ON THE BEHAVIOURAL ECOLOGY AND VOCAL COMMUNICATION OF THE BROWN-HEADED PARROT (*Poicephalus cryptoxanthus*)

by

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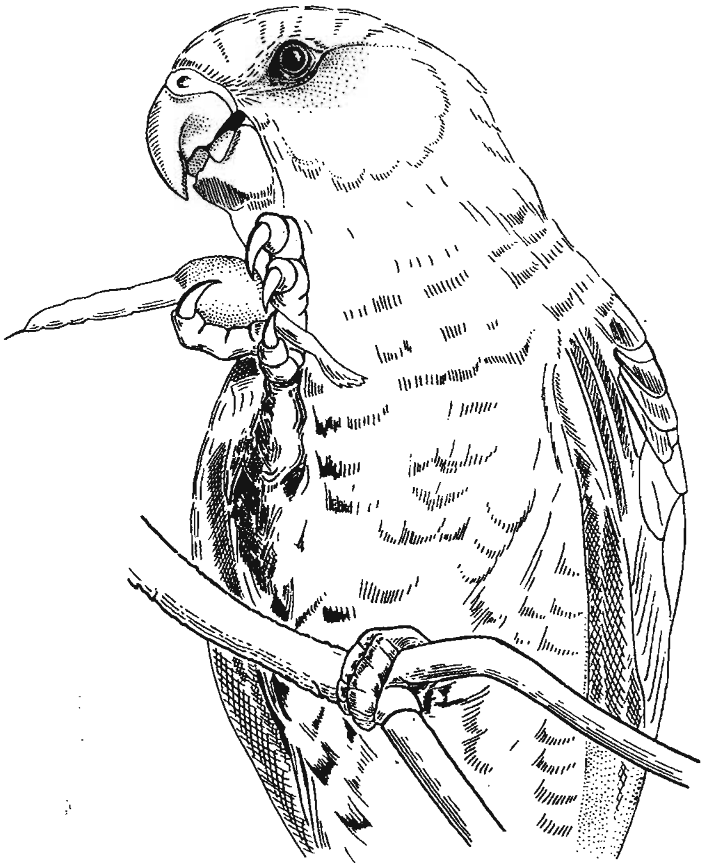

PREFACE

The work for, and the preparation of this thesis were done whilst the author was a full time student in, first the Department of Zoology and Entomology and latterly in the School of Botany and Zoology, University of Natal, Pietermaritzburg, from March 1996 to September 2002. Supervision was by Professor Michael R. Perrin and Professor Michael Lawes.

These studies represent original work by the author and have not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.

Signed......................................

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It is unlikely that this work is without error and although I have acknowledged the parts played by other parties, any shortcomings as may exist, I fairly claim as my own.

This study is respectfully dedicated to

BEN and **QUARTA PRETORIUS**

and

to the memory of my late

MOTHER and **FATHER.**

After you have exhausted what there is in
business and politics, what remains?
Nature

W. Whitman *(1819 - 1892)*

LIST OF CONTENTS

Abstract

The Brown-headed Parrot (*Poicephalus cryptoxanthus*) is a poorly known species inhabiting open woodland in south-eastern Africa. This study elucidates critical aspects of the species ecology and although each of these categories impinge on one another, it concentrates on two broad biological aspects, diet and breeding biology, and vocalizations.

The species has a generalist diet, switching from one suite of food species to another as and when those species become available, with no species critical for its survival. Analysis of dietary items throughout the year and comparison with handling times and availability reveals that at no time is the species under dietary constraint.

Evidence from association indices and behavioural observation shows that the popular view that the Brown-headed Parrot forms pairs just before breeding is erroneous. Birds retain pair bonds and the bond is long-term, lasting at least throughout the year. Congregations are therefore of a classical fission/fusion type with the sub-units being the paired males and females.

A mathematical model of the growth of captive chicks is presented, as a guideline to alert potential breeders of Brown-headed Parrots of malnutrition or disease. The species is a secondary cavity hole nester and whilst, the breeding biology of the species is summarised, the importance of large and old trees for breeding opportunities of the species is emphasised. This theme is continued by testing various adaptive hatching hypotheses as possible explanations of asynchronous hatching in the species. It is suggested that asynchronous hatching may be an adaptive strategy moderating against the number of suitable nesting cavities.

The vocalization repertoire of the Brown-headed Parrot is described and seven separate vocalizations are recognized. None of these are associated with sexual situations, offering further evidence of a long-term pair bond.

Evidence is offered that Brown-headed Parrot chicks can recognise their parents from individual vocal signatures supporting previous evidence from a number of species where chicks may mingle with unrelated chicks. Conversely, parents seem to be unable to recognise their chicks in the same way. It is concluded that this inability may be a result of strong one-way selection pressure, where the costs outweigh the benefits for parents with more than one chick or may be related to the experimental design.

Individual recognition by voice implies individual voice differences and the adult *double chip* contact call is analysed using multivariate statistical techniques. The analysis separates individuals on the basis of frequency and temporal patterns and it is concluded that these parameters may allow individual voice differentiation.

Finally, high frequency aspects of the *double chip* contact call are examined. These frequencies lie above the normally accepted upper threshold of avian hearing. From laboratory and field experiments, behavioural evidence is presented suggesting that the Brown-headed Parrot reacts to these frequencies and may use their degradation as a means of ranging distances to conspecifics.

Chapter 1

Introduction

The term “parrot” dates from the early 1500s and seems to derive from the French Pierrot or Perrot, a diminutive of Pierre (Rowan, 1983). The general body shape of these birds is compact with a short neck. Probably the most diagnostic feature of parrots is the strongly hooked beak, with a fleshy cere, through which the nostrils open. The strongly down-curved upper mandible fits over a broad and up-curved lower mandible. The upper mandible of the beak articulates with the skull. The tongue is especially large and fleshy, usually rounded at the tip. The legs are comparatively short and the feet are zygodactyl. The second and third digits point forwards with the first and fourth pointing backwards. The plumage is firm and sparse with the dominant colour being green, however the presence of yellow, red, blue or purple makes some species extremely colourful.

With a few exceptions, parrots are arboreal and many use the bill as a third foot to hook a branch or area of rough bark. Parrots are generally confined to tropical or sub-tropical areas where they are gregarious, living in small flocks of a few birds, however, larger flocks may assemble at a favoured food or water source.

Most parrots are vegetarian and eat husked grains or seeds, notable exceptions being *Calyptorhynchus* that is at least partly or totally insectivorous (Forshaw 1989) and the Kea (*Nestor notabilis*), which is partly carniverous. Characteristically they husk the food by manipulating it with their feet and bring the food to their beak. Only the parrots and the owls share this faculty amongst birds. All other birds must bring the beak to the feet (Rowan 1983).

Little is known about the social or breeding behaviour and organisation of wild parrots. Brereton (1963) pointed out that courtship feeding and allopreening seem to be widespread within the order. Many species are secondary, cavity hole-nesters. That is, they nest in cavities in tree trunks or boughs but are unable to excavate the hole, although some species are known to enlarge or reshape the entrance (Rowan 1983). In general, parrots neither line or bring nesting material to the cavity and lay one to ten eggs, at two-day intervals. Incubation can be by both parents or most commonly, by the female only. In the latter case, she will leave the nest to be fed by regurgitation from her partner.

The length of the incubation and nestling period is extremely long, from 6 weeks to 3 months. Lack (1968) has pointed out that in most avian orders the nestling period is roughly equivalent to the incubation period. However, the nestling period of parrots may be one and a half to twice that of the incubation period. He suggests that the reason is that the young are hatched at an early stage of development.

Parrots are remarkable for their vocal dexterity. Many individuals develop an ability to mimic human speech or other sounds heard frequently, though this ability varies between species and individuals. Although mimicry is not unique in the bird kingdom, the parrots are unique in that they rarely demonstrate their ability in the wild, where they communicate by means of various species-specific screams and whistles.

Taxonomic Relationships of Parrots

Both Rowan (1983) and Forshaw (1989) have emphasised the homogeneity of parrots as a taxonomic group, however, the taxonomic relationships within the order have remained controversial with separation into lower taxonomic assemblages being based on minor differences.

The first attempts at biological classification of the parrots recognised seven families within a single order, the Psittaciformes (Salvadori 1891). Since then various authors have presented new taxonomic arrangements based on minor anatomical, physiological or morphological characteristics (Thompson 1900; Reichenow 1913; Peters 1937; Condon 1941; Cain 1955; Verheyen 1956; Glenny 1957; Brereton & Immelman 1962; Brereton 1963; Gysels 1964; Sibley & Alquhist 1972; Sibley & Alquhist 1990; Sibley & Monroe 1990). In 1975, Smith presented an essay on parrot systematics and it is this arrangement that is now generally accepted (Forshaw 1989). In this system the order

Psittaciformes has one family, the Psittacidae, which comprises three subfamilies, the Loriinae, the Cacatuiinae and the Psittacinae. The latter two subfamilies are further subdivided into a number of tribes.

The order comprises some 330 species (Collar & Juniper 1991) of which 17 are indigenous to the African continent, with one introduced species, the Rose-ringed Parakeet (*Psittacula krameri*). In southern Africa, Maclean (1993) lists seven indigenous species. White (1965) places three of these species, Meyer's Parrot, (*Poicephalus meyeri* (Cretzschmar) 1827), Ruppell's Parrot (*P. rueppellii* (Gray) 1849) and the Brown-headed Parrot (*P. cryptoxanthus* (Peters) 1854) in a superspecies, based on similarity in size, behaviour and voice.

The Study Species, *Poicephalus cryptoxanthus*

No comprehensive study has, as yet, been undertaken on the biology of the Brown-headed Parrot (*Poicephalus cryptoxanthus*) in the wild, published information being limited to general accounts of distribution, breeding habits and feeding behaviour.

Distribution

The species apparently has a wide ecological tolerance although throughout its range it is always associated with woodland (Benson & Benson 1977; Hanmer 1976; Britton 1980; Irwin 1981; Maclean 1993). Within its distribution (Figure 1.1), it has been described as "common" (Maclean 1993), "fairly common" (Forshaw 1989), "locally common" (Sinclair *et al.* 1993) and "not uncommon" (Rowan 1983).

