimicry hypothesis comes into play. A young bird establishing a territory may be able to reduce the aggression directed towards it by neighbours if it copies the songs of the neighbours with which it is interacting, thus giving the deceptive impression of being an established member of the local neighbourhood.

The question though is whether the established residents are likely to be fooled by this mimicry, i.e. how good is their ability to discriminate between known, established neighbours and new mimics?

Neighbour discrimination implies long-term memory of songs, and, in species where males have repertoires, many songs may have to be learned (Stoddard *et al.* 1992). If birds are limited by the number of songs they can commit to memory, neighbour recognition may be enhanced if neighbouring birds share similar repertoires. Whilst some studies have demonstrated that memory does not appear to constrain individual recognition in species with repertoires (Stoddard *et al.* 1991, 1992; Weary *et al.* 1992), no study has adequately tested what features repertoire species use in individual recognition. Therefore, the hypothesis that a male may find it easier to recognise another male as a neighbour if that bird shows significant matching with its own phrase types cannot be discounted. Should this be the case, then it would indeed be possible for a bird mimicking the repertoires of its neighbours to fool them into believing it is an established resident.

5.4.9 Song matching

Song matching occurs when a bird responds to a rival by singing phrases from its repertoire that resemble or match those just sung by that rival (Krebs *et al.* 1981). Matching of phrase types in countersinging duels between rivals has been observed in many species (Hinde 1958; Lemon 1968a,b, 1974; Dixon 1969; Kroodsma 1971, 1979; Krebs *et al.* 1981; Todt 1981; Falls *et al.* 1982; Kramer & Lemon 1983; Kramer *et al.* 1985).

Suggestions about the significance of song matching in communication have included its use as 1) a form of "vocal threatening" to regulate distances between conspecific neighbours (Todt 1981), and 2) to signal the likelihood of attacking an intruder by the probability of matching an intruders song (Krebs *et al.* 1981; Falls *et al.* 1982), but there has been little direct evidence.

In the Blackeyed Bulbul, the probability of a bird being able to match the phrases of a stranger, or vice versa, is low due to extreme repertoire variability. On the other hand, a territorial bird should be able to match most of the phrase types of a neighbour due to the similarity in repertoire composition of neighbouring birds. Whilst I have not directly quantified this effect, I did notice that birds singing closer together often matched phrase types in their songs. I therefore suggest that song matching may act as a previously undescribed form of neighbour recognition, with a territorial resident more likely to attack a bird that is unable to match its own phrase types sung in a counter-singing duel.

The pattern of phrase type variation in bulbuls lends itself well to this hypothesis of neighbour/stranger discrimination on the basis of phrase type matching. The degree of phrase type variation (64 phrases recorded among 51 birds) and the fact that each individual has a limited repertoire (median of 5), could indicate a memory constraint on individual recognition if all neighbours had different repertoires.

Furthermore, if one accepts that a bird is capable of discrimination solely on the basis of voice quality, then an alternative explanation for the observed highly structured pattern of song sharing among neighbours is required.

5.4.10 Co-operative territorial defence?

Getty (1987) used a game theoretical approach to develop a model based on the dear enemy prisoners dilemma to explain why territorial residents so consistently defeat potential usurpers. By collectively monopolising a limited habitat or resource space, the established neighbours create a class of excluded "floaters" (Figure 5.11). For the neighbours, these strangers represent a common outside threat since:

1. the stranger may threaten a portion of their territories too, and
2. the neighbours will have to pay the costs of renegotiating dear enemy relationships should the stranger successfully replace the former resident.

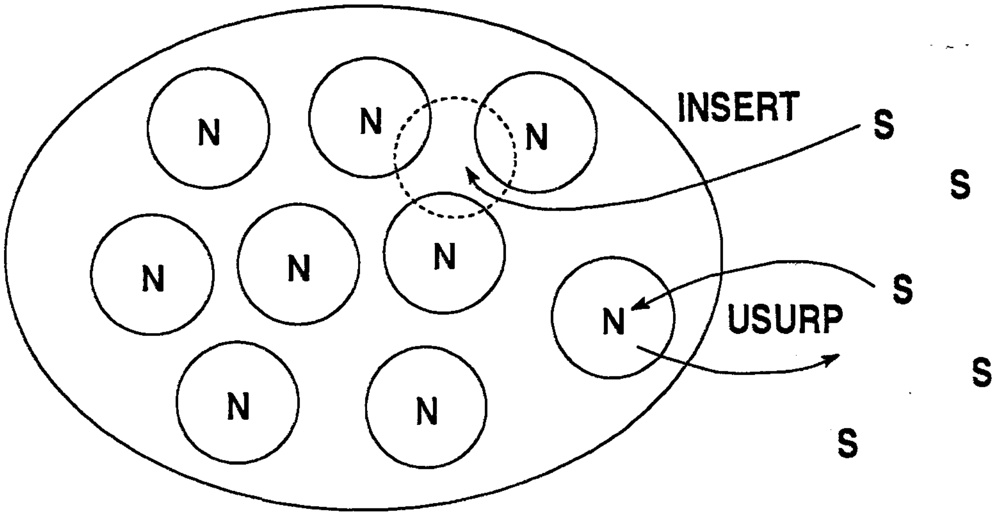


Figure 5.11 A schematic representation of an oligopoly of territorial neighbours (N) monopolizing the habitat. Floating strangers (S) threaten to:
1. insert into the habitat by carving out portions of several territories, or
2. usurp entire territories (from Getty 1987).

Getty therefore argued that territorial neighbours should form "defensive coalitions" to assist one another in defending their territories against intrusion by strangers.

If it can be assumed that song matching assists neighbour/stranger discrimination, then the existence of microgeographic structure in song populations such that local dialect clusters of neighbouring males share song types or have similar song structures, as described in this study and others already referred to, can be argued to provide indirect support for Getty's model.

To summarise then, the observed pattern of song variation in a Blackeyed Bulbul population such that neighbours share similar repertoires of phrase types and the degree of song similarity decreases rapidly with increasing distance between birds or neighbour groups could enable neighbour/stranger discrimination, which in turn, may assist neighbours in a system of co-operative territorial defence.

To the best of my knowledge, this form of co-operative territorial defence has yet to be demonstrated. It is interesting to note though, that in the polygynously breeding Redwinged Blackbird *Agelaius phoeniceus*, groups of male neighbours co-operate with females in nest defence and that females may choose groups of males in "breeding neighbourhoods" rather than individuals (Beletsky & Orians 1991).

5.4.11 Territorial song in *P. nigricans* and *P. capensis*

In the course of recording the songs of the other two bulbul species, I have observed the same pattern of phrase type variability and song sharing amongst neighbours. This leads me to suggest that it is highly probable that these two species have very similar territorial song systems to *P. barbatus*.

Observations I made on *P. nigricans* during the breeding season on the lower Orange river suggest that population density may be a complicating factor modifying territorial behaviour. In this area, bulbuls are superabundant. During the dawn chorus, singing males were separated by as little as 30 m, and although still site-specific, were clearly defending much smaller areas than Blackeyed Bulbuls in Grahamstown. After sunrise, territorial behaviour seemed to tail off, with birds intermingling and gathering in flocks in suitable fruiting trees to feed.

Liversidge (1970) noted a similar situation for *P. capensis*; males had specific song perches, but did not vigorously defend their territories. He further stated that territorial song was only heard when nesting activity was under way during incubation, making no mention of the dawn chorus. This leads me to suspect that he was unaware of their dawn chorus singing behaviour, since I have definitely observed it at many localities across the distribution of this species.

Clearly though, the dynamics of territorial behaviour may differ quite significantly between localities, influenced in part by population densities.

5.4.12 Territorial behaviour in the non-breeding season

In my Grahamstown study area, many pairs appeared to roost on their breeding territories during the non-breeding season. Whilst singing during the dawn chorus was much reduced, short snatches of announcement song could be heard regularly through the winter months. It would therefore appear that whilst the birds gather gregariously into feeding flocks during the day, some form of territory maintenance may still take place.

5.4.13 Why are bulbuls territorial?

Territoriality has been variously defined as the exclusion of intruders from a fixed area by some combination of advertisement (e.g. song), threat and attack (Brown 1975), or the maintenance of a fixed portion of an individuals home range such that it has priority of access to one or more critical resources over others (Kaufmann 1983).

Arguments over the functions of territoriality have centred on two main themes: social stimulation and resource acquisition (Kaufmann 1983). Darling (1952) argued that the main value of territoriality is to provide peripheries of social contact with neighbouring conspecific territory holders. The resulting acts of defence, he believed, are needed to bring birds into reproductive condition. Kaufmann (1983) argued that there is little evidence for this hypothesis and that it fails to take into account more plausible alternative explanations.

Wynne-Edwards (1962) argued that the adaptive function of territoriality is as a spacing mechanism to keep the population within the carrying capacity of the habitat by limiting reproduction. This theory depends on selection between demes (group selection) rather than between individuals, a phenomenon that most biologists believe occurs only in rare circumstances.

Territoriality is now generally regarded as a form of more or less direct competition for critical resources in short supply, and all aspects of territorial behaviour are seen as resulting from individual selection (Brown 1964; Kaufmann 1983). Resources might include a mate, food or the most suitable nesting sites or habitat.

Whilst it is not known at what age a young bird becomes paired with a mate for the first time, the pair bond in bulbuls is strong, with the birds probably pairing for life (Liversidge 1970; *pers. obs.*). Thus territoriality is unlikely to function in mate acquisition in bulbuls, especially since the advertisement song appears to have a mostly intrasexual function.

Extra-pair copulations have been widely reported in birds (Gowaty & Karlin 1984; Burke & Bruford 1987; Westneat 1987; Wrege & Emlen 1987; Brown & Brown 1988; Hoffenberg *et al.* 1988; Sherman & Morton 1988; Rowley & Russell 1990; Gelter *et al.* 1992), and it has been suggested that territorial behaviour, and in particular the dawn chorus singing, may function in paternity protection (Greig-Smith 1982; Mace 1986, 1987a,b; Moller 1988; Part 1991). In the Blackeyed Bulbul, however, the advertisement song is not directed at the female, who often moves out of sight of the singing male, hardly the hall-marks of mate-guarding behaviour.

The availability of food is extremely difficult to quantify and consequently nearly impossible to confirm as a limiting factor in bird populations. This is possibly the reason why it is so often glibly invoked in many studies of competition. Liversidge (1970) found a superabundance of fruit in the breeding territories of *P. capensis*, and concluded that food was an unlikely limiting factor for this predominantly frugivorous bird. He, however, overlooked the fact that the developing chicks are fed mostly on arthropods. Orians and Willson (1964) have suggested that the rate at which food can be delivered to the nestlings may have a particulary important effect on reproductive success.

Bulbuls do not require specialized nest sites, so this is unlikely to be a limiting resource. Certain habitat features may influence nest predation rates and ultimately breeding success, resulting in competition for the best nesting habitat. However, it is difficult to envisage how this factor alone could be responsible for the fairly large size of the territories, unless the degree of nest dispersion affects predation rates.

Andersson and Wiklund (1978) regard predation as one of the most important selective pressures influencing the optimal spacing pattern in any population. Nest predation rates in birds are usually high, in the range 25-90% (Lack 1966, 1968; Clark & Wilson 1981; Schieck & Hannon 1993; *pers. obs.*), and must act as a powerful selective force. Liversidge (1970) recorded 60 % nest-predation levels for *P. capensis*. The consequences for individuals sharing a natural enemy have been argued, in general terms, to be identical to more conventional forms of competition for limited resources (Williamson 1957), and to have structured many aspects of species' niches in ecological and evolutionary time (Jeffries & Lawton 1984). Such considerations have led to the hypothesis that well-camouflaged prey, such as bird nests, should be over-dispersed i.e. having inter-individual distances which greatly exceed the distance from which predators usually detect them directly (Tinbergen *et al.* 1967; Dunn 1977; Andersson & Wiklund 1978; Schieck & Hannon 1993; see Andren 1991 for a dissenting opinion). A logical extension of this is the argument that territoriality itself may have evolved to space out breeding individuals under such selective pressures.

Krebs (1971), in a classic study on the Great Tit *Parus major*, found that territory size variations from year to year were the result of interactions between the birds themselves, rather than direct adjustments of territory size to fluctuations in some environmental resource (e.g. artificial food supplements). Furthermore, when he removed established territorial pairs, the removed birds were rapidly replaced by largely first-year birds from the surrounding habitat that was suboptimal in terms of reproductive success. These results show that territorial behaviour in this species limits breeding density in optimal habitat as a consequence of the spacing out of birds, with the possible advantage of acting as a defence against predation.

Returning to bulbuls once more, there is no immediately obvious critical resource or factor responsible for the territoriality of Blackeyed Bulbuls. However, since territories can be multipurpose areas, it is difficult to evaluate which factor or combination of factors might be responsible for the evolution of territorial behaviour, and indeed the evolutionary significance of territoriality itself (Orians & Willson 1964).

5.4.14 Recommendations for further research

This study of the territorial song of *P. barbatus* has basically only described a very interesting system. The great variability in song phrases and the ease with which they can be distinguished, make this species an ideal study subject. Furthermore, no other species in the extensive literature exhibits quite the degree of microgeographic structure in song populations as does *P. barbatus*. Had this species been the "white rat" of the ornithological world in place of the ubiquitous Whitecrowned Sparrow *Zonotrichia leucophrys*, I am certain that our understanding of the biology of bird song dialects would be substantially clearer than it is today.

Many interesting hypotheses have been generated by this study, but until they are actually rigorously tested, they shall remain just that. There are two different research approaches that can be followed to accomplish this. The first is a labour-intensive, long-term population study, whose first requirement is that all territorial males, and possibly their females, be captured on their territories at the start of each breeding season and given colour-ring combinations. Males, and often their mates, respond strongly to song playback, and should not be too difficult to mist-net in this manner. With the birds individually identified, their survival, reproductive success, changes in song structure, and the dynamics of their territorial behaviour can be followed on an annual basis. Following juvenile recruitment and dispersal would be extremely useful in gaining an idea of when their adult songs are learned and how far from their natal territories they eventually establish territories of their own. This would require locating nests and ringing the nestlings shortly before they left the nest.

The second approach would primarily involve song playback studies, strictly following the guidelines laid down by Payne (1981b), Kroodsma (1989a,b, 1990) and Searcy (1989), but see also Weisman & Ratcliffe (1987). The first question to be addressed should be whether territorial residents do react more strongly to the song of a stranger than to a known neighbour.