Three subspecies have been recognised based on colouration and size (Forshaw 1989). The nominate race *P. cryptoxanthus cryptoxanthus* ranges from Northern KwaZulu-Natal northwards to southern Mozambique and southeastern Zimbabwe. *P. cryptoxanthus tanganyikae* is distinguished in having a much paler and more greenish plumage with less brown on the head, throat, neck and rump. The underparts appear to be brighter and more yellowish. It occurs north of the Save River in Mozambique, southern Malawi, eastern Tanzania and coastal Kenya. The existence of a third subspecies *P. cryptoxanthus zanzibaricus,* confined to the islands of Zanzibar and Pemba, is now doubted. Clancey (1977) found no difference in size between the modern birds of Zanzibar and those from the mainland. He concluded that if the subspecies existed then it is now extinct, either because of the direct intervention of man trapping the birds or by interbreeding with immigrant *P. c. tanganyikae* from the mainland. Similarly, whilst Forshaw (1989) reports morphological measurements for *P.c. zanzibaricus,* he also concludes that the existence of the subspecies is dubious. Morphometric measurements of the three sub-species are given as Table 1.1.

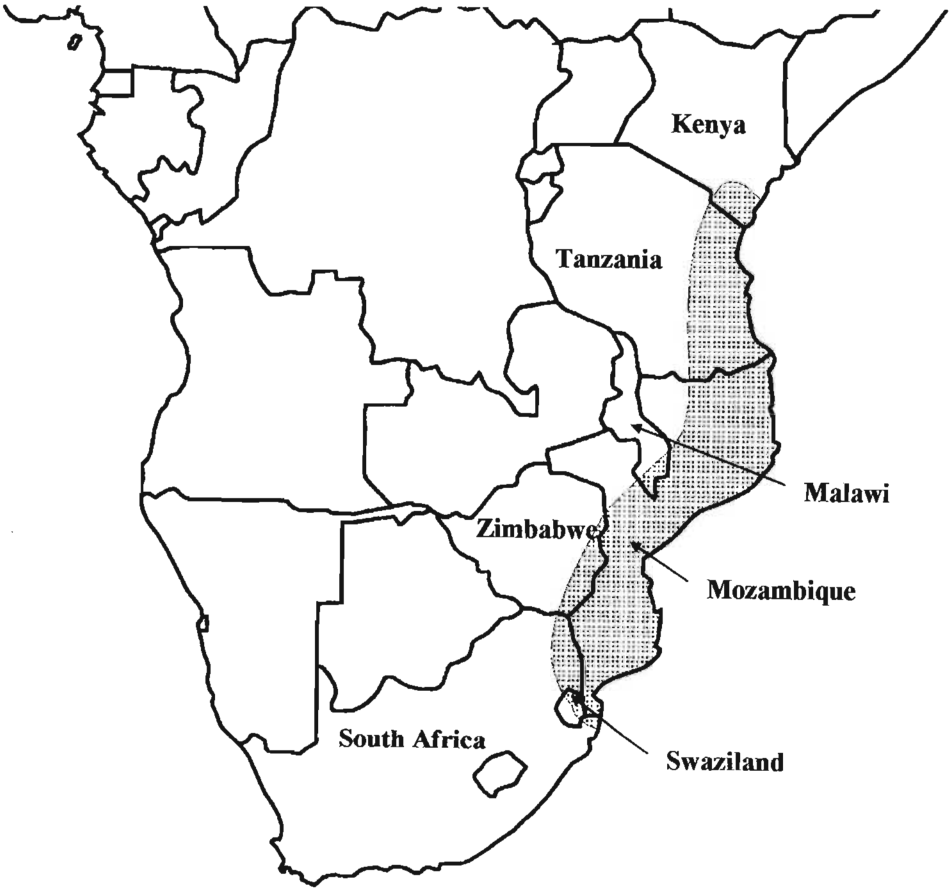

Figure 1.1: Map of Sub-Equatorial Africa, showing the distribution of the Brown-headed Parrot as shaded area.

General Description

Subspecies	n	Sex	Wing	Culmen	Tail	Tarsus
Poicephalus cryptoxanthus cryptoxanthus	49	M	157.7	21.7	68.4	–
	34	F	151.0	20.5	65.8	–
Poicephalus cryptoxanthus tanganyikae	24	M	155.3	21.8	62.9	17.4
	24	F	149.7	21.0	61.3	16.8
Poicephalus cryptoxanthus zanzibaricus	3	M	159.3	21.3	64.0	18.3
	2	F	156.0	21.5	--	17.5

Table 1.1 : The mean measurements (mm) of the wing, culmen, tail and tarsus lengths of the 3 subspecies of *Poicephalus cryptoxanthus*. Adapted from Clancey (1977) and Forshaw (1989).

Maclean (1993) reports the length of the adult to be between 22 and 24 cm. The general plumage colour of the Brown-headed Parrot is green, indeed Sinclair *et al.*, (1993) describe the species as "the greenest parrot of the sub-region". The under wing coverts are bright yellow, although the extent of this is variable. It is from this yellow that the specific name derives, *kryptos* being Greek for hidden or concealed and *xanthos* meaning yellow. Forshaw (1989) maintains that the underparts and lower back are paler green, as is the margins of the feathers on the underparts, with this colouration becoming more pronounced towards the vent and thighs. The rump is very bright, almost metallic green. The neck is grey-brown merging to brown on the head but merging to greenish on the mantle. The tail is edged olive-brown and tipped green. The iris is greenish yellow (Maclean 1993) or yellow (Forshaw 1989) and the legs and feet are blackish grey. The bill is dark, almost black above, merging to whitish below. The immature is always described as "duller than the adult and yellowish below" (for example, Maclean 1993). The flight is described as "fast and direct" (Forshaw 1989).

Breeding Biology

Brown-headed Parrots nest in cavities in trees up to 10 m above ground (Maclean, 1993). Maclean (1993) reports the breeding season to be April to October in the Southern African Sub-region, with 2 to 3 (usually 3) eggs being laid. The eggs are glossy, white and rounded (Maclean 1993) or slightly elliptical (Forshaw 1989). Schonwetter (1964) reported that a single egg in the British Museum Collection measured 27.2 x 22.9 mm, whilst Maclean (1993) gives an average dimension of 32.5 x 26.3 mm (n = 3). Incubation is by the female only and lasts between 26 and 30 days (Maclean 1993). During this time the female is fed by the male (Low 1980). The nestling period is reported as 12 weeks, whereupon the young are fed exclusively by the male for a further 4 weeks, when the chicks are independent (Low 1980).

Clancey (1977) states that the Brown-headed Parrot and Meyer's Parrot (*P. meyeri*) "hybridize freely" along a narrow zone of sympatry between the Motale River in northeastern Northern Province and the Sabi River in Zimbabwe. However, Rowan (1983) has questioned this statement on the grounds that it presupposes that the two species *are* sympatric. Harwin (1972) observed that *P. cryptoxanthus* was present along the Nuanetsi, Sabi and Lundi Rivers, whilst *P meyeri* was absent. Benson (1942) recorded a similar geographical replacement in Malawi and Rowan (1983) stated that not only do they not occur together in the Northern Province but field observers have the impression that they rarely if ever occur together. Further, Rowan (1983) pointed out that mixed pairs or parties are unknown and that no record of them hybridizing existed from captive records. However, in 1985, Brickell, reported producing hybrids of Meyer's x Ruppell's, Brown-headed x Niam-Niam and Brown-headed x Meyer's.

Diet

Brown-headed Parrots have been variously described as eating wild figs (*Ficus* spp.), the berries of cassava, the pods of *Acacia* spp. and probing for nectar in *Aloe marlothii* inflorescences (Oatley 1964). Juniper & Parr (1998) report them eating cassava (*Manihot esculenta*), Baobab seeds, coconut palm flowers, tree shoots as well as the pods of *Acacia nigrescens* and *Albizia gummifera*. Vincent (1934) and Fuggles-Couchman (1939) have also referred to specific dietary items as well as describing the species as a pest attacking millet and ripening maize in cultivated land. Both Maclean (1993) and Forshaw (1989) have given more generalized descriptions of the diet and the former author states that flocks of up to 50 birds can congregate at a good food source.

Voice

Brown-headed Parrots are described as noisy, especially in flight (Forshaw 1989). Maclean (1993) describes two calls, "a strident *chree-oo...chree-oo* and a sharp *kreek*", whilst Mackworth-Praed and Grant, (1952) reported that feeding was accompanied by "conversational chattering".

Objectives and Hypotheses

With a paucity of scientific data on the species, the present study was directed at investigating the general biology, reproductive characteristics and habitat requirements of the species. A further motivation was to investigate the vocal communication of the species.

Although these general aims may impinge in detail, a number of specific objectives arise.

Behavioural Ecology

Diet

For the majority of birds the food supply is not constant (Karr 1990). Long-term changes such as habitat degradation or alteration may cause a species to vacate a habitat entirely, however, long-term, reasonably predictable change such as seasonal changes in food availability may cause a species to migrate to areas where food can be found (Koen 1992). Whilst this strategy is followed by many temperate species, successional seasonal changes in food abundance and availability are exploited by many tropical and sub-tropical birds by altering their diet (Morrison *et al.* 1985; Klasing 1998). There is no evidence to show that Brown-headed Parrots migrate, in the strictest sense, although local movements occur in some *Poicephalus* species (Juniper & Parr 1998). They must therefore, modify their diet in accordance with the fluctuations of seasons.

The dietary preferences of the species have previously been only described in the vaguest terms, suggesting that the species' diet consists of fruit, nuts and berries (Maclean 1989). Therefore, this study investigates the proximate factors governing the annual diet of Brown-headed Parrots. In particular, I considered what they eat and why. The first of these questions is one of natural history but to answer the second requires the testing of the hypothesis that; all the vegetation is available to Brown-headed Parrots and that their dietary constituents are not chosen because of nutritional content, palatability, accessibility or item size.

Social Structure

Very little is known about the social structure of this species. It has been suggested that the species is highly gregarious at certain times of the year and that the pair-bond is not permanent (Maclean 1989; Forshaw 1989). Whilst many parrots are gregarious, most form pair bonds, which are intact throughout the lives of the partners (reviewed in Forshaw 1989). Why then, should the Brown-headed Parrot behave like a typical parrot species in regard to sociality in larger groups yet form new pair groupings during the breeding season? The hypothesis tested is that the Brown-headed Parrot does not form pair bonds, which last longer than the breeding season. An obvious corollary of this hypothesis is that if it is accepted then how does the breeding pair bond form?

Allied to these questions is the formation and function of larger seasonal groups and the cohesion within them. Do such groups have an adaptive significance or are they a by-product of food patchiness?

Breeding Behaviour

Although it is known to be a secondary cavity hole-nester, little is known about the types or species of tree Brown-headed Parrots prefer to nest in or why. I will therefore test the hypothesis that the parrots have no preferential tree species and that any tree hole is a potential and viable nesting site. Newton (1994) suggests that many hole-nesting birds are either excluded from breeding or are kept at low abundance levels as a direct result of being unable to find suitable nest sites. I investigate the question of whether suitable nest holes are limiting factors on the numbers of birds able to breed in any one area. Further, I will consider the question of interspecific competition for nesting sites.

Information concerning the breeding biology of Brown-headed Parrots is restricted and anecdotal. By collecting and collating data from Brown-headed Parrot breeders, the chick growth curves are reported offering a general growth guide.

Lastly, Verner and Willson (1969) have shown that in general, the males of sexually monomorphic species participate more in nesting activities than does the male in dimorphic species, whilst Armstrong and Juritz (1996) have predicted that Brown-headed Parrots may be communal breeders. The epimeletic behaviour will therefore be examined and the prediction that non-breeding birds help at the nest will be examined.

Vocal Communication

Amongst the varied sensory channels open to birds for communication, sight and sound are by far the most “important”. Although visual communication is crucial for many species (Miller & Emlen 1975; Stoddard & Beecher 1983; Whitfield 1986, 1987), as demonstrated by their elaborate plumage and colouration, visual signals have several disadvantages. Darkness, poor light, dense foliage or physical obstructions all produce events when the individual can be partially or wholly hidden from view (Hailman 1977, 1979;

Endler 1990, 1992, 1993). Clearly this is inadequate if the bird's "intention" is communication. Sound travels over long distances, can be heard at all times of the day and can penetrate dense foliage (Richards & Wiley 1980; Wiley & Richards 1982). A further advantage is its non-permanency. Vocalisations can be produced only when required with large amounts of information being transmitted quickly and efficiently (Catchpole & Slater 1995). Avian vocalisations can be separated into songs and calls, although this differentiation should not be seen as definitive. Bird song has been defined by Catchpole & Slater (1995) as "tending to be long, complex vocalisations produced by males during the breeding season", whilst "calls tend to be shorter, simpler and produced by both sexes throughout the year".

The first objective descriptions of bird song using spectrographs were published almost 50 years ago (Borror & Reese 1953, Kellogg & Stein 1953; Collias & Joos 1953). Subsequent advances in recording and analysis instrumentation has allowed bioacoustics to provide insights into disciplines as diverse as communication theory (Hailman *et al.* 1985), voice cognition (Pepperberg 1993), taxonomy and systematics (Marshall 1978; Payne 1986; Cocroft & Ryan, 1995), speciation (Martens & Nazarenko 1993), behavioural genetics (Baptista & Gaunt 1994; Baptista 1996), behavioural ecology (Payne *et al.* 1988) and in the last few years its use as a conservation tool has been recognised (Baptista & Gaunt 1997). By and large these studies have concentrated on passerines, especially oscines and relatively little work has been conducted on calling species (Bretagnolle 1996). Whichever species has been studied, a first and necessary step is to describe the singing or calling repertoire of the species correlating this information to its life history, habitat and behaviour (Bertram 1970; Beightol & Samuel 1973; Miller & Gottlieb 1976; Barklow 1979; Hausberger *et al.* 1994).

This descriptive phase facilitates a transition towards hypothesis testing and question generation, such as those regarding parent offspring recognition or individual recognition amongst adults (Bailey 1978; Pidgeon 1981; Falls 1982; Storey 1984; Wooller *et al.* 1984). However, the descriptive phase should not just be seen as a means to an end. Kroodsma *et al.* (1996) have emphasised the importance of this phase, especially in species which a) have not been previously studied and b) are experiencing declines in overall abundance. This scenario exists in most of the world's parrot species, which remain the least studied of all vertebrate families (Collar & Juniper, 1991).

Vocal Communication of Brown-headed Parrots

No study exists on the vocal communication of the Brown-headed Parrot, published information being restricted to onomatopoeic descriptions in field guides of the sounds made (e.g. Maclean 1993; Sinclair *et al.* 1993). No attempt has been made in the past to consider the ecological context of the calls or analyse the calls in a critical manner. The first section of this part of the study remedies this situation by presenting sonograms of typical calls of the species and the behavioural context in which these calls are produced. Behaviour can be defined as an evolutionary adaptive response to specific requirements of an organism's environment (Maclean 1990). It can involve more than one individual i.e. flocking, more than one species, i.e. feeding or be a process applied by an individual to itself i.e., preening, but each behavioural activity produces a beneficial reward greater than the cost of the behaviour (Miller 1988). As such, behaviours determine the time budgets of species and individuals. However, a corollary of avian behaviour includes a species' repertoire of songs or calls. Therefore, as well as outlining a generalised ethogram of Brown-headed Parrots, describing, with accompanying illustrations, maintenance activity and feeding, agonistic, epigamic, etepimeletic, exploratory and play behaviours, I correlate these processes with accompanying vocalisations. Although necessarily descriptive, it provides a template upon which the rest of the study is based.

Earlier pilot studies showed that Brown-headed Parrots take up a pseudo-colonial breeding strategy after the chicks have fledged (Taylor per. obs.). The various benefits and disadvantages of colonial breeding are described by Lack (1968) who pointed out that some form of parent-offspring recognition is a prerequisite for coloniality to be evolutionarily stable. This prediction has been shown to be true in all studies of colonially nesting birds so far studied (Davies & Carrick 1962; Fagen 1973; Beer 1979; Stoddard & Beecher 1983; Beecher *et al.* 1986; Mathevon, 1997; Aubin & Jouventin 1998;

Lengagne *et al.* 1999) with the channel used being individual voice recognition. In adopting a pseudo-colonial breeding system where the chicks are mobile, Brown-headed Parrots face the same problem. In order for parents to feed their own young they must be able to tell them apart from "foreign" chicks. The first hypothesis here is that Brown-headed Parrot chicks and adults do not recognise each other by voice, and subsequently another recognition system operates, or adults feed chicks randomly.

If the above hypothesis is rejected then there must exist individual voice signatures either in the chicks or in the adults. Therefore, I next test the hypotheses that; no difference exists in the voices of individual chicks or the adults.

Finally, I investigate the ability of Brown-headed Parrots to produce frequencies in their calls above the currently accepted highest frequency threshold of avian hearing. Dooling (1992) has stated that the Strigiformes have the most acute hearing in higher frequencies, the upper threshold being 11.2 kHz. In a pilot study sonograms of some calls of Brown-headed Parrots exceeded this boundary. I therefore test the hypothesis that these high frequency elements are functionless artefacts of the sound producing mechanism and cannot be heard by Brown-headed Parrots.

Conservation of Brown-headed Parrots

It is now generally recognised that Brown-headed Parrots are undergoing a rapid and serious decline in numbers and distribution (Juniper & Parr 1998; Taylor & Horsfield 2001a & b). The last chapter of this study will make recommendations for the conservation of this species in the context of the information and data presented in this thesis.

Summary

Like most parrots, the Brown-headed Parrot is a poorly known species and in this chapter, I have detailed the paucity of information that exists on the species, and detailed the general context of the study, and identified the purpose of this work. Davies (1992) has pointed out that detailed studies of a particular species for their own sake have become less fashionable, current trends being to think of an idea then a species to test those ideas. Like Davies, I have found this single-species study has generated other interesting questions which have arisen from direct observation of the bird in the wild rather than from the theoretical literature. These questions are posed in the following chapters, however, to avoid repetition it is appropriate that a detailed description of the study areas is given and experimental methods which are common to these sites. This is the subject of the next chapter.

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Chapter 2

Study Areas and General Methods

The Study Areas

Three study areas were used during this study, two in the Kruger National Park (KNP) and one in southern Mozambique. The choice of study area was governed both by the presence of the study species and the ease of being able to carry out research in the area. A third criteria, was to choose study areas where different biotic and abiotic conditions prevailed, thus offering an opportunity to compare three populations of Brown-headed Parrots.

Punda Maria

Punda Maria lies in the north west of the Kruger National Park in South Africa (Figure 2.1). The rest camp lies at 22° 41' S and 31° 01' E at an altitude of 462 m. a.s.l.

The altitude of the area varies between 420 and 580 metres. Punda Maria has a moderate climate with most of the rain falling in summer (Figures 2.2 & 2.3).