The significance of repertoire size and the discreteness of song or phrase-sharing groups has received little attention in the literature (see Kroodsma 1990). The Blackeyed Bulbul, with its high degree of phrase type variation, but limited repertoire size, makes an ideal subject for studying issues relating to repertoire size.

Determining the degree of phrase-type matching between singing neighbours would be a relatively simple study, but assessing the possible significance of this to individual and/or "neighbourhood" recognition is likely to be difficult. Should the results of these studies yield positive results though, the final test of the possible existence of a co-operative territorial defence system would be the most challenging of all.

CHAPTER SIX

HYBRIDIZATION AND HYBRID ZONES WITHIN THE *Pycnonotus* SPECIES COMPLEX

6.1 INTRODUCTION

A hybrid zone has been variously defined as an interaction between taxa which have diverged genetically so that interbreeding between individuals from the divergent populations results in progeny recognizably different from the parents (Gartside *et al.* 1979), or as a cline or set of clines between taxa for genes and the distinguishing characters they determine (Hewitt 1988). Mayr (1963, 1970) interpreted hybrid zones as evidence of secondary contact between previously isolated populations. Others have suggested alternative mechanisms for the evolution of abrupt discontinuities in a continuous series of populations (Clarke 1966; Endler 1977; White 1978; De Meeus *et al.* 1993 and references therein). These alternatives have been severely criticized (see Mayr 1970, 1982) and will therefore not be further considered.

To date, over 170 reasonably clear hybrid zones have been documented amongst plants and animals (Barton & Hewitt 1989). Most hybrid zones are narrow relative to the species' range and to the distance moved in a generation; they are often only a few hundred metres wide and yet may be several hundred kilometres long (Barton & Hewitt 1985, 1989).

Three major hypotheses have been put forward to explain and predict the dynamics of hybrid zones. When the occurrence of hybrid zones amongst a wide variety of animal taxa was first appreciated, they were, in accordance with the state of evolutionary theory at the time, regarded as ephemeral. Natural hybridization was predicted to lead to one or other of two scenarios:

1. speciation, or
2. fusion of the allopatric populations through introgressive hybridization (Dobzhansky 1940, 1970; Sibley 1957; Remington 1968).

The first scenario involves taxa that have diverged through differential mutations, selection and coadaptation to the extent that hybridization would disrupt the distinctly coadaptated gene pools.

This results in selection against the inferior hybrids which would lead to reinforcement of premating reproductive isolating mechanisms. This in turn would lead to assortative mating, reduced hybrid production at the contact, and eventual speciation.

In the second scenario, if the two isolates have not diverged to the extent to which hybrids are selected against, the fully fertile hybrids will be the means of introgressive hybridization and complete fusion between the two taxa, or the swamping of the smaller taxon will occur.

Most hybrid zones have since been shown to persist and remain relatively stable through time, with neither increased reproductive isolation nor fusion taking place. Furthermore, current thinking holds that the evolution of reproductive character displacement (Brown & Wilson 1956) and ecological differentiation (Mayr 1963), which together would allow broad geographic overlap, are prevented for two reasons. Firstly, such mechanisms will be favoured by selection only in the area of interaction where an individual's fitness is lowered by any mating with a non-conspecific individual. Secondly, continuing immigration of individuals from parental populations adjacent to the zone of interaction will result in "genetic swamping" of the products of localized reinforcing selection (Thaeler 1968; Alerstam *et al.* 1978).

The two more recent hypotheses have arisen to account for the dynamics of persistent hybrid zones. The first, which has been termed the "bounded hybrid superiority" hypothesis, was first proposed by Anderson (1948). It suggests that a hybrid zone is located at an ecotone between the habitat preferred by one taxon and that preferred by the other. If intermediate habitats are found within the ecotone, then hybrids, with part of their genome adapted to each habitat, might be fitter there than either parental taxon. The theory predicts that hybrids have heterozygotic fitness within the ecotone, but reduced fitness in either of the habitats outside the ecotone where one or other parental taxon is better adapted. Moore (1977) suggested that this hybrid superiority maintains many vertebrate hybrid zones.

The second hypothesis, termed the "dynamic-equilibrium" hypothesis was first formulated by Bigelow (1965) and Bazykin (1969) and refined by Barton (1979a,b) and Barton and Hewitt (1981, 1985, 1989). This hypothesis characterizes hybrids formed at the secondary contact of related taxa as having reduced or null fitness as a consequence of the breakdown of coadapted parental genomes. Hybrids may be at a disadvantage because they have low viability or fecundity, or because they attain a low mating success. Since only populations within the often narrow hybrid zone experience selection against hybridization, gene flow from the allopatric areas into the hybrid zone would genetically swamp the alleles which may cause individuals to avoid hybridizing. Thus Barton and Hewitt (1985, 1989) believe that most hybrid zones are "tension zones"; clines maintained by a balance between random dispersal and selection against hybrids.

To date, only isolated instances of hybridization have been reported within the *Pycnonotus* bulbul species complex (summarized in Chapter 1). In this chapter, classic narrow hybrid zones between each of the three species pairs will be described, and their significance with respect to the population ecology and population genetics of the species complex will be discussed.

6.2 METHODS

Five wide-ranging field trips were undertaken to determine both the exact distribution limits of the three species in the eastern Cape region, and the extent and nature of any hybridization taking place. These trips took place on 5-7 June 1992, 15-17 July 1992, 31 July - 3 August 1992, 6-11 September 1992 and 22-24 May 1993.

For the most part, this survey was conducted by driving and stopping at frequent intervals to locate and identify any bulbuls. A total distance of 1 400 km was traversed in and around the areas of contact between the species.

Bulbuls were observed through Nikon 10x40 binoculars and on occasion, a 20x telescope. These sightings were then plotted on 1:250 000 topographical maps. Map numbers used were 3224 (1987), 3226 (1985) and 3324 (1981). All place names referred to in this chapter are taken from these maps (see Appendix 6.1 for all locality coordinates).

On the trip of 15-17 July 1992, 43 bulbuls were mist-netted on the farm Glen Ross. These birds were measured, described, photographed, ringed and released.

Once hybrid zones between each of the three species pairs had been established, a decision was made to collect birds from eight different localities along a 'transect' across the *P. barbatus*/*P.*

nigricans hybrid zone, and to collect examples from each of the *P. barbatus/P. capensis* and *P. nigricans/P. capensis* hybrid zones for phenotypic and genetic analysis.

The localities across the *P. barbatus/P. nigricans* hybrid zone included the farms Saxfold Park (8 birds), Waterfall (10 birds), Glen Lyndon (10 birds), Glen Ross (10 birds), Glen Isle (10 birds), Geluk (10 birds), Rietvlei (8 birds) and Altyd Somer (10 birds) (Figure 6.1).

At first the birds were captured with mist nets and transported back to Grahamstown where they were housed in a large outdoor aviary until sacrificed. Birds collected in this way included nine from Glen Ross (collected 15-16 June 1993), two from Rietvlei (collected 23 July 1993), seven from Geluk (collected 24-25 July 1993), all sacrificed on 1 August 1993, seven from Waterfall (collected 2-4 August 1993; three later escaped), one from Glen Ross (collected 5 August 1993) and three from Glen Isle (collected 6 August 1993; one later escaped), all of which were sacrificed on 10 August 1993). The remaining birds were shot between 13 and 19 August 1993.

A further three individuals on the farm Waterkloof in a *P. nigricans/P. capensis* hybrid zone and six individuals on the farm Protest in a *P. barbatus/P. capensis* hybrid zone were shot between 4 and 5 September 1993 (Figure 6.1).

For each bird, the following were recorded immediately after capture or death:

1. weight,
2. wing length - maximum chord,
3. tarsus length - back of knee joint to distal edge of last complete scale,
4. bill length - base of the skull to the tip of the bill,
5. bill width - at the posterior edge of the nasal openings, and
6. bill depth - at the posterior edge of the nasal openings.

A measure of bill volume was obtained by multiplying bill length, width and depth. The colour of the eye-wattle on birds within the *P. barbatus/P. nigricans* hybrid zone was recorded on a scale of 1 to 4 (see Figure 6.2), where 1 = black wattle (typical of *P. barbatus*), 2 = wattle partly black / partly infused with yellow, 3 = wattle yellow throughout, and 4 = wattle orange throughout (typical of *P. nigricans*).

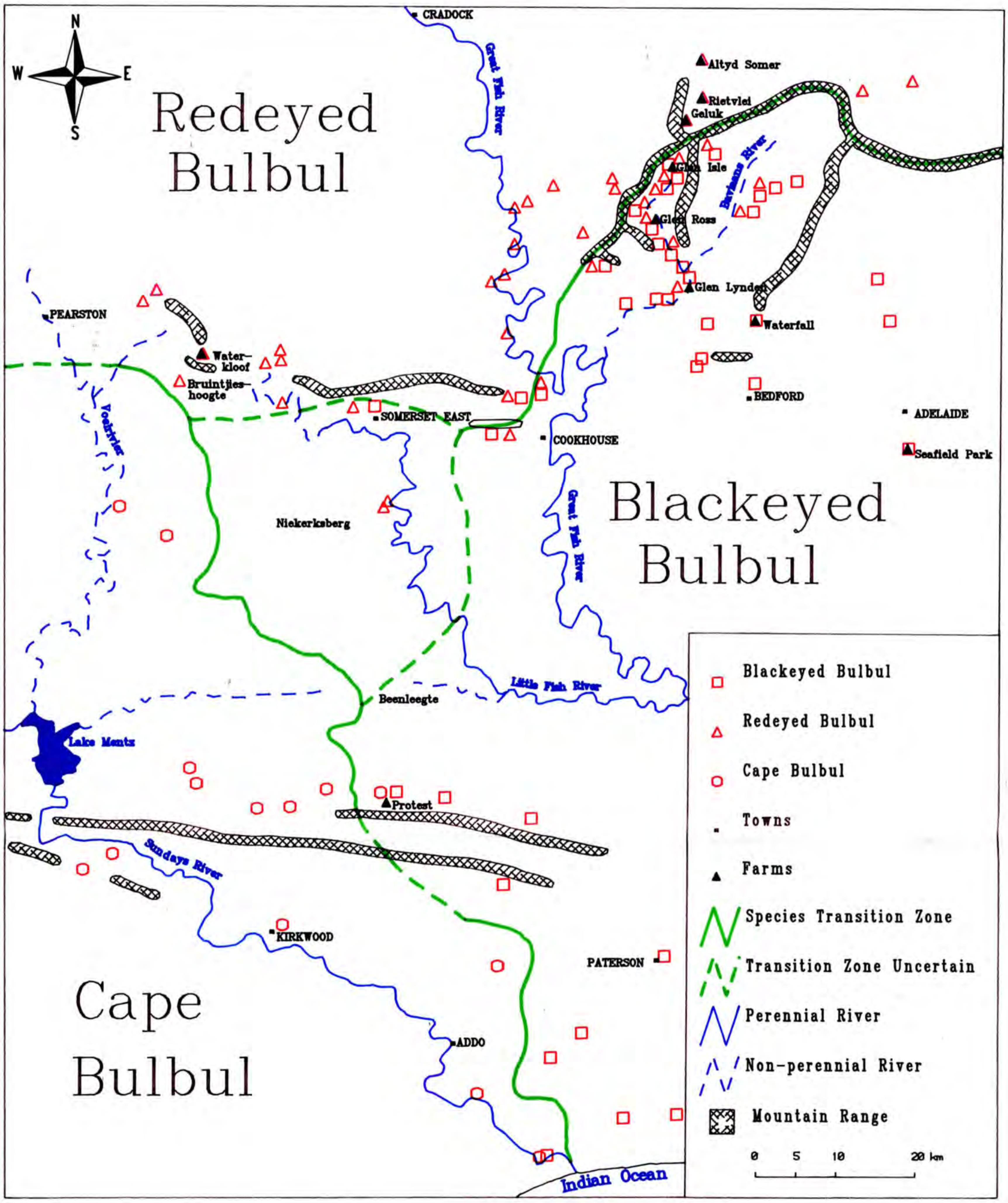


Figure 6.1 Map of the eastern Cape region surveyed for *Pycnonotus* bulbuls, showing the approximate transition zones between the three species. See Appendix 6.1 for a detailed summary of survey results.

The eye-wattles were removed and stored in vials containing 95% alcohol for later measurement under a 10x25 dissecting microscope. The birds were individually skinned immediately after death; the skin being prepared as a museum study skin and the carcass being labelled and immersed in a dewar of liquid nitrogen for later mitochondrial DNA analysis. The mitochondrial DNA analyses are being performed by Dr M.F. Essop at the University of Cape Town. Unfortunately, the results were not yet available by the time this thesis went to print.

6.3 RESULTS

6.3.1 *P. barbatus/P. nigricans* hybrid zone

A hybrid zone between these two species extended from the Somerset East area, the southernmost point of contact between the two species, to at least the Baviaans river valley. Areas to the east of this valley were not visited (Figure 6.1).

The two parental populations were generally separated by a range of mountains running SW-NE, with the hybrids to be found in the valleys and kloofs on either side. The vegetation on either side of the range differed quite noticeably. I was usually able to predict, on the basis of the vegetation, which species would predominate in any area visited. On the northern side of the range, the vegetation was typically karoid and dominated by *Rhus lancea* and *Acacia karoo*. On the southern side it contained many Subtropical Thicket (Palmer 1988) components, such as *Ochna arborea*.

Bulbuls were plentiful within the hybrid zone. I observed a noisy congregation of well over 100 birds, many of which were obvious hybrids, in a bushy kloof on the farm Daggaboerhoek on 7 June 1992. This is the largest foraging flock of bulbuls I have encountered anywhere. The birds appeared to have congregated there because the kloof was sheltered from the strong wind prevailing that day. Further, the ease with which 43 birds (mostly hybrids) were mist-netted at Glen Ross demonstrated no shortage of birds there either.

The width of the zone of contact in which hybrids were to be commonly seen was usually no more than 20 km. The transition from predominantly black-eyed birds to predominantly red-eyed birds was much sharper, and usually within 10 km. One might have expected the transition to be less well defined where the zone crossed the Fish river valley north of Cookhouse, where there is no possible geographic barrier, but this was not the case.

6.3.2 Description of *P. barbatus* x *P. nigricans* hybrids

A typical *P. barbatus* has a narrow black wattle and a very dark brown iris, whilst a typical *P. nigricans* has a wide, bright orange wattle and a rich brick-red iris (see Figure 6.2).