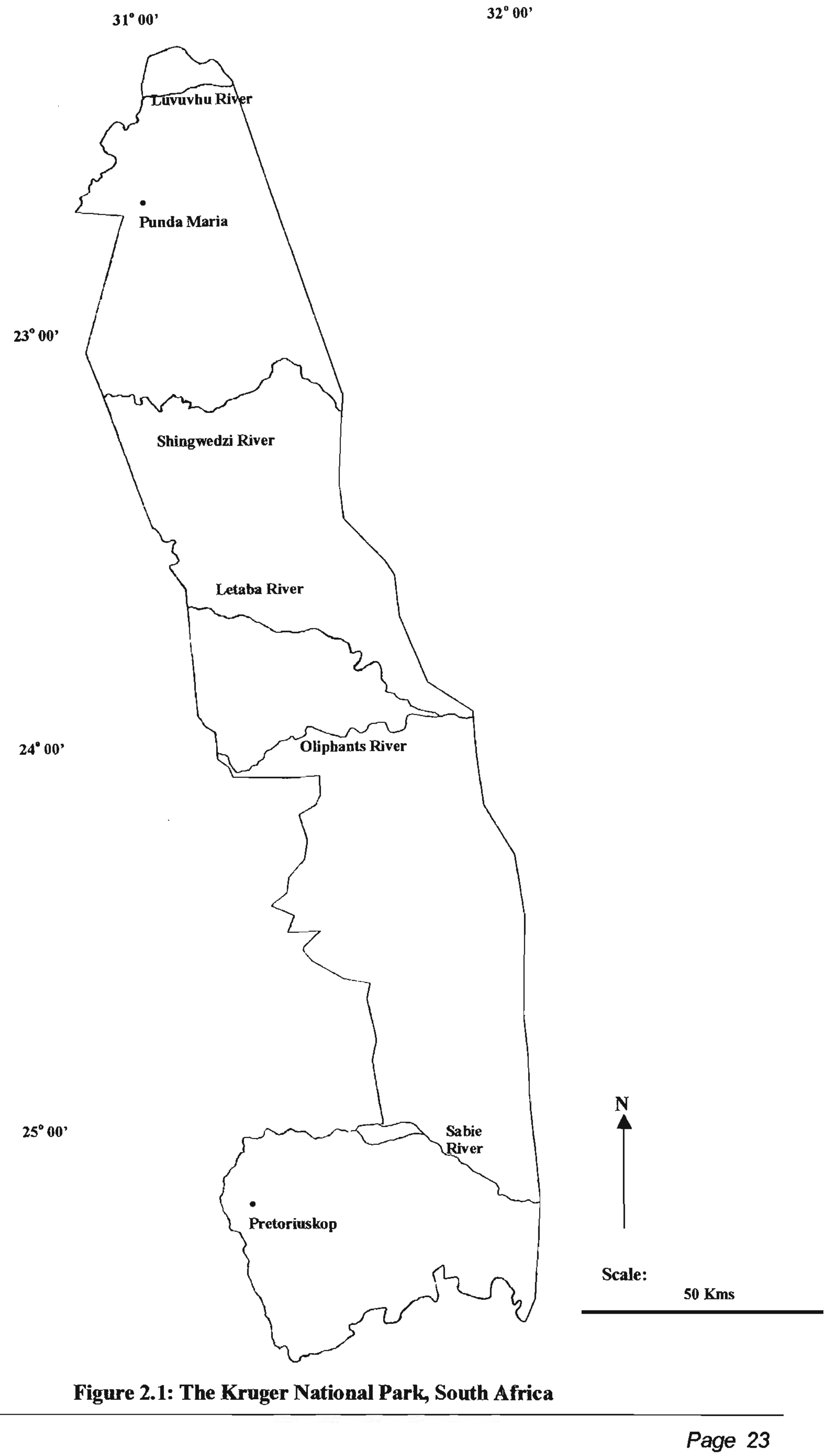

Figure 2.1: The Kruger National Park, South Africa

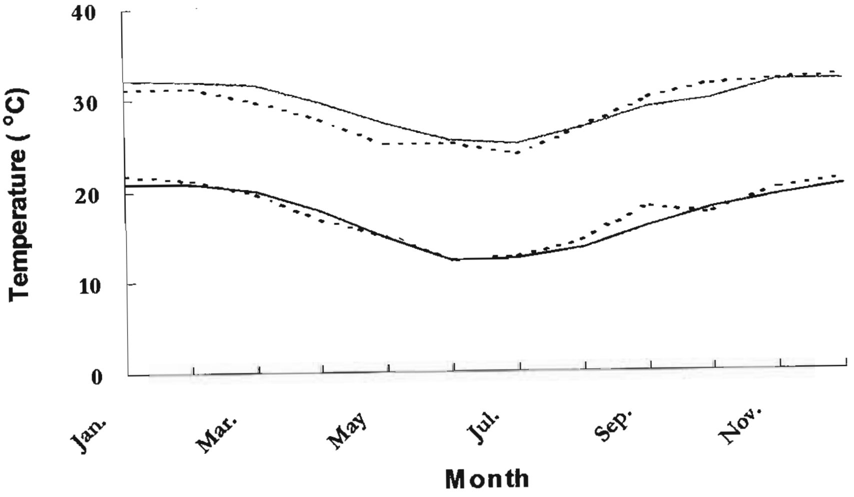

Figure 2.2: Monthly temperature for Punda Maria. For comparison, the maximum and minimum daily means are shown for the period 1961 – 1997 (solid line) and 1995 – 1997 (dotted line). Source: S.A. Weather Bureau.

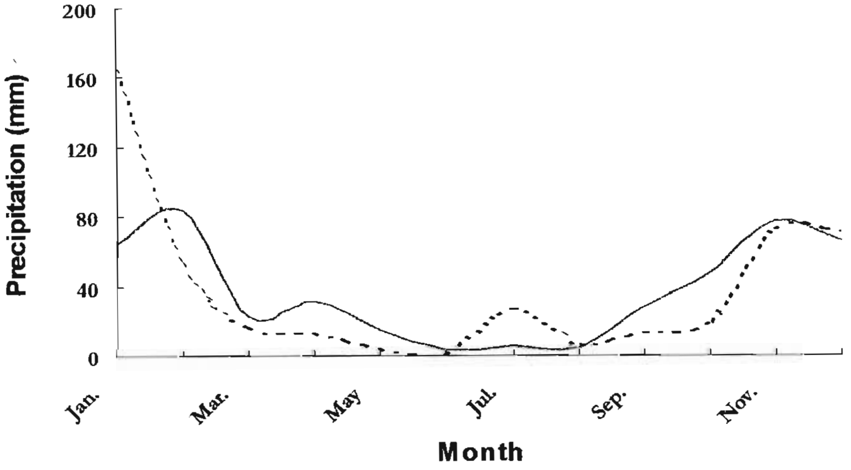

Figure 2.3: Monthly precipitation for Punda Maria. For comparison, the daily mean is shown for the period 1961 – 1997 (solid line) and 1995 – 1997 (dotted line). Source: S.A. Weather Bureau.

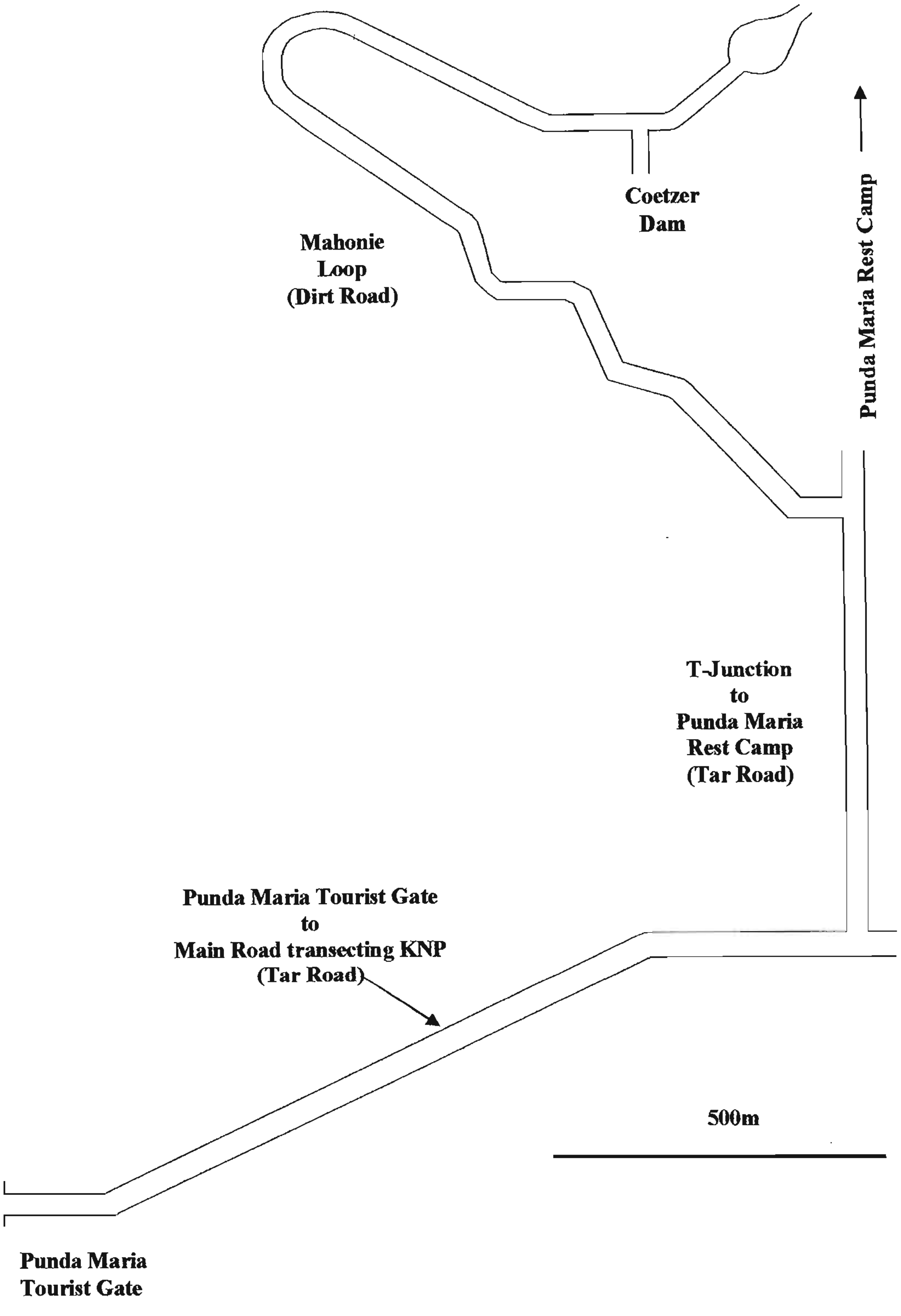

Figure 2.4: Punda Maria between Punda Maria Tourist Gate and Coetzer Dam (see text for details).

The area supports two markedly different vegetation communities of which one can be further subdivided. Surrounding the rest camp and immediately to the west of it, the soil is sandveld on waterberg sandstone with intrusions of diabase sills and dolerite dykes. Gertenbach (1983) points out that these intrusions have a major influence on the soil type and consequently on the vegetation. The soils vary from lithosols in the higher altitudes to deep sandy soils and brackish soils in the valleys. Van Rooyen (1978) divides the vegetation into four clearly defined communities. In the following section common names of trees are those given by van Wyk (1994).