The wattles of the phenotypic hybrids varied greatly. The range of variation included: black wattles with a faint yellow infusion in the hind quarter (code 2), wattles with the hind half faint yellow and the front half black (code 2), wattles completely dull yellow (code 3), wattles completely dull orange (code 4), and wattles bright orange (code 4) (Figure 6.2). The orange wattles within the hybrid zone were often noticeably thinner than one would expect from a typical *P. nigricans* wattle.

Iris colour of hybrids ranged from dark brown to light brown to reddish brown to brick-red (see Figure 6.2) but due to the difficulty in determining the iris colours of dead birds, this feature was not quantified.

The plumage of a typical *P. barbatus* in the eastern Cape consists of a dark brown throat, a brown breast whose feathers have only narrow pale fringes, and a dull white belly (Figure 6.3). The plumage of a typical *P. nigricans* from the E Cape consists of a black throat, an almost sooty-brown breast whose feathers are fringed whitish, giving a characteristic scaly effect, and a pure white belly (Figure 6.3). The plumage coloration of the hybrids is variably intermediate between that of the two parental species. It was not uncommon to see hybrids with orange wattles (typical of *P. nigricans*) but plumage characteristic of *P. barbatus*, and vice versa. Whilst the plumages of the two parental species are distinct, the intermediate plumages of most hybrids proved to be exceptionally difficult to quantify, and are therefore not included in this summary.

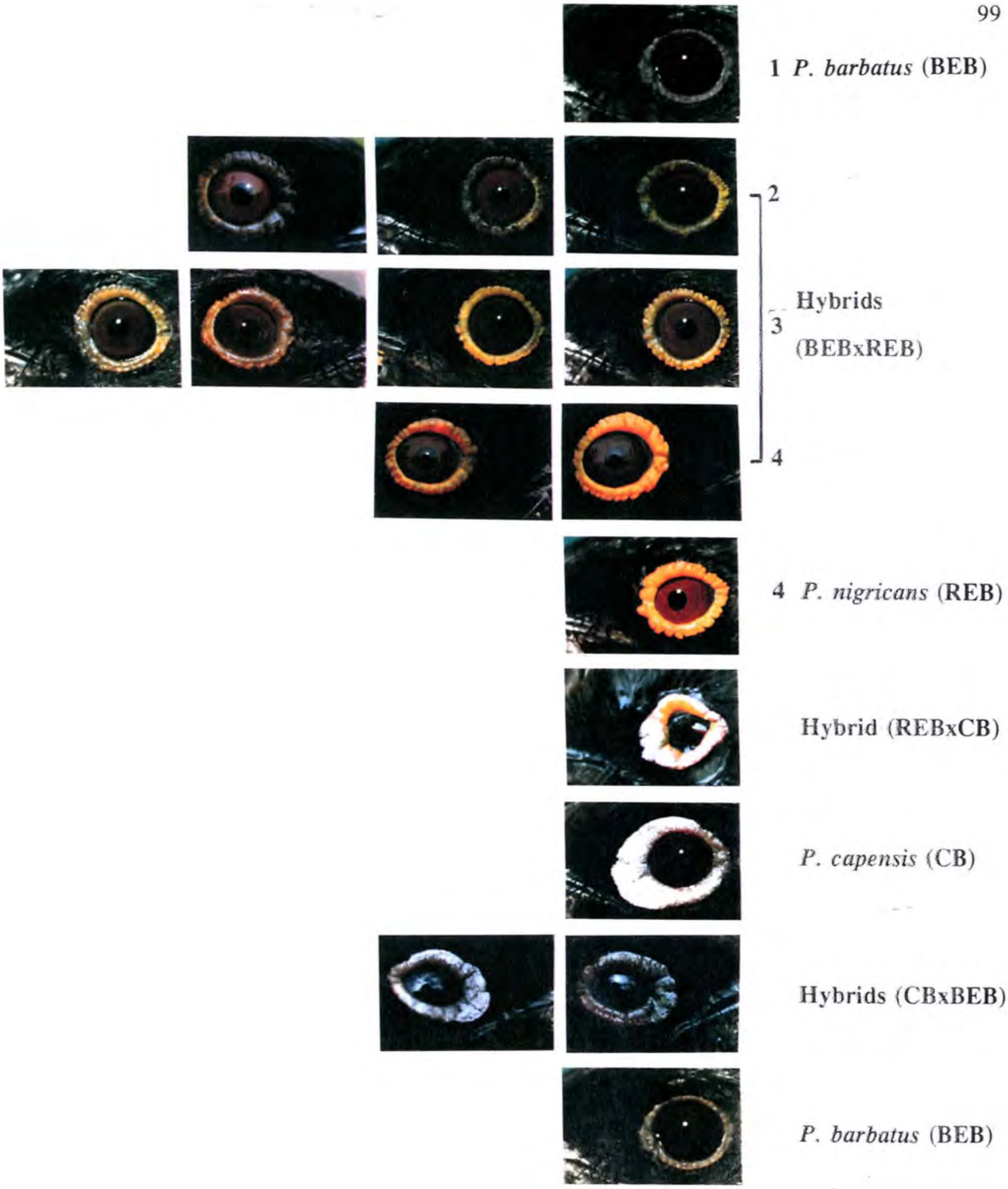


Figure 6.2 Eye-wattles of the three *Pycnonotus* species and their hybrids. Numbers 1-4 refer to eye-wattle colour codes (see text). Note differences in iris colour, particularly amongst the *P. barbatus* x *P. nigricans* hybrids.

Figure 6.3 Photographs of the throat, chest and belly plumage of *P. barbatus* (left) and *P. nigricans* (right).

Appendix 6.1 groups birds seen through binoculars as:

1. essentially black-eyed,
2. essentially red-eyed, and
3. of intermediate wattle coloration.

It must be remembered that the first two groupings do not necessarily correspond to the two pure species; it is not possible to distinguish the finer differences of many hybrid wattles through binoculars. A truer survey of hybrid phenotypes within the hybrid zone is discussed under 6.3.3 below.

6.3.3 Transect through the *P. barbatus/P. nigricans* hybrid zone

Figure 6.4 depicts the frequency of eye-wattle colours at the eight localities on the transect across the *P. barbatus/P. nigricans* hybrid zone, whilst Figures 6.5 to 6.7 depict the variable means and standard errors for the features that were quantified. Table 6.1 lists the statistical significance values for between-locality comparisons for each variable.

Table 6.1 Statistical significance (*P*) values for between-locality comparisons for variables quantified at eight localities along the transect across the *P. barbatus/P. nigricans* hybrid zone.

Variable	***P* value**
Wattle code	0.000
Wattle width	0.000
Weight	0.001
Bill width	0.002
Bill length	0.010
Bill volume	0.063
Tarsus length	0.068
Bill depth	0.121
Wing length	0.692

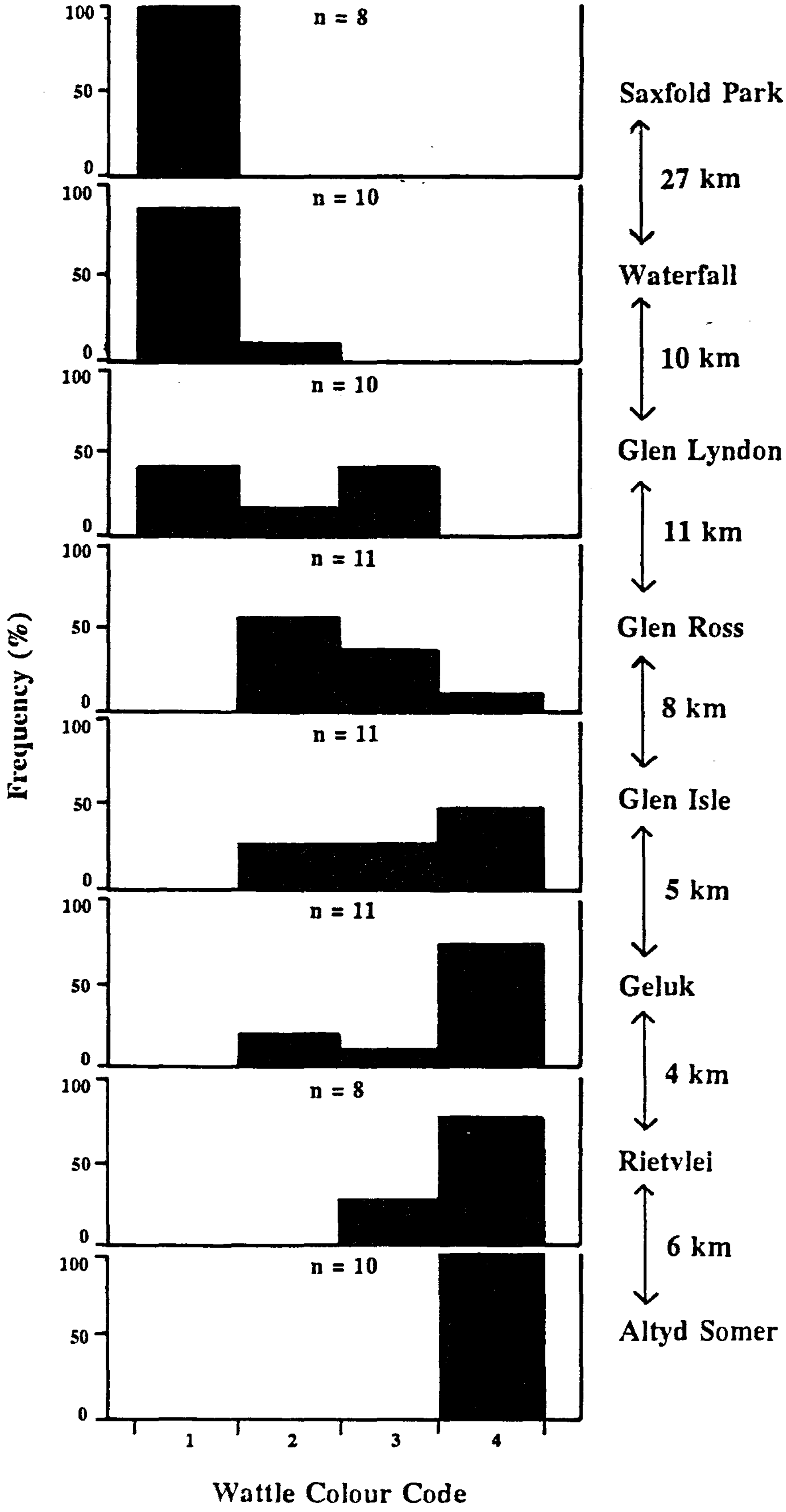


Figure 6.4 Frequency of eye-wattle colours (coded 1-4) at the different localities on the transect through the *P. barbatus/P. nigricans* hybrid zone. Straight line distances between localities are provided.

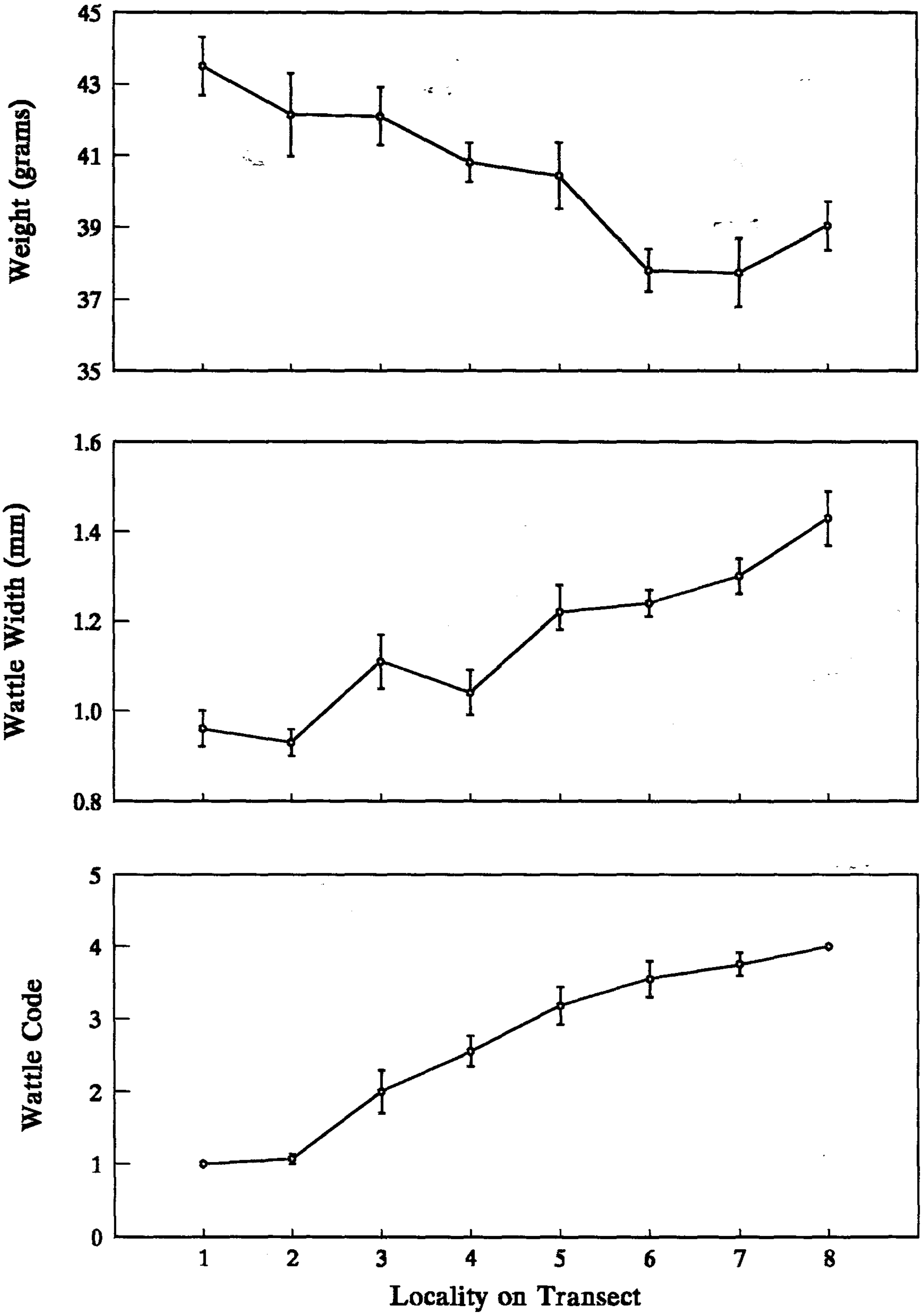


Figure 6.5 Weight, wattle width and wattle code means and standard error bars for localities across the *P. barbatus/P. nigricans* hybrid zone. Locality 1 = Saxfold Park, 2 = Waterfall, 3 = Glen Lyndon, 4 = Glen Ross, 5 = Glen Isle, 6 = Geluk, 7 = Rietvlei, 8 = Altyd Somer.

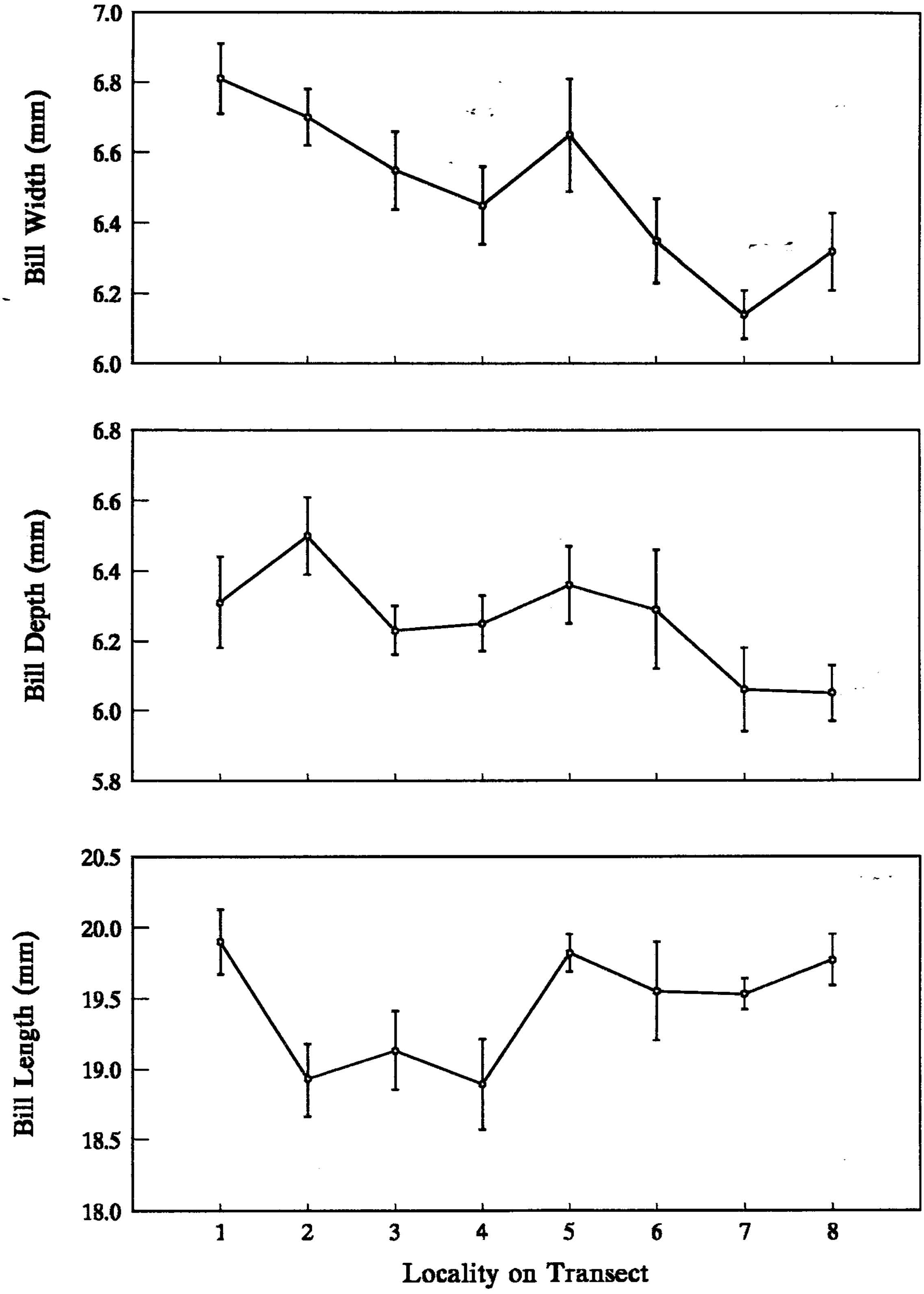


Figure 6.6 Bill width, depth and length means and standard error bars for localities across the *P. barbatus/P. nigricans* hybrid zone. Locality 1 = Saxfold Park, 2 = Waterfall, 3 = Glen Lyndon, 4 = Glen Ross, 5 = Glen Isle, 6 = Geluk, 7 = Rietvlei, 8 = Altyd Somer.

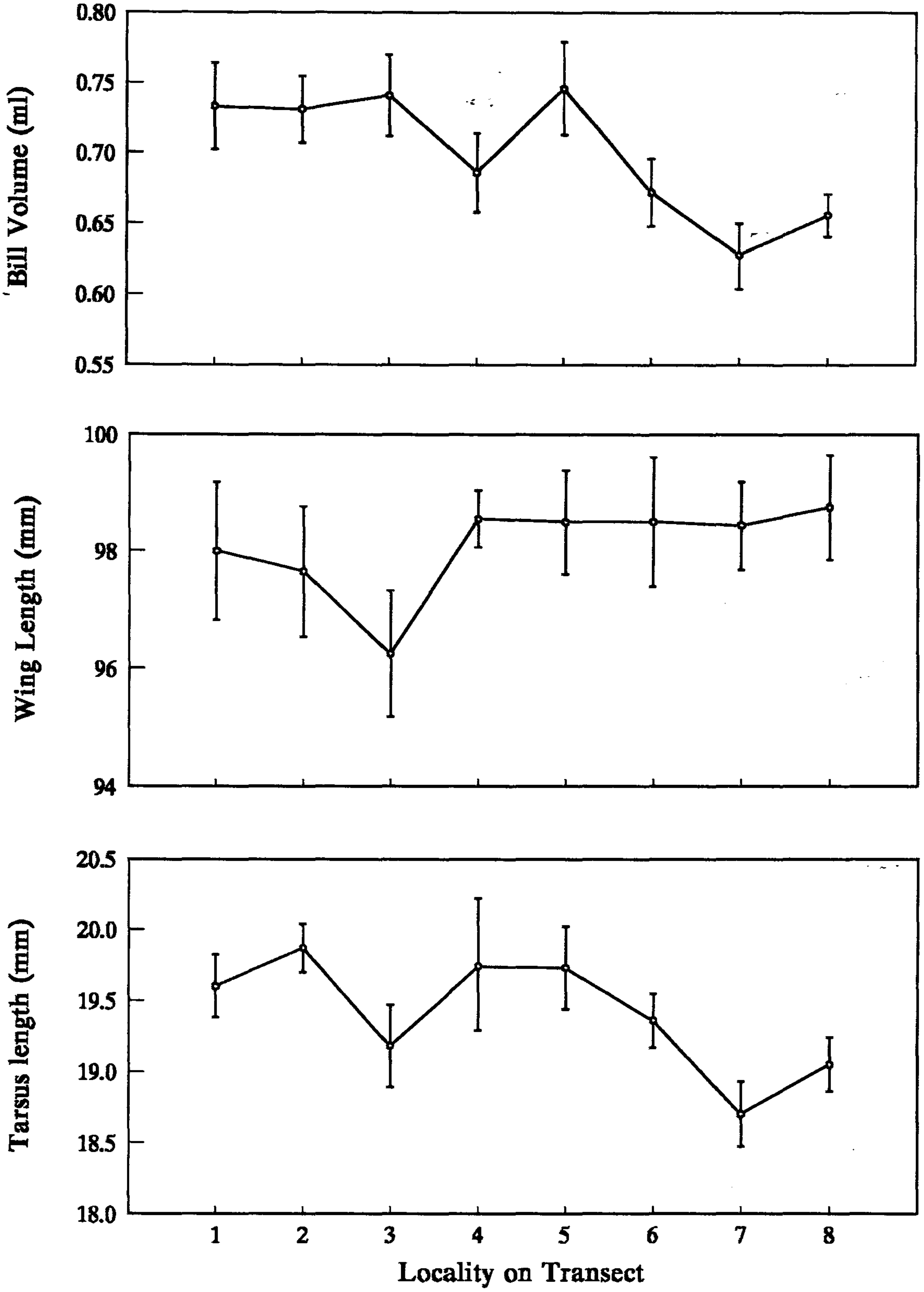


Figure 6.7 Bill volume, wing length and tarsus length means and standard error bars for localities across the *P. barbatus/P. nigricans* hybrid zone. Locality 1 = Saxfold Park, 2 = Waterfall, 3 = Glen Lyndon, 4 = Glen Ross, 5 = Glen Isle, 6 = Geluk, 7 = Rietvlei, 8 = Altyd Somer.

From Saxfold Park to Altyd Somer, there is a statistically significant trend of decreasing weight, from values of 43.5 g to 39.1 g. Bill width follows a similar and significant trend, decreasing from a mean of 6.81 mm at Saxfold Park, to 6.32 mm at Altyd Somer. Wing length, tarsus length, bill depth and bill volume are not significantly different between localities. Whilst bill length is significant, there is no definite trend across the hybrid zone. Interpretations of these trends, or lack thereof, should be cautious, in view of the small sample sizes.

The two variables that show the most strongly significant between-locality differences, and the most definite trend across the hybrid zone, are wattle width and wattle colour code (Table 6.1 and Figure 6.5). Average wattle width increased 49% across the hybrid zone, from a mean value of 0.92 mm at Saxfold Park to 1.37 mm at Altyd Somer. Wattle colour frequencies change from 100% black-wattled birds at Saxfold Park, through the various intermediates, to 100% orange-wattled birds at Altyd Somer (Figure 6.4).

Saxfold Park lies outside the phenotypic hybrid zone, in an area of pure *P. barbatus*. Waterfall lies on the extreme edge of the hybrid zone; only one of the ten birds captured there had a hybrid wattle, and I saw no sign of hybrids amongst a number of large bulbul flocks observed through binoculars. Glen Lyndon to Geluk fall within the hybrid zone proper, with Glen Ross in the centre. The frequency of wattle colour codes amongst the 11 birds captured for the transect analysis at Glen Ross was 1 (0%), 2 (55%), 3 (36%) and 4 (9%) (Figure 6.4), whilst wattle code frequencies amongst the 43 birds mist-netted in July 1992 were 1 (16%), 2 (46%), 3 (19%) and 4 (19%). Rietvlei lies on the edge of the *P. nigricans* end of the hybrid zone. Whilst three of the eight birds shot here on 19 August 1993 had hybrid wattles, all previously captured birds (for the work described in Chapter 2), and those observed through binoculars on at least four visits, did not exhibit definite hybrid phenotypes. Altyd Somer, 6 km from Rietvlei and only 23 km from a centre of the hybrid zone (Glen Ross), lies outside the phenotypic hybrid zone; only typical *P. nigricans* were seen and captured here. Waterfall, via Glen Lyndon, is 21 km from Glen Ross. Whilst the straight line distance between Waterfall and Rietvlei is 33 km, it does not run at 90° through the hybrid zone (Figure 6.1). A more accurate estimation of the width of the phenotypic hybrid zone is approximately 20 km.

The results of this analysis indicate that there is a sharp step cline in at least four phenotype character variables across a narrow hybrid zone.

6.3.4 The *P. barbatus/P. capensis* hybrid zone

The contact zone between these two species is clearly defined north of the Suurberg mountain range. In this region, the watershed of the Sundays River catchment forms the boundary; *P. capensis* to be found in the Sundays River catchment system to the west of the watershed, and *P. barbatus* to the east.

The western slope is steeper and more vegetated with bushy Succulent Thicket (Palmer 1988); here I noted the occurrence of *P. capensis* at several localities. This species is quite common in the south but becomes progressively sparser, as the vegetation becomes distinctly more arid, further north towards Bruintjieshoogte.

The eastern slope is gentle, and in this high-lying area, the vegetation consists mainly of Montane Grassland with shrubs and dwarf shrubs (Palmer 1988). In this habitat, bulbuls were clearly rare. Whilst I only saw *P. barbatus* to the south, I predict its occurrence in the areas to the north on the basis of the observed vegetation.

North of the Niekerksberg the habitat becomes more arid, with Thorny Shrubland (Palmer 1988) vegetation, and here I found only *P. nigricans* in the Little Fish river valley. On the farm Eureka (32°51 'S 25°40 'E) however, Mr Brian von Holdt recorded the presence of both *P. barbatus* and *P. nigricans* for most months in the years 1987 and 1988. I visited this area on 3 August 1992 after it had experienced several years of severe drought. Mr von Holdt could not recall seeing *P. barbatus* recently then, and also ascribed its absence to the drought. Interestingly, he recorded *P. capensis* on the farm in the months May - June 1987 and June - August 1988, but never more than a 2-3 birds.

The low-lying area running east-west through Beenleegte (33°05 'S 25°36 'E), south of the Niekerksberg, constitutes arid grassland, and is not an area that bulbuls would inhabit. Thus much of the country north of the Beenleegte valley, west of the Great Fish river and south of the Somerset East - Cookhouse mountains must constitute marginal habitat for *P. barbatus*, especially during drought periods. This may explain why I failed to see this species on my single visit to the region.

Through the Suurberg mountains themselves, the contact zone between *P. barbatus* and *P. capensis* could not be defined very accurately. Near the Sundays River itself, I saw a couple of *P. capensis* individuals, but they were by no means common there. Further east, I saw a single *P. capensis* on the outskirts of Kirkwood. I searched the kloofs adjacent to the roads leading to the farms Paardekraal (33°21'S 25°32'E) and Slagboom (33°22'S 25°40'E) but neither heard nor saw any bulbul. These kloofs were fairly well wooded with Subtropical Thicket and montane forest elements, and certainly appeared to be suitable habitat for bulbuls. A little further east again, I saw a pair of *P. barbatus* near the Suurberg Hotel (33°20'S 25°45'E). Thus the transition zone between the two species appears to be located somewhere between this point and Kirkwood, a band some 20 km wide in which neither species appears to be very common.

Just south of the mountains in this area, the rolling hills are clothed in a dense and unbroken swathe of Subtropical Thicket, in which no bulbuls were found. This is not surprising since they are not known to inhabit unbroken forest.

In the rather arid vegetation along the Sundays river south of Kirkwood, only *P. capensis* was recorded, although never commonly. Around the camp-site in the NW corner of the Addo National Park, I found two pairs of *P. capensis*. On the farm Orlando, just 14 km to the SE, I recorded only *P. barbatus* in habitat I would consider suitable for that species. Mr Andrew Royal also records only *P. barbatus* on this farm. I therefore believe that the transition zone between the two species probably follows the higher ground on the eastern edge of Addo National Park, where the vegetation changes from dwarf succulent Noorsveld in the west to taller Subtropical Thicket bush clumps in grassland in the east.