The *Burkea africana/Pseudolachnostylis maprouneifolia* tree savannah occurs on deep sand and the woody component is dominated by *Burkea africana* (Wild Seringa), *Pseudolachnostylis maprouneifolia* (Kudu Berry), *Terminalia sericea* (Silver Cluster-Leaf) *and Combretum collinum* (Weeping Bushwillow), *C. zeyheri* (Large-fruited Bushwillow), *C. apiculatum* (Red Bushwillow) and *Diospyros mespiliformis* (Jackal Berry).

The *Kirkia acuminata/Afzelia quanzensis/Combretum apiculatum* tree savannah occurs on the steep slopes with stony soils. It is moderate tree savannah (Gertenbach, 1983). The common tree species are *Kirkia acuminata* (White Seringa), *Afzelia quanzensis* (Pod Mahogany), *Combretum apiculatum*, and *Croton gratissimus* (Lavender Feverberry). Otherwise species which are rare in other areas of KNP, occur here commonly, including *Entandrophragma caudatum* (Mountain Mahogany) and *Rhus leptodictya* (Mountain Karree).

The *Androstachys johsonii/Croton pseudopulchellus* dry woodland occurs on the drier slopes of the mountains. As well as the 2 species it is named after (Lebombo Ironwood and Small Lavender Croton, respectively), other typical tree species of this area are *Combretum apiculatum, C. mossambicense (Knobbly Creeper), Ficus soldanella* (Large-Leaved Rock fig), *Cassia abbreviata* (Sjambok Pod) and *Adansonia digitata* (Baobab).

The diabase intrusions support the fourth community. It is a shrub dominated community on clay soil. *Combretum hereroense* (Russet Bushwillow), *C. collinum C. imberbe* (Leadwood), *C. mossambicense, Acacia nigrescens* (Knobthorn) and *A. gerrardii* (Red Thorn) are the dominant tree species.

A clear demarcation occurs to the east of these communities as the substrate gives way to ecca-shale (Gertenbach 1983). Van Rooyen (1978) describes the area as a high tree savannah. The major component of the high canopy is *Colophospermum mopane* (Mopane) between 10 and 15 m. tall. The major component of the middle canopy and shrub layer comprises *Acacia nigrescens, A. tortilis (Umbrella Thorn), Combretum imberbe, C. hereroense* and *Dichrostachys cinerea* (Sickle Bush).

A transect was selected, which incorporated much of the soil types and, therefore, vegetative diversity of the area (Figure 2.4). The transect began at the Punda Maria tourist gate on a tar road and progressed in an easterly direction. To the south of this section the prevailing vegetation was closed mixed woodland dominated by *Terminalia* spp., *Combretum* spp. and Mopane. To the north, the vegetation was typical high tree savannah as described by van Rooyen (1978). The transect circumnavigated this area becoming alternatively, the western, then southern boundary (Figure 2.4). The transect turned north at the t-junction heading towards Punda Maria Restcamp, again following the tar road. The eastern boundary at this point consisted of grassland with a patchily distributed shrub layer, mostly consisting of *A. tortilis* and *D. cinerea.* Six hundred meters along this road, the Mahonie loop begins on the east. The Mahonie loop is a 23 km tourist, game-viewing, circular route on a dirt road. The northern boundary of the transect at this point was tree/shrub savannah dominated by *Cassia abbreviata.* This biome gradually gives way to closed mixed shrub before opening out to the high tree savannah surrounding Coetzer Dam. The dam is a man-made trough, provisioned by a windmill drawing up ground water. An artificial elephant water tank is also close-by. On the opposite side of the dirt road and after circumnavigating the high tree savannah, the eastern boundary consisted of an incline of shale dominated by *K. acuminata, A. quanzensis* and *E. caudatum.* This gradually merged into tree savannah dominated by *B. africana, P. maprouneifolia* and *D. mespiliformis.* This vegetation continued to the east side of the transect opposite Coetzer Dam. The transect was 6.9km and driven at an average speed of 10km per hour. The starting point for each transect run was chosen at random each day and subsequent runs were began at that end point.

Pretoriuskop

Pretoriuskop lies in the south-western corner of the KNP (Figure 2.1). The rest camp lies at 25° 10' S and 31° 16' E at an altitude of 600 m. a.s.l. The area has a moderate climate and the annual rainfall varies between 600 and 1000 mm p.a. (Gertenbach, 1980) with most of this falling between October and April (Figures 2.5 & 2.6).

The underlying geology of the area is granite and gneiss, resulting in an undulating landscape, characterised by rocky kopjies and deep incisions. These incisions allow the formation of seasonal spruits. The soil varies from sand to sandy loam and is deeply leached (Gertenbach, 1983). Acocks (1975) describes the vegetation as lowveld sour bushveld and Van Rooyen (1978) describes it as open tree savannah. Van der Shijff (1957) and Pienaar (1963) both provide detailed inventories of the plant species present. The woody component is dominated by *Terminalia sericea, Combretum collinum suluense C, zeyheri, C. apiculatim, C. molle* and *Dichrostachys cinerea. Ficus sycomorus* (Sycamore Fig) which is a common riverine species in the KNP, occurs here on the uplands because of the relatively high rainfall and high water retention of the soil. Many of the rarer KNP tree species are abundant in this area, especially *Acacia sieberana* var. *woodii* (Paperbark Acacia). The dominant tree species' within the rest camp are *Erythrina lysistemon* (Common Coral Tree) and *Trichilia emetica* (Natal Mahogany).

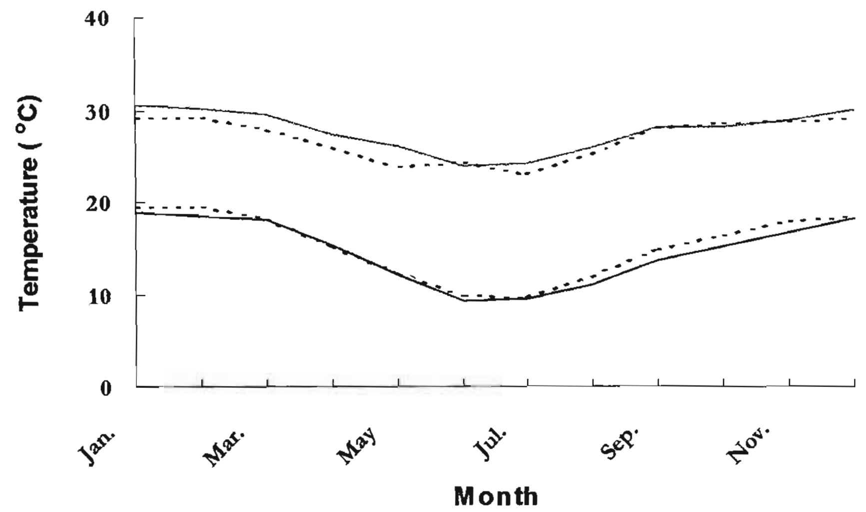

Figure 2.5: Monthly temperature for Pretoriuskop. For comparison, the maximum and minimum daily means are shown for the period 1961 – 1997 (solid line) and 1995 – 1997 (dotted line). Source: S.A. Weather Bureau.

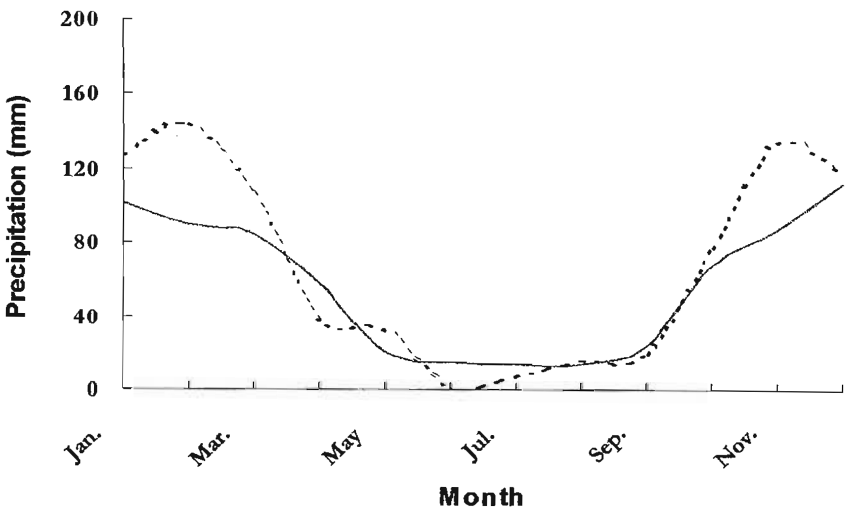

Figure 2.6: Monthly precipitation for Pretoriuskop. For comparison, the daily mean is shown for the period 1961 – 1997 (solid line) and 1995 – 1997 (dotted line). Source: S.A. Weather Bureau.

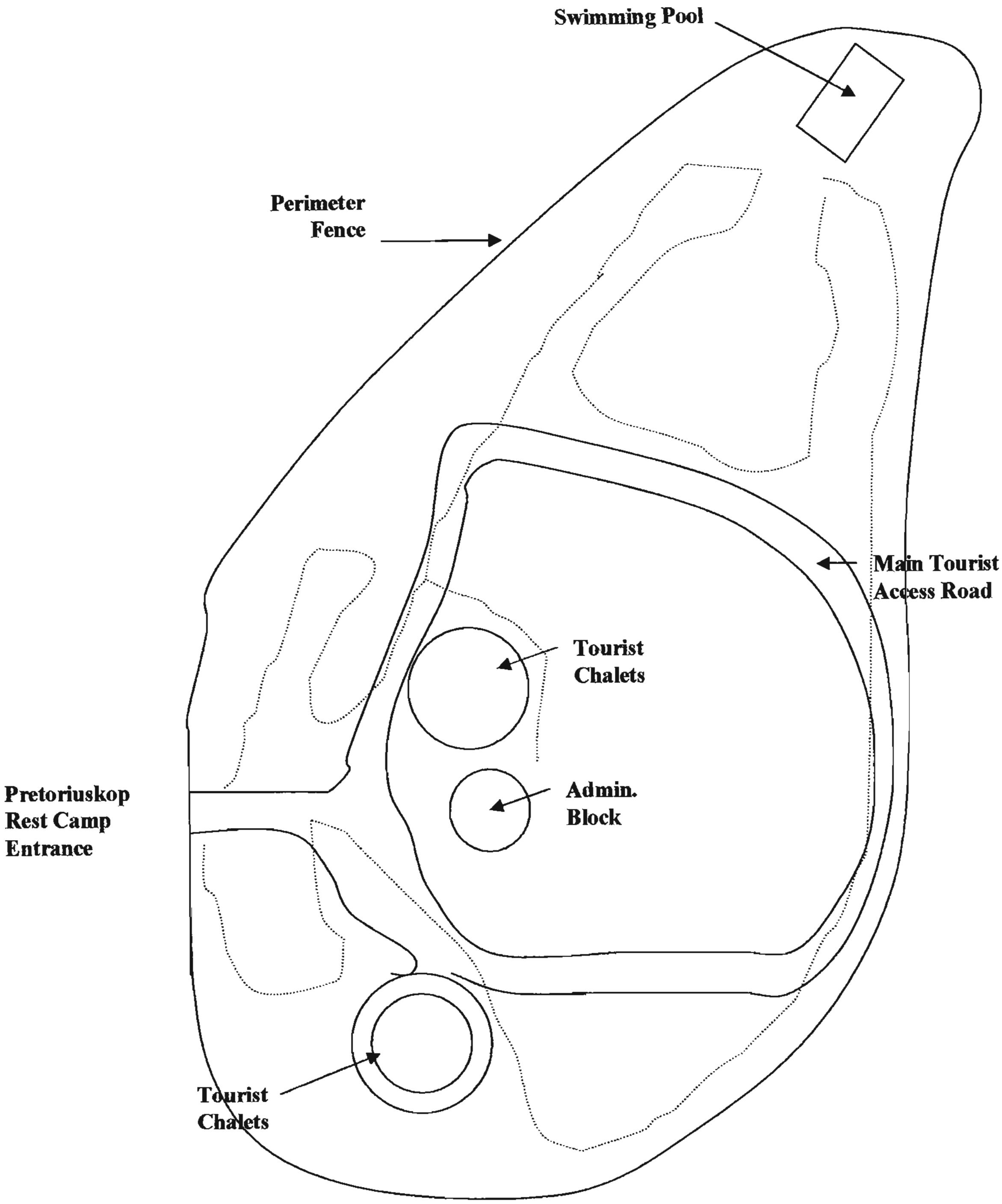

Figure 2.7: Transect (dotted line) used within the campsite at Pretoriuskop Rest Camp.

A transect was selected within the confines of Pretoriuskop restcamp, however by incorporating the mixed vegetation within the camp and by following the perimeter fence as much as possible much of the vegetative diversity of the area was included (Figure 2.7). The transect began at the entrance to Pretoriuskop restcamp and progressed in a northerly direction before cutting back south to join the main tourist access road. This section consisted of a lawn dominated by *T. emetica* and *E. lysistemon*. The transect then continued along an avenue of *E. lysistemon* towards the Administration block, before returning to the road. At this point on the road the dominant vegetation was *T. emetica*. The transect then followed the perimeter fence north. The vegetation towards the east was mixed *Terminalia/Combretum* spp. and D. *cinerea,* with interspersed *Sclerocarya birrea* (Mareola). This vegetation type continued outside the perimeter fence on its north and west boundary. The woody component within the restcamp around the swimming pool area was mixed *T. emitica* and *S. birrea*. This continued to the most southern part of the transect where it gave way to sparse woodland (A. *sieberana* var. *woodii* and *Rhus rehmanniana* (Blunt-leaved Taaibos) on sand. The transect then continued north towards the starting point, again across lawn dominated by *T. emetica* and *E. lysistemon*.

The transect was 5.4 km and walked. The starting point for each transect run was chosen at random each day and subsequent runs were began at that end point.

Ponta Malongane

The study site at Ponta Malongane in Mozambique lies at 26° 48' S and 32° 53' E on the Indian Ocean (Figure 2.8). No detailed data exist on the temperature or rainfall, however, it is a summer rainfall region, receiving an average annual precipitation of between 800 and 1000 mm, with most of this falling between September and April. The area was formerly seabed and as such, the dominant soil type is deep sand, nevertheless, three distinct terrestrial biomes exist. To the south of the Reserva Especial do Maputo (REM), a *Themeda*

– *Turbina* complex, dominates the extensive grasslands. Interspersing this grassland are wetland areas and woodland “islands”. The wetland areas are supported by a complex and shifting non-permanent lake system fueled by rising ground water. The woodland islands are dominated by *Albizia*, *Afzelia* and *Sclerocarya* spp. (Clancey, 1996).

A second woodland type is abandoned *Eucalyptus nigra* plantation. These plantations dominate the western boundary of the REM. They were planted after independence in 1975 but soon after were abandoned with the beginning of the civil war in Mozambique. The trees are about 20 years old. The third major biome is the virgin sand-dune forest along the coast, dominated by *Mimusops caffra* (Coast Red-Milkwood) and a dense shrub layer.

A transect was selected, which roughly followed the eastern boundary of the REM (Figure 2.9) at the southern end of the transect the vegetation on both sides was abandoned *E. nigra* plantation. This began to thin on the eastern side of the transect. The dirt road then veered to the east, following the REM boundary, with *A. quanzensis* being the dominate woody species. Towards the north the dominant species remained *E. nigra*.

The total length of the transect was 7.2 km. Some locals suggested that spread through the plantations were small minefields dating from the civil war, however, evidence was regularly found of elephant utilizing these areas. Therefore, the transect was driven at an average speed of 10km per hour. The starting point for each transect run was chosen at random each day and subsequent runs were began at that end point.

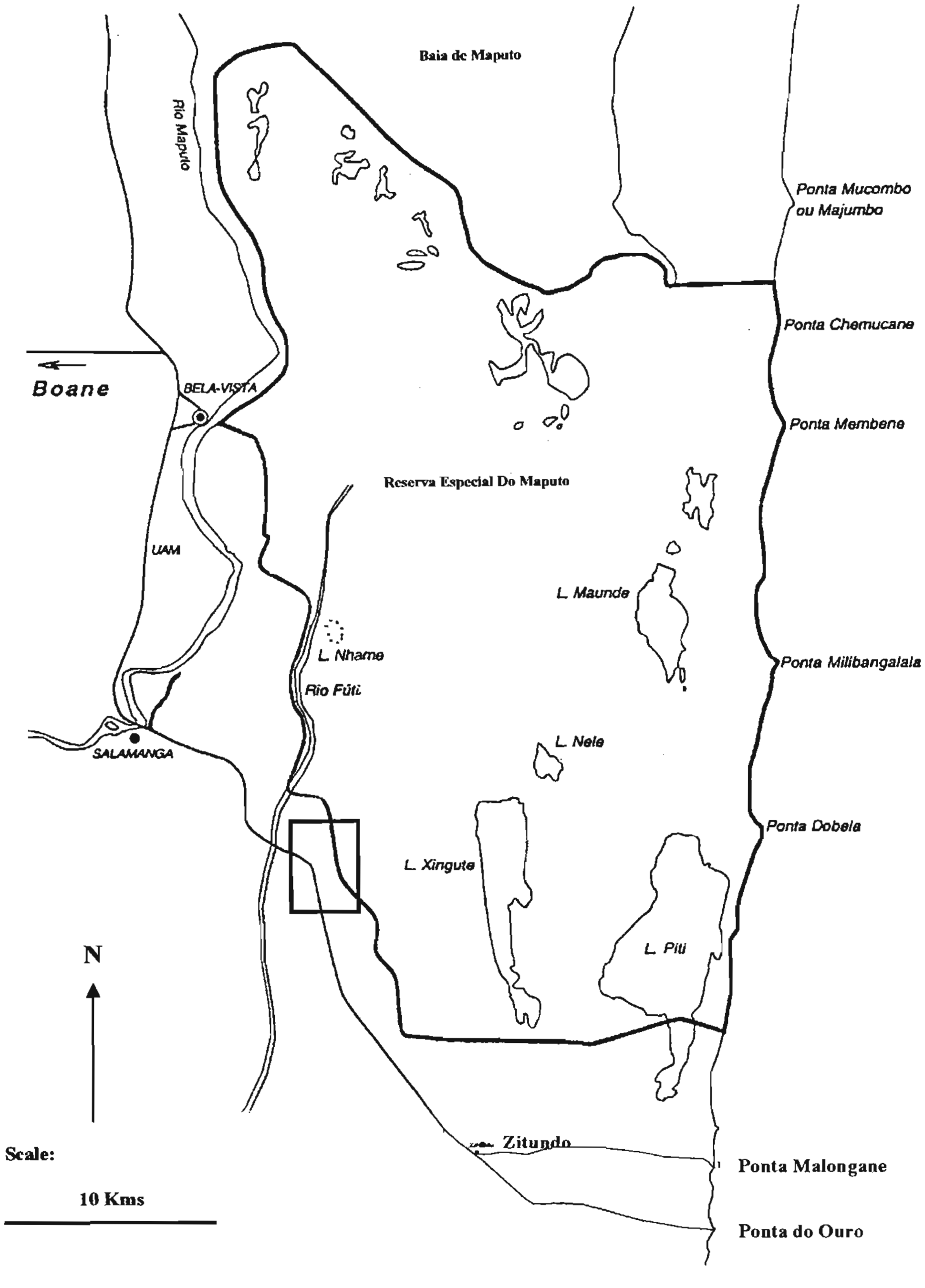

Figure 2.8: Map of southern Mozamique. The heavy black line marks the boundary of the Reserva Especial do Maputo. Single lines signify the road system. Double lines signify the river systems. The bold rectangle is expanded on the following page.