The zone probably then follows the higher ground around the Addo Heights, reaching the coast at the Sundays River mouth itself. Around Colchester I have seen a number of *P. capensis* and the odd *P. barbatus*. Ten to fifteen kilometres NE of the Sundays River mouth, in the Congoskraal area, I found large flocks of *P. barbatus* on 22 May 1993.

To summarize then, the survey revealed the following:

1. *P. barbatus* and *P. capensis* are seldom found together in the same locality. Their distributions overlap very little, and the transition from the one to the other occurs within 10-20 km.

2. The transition between the parapatric distributions of these two species generally follows the transition between the Sundays river valley Noorsveld and Succulent Thicket, and the Subtropical Thicket vegetation types. This in turn generally follows the eastern lip of the Sundays river catchment area.

3. The transition zone is characterized for the most part by low densities of birds of both species. Densities may increase sharply within a few km of the transition zone though.

4. No evidence of hybridization was found along most of the length of the transition zone, with one notable exception.

On visiting the farm Protest on 25 May 1993 I observed several fairly large bulbul feeding flocks. Most of these birds were clearly *P. barbatus* x *P. capensis* hybrids, although all birds observed on this occasion had essentially black eye wattles and no true *P. capensis* were seen.

This farm is located at the upper end of a valley just over the eastern edge of the Sundays river catchment escarpment, and just north of the Suurberg mountain folds. Whilst generally rather open, there were scattered clumps of Subtropical Thicket containing fruiting plants, with the lower watercourses becoming progressively bushier. A little earlier, I had seen a small flock of typical *P. capensis* on the farm Olievenfontein, only nine km away on the western edge of the catchment escarpment. Clearly, quite extensive hybridization had taken place in the vicinity of Protest, in an area where both species were to be found in close contact and in quite large numbers.

6.3.5 Description of *P. barbatus* x *P. capensis* hybrids

P. capensis differs from the other two species in having the head, chest and upper belly a uniform sooty brown instead of black, brown and white; only the lower belly is whitish and whilst the crown feathers are a slightly darker brown, they are by no means black. The most striking feature of *P. capensis* is the broad white wattle around the eye.

The plumage of the hybrids observed on 25 May 1993 varied from birds having a black head and a darker brown wash to the belly than is usual for *P. barbatus,* to birds possessing the plumage characteristics of typical *P. capensis* but lacking white on the wattle. Some did appear to have enlarged black wattles though.

The contact call of *P. capensis* is audibly different from that of *P. barbatus* (see Chapter 4). Whilst most of the birds were heard to give the *P. barbatus* contact call, I did hear the odd *P. capensis* contact call and even calls that sounded intermediate between the two. Unfortunately I was unable to obtain recordings of these.

Of six birds shot on Protest on 5 September 1993, only two were typical *P. barbatus* in all respects. The remaining four were clearly hybrids, and included:

1. a bird with plumage typical of *P. capensis* (brown head and belly) that had an enlarged off-white eye wattle (Figure 6.2),
2. a bird with plumage typical of *P. capensis,* but with an enlarged black wattle clearly intermediate between that of *P. barbatus* and *P. capensis,*
3. a bird with a black head and the brown of the chest extending quite far down the flanks and belly (i.e. intermediate between *P. barbatus* and *P. capensis*) and a slightly enlarged black wattle that was yellowish along the inner edge, and
4. a bird with plumage typical of *P. barbatus* and a narrow black wattle infused with yellow in the hind quarter (i.e. as in a *P. barbatus* x *P. nigricans* hybrid).

The enlarged black wattle of 2) above was also found to be tinged yellow on its inner surface once it had been dissected out.

6.3.6 The *P. nigricans/P. capensis* hybrid zone

An area of contact between these two species was located within the Bruintjieshoogte and Durandsberg area on the extreme NE lip of the Sundays river watershed (Figure 6.1). A band of Succulent Thicket running up the steeper western slope of the escarpment appears to allow *P. capensis* to penetrate as far north as the Bruintjieshoogte, where Liversidge (1970) recorded the presence of this species.

To the west of this point, from east of Pearston to the Sundays river near Graaff Reinet, runs the Camdeboo, an area of arid grassland and Dwarf Shrubland (Palmer 1988) unsuitable for any bulbul. This must act as a barrier between the two species. I found no bulbuls along the upper Voëlrivier for example. Farmers here report only seeing bulbuls during wet years when the trees and shrubs are fruiting. Unfortunately they could not identify the species.

Twenty kilometres south of the Bruintjieshoogte, I found *P. capensis* in low numbers. Ten kilometres NW of Durandsberg I found *P. nigricans* in large numbers on the farm Struishoek.

On 2 August 1992 I observed three bulbuls near the main road below Bruintjieshoogte (32°40'S 25°19'E), all apparent hybrids in plumage, although all possessed dull orange wattles. On 1 August 1992 I observed 11 bulbuls on the farm Waterkloof on the northern slope of the Durandsberg, of which six were typical *P. nigricans* and five apparent hybrids with orange to dull orange wattles but intermediate plumage.

6.3.7 Description of *P. nigricans* x *P. capensis* hybrids

The three birds observed at Bruintjieshoogte on 2 August 1992 all had dull orange wattles. Two had dark brown throats and heads, brown chests and a brown wash on their bellies, giving an overall brown appearance. The third had a black head and throat, but the brown of the chest extended all the way down the belly. This was also the appearance of a single hybrid observed on the farm Struishoek.

Of the 11 birds seen well on the farm Waterkloof on 1 August 1992: four were typical *P. nigricans* with the bright orange wattle, black head and throat, scaly sooty-brown chest and white belly; two were typical of *P. nigricans* except for having a blackish-brown head and throat; two had a dark-brown head but pale belly; two had a dark-brown head and throat and a pale brown wash extending to the upper belly; and one had a dark-brown head and the brown of the chest extending all the way down the belly to the legs i.e. the plumage typical of *P. capensis*. All 11 birds had orange to dull orange wattles, and no evidence of abnormal enlargement of the wattle.

Of the three birds shot on Waterkloof on 4 September 1993, one was a typical *P. nigricans* with orange wattle, black head and pale belly, the second had an orange wattle, but a dark brown head and a brown wash down the flanks and belly, whilst the third had plumage typical of *P. capensis* and a striking hybrid wattle that was much enlarged and coloured pale orange on the inside and white on the outside (see Figure 6.2).

6.4 DISCUSSION

The results of this survey can be summarized as follows:

1. *P. barbatus* and *P. nigricans* meet in fairly large numbers along a contact zone defined for the most part in my E Cape study area by a mountain range. The transition from one species to the other is sharp and follows the transition between two distinctly different vegetation types. Within a 20 km wide contact zone, extensive hybridization has occurred and almost certainly still continues. Thus most birds presently found within the zone are hybrids, constituting a "hybrid swarm".

2. *P. barbatus* and *P. capensis* meet along a contact zone characterized, for the most part, by low densities of birds of one or both species. In these areas of low bulbul densities, no evidence of hybridization was detected, although the number of sight records are far from satisfactory. Only one locality was found at which extensive hybridization has taken place. Interestingly, this was in an area where both species were to be found in fair numbers. Once again, the transition from one species to another is sharp (within 10 km) and follows the transition between two different vegetation types.

3. *P. nigricans* and *P. capensis* meet at the edge of the study area, on the extreme NE lip of the Sundays river watershed. The exact point of transition was not established, but rather extensive hybridization had clearly taken place. This zone was characterized by relatively large numbers of *P. nigricans* and small numbers of *P. capensis*. Once again, the transition was sharp (probably within 10-20 km) and followed the transition between two vegetation types on a mountain range.

6.4.1 Degree of distributional overlap

Liversidge (1970) gave a good summary of the known cases where two *Pycnonotus* bulbul species had been sighted together. At that time there were specimens of *P. nigricans* from the Orange river mouth, but sight records of only *P. capensis*. SABAP data now shows *P. nigricans* to be resident in this area, with no records for *P. capensis* (Figure 3.1). The two species are recorded together at various localities in Namaqualand, where *P. nigricans* appears to be a vagrant and *P. capensis* more or less resident where the habitat is suitable.

In the southern and eastern karoo there appears to be little overlap, despite both species often being recorded from the same quarter degree squares in the SABAP data. There are sight records from Laingsburg for both, and regular sightings of both from Prince Albert (Richard Dean *pers. comm.*). Liversidge states that these two towns have provided suitable man-made habitat for *P. capensis* to wander beyond its normal distribution. Similarly, the two species have been recorded in the towns Graaff Reinet, Jansenville, Pearston and within 50 km of Steytlerville. In the Swartberg mountain range, *P. capensis* occurs naturally along the southern foothills whilst *P. nigricans* occupies the arid northern slopes.

Liversidge (1970) recorded only *P. capensis* at Bruintjieshoogte, a locality where I found only two red-eyed hybrids. Clearly some interchange fluctuation has taken place here. Generally though, it appears as if there is very little overlap between these two species and that the transition from the one to the other is sharp.

Liversidge (1970), in his study of *P. capensis* in the Sundays river valley, never recorded this species together with *P. barbatus*. He found that a mere 13 km separated the species at Colchester and 24 km separated records of *P. barbatus* near the Suurberg and *P. capensis* in Addo National Park. These observations correlate very well with my own, suggesting that the transition between the two species is sharp and with little or no overlap.

P. barbatus and *P. nigricans* have been noted to overlap with ecological segregation in NW Botswana, where *P. nigricans* occupies drier areas and *P. barbatus* the vegetation along streams (Irwin 1958). Liversidge (1970) reported mixed feeding flocks at Maun though. Further overlap without ecological segregation has been reported from riverine forest on the Zambezi river at Livingstone in southern Zambia (Holliday 1965), and on the Limpopo river in the north-eastern Transvaal (Liversidge 1985).

Hybrids have been reported from Angola (White 1956), Pretoria (Clancey 1980), Potchefstroom (Markus 1963), Fochville (Markus 1966, 1967) and of course near Bedford (Liversidge 1970), indicating that overlap has taken place at these localities. The records from Potchefstroom and Fochville fall within the south-western Witwatersrand region that is becoming recognised as a zone of fairly broad overlap and hybridization between these two species (Andrew Hart and Stuart Grant *pers. comm.*). The habitat in this region of highveld grassland has been considerably altered by man's farming activities and urbanization. This has created suitable tree and shrub-filled habitat for these two species in a zone of transition where possibly neither had occurred earlier (Liversidge 1970).

Once again though, it would appear as if there is little overlap between the two species along the length of their contact zone stretching from the eastern Cape Province of South Africa to Benguela in SW Angola.

These observations on the distributions of the three species are in agreement with the latest SABAP data (dealt with in Chapter 3), that suggest there is little overlap between the three species throughout South Africa.

6.4.2 Habitat alteration

Both Mayr (1970) and Stebbins (1950) regarded the breakdown of habitat barriers, mostly as a result of human interference, to be the single most important cause of hybridization in animals and plants respectively. Whilst some studies have certainly demonstrated such an effect (see Mayr 1970, also: Hubbs 1955; Wasserman 1957; Anderson 1971; Cooke *et al.* 1988; Lawson *et al.* 1991; Hairston *et al.* 1992), the vast majority have found stable, narrow hybrid zones under completely natural conditions (see Barton & Hewitt 1985, also: Howard 1986; Bert & Harrison 1988; Wooten *et al.* 1988; Baker *et al.* 1989; Good 1989; Rand & Harrison 1989; Dessauer & Cole 1991; Hairston *et al.* 1992; Scribner 1993).

It should be pointed out, anyway, that hybrid zones have to be considered natural phenomena, even if human alteration of the habitat has acted as a catalyst, and cannot be swept under the carpet when considering their implications for species concepts and evolutionary theory.

Liversidge (1970, 1985) laid heavy emphasis on the hypothesis that man's alteration of the habitat has been primarily responsible for subsequent overlap and hybridization between *Pycnonotus* bulbuls. Whilst this certainly appears to have been a factor in the south-western

Witwatersrand hybrid zone, I believe it to be of no significance in the hybrid zones I report here for the eastern Cape, where there has been minimal habitat alteration.

6.4.3 Fitness of hybrids

Evidence for the reduced fitness or inviability of hybrids has included the absence or rarity of F_2 and backcross individuals (Arntzen & Wallis 1991) and a reduction, or trough, in population density at the centre of the hybrid zone (Barton 1980). The large range in variation shown by the *Pycnonotus* bulbul hybrids, particularly those within my better studied *P. barbatus/P. nigricans* hybrid zone, strongly suggests that the hybrids are viable and that much backcrossing and post-F1 recombination has taken place. Backcrossing can lead immediately to forms so closely resembling the recurrent parent that whilst they have greater variability genetically, morphologically there is little suggestion of hybrid ancestry (Anderson 1953). Backcrossing, especially when repeated, therefore masks the products of hybridization, particularly introgressive hybridization away from the centre of the hybrid zone. Taking this factor into consideration, it is highly likely that most bulbuls in the centre of the hybrid zone at least, are hybrids, constituting a "hybrid swarm".

No depression in population density was observed in the *P. barbatus/P. nigricans* hybrid zone; large numbers of birds are found at the centre of the zone, where most of the birds are hybrids constituting a hybrid swarm. Thus there appears to be no selection against the hybrids, *per se*, within the hybrid zones. Unfortunately there is little direct evidence of hybrid viability/inviability, apart from Liversidge's record of a male '*P. nigricans*' and a *P. barbatus* x *P. nigricans* hybrid that produced young successfully (Liversidge 1970).

A more direct indication of hybrid fitness can be obtained from a measure of introgression on either side of the hybrid zone. The term introgression designates the incorporation of genes of one species into the gene complex of another species as a result of successful hybridization (Mayr 1970). The results of the mitochondrial DNA analyses, once they become available, should provide valuable information in this regard. Preliminary results of the pure species samples from various localities across southern Africa have found a 4.6% mitochondrial DNA sequence divergence between *P. nigricans* and *P. capensis*, a 4.5% sequence divergence between *P. nigricans* and *P. barbatus*, and a 1.2% sequence divergence between *P. barbatus* and *P. capensis* (M.F. Essop and T.M. Crowe *pers. comm.*). These values fall within the range of interspecific sequence divergences between closely related species (Avise & Zink 1988), indicating that mitochondrial sequence divergence should be a useful variable for analyzing introgression.

Closer analysis of the cline in body weight across the hybrid zone (Figure 6.5) reveals the possibility of directional introgression. *P. barbatus*, with an average weight of 38.9 g (range 23-52.9 g), is a larger and heavier species than *P. nigricans*, with an average weight of 30.8 g (range 21.6-37.4 g) (Maclean 1985; Keith 1992a). In the eastern Cape, *P. barbatus* is heavier (with an average weight of approximately 42 g) than over the rest of its African range (Crowe *et al.* 1981). In the vicinity of Grahamstown, 70 km SE of the hybrid zone, the average weight of 98 *P. barbatus* was 41.1 g (ringing records of A.J.F.K. Craig). Whilst average weights at the *P. barbatus* end of the hybrid zone are roughly equivalent to those of pure *P. barbatus*, average weights at the *P. nigricans* end of the hybrid are substantially heavier than those quoted for the species (Maclean 1985; Keith 1992a). This might indicate directional introgression of *P. barbatus* genes into adjacent *P. nigricans* populations. Whilst the data are too scanty for serious consideration, an hypothesis of selection favouring birds of larger size is worthy of further investigation.

6.4.4 Age of hybrid zones

The first question to be addressed is whether hybridization between these three species has occurred only recently, or whether these are stable hybrid zones that have been in existence since initial contact between the species first took place.

Liversidge (1970) records observing three breeding pairs of *P. barbatus/P. nigricans*, including a *P. nigricans/P. nigricans* x *P. barbatus* hybrid pair that successfully produced three young "at Bedford". Whether this was the town of Bedford itself, where I have recorded only *P. barbatus*, or within the Baviaans river valley 10 km to the NW, is unknown. Liversidge reasoned that the habitat had changed over the years with the encroachment of *Acacia karoo* as an indicator of drier conditions, and that this factor coupled with a prolonged drought had "brought *P. nigricans* in as a common species where as previously *P. barbatus* had occasionally occurred". A local farmer, Mr. Victor Pringle, has reported seeing hybrids. Craig and Hulley drove through this valley in December 1983, October 1986 and November 1988 specifically looking for the two species, but saw only *P. barbatus* along the length of the valley.

My survey in this area was also conducted at a time of prolonged drought, but unlike Liversidge's observations, I found either *P. barbatus* or hybrids to be most common at different localities, with few typical *P. nigricans* observed. That drought has been responsible for the movement of dry-country birds into new, previously more mesic areas, is well documented in southern Africa. *P. nigricans* has been recorded quite far east of its normal range in Pretoria and the northern Transvaal during dry years. Clearly then, drier conditions may well have caused the movement of *P. nigricans* from the NW side of the Baviaansrivierberge, where it is a common resident, over and into the valleys on the SE side where *P. barbatus* is a common resident, precipitating hybridization between the two species.

Liversidge (1970) thus regarded hybridization between these two species as limited and of recent origin. Such a view, however, ignores the fact that droughts are part of a natural weather cycle that has been repeating itself for millennia. Furthermore, *Pycnonotus* bulbuls are likely to have occupied their present parapatric distributions in this area, and therefore to have been in close contact, for at least the past few thousand years. These bulbuls also gather into flocks that are capable of wide-ranging movements in search of suitable feeding sites during the winter months. Of interest in this regard are the records Mr von Holdt made of Cape Bulbuls visiting his farm only in the winter months of 1987-1988, 25 km outside of the normal limit to their distribution (Figure 6.1).

If these three factors are considered together, a picture of regular interactions between these species begins to emerge. Since many opportunities for hybridization would thus have been provided, I believe that hybridization has been taking place for centuries, and that the hybrid zones are stable in time. The evidence supporting this statement is, of course, far from conclusive, but the results of the mitochondrial DNA analyses should provide greater clarification.

I attribute the paucity of hybrid reporting to three factors:

1. the location of the hybrid zones in isolated farming regions that professional ornithologists rarely visit,
2. the narrowness of the zones, and
3. subtle differences between hybrids and the true species that render them difficult to identify. For instance, the farmer and his wife on the farm Protest are both keen bird-

watchers and used to submit monthly lists for SABAP. When I asked what bulbuls they had recorded for the farm, they said that *P. barbatus* was the common species, but that *P. capensis* was a regular visitor in small numbers. They were unaware that many of the birds present on the farm were in fact hybrids between these two species.

6.4.5 Maintenance of the hybrid zones

On the basis of my observations and the arguments presented, I believe that hybridization between the three *Pycnonotus* bulbuls:

1. is widespread in the E Cape,
2. is probably a lot more widespread over the rest of their distributional contact zones than is currently recognised,
3. has probably been taking place since contact between previously allopatric populations was first established, and
4. has resulted in the formation of classic hybrid zones that are narrow and stable in time.

The question that now needs to be addressed is what factors are responsible for the maintenance of these narrow zones of extensive hybridization. The dynamic equilibrium hypothesis (Barton & Hewitt 1985, 1989) holds that a hybrid zone is a tension zone maintained by a balance between random dispersal and selection against hybrids. Circumstantial evidence from this study suggests, however, that the hybrids are fully viable. Some factor other than reduced hybrid fitness *per se* must, therefore, be responsible for restricting gene flow across either side of the hybrid zone. Such a suggestion is supported by a number of studies that have found little or no evidence of hybrid disadvantage or inviability (summarized in Moore 1977; also Bull 1979, Patton *et al.* 1979, Rising 1983, Moore & Buchanan 1985, Howard 1986, Moore & Koenig 1986, Moore 1987, Woodruff & Gould 1987, Bert & Harrison 1988, Dessauer & Cole 1991, Hairston *et al.* 1992, and Saino & Villa 1992). There are two possible factors at play, namely:

1. ecological segregation of the populations (habitat choice), or
2. selection gradients in direct response to environmental gradients.

Since the two "species" of bulbul recognize one another as conspecific, a hypothesis of interspecific competition (competitive exclusion) limiting distributional overlap becomes superfluous.

The transition between the distributions of *Pycnonotus* bulbuls is strongly correlated with the transition between different vegetation types in the E Cape study region. The results of Chapter 3 further suggest that the three species occupy distinctly different habitat types, as characterized by a complex of environmental variables. The hybrid zones thus follow what are probably rather steep environmental gradients on ecotones. This is a characteristic of most hybrid zones studied to date (see Moore 1977, Barton & Hewitt 1985; also Cook 1975, Harrison 1986, Howard 1986, Moore & Koenig 1986, Moore 1987, Woodruff & Gould 1987, Bert & Harrison 1988, Kohlmann *et al.* 1988, Saino & Villa 1992), and probably reflects a direct relationship between environmental variation and the forces of selection operating within the hybrid zone.

The bounded hybrid superiority model (Moore 1977) suggests that selection actually favours hybrid genotypes along the environmental ecotone between the habitats occupied by the two parental populations. Barton and Hewitt (1989) argued against such an hypothesis on two points. Firstly, they argued that the model predicts the predominance of only a few hybrid genotypes under such selection, and that by contrast, hybrid zones contain a mix of gene combinations, with associations of similar magnitude between all pairs of genes. Secondly, they argued that the superiority of hybrids cannot account for the long, narrow strips of roughly even width that are typical of most zones.

It is unfortunate that most individual studies and the major revisions of hybrid zone dynamics have focused so exclusively on characterizations of genotype-specific fitness in terms of increased (Moore 1977) or reduced (Barton & Hewitt 1985, 1989) fertility and/or viability of hybrids alone, rather than on differences in specific ecological characteristics, or differences in environmentally-associated fitness, between parental types or among parental and hybrid genotypes (Scribner 1993).

6.4.5.1 Ecological characteristics

Two populations differentiating in allopatry might evolve to occupy two quite different habitat types. These two populations might subsequently resume contact along a border or ecotone between these two habitat types. If the mate recognition systems have not changed significantly, and individuals within the two groups still recognise one another as suitable mates, interbreeding will occur. The SMRS of a population is likely to be highly conservative and resistant to change (Paterson 1978, 1982). Furthermore, if the SMRS is not specifically linked to the habitat requirements of the population, it may not undergo changes in parallel with changes in the ecological tolerance of that population. This is of course assuming that pleiotropy is not a significant factor.

In becoming adapted to the two different habitat types, the two populations may have evolved to the point where they also select only the habitat type in which they evolved. Thus the failure of either of the two populations to spread across the ecotone into the adjacent habitat may be due to it being perceived as unsuitable habitat by the individuals of that population. Hybrids, with their intermediate phenotypes, might select the intermediate habitats within the narrow ecotonal belt. Heterogeneous phenotype dispersion, reflecting differential habitat selection, could result in nonrandom mating (Saino & Villa 1992). A combination of these two factors could restrict gene flow across the hybrid zone and be responsible for the maintenance and stability of the zone.

Determining whether, as Harrison (1986) put it, "individuals select habitats or habitats select individuals" is not as easy as it might first appear. Whilst there is evidence to suggest that habitat segregation between closely related species can result from the selection of different habitats (Schroder & Rosenzwieg 1975; Douglass 1976; Howard & Harrison 1984), there is little direct evidence for it playing much of a role in narrow hybrid zone dynamics (Harrison 1986; Saino & Villa 1992). On the other hand, there is abundant evidence of the importance of differential selection gradients operating on the different genotypes across the hybrid zone (whether due to reduced or increased hybrid fitness, or to differences in environmentally associated fitness between parental types or among parental and hybrid genotypes) in hybrid zone dynamics (see Moore 1977; Barton & Hewitt 1985, 1989; Scribner 1993). Particularly illuminating are studies in which hybrid zones have been shown to move in response to changing environmental conditions e.g. climate (Cook 1975; Rising 1983) or in response to directional selection (Hairston *et al.* 1992).

6.4.5.2 Environmentally associated fitness

At this point, it is illuminating to consider the ideas expressed by Templeton (1989). Using the framework of Hutchinson's niche theory, he considers the situation where two genetically differentiated populations share the same fundamental niche, but differ in their ability to exploit that niche. The fundamental niche is defined by the intrinsic (i.e. genetic) tolerances of the individuals to various environmental factors that determine where the individuals are potentially capable of surviving and reproducing. The realized niche refers to that subset of the fundamental niche that is actually occupied by a species. The realized niche is usually a proper subset of the fundamental niche because of the lack of opportunity to occupy certain portions of the fundamental niche (e.g. due to geographical barriers) or because of biotic interactions that prevent the exploitation of the entire range of ecological tolerance.

Let us now consider the situation where these two populations have diverged genetically to some extent in allopatry to become diagnosably different and occupying different "adaptive peaks" within the "rugged landscape" (*sensu* Kauffman 1993) of their shared fundamental niche. On resumption of contact between the two populations, they may continue to recognise one another as conspecific, and hybridize.

Now, if the point of secondary contact occurs at the edges of the adaptive peaks of the two populations' gene pools superimposed on an environmental gradient such as that associated with an ecotone between two different habitat types, then gene flow between the two populations might be restricted by a differential gradient in the forces of selection acting on the two differentially adapted gene complexes across the environmental gradient. According to the principles of natural selection, at a given time in a given environment, each genotype has a different fitness, i.e. a different probability of reproductive success (Mayr 1970). Natural selection is a statistical phenomenon, and even very slight differences (as little as 0.1%) in the selective value of competing genes appear able to cause evolutionary change (Fisher 1930 and Haldane 1932 in Mayr 1970). Thus natural selection should favour one gene complex over another at each end of a selection gradient, if the two are differentially adapted. In the middle of the gradient, neither should be differentially selected for.

All three *Pycnonotus* species occupy a wide variety of habitat types within their ranges (discussed in Chapter 1). The habitat generalism of these highly successful birds strongly suggests that each species should be capable of colonizing at least some of the habitats outside of its present distribution limits. The nature of the mutually exclusive *Pycnonotus* bulbul distributions (narrow contact zones across the length and breadth of southern Africa), the sharpness of the transition from one to the other, and the correlation of this transition with the ecotone between two different habitat types, strongly suggests that differences in environmentally-associated fitness between parental phenotypes or among parental and hybrid phenotypes along an environmental gradient is preventing the spread of the one species into the habitat occupied by the other.

P. barbatus, and probably the other two species also, are territorial during the breeding season (see Chapter 5). The very fact that the males defend territories indicates that competition for some critical resource, be it food, a mate or a breeding space, is taking place. If the two species in a zone of contact recognise one another as conspecific, as they do in a hybrid zone, then they are certainly likely to compete for the critical resources in the same way that conspecifics do. Natural selection dictates that the better-adapted genotypes will replace those that are less well adapted. In this manner, competition and the forces of selection acting on two differentially adapted gene complexes ("species") across an environmental gradient are likely to severely retard the spread of either "species" across the zone of contact into the habitat occupied by the second "species".

Since the evidence for this hypothesis is largely circumstantial, though, the alternative hypothesis of ecological segregation or habitat choice being responsible for the observed distribution patterns of the three *Pycnonotus* species cannot be dismissed out of hand. Clearly, further research is required to distinguish between these two competing hypotheses before any firm conclusions can be drawn.

CHAPTER SEVEN

SYSTEMATIC REVIEW OF THE SOUTHERN AFRICAN *Pycnonotus* BULBUL SPECIES COMPLEX

7.1 Species concepts

Hybrid zones pose interesting questions for the systematist for they contrast two views of the species: as a set of populations delimited by genetic barriers to gene exchange; and as set of populations maintained in a particular stable equilibrium by selection and/or gene flow (Barton & Hewitt 1985). Hybrid zones also present the taxonomist with unique problems for naming and classifying hybridizing taxa. This has lead some authors to consider hybrid zones to be the testing or proving grounds of species concepts (Barton & Hewitt 1985, 1989), whilst others generally overlook the problems that the existence of hybrid zones create for species concept theories, or argue that they do not necessarily contribute to clarification of species limits (Mayr 1970; Cracraft 1983; Paterson 1985; McKitrick & Zink 1988). These differences of opinion centre largely on differences in species concept theory adhered to by the different authors. Any attempt at assigning taxonomic rank to the taxa within the *Pycnonotus* bulbul species complex, and slotting them into a broader evolutionary framework, requires closer examination of these different species concepts. I would like to stress that I am examining these concepts as far as they apply to sexually reproducing organisms only.

7.2 What is a species?

The term species is difficult to define because it is used for a taxonomic category, a biological concept and a unit of evolution (Cranston *et al.* 1991).