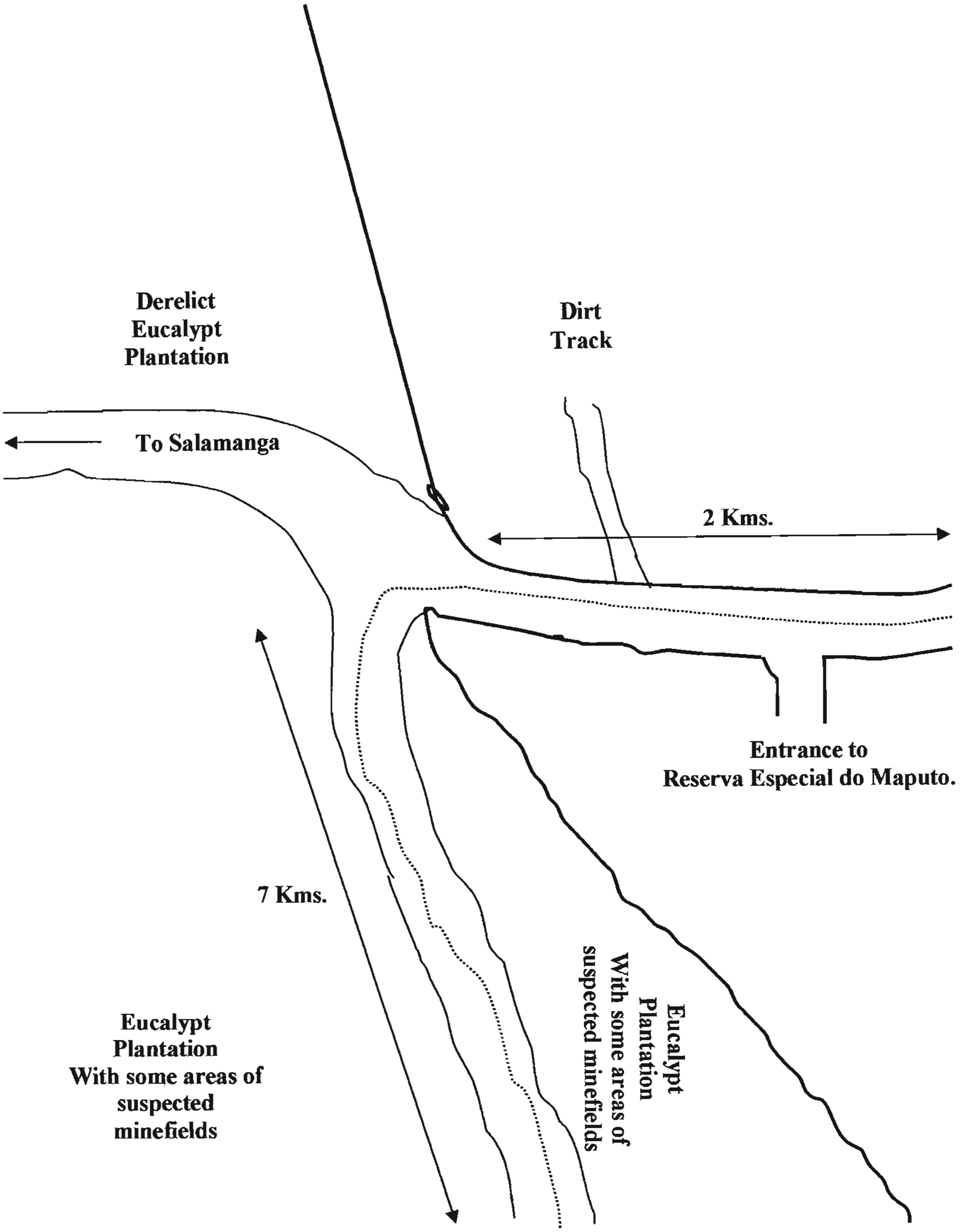

Figure 2.9: Expansion of bold rectangle from figure 2.8, showing Ponta Malongane transect (dotted line). Figure is not to scale but relevant measurements have been indicated. Bold line represents the border of the Reserva Especial do Maputo.

]

Individual Recognition

Rowan (1983) points out that in some individuals yellow feathers may be scattered on the plumage or the yellow may extrude from under the wing and be visible at the wing bend. The extent of the yellow is highly variable and in the pilot stages of this study it was possible to use the patternation to identify individuals (Figure 2.10)

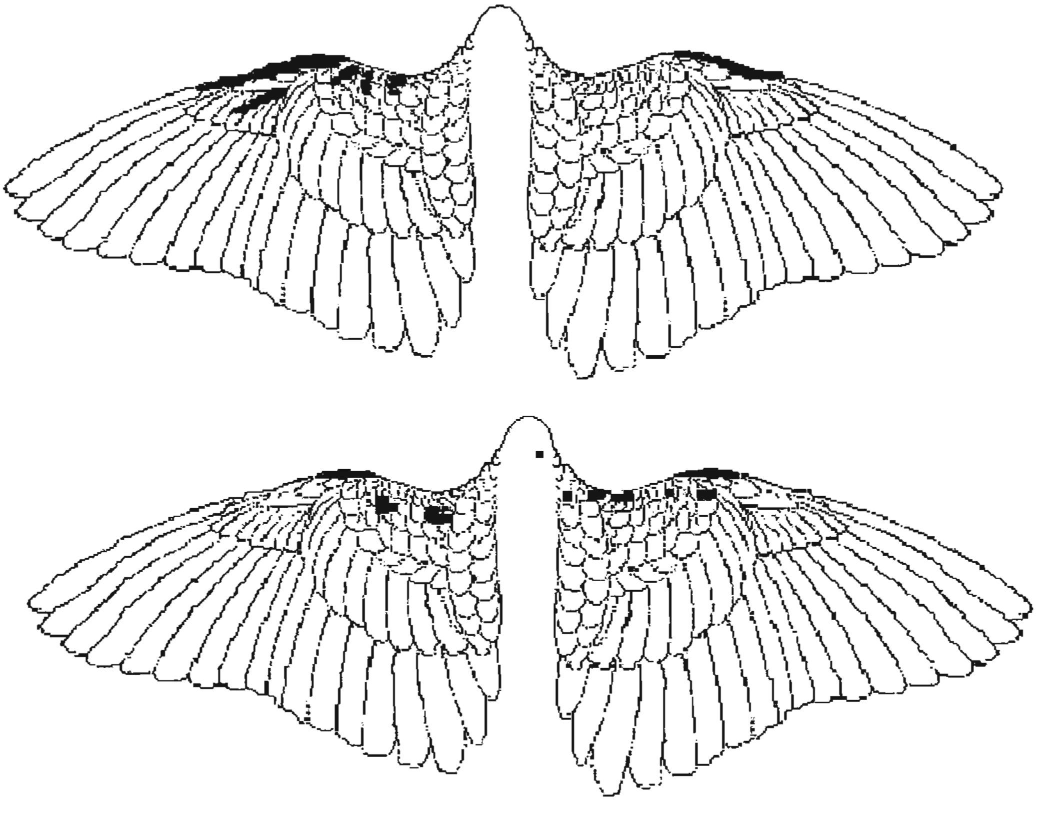

Figure 2.10: Two examples of individual plumage differences, which allowed individual Brown-headed Parrots to be identified. Top bird is PM7, the 7th bird to be individually identified at Punda Maria. Bottom bird is PM12. The black spots represent yellow patches of feathers.

Although this method of identification proved to be invaluable it did not allow the entire population, at any study site, to be identified. The visible yellow extrusion of some individuals only occurred at the wing bend, whilst some individuals showed no visible yellow.

Observations

All field observations of parrots were made using either an Optolyth field telescope or Zeiss 10 x 40 binoculars. The telescope was fitted with a 20x to 60x zoom eyepiece mounted on a car window mount or a free standing tripod.

Recording Vocalisations

Two recording systems were used to record parrot vocalisations in the field. Early recordings were made on a Marantz CP230 cassette recorder with a TEAC UEM – 83 Super-Cardioid microphone. This microphone has a super-cardioid pick-up pattern and the unit has a frequency response of 50 to 18,000 Hz. All Dolby and MPX filters were switched off during recordings and the bias set at the manufacturers recommended level for the TDK CrO_2 tape used. Whilst recording, comments on the behaviour of the birds were spoken into the microphone. Sampling theory states that the minimum sampling frequency (number of samples per second) is twice the highest signal frequency. This means that a signal containing frequencies between 20 Hz and 20 kHz has to be sampled at a rate of at least 40,000 samples per second (a sampling frequency of 40 kHz). As the maximum frequency of the calls was around 9.5 kHz., the sample rate was set at 22,500 samples per second to avoid aliasing the signal. The analogue recordings were then transferred into digital format using “Batsound”, a sound analysis program (Pettersson Electronics, AB, Sweden). Undesired artifacts of the sound, tape noise and extraneous sound were then filtered or attenuated using a Butterworth filter. This has a maximally flat frequency response in the range of frequencies, which should not be attenuated by the filter. Typically this was set to remove frequencies below 500 Hz. No filter was used on the upper level of the signal.

Spectrograms were then produced using a Fast Fourier Transformation (FFT) length of 512 and a Hamming time window.

In later recordings, a TASCAM DA-P1 DAT-Recorder was used. This was fitted with a Sennheiser ME67 shotgun microphone and a Sennheiser K6 wind shield. Again this microphone is a supercardioid type. The TASCAM was set at a sampling rate of 48 kHz for all recordings, allowing the microphone to operate at its fullest frequency response of 50 to 20,0000 Hz.

All recordings were transferred to computer using the software Batsound Ver. 1.2 (Pettersson Elektronik, AB, Sweden). This software is a real-time sound analysis system for use with IBM compatible computers. The software, as well as allowing sound storage, play back, editing and analysis facilities, generates real-time displays of spectrogams and power spectra.

The sound files were transferred to a writeable CD, using a HP CD-Writer 7500 series. This allowed for permanent storage of the sound files.

The sound files were then analysed using spectrograms generated by the sound analysis program, Avisoft-SASLab Pro, Ver. 3.95f (Raimund Specht, Berlin), using a cursor resolution of 3 decimal places in the time domain and 1kHz in the frequency domain.