The taxonomic species is defined purely on morphological grounds, based on the description of the type specimen. It is an artificial concept, with species status determined in terms of diagnosable similarities and differences in morphology, with no consideration of the ecological, behavioral and genetic relationships between its constituent members. Nevertheless, taxonomic species often, but not always, appear equivalent to biological species.

The biological concept views the species as consisting of one or more populations, defined, for sexually reproducing taxa, as communities of potentially interbreeding individuals at given localities. Species status is thus determined on the basis of inference of reproductive discontinuity from other presumably related species (Mayr 1989). The biological concept essentially views species unidimensionally, at a specific time.

As an evolutionary unit, the species is viewed as a group of organisms sharing a common evolutionary fate through time. Owing to mutation, genetic recombination, and selection, a species has the capacity to change, or evolve, over time. In a stable environment, with no selective pressure for change, the species is likely to remain in stasis due to the stabilizing effects of gene flow. If the environment should change such that the "adaptive peak" (*sensu* Kauffman 1993) of the species no longer fits the environment, there will be a selective pressure favouring positive change.

There are two schools of thought as to the tempo of this change. The first, the theory of punctuated equilibrium, arose to explain the apparent lack of intermediates between lineages ("gaps") in the fossil record. It holds that brief periods of rapid genetic change (during which speciation can take place) punctuate long periods of stasis (Eldredge & Gould 1972, 1988, 1993). The alternative neo-darwinist school has favoured progressive, gradual change continuing over long periods, with eventual speciation possible (phyletic gradualism) (e.g. Sheldon 1987, 1990). In the words of Sheldon (1990), though, "punctuated equilibrium and phyletic gradualism are theoretical ends of a wide spectrum of possible evolutionary patterns".

Whatever one's view on the tempo of population differentiation, it is generally accepted that speciation in sexual species nearly always takes place when small populations become geographically isolated from the main body of their species. Because of their small size, such populations may represent an atypical and impoverished sample of the parental gene pool. Any chance mutations or gene combinations that are favoured by selection will have greater effect in such small populations and are less likely to be diluted by gene flow. Small populations usually become extinct, but when they do not, they can evolve into new species in a relatively short time. The end result is that the number of organisms intermediate between the ancestral and descendant species is reduced considerably, effectively narrowing the boundaries between ancestral and descendant populations (Hull 1976).

Now let us consider a species expanding its range, for instance after speciating in a small, isolated population. Founder populations colonizing new habitats are quite likely to encounter different environmental regimes favouring slightly different adaptations. If gene flow between these "coloniser" populations and the "core" population is sufficiently slow or restricted (see Ehrlich & Raven 1969, Ehrlich *et al.* 1975, and McKechnie *et al.* 1975), local differentiation can take place. The ecological "landscape" is only rarely so uniform that a species (or part of it) consists of a single continuous population. A species is therefore more likely to be subdivided into numerous partially isolated local populations as it expands its range (Mayr 1970). The end result in populations distributed through a much expanded species' range might be a continuous cline with or without discrete steps between partially isolated populations.

The polytypic species can therefore be viewed as a series of interconnected or allopatric populations, any one or a number of which may be genetically static, or changing by gradual or rapid (in small isolated populations) evolution. In this way, populations of a species can, through evolutionary time, give rise to new species through a series of intermediates. This is the essence of the species as an evolutionary unit. As Mayr (1969) observes, "species are the real units of evolution; they are the entities which specialize, which become adapted, or which shift their adaptation". At this point, it should be observed that, in the allopatric model of speciation, it is the population, and not the species, that is the real unit of evolution.

A problem arises, though, when biologists attempt to define a species in space *and* time, and delimit descendant species from the ancestral species.

The definition of what constitutes a species is built on a species concept and the concept itself profoundly affects the way in which investigators view the origin of the species they study (Wiley 1978).

Whilst most evolutionary biologists acknowledge that there is a relationship between the conceptual framework with which we view species and the processes we believe give rise to them, there is less agreement on its extent and desirability (Chandler & Gromko 1989). Wiley (1978) apparently favours an explicit relationship, by suggesting that a concept "must clearly specify what types of species origins are possible and what types are not". Sokal (1973) looks to the "major speciational mechanisms" to suggest a "generally useful species definition".

Similarly, Templeton (1989) seeks to relate a species concept directly to a mechanistic framework of speciation. Others have sought to separate concept from process. McKitrick and Zink (1988) seek a "consistent species concept, irrespective of process". Cracraft (1983) has argued against a conceptual framework derived from our preconceptions of evolutionary processes, stating that it biases and hampers the study of these processes.

Chandler and Gromko (1989) argued that the most obvious link between concept and process, though, is the general constraint that species concepts should not be inconsistent with a process of evolutionary change. Species taxa are variable and changing entities (in the spatiotemporal sense) related through a pattern of common ancestry. Therefore, species concepts cannot ignore the fact that the entities they seek to explain arise through the gradual or rapid accumulation of genetic differences with respect to the ancestral species.

Hull (1976) eloquently pointed out that rarely in areas of intellectual dispute is one position superior in every respect to its competitors. Rather, one must weigh the strengths and weaknesses of competing hypotheses and choose accordingly.

7.3 The Isolation Species Concept (ISC)

The isolation species concept is widely referred to as the biological species concept (BSC), but I follow Paterson (1985) in naming it the isolation concept to avoid confusion with the biological concept of a species (Cranston *et al.* 1991) referred to earlier.

The isolation species concept, as summarised by Mayr (1942, 1963, 1969, 1970) and Dobzhansky (1940, 1970) is without question the dominant view of species. Mayr (1963) defined the species as "groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups". Similarly for Dobzhansky (1970), species are "systems of populations; the gene exchange between these systems is limited or prevented by a reproductive isolating mechanism or perhaps by a combination of several such mechanisms". Within the framework of the ISC, hybrid zones are regarded as ephemeral, and as existing between two taxa that have either not diverged sufficiently to speciate, or which are in the process of speciation. Hybridization is predicted to lead to one of two scenarios: 1) speciation through the acquisition of reproductive isolating mechanisms as a result of the lower Darwinian fitness of the hybrids, or 2) fusion of the two previously allopatric populations through introgressive hybridization.

Under the ISC therefore, the three southern African *Pycnonotus* taxa would be regarded as semispecies, and classified as three subspecies within a single polytypic species that may of may not continue to evolve into true species.

The ISC is a relational species concept, defining a species in terms of its relationships with other species. This view of species and speciation is coming under increasing criticism due to the irrelevance of isolating mechanisms under the classic allopatric model of speciation and an increasing body of evidence suggesting that premating isolating mechanisms can seldom, if ever, evolve as adaptive features (Ehrlich 1961; Bigelow 1965; Sokal & Crovello 1970; Walker 1974; Paterson 1978, 1982, 1985; Levin 1979; Templeton 1981, 1987, 1989; Cracraft 1983; West-Eberhard 1983; Lambert *et al.* 1984; McKitrick & Zink 1988; Sanderson 1989). As stated by Templeton (1989), the ISC is actively misleading in that it confuses the process of speciation with the product (isolation).

7.4 The Recognition Species Concept (RSC)

Paterson (1978, 1980, 1981, 1982, 1985) avoided the confusion generated by the ISC by looking at the so-called isolating mechanisms from a different perspective, and emphasizing that the achievement of intraspecific fertilization is of far greater evolutionary consequence than the prevention of interspecific matings. He defines the species as "the most inclusive population of individual biparental organisms which share a common fertilization system". The members of a species share a common specific-mate recognition system (SMRS) which functions to ensure effective syngamy within a population occupying its preferred habitat. Since the characters of the SMRS are adapted to function efficiently in this preferred habitat, changes in the genome of a small isolated subpopulation of the parental species which facilitate the achievement of syngamy under the new conditions fortuitously makes effective signalling impossible between members of the daughter and parental populations. Speciation is thus viewed as an incidental effect of general adaptive changes in small isolated populations.

The existence of extensive hybridization suggests that the *Pycnonotus* taxa share a common SMRS at a number of localities in space and time. Under the RSC then, the taxa would be regarded as belonging to the same species. The RSC makes no taxonomic decisions below the level of species. A weakness of the RSC, therefore, is its failure to recognise the polytypic species and the importance of population genetics to the study of evolution and speciation.

Paterson (1993) criticized the polytypic "structural" species approach on the basis that it "led to obfuscation, not clarification, of evolutionary and ecological understanding". Since the RSC recognizes the two or more taxa hybridizing along a narrow hybrid zone as belonging to a single species, the same criticism can be levelled at Paterson's approach.

The existence of stable, narrow hybrid zones, particularly those in which there is evidence of significant hybrid disadvantage (Barton & Hewitt 1985, 1989), creates an intractable problem for the operational definition of the RSC (Newberry & Brothers 1990), which predicts the extinction of the rarer population or the elimination, through selection, of the rarer chromosome arrangement (Paterson 1978).

7.5 The Evolutionary Species Concept (ESC)

The evolutionary species concept defines a species as "a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978). A corollary of this definition is that species must be reproductively isolated from one another to maintain their separate identities, tendencies and historical fates (Wiley 1978).

Considering this species definition and its corollary, the ESC is faced with a problem in dealing with the *Pycnonotus* taxa. The three taxa clearly evolved as separate units in allopatry (i.e. are separate lineages), and continue to maintain their separate identities in parapatry, despite a narrow zone of hybridization (i.e. lack of reproductive isolation). Faced with such a situation, the ESC has a problem in judging quite what constitutes a "common" evolutionary fate. By falling back on the theories of speciation through reinforcement, or introgressive hybridization, the ESC suffers the same weaknesses as the ISC in failing to recognize that stable hybrid zones can, and do, exist.

7.6 The Phylogenetic Species Concept (PSC)

Within the framework of the phylogenetic species concept, a species is defined as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent (i.e. which are monophyletic)" (Cracraft 1983). Cracraft (1983) views speciation as the "phylogenetic deployment of differentiated taxonomic units through space and time" and argues that "if reproductive discontinuity does not precisely correlate with this deployment, then any definition of these taxonomic units solely in terms of that discontinuity will logically result in phylogenetic history (speciation) being reconstructed incompletely, at best, or incorrectly, at worst".

Under the PSC, the *Pycnonotus* taxa outside of the hybrid zones will be regarded as separate species on account of their being diagnosably distinct and having had separate phylogenetic and biogeographical histories during allopatric divergence. The PSC has a problem in dealing with the hybrid swarm populations though, since 1) in the words of Cracraft (1983), it is unable to assign the hybrids to either of the parental species, and 2) advocates of the PSC (Cracraft 1983; McKitrick & Zink 1988) reject the recognition of more than one kind of species. This raises two important questions. Firstly, is it valid to exclude hybrid populations from species categories and simply assign them the label of "hybrids between species A and B"? Most evolutionary biologists would answer "no". Secondly, assuming that introgression does take place, at what level of genetic 'hybridity' is an introgressed individual assigned to the grouping "parental species" or "hybrid"? This poses a serious problem to advocates of the PSC who laud the 'objectivity' of the phylogenetic approach over the 'subjectivity' of the approach of the other species concepts.

Frost and Hillis (1990 in Echelle 1990) emphasize that the primary disadvantage of the PSC is the potential for recognizing "extremely transitory components (i.e. local demes)" as species. An illuminating example in this regard is the species *Homo sapiens* (Wijsman & Cavalli-Sforza 1984). Under the strict definitions of the PSC, the different 'races' of the human population would be recognized as separate species; they are diagnosably distinct and usually have separate phylogenetic and biogeographic histories on account of behavioral customs and geographic barriers. Any other species concept regards such a view as untenable since the various human populations form a single intercommunicating gene pool, the internal cohesion of which is being constantly strengthened with the steady improvement in communication and means of transport (Mayr 1970).

Echelle (1990) effected an inadequate reply to this criticism with the statements "a deme would be recognised as a different phylogenetic species only if it exhibits one or more fixed character differences" and "two populations fixed for different traits represent only one species if a third population is polymorphic for the traits". This argument misses the point since two populations may exhibit fixed character differences in allopatry, but on secondary contact may interbreed freely to produce a population of intermediate character. In such a situation, the "species" would indeed be ephemeral, and can only be accommodated if a reticulate evolutionary theory is proposed.

7.7 Species as evolutionary units

At this point, one might be excused for thinking that the PSC has no merits as a species concept in its own right. However, an advantage of this species concept over the others is revealed if one examines the species as an evolutionary unit. Implicit in the theories of all the species concepts summarized here, is the view that the species has reality in nature. The cohesion of the species is maintained through natural selection favouring genetic relatedness and the homogenizing effects of gene flow. Therefore, the species itself is regarded as an evolutionary unit. This is fine for a population or a series of populations connected through interbreeding and gene flow; they share a common evolutionary fate as a cohesive unit. A problem of definition is encountered when this cohesion is broken though, such as through the splitting off of a small allopatric population. From the moment of isolation, natural selection can direct the evolutionary fates of the two allopatric populations in different directions, and they cannot be regarded as a single evolutionary unit any longer. It is the two populations that are now separate units of evolution. The "biological" species concepts (ISC, RSC and ESC) are forced to concede that a species is ontological only at a given place and time (Mayr 1987). The PSC has less of a problem in dealing with this situation, since it will recognize the two as independent units of evolution, since they will now have independent phylogenetic and biogeographical histories, but will only assign them species status once they have diverged sufficiently to become "diagnosably" distinct.

This is not to say that the PSC has the perfect definition of the species as a unit of evolution though. Allopatric populations as separate units can meet secondarily and fuse to form a single evolutionary unit once more. Thus the definition of species in the PSC requires acceptance of a reticulate evolutionary framework. Such a suggestion is, however, totally unacceptable to the zoological community at the present time.

7.8 The status of the species in zoology

As can be seen from the arguments presented above, none of the currently recognised species concepts can fulfil their claims of providing a universally acceptable species definition that can accommodate even the restricted subset of all biparental sexually reproducing organisms, let alone all living organisms. The existence of stable hybrid zones, and in particular the existence of hybrid swarms that are viable in the Darwinian sense, poses unique problems to each of them. These problems are generally overlooked by advocates of the various species concepts, who either neglect or are ignorant of the extensive literature on the subject of interspecific hybridization. The statement by Lambert *et al.* (1987) that "hybrids in nature are either not recorded or are present in extremely low frequencies", illustrates this point.

Clearly then, unless these concepts can moderate their definitions to accommodate the "grey areas" of speciation that stable hybrid zones represent, there is room for the advancement of a new species concept that will. Cain (1954) and Scudder (1974) suggested that many kinds of species exist, such as sibling, ring, polytypic, morphological, hybrid, and paleospecies, and that each requires the application of a different species concept. If asexual organisms are to be included, this suggestion is not without its merits, although in the narrower field of biparental sexually reproducing organisms it has been rejected on the basis that taxa are then incomparable (McKitrick & Zink 1988).

Consideration of these problems with species definitions attracts a return to an essentially nominalistic species concept. According to this viewpoint, nature produces only individuals; species are merely human mental constructs that conveniently divide a supposed biological continuum, and have no real existence in nature. This is a radical departure from conventional thinking and the current dogmas. Whilst such thinking (e.g. Kauffman 1993) may well be what is required to stimulate the search for a lasting answer to the species problem, it is not within the scope of this study to discuss such hypotheses.

7.9 The *Pycnonotus barbatus* superspecies

What is clear from the ideas summarized above is that if an ontological species concept is to be formulated, it must be based on a population genetic framework if it is to be biologically meaningful and is to promote our understanding of the evolutionary process. Thus the three *Pycnonotus* bulbul taxa within my eastern Cape study area, currently recognised as *P. barbatus*, *P. nigricans* and *P. capensis*, can be regarded as three distinct, differentiated and differentially adapted populations, with gene flow between the populations possibly being restricted by selection operating on the differentially adapted genomes in the different local environments.

Such a framework is also helpful to our understanding on the population-level variation within the currently recognised *Pycnonotus* species. *P. barbatus*, for example, comprises 10 currently recognised and well-marked races in this highly polytypic species whose distribution stretches through Africa (Keith 1992a). Certain of these races have brown, as opposed to black, heads and white, as opposed to yellow, undertail-coverts. These races meet with or without intergradation or hybridization. The white-vented *P. b. arsinoe* meets the yellow-vented *P. b. tricolor* without intergradation for example (Keith 1992a). Hall and Moreau (1970) believe that in the past, African *Pycnonotus* bulbuls had a sporadic distribution which allowed several populations to diverge to near-specific status in allopatry. Clearly, these well-differentiated populations reflect differential adaptations to local or regional environments, and in some cases, can be as distinct from one another as are the currently recognised species within the eastern Cape. Certainly, Hall & Moreau (1970) report that in eastern Abyssinia, where four races are found, ecological segregation seems to have prevented free hybridization.

Whilst negotiating the minefield of designating taxonomic rank to these differentiated populations is not within the scope of this study, it is clear that a revision of the genus is warranted in the light of these findings.

The complexity of the situation is further illustrated by an examination of the *Pycnonotus* bulbuls distributed through the Middle East, Arabia, and Asia. Here, a further five species, *P. xanthopygos, P. leucotis, P. leucogenys, P. cafer* and *P. aurigaster* are generally allopatric, but have formed narrow hybrid zones at most points of contact (Hall & Moreau 1970).

The fact that various taxa hybridize indicates that they are not true species, but the fact that this hybridization is restricted to narrow, stable hybrid zones, and that the taxa have retained their individual identities after the resumption of contact, suggests that they cannot be regarded as truly belonging to a single species either.

In conclusion then, the three *Pycnonotus* taxa in the eastern Cape, currently recognised as *P. barbatus*, *P. nigricans* and *P. capensis*, together with at least some of the well-differentiated races within the *P. barbatus* taxon, can, in the population genetic sense, be regarded as "semispecies" within a "superspecies". In this regard I follow Hall and Moreau (1970) and Keith (1992a) in recognizing a *Pycnonotus barbatus* superspecies that includes the Middle Eastern, Arabian, and some of the Asian taxa.

APPENDICES

Appendix 4.1 Summary statistics of the song variables for each of the *Pycnonotus* species. BEB = *P. barbatus*; REB = *P. nigricans*; CB = *P. capensis*; HiF = figure highest frequency; LoF = fig. lowest freq.; FRnge = fig. freq. range; StF = fig. starting freq.; EndF = fig. ending freq.; FSuc = freq. range between EndF and StF of figures in a phrase; Int = pause between successive figures in a phrase; FigDur = fig. duration; Fig/Int = ratio of fig. duration to duration of the following pause; ModR = fig. segment modulation rate; FigNo = no. of figures per phrase; PhDur = phase duration; Infpt = no. of inflection points per phrase; $\bar{X}$ = mean; SD = standard deviation; n = sample size; * = significantly different from the other species at $P < 0.05$ (Kruskal-Wallis test with Mann-Whitney U test for multiple range analysis).

Species		Song Feature												
		HiF (kHz)	LoF (kHz)	FRnge (kHz)	StF (kHz)	EndF (kHz)	FSuc (kHz)	Int (sec)	FigDur (sec)	Fig/Int	ModR (kHz/sec)	FigNo	PhDur (sec)	InfPt
BEB	$\bar{X}$	2.665*	1.527	1.138*	2.060	2.312	0.677	0.196	0.107	0.737	26.31*	4.976	1.314	7.833
	SD	0.424	0.303	0.460	0.601	0.511	0.476	0.105	0.047	0.703	25.55	1.047	0.316	3.245
	n	209	209	209	209	208	167	167	209	167	533	42	42	42
REB	$\bar{X}$	2.971*	1.530	1.442*	2.095	2.415	0.690	0.196	0.129	1.163	30.27*	4.677	1.309	8.161
	SD	0.549	0.315	0.505	0.622	0.562	0.516	0.118	0.048	1.297	28.38	1.013	0.270	3.034
	n	144	144	144	144	144	112	113	144	113	395	31	31	31
CB	$\bar{X}$	3.446*	1.753*	1.692*	1.941	2.963*	1.088	0.198	0.149	1.157	41.81*	5.000	1.361	10.21*
	SD	0.514	0.202	0.514	0.425	0.644	0.651	0.121	0.305	2.093	26.93	1.474	0.325	3.912
	n	120	120	120	120	120	96	96	119	96	368	24	24	24

Appendix 5.1 Percentage of song output made up by different phrases in the 51 male Blackeyed Bulbuls recorded in the 1991/'92 breeding season in suburban Grahamstown. N = repertoire size; n = phrase-sharing group s ize.

Phrase Number

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	N
1	2				23				33																																	13				29																					5
2					22		21		10																																	22	13	3	7																						7
3				21	20		13		23	23																																																							5
4				50			50		1																																																									3
5	26			44			26		3	1																																																							5
6	26			22			25	7	15	5																																																							6
7	4			17			4			58	17																																																						5
8				45							48																																									7														3
9	27			13			38		18							4																																																		5
10	35			26			28		6		4																																																						5
11	7			46			19			6	22																																																						5
12				11			22	3	14	28		13																																			8	1																			8
13				21	21		31		13	15																																																							5
14				40			48		12																																																								3
15				38			42		20																																																								3
16	12			48			29	5	6																																																								5
17	30			26			12	16																																																								4
18	12			14			32	6	15	21																																																							6
19	14						44	7	13	16																								6																																6
20				2			48		9	12							8	12	4	1														3																																9
21				1			17		15	28							3	14	14	8																																														8
22							19			19								39	23																																															4
23				17						22							9		27	25																																														5
24							15			58									26																																															3
25										3						39			21	2	5					5																																							25	7
26																9			18																																					10	26	20	5	6		5			8
27												23							37	17	22																																													4
28												1				21			44	19	6			1		2															6																							5		9
29												4	24						23	34	15																																													5
30												5	27						1	14	6	10		10	7			9																																						9
31													30						17	26	3			12	2										11																															7
32												18							6	53				8	14																																									5
33													11						28	8				25	22								7																																	6
34													11						7	20	13	20		7	3			19																																						8
35													19		7				12			8			12			26			16																																			7
36													21		15				6	18					12			18			3																																			7
37													20		2										21			15																																		42		5
38																									9		33				57																																			3
39													14	5					1				14			15			18		21	12																																		8
40																																				27	10	40	10	13																										5
41													19						28						3				11		39																																			5
42																			39	9									18		15																		18																		5
43																			69												31																																			2
44		29		25															12																																	15		19												5
45					20	13																																											11	13			20	15	2	5										8
46						39																																													61																2
47				25							18																																29						29																		4
48				22							4																																20						40	13																5
49			2	25			11																																				14						36	12																6
50					24		15		7	5																																			28							3										18				7
51					24		24																																						47																5				4
n	11	1	1	23	7	2	24	6	18	16	6	6	10	1	3	4	3	3	22	14	7	3	1	6	10	3	1	5	3	0	7	1	1	2	1	1	1	1	1	1	1	2	4	1	1	3	1	1	5	3	1	1	3	1	2	1	1	1	1	1	1	2	1	2	1	

Appendix 6.1 Summary of field trip observations and *Pycnonotus* bulbul counts in the vicinity of the contact zones between the three species. BEB = *P. barbatus* (eye-wattle predominantly black); REB = *P. nigricans* (eye-wattle predominantly orange); CB = *P. capensis* (eye-wattle predominantly white); Hybrid BEB/REB determined as bird with indeterminate wattle colour (black/orange); Hybrid REB/CB determined as bird with intermediate plumage and/or wattle; Hybrid BEB/CB determined as bird with intermediate plumage and/or wattle; T = total number of bulbuls seen at each locality. Birds only counted if observed well through binoculars or telescope.

Locality	Coordinates	BEB	REB	CB	Hybrid BEB/REB	Hybrid REB/CB	Hybrid BEB/CB	T	Comments
Walkersvale	32°35'S 26°16'E	2						2	Typical *P. barbatus*
Linton	32°31'S 26°15'E	2						2	Typical *P. barbatus*
Spring Valley	32°15'S 26°17'E		1					1	
Palmietfontein	32°16'S 26°13'E		5					5	
Fair View	32°08'S 26°20'E		1					1	
Altyd Somer	32°14'S 26°01'E								30+ birds, all typical *P. nigricans*
Rietvlei	32°17'S 26°01'E								Only REB seen and caught on several visits
Geluk	32°19'S 25°59'E		3					3	
Glen Garry	32°22'S 26°02'E	3	3					6	
Langkloof	32°19'S 26°01'E		5		1			6	
Mt Pleasant	32°24'S 26°08'E	4						4	
Huntley Glen	32°25'S 26°06'E	2	2					4	
Camerons Glen	32°21'S 26°06'E								30+, mostly BEB, few REB
Avondale	32°34'S 26°00'E	4						4	
Lichenstein	32°35'S 26°02'E				1			1	
Waterfall	32°35'S 26°05'E								50+ BEB
Bell-Vue	32°38'S 26°01'E	1						1	
The Ruins	32°38'S 26°01'E	4						4	
Bedford	32°40'S 26°05'E	5						5	
Waldeck	32°33'S 25°58'E	4			1			5	
Belvedere	32°33'S 25°55'E	3			1			4	
Daggaboerhoek	32°31'S 25°53'E	21	9		4			34	100+ birds in loose flock

Appendix 6.1 continued

Locality	**Coordinates**	**BEB**	**REB**	**CB**	**Hybrid BEB/REB**	**Hybrid REB/CB**	**Hybrid BEB/CB**	**T**	**Comments**
Glen Lyndon	32°32'S 26°00'E								30+ birds, mostly BEB, few REB
Lynedoch	32°31'S 25°55'E	2						2	
Fair Holt	32°29'S 25°58'E	6			1			7	
Glen Ross	32°27'S 25°57'E	33	16		7			56	150+ birds seen on 4 visits, mostly BEB and hybrids
Belmont	32°26'S 25°56'E	12	2					14	
Venn Grove	32°24'S 25°53'E	2	1		1			4	
Glen Isle	32°23'S 25°58'E								10+ birds, equal BEB and REB
Donkerhoek	32°24'S 25°55'E		16					16	Typical *P. nigricans*
Laborare	32°24'S 25°49'E		4					4	Typical *P. nigricans*
Cloverfields	32°26'S 25°46'E		4					4	Typical *P. nigricans*
Leeukloof	32°29'S 25°46'E		3					3	Typical *P. nigricans*
Elandsdrift	32°31'S 25°45'E		2					2	Typical *P. nigricans*
Kerkplaas	32°32'S 25°44'E	1	13					14	
Klipfontein	32°36'S 25°45'E		1					1	
Spreeukloof	32°41'S 25°46'E	7	1		8			16	
Olivewoods	32°45'S 25°45'E	5	8		2			15	
Bosberg N.R.	32°42'S 25°34'E	1	6					7	
Kranskloof	32°50'S 25°35'E		3					3	
Goedehoop	32°42'S 25°27'E		2					2	
Buffelsfontein	32°38'S 25°26'E		7			1		8	
Lunsklip	32°37'S 25°27'E		2					2	
Waterkloof	32°38'S 25°20'E		6			5		11	
Bruintjieshoogte	32°40'S 25°19'E					3		3	
Struishoek	32°33'S 25°17'E		5			1		6	
De Draai	32°50'S 25°14'E			2				2	Typical *P. capensis*

Appendix 6.1 continued

Locality	**Coordinates**	**BEB**	**REB**	**CB**	**Hybrid BEB/REB**	**Hybrid REB/CB**	**Hybrid BEB/CB**	**T**	**Comments**
Skietfontein	32°52'S 25°18'E			6				6	
Perdepoort	33°16'S 25°01'E			6				6	Flock of 30+ *P. capensis*
Waterplaas	33°18'S 25°02'E			2				2	Typical *P. capensis*
Brakfontein	33°18'S 25°12'E			1				1	Typical *P. capensis*
De Dorings	33°17'S 25°14'E			1				1	Typical *P. capensis*
Kirkwood	33°23'S 25°27'E			2				2	Typical *P. capensis*
Wapadspoort	33°12'S 25°20'E			5				5	Typical *P. capensis*
Doringhoek	33°14'S 25°28'E			4				4	Typical *P. capensis*
Olivenfontein	33°13'S 25°31'E			4				4	Typical *P. capensis*
Protest	33°14'S 25°36'E	1					3	4	20+ birds, hybrids and BEB
Shadwell	33°15'S 25°47'E	2						2	
Suurberg	33°20'S 25°45'E	2						2	
Addo N.P.	33°27'S 25°45'E			4				4	
Barkely Bridge	33°37'S 25°43'E			4				4	
Orlando	33°32'S 25°52'E	2						2	
Addo Heights	33°34'S 25°49'E	1						1	
Colchester	33°42'S 25°49'E	1		2				3	
Oakhill	33°39'S 25°55'E	1						1	
Congoskraal	33°39'S 25°59'E	10						10	Typical *P. barbatus*
Oxton	33°37'S 25°59'E	8						8	Typical *P. barbatus*

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