Birds in Captivity

Both adult Brown-headed Parrots and chicks were kept in captivity throughout this study. Additionally data was collected from birds in Concord, California, USA and from birds kept at the University of Milan, Italy. In all cases adults were housed in 1.2m x 1.2m x 1.8m suspended cages. Water was available at all times and was changed each day. Dietary items offered included sunflower seeds, oats, wheat, barley and sorghum, all of which was soaked overnight apart from the feeding regime in Milan, where the items were boiled briefly and allowed to cool. Additionally, fresh vegetables and fruit were also offered to the birds. Food was restricted so that most of it was consumed by the end of the day and any surplus was removed. On alternate days, vitamin, mineral and a probiotic was sprinkled onto the seed.

All cages were also supplied with a nest-log, 400-450mm high and 250mm diameter with a 50mm entrance hole. The type of wood varied and the nest-log also has a 150mm diameter inspection hatch at the top. Breeding pairs, were given unlimited food and the chicks were removed after hatching to encourage double clutching. Chicks were fed a formula of proprietary parrot chick food mixed with water and a probiotic, through a syringe with a tip attachment until their crop was full. An attempt was made to weigh the chicks to the nearest gram each day until they fledged. However, for a variety of reasons, especially in the USA, where the chicks were being sold as they neared weaning, this was not possible.

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Chapter 3

Diet of the Brown-headed Parrot

Introduction

Many authors have described Brown-headed Parrots eating specific items (Vincent 1934; Fuggles-Couchman 1939; Juniper & Parr 1998) or given more general dietary descriptions (Forshaw 1989; Maclean 1993). However, these descriptions, which are reviewed in Chapter 1, lack temporal, spatial or quantitative detail. Generally, it is agreed that the Parrots eat a mixture of berries, seeds and fruits but in mixed woodland in the tropics, the availability of these items may vary both seasonally and from year to year (Karr 1990) and their occurrence may be highly unpredictable (Lawes, Henzi & Perrin 1990; Koen 1992).

Therefore here I address the issue of what exactly do Brown-headed Parrots eat? A bird's perception of food availability is different from a human researcher's perception of availability (Hutto 1990). Lacking knowledge of the species full feeding constraints, sampling the "kind" of food existing in an area and concluding that it is available to a species, at best introduces bias to a study (Morrison *et al.* 1990; Block & Brennan 1993) or is merely conjecture (Hutto 1990). Furthermore, extrapolation from parameters of observer-defined availability to the user-defined parameters of the bird species ignores differences in sampling techniques (Heinrich & Collins 1983), inaccessibility (Moermond & Denslow 1983) and mechanical (Sherry & McDade 1982) and chemical defences of the prey species (Janzen 1980). Therefore, a contrast between the perceived food supply and the actual species utilisation by Brown-headed Parrots was not attempted. Instead, the principal aim was to describe the diet of Brown-headed Parrots throughout the year.

Methods

Detailed descriptions of the study areas and transects are given in chapter 2. At least three transects were attempted each day at each site, two in the morning and one in the afternoon, with the first beginning between just after dawn (Table 3.1). The duration of each transect run was dictated by events. When seen, parrots were observed until they flew away; a transect run with no sightings lasted < 30 minutes. 1360 transect runs were made (Table 3.1).

Site	No. of Runs	Date	Min. Time	Max. Time	Mean Time
Punda Maria	**368**	**2nd June 1996 – 12th Apr. 1997**	**28**	**217**	**163**
Mozambique	**217**	**15th June – 24th Dec. 1997**	**33**	**104**	**71**
Pretoriuskop	**749**	**1st Mar. 1998 – 2nd April 1999**	**37**	**241**	**174**

Table 3.1: Number and duration of transect runs made to observe Brown-headed Parrots. The minimum and maximum time taken to complete each run and the mean time is given in minutes.

Any feeding behaviour of individuals or groups was recorded as and when observed on a transect. The species of each dietary item was noted as was the plant part consumed and the date. Which part of the prey species being consumed was also recorded. Tree nomenclature follows Palgrave (1977).

Results

Species Utilised

A distinction was made between intensive feeding and intermittent feeding. Intensive feeding by Brown-headed Parrots was characterised by consumption of a succession of food items. Intermittent feeding was characterised by birds indulging in a variety of behaviours, which could, but not necessarily include, feeding e.g. allopreening, preening or sleeping. Intensive feeding began an hour after dawn and continued for the next 4–5 hours. Intensive feeding resumed in mid-afternnon and continued until an hour before sunset, when they usually drank.

The parrots were exclusively arboreal when feeding. All dietary items derived from trees or shrubs, no grass seeds were eaten.

The actual number of tree species utilised monthly at each site for food is summarised in Figure 3.1.

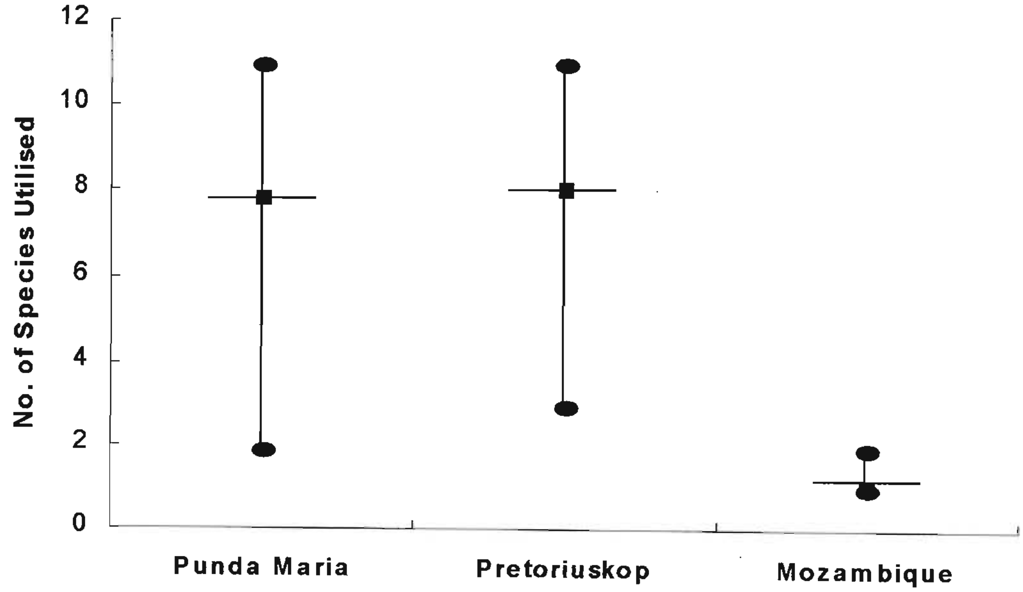

Figure 3.1: Plot of maximum and minimum number of tree species utilized per month over one year and the mean annual number of tree species utilized by Brown-headed Parrots for food at the three study sites.

No significant difference exists between the mean number of species utilized at the two KNP sites (Mann-Whitney, W= 157.5, $p > 0.05$), although the variance is larger at Punda Maria (8.15) compared with Pretoriuskop (4.91), indicating a relatively wider range of prey items. This is further validated by considering the number of species eaten by parrots each month (Figure 3.2). Regression indicated no statistically significant difference between the absolute numbers of tree species utilised per month at the two KNP sites ($r^2 = 0.838, f = 1.00, df = 1$). The number of tree species utilized declined from September, from a high in the winter months of between 8 and 11 to only two and three at Pretoriuskop and Punda Maria respectively in December. Few dietary items were recorded at the Mozambique site, however, the situation in southern Mozambique was compounded by two factors. The study area became inaccessible after the summer rains leading to abandonment of the site. Secondly observation was limited to the east of the site as a result of suspected minefields.

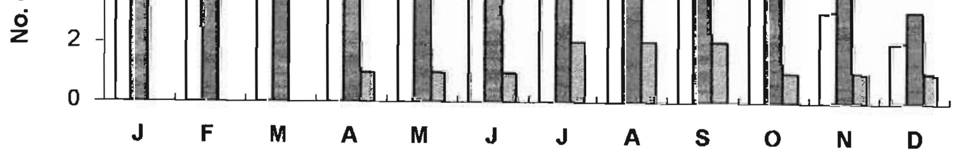

Figure 3.2: The number of tree species utilised by Brown-headed Parrots each month at the 3 sites. Unshaded denotes Punda Maria, shaded, Pretoriuskop and solid, Mozambique.

Seasonal changes in the vegetative diet of Brown-headed Parrots in terms of species composition and the parts of the prey items eaten are presented (Figure 3.3). Two points should be noted. The list is not exhaustive as they certainly eat other species outside the distributional range of this study (see Juniper & Parr 1998). Furthermore, they were unable to handle the fruits of *Sclerocarya birrea* (Marula) or *Strychnos madagascariensis* (Black Monkey Orange). The former fruit is hard, spherical and 2.5 cm in diameter. Individuals bit into them *in situ* until the fruit dislodged and fell to the ground. No attempts were made to retrieve these items. The fruit of the Black Monkey Orange is also spherical, 8 cm in diameter and covered with a thick woody shell (Palgrave 1977). Birds fed on the parts of the fruit discarded by vervet monkeys (*Cercopithecus (aethiops) pygerythrus*). This was the only time, apart from drinking, that Brown-headed Parrots were seen on the ground.

The seeds of *Cassia abbreviata* (Sjambok Pod) are contained in pods up to 90 cm long. The pod has a woody outer coat and the seeds are contained within green flesh. To open the pod, birds first clung to the length of the pod and bit into it repeatedly, until a hole was made. The coat was then pulled off up the length of the pod and the seeds extracted. The green flesh was discarded. Opening a virgin pod took about 57 bites and the mean time from beginning a new pod to extracting the first seed was 62.5 seconds (n = 39).

All other food items were plucked from a tree and held in one foot. Parrots did not discriminate between the pod or the seed in the pods of the *Acacia* species, which were eaten whole. Although the *Acacia* pods were picked from the tree and held in the foot, the pods were heavy in comparison with other food items. No pods were ever entirely comsumed. Usually they were dropped during manipulation, but unlike the fruit of *Strychnos madagascariensis* no attempt was made by parrots to retrieve the dropped pods. The seed "wings" of *Combretum* and *Terminalia* species were removed before consumption of the seed, which was swallowed whole, as were the small fruit of *Rhus rehmannianii.*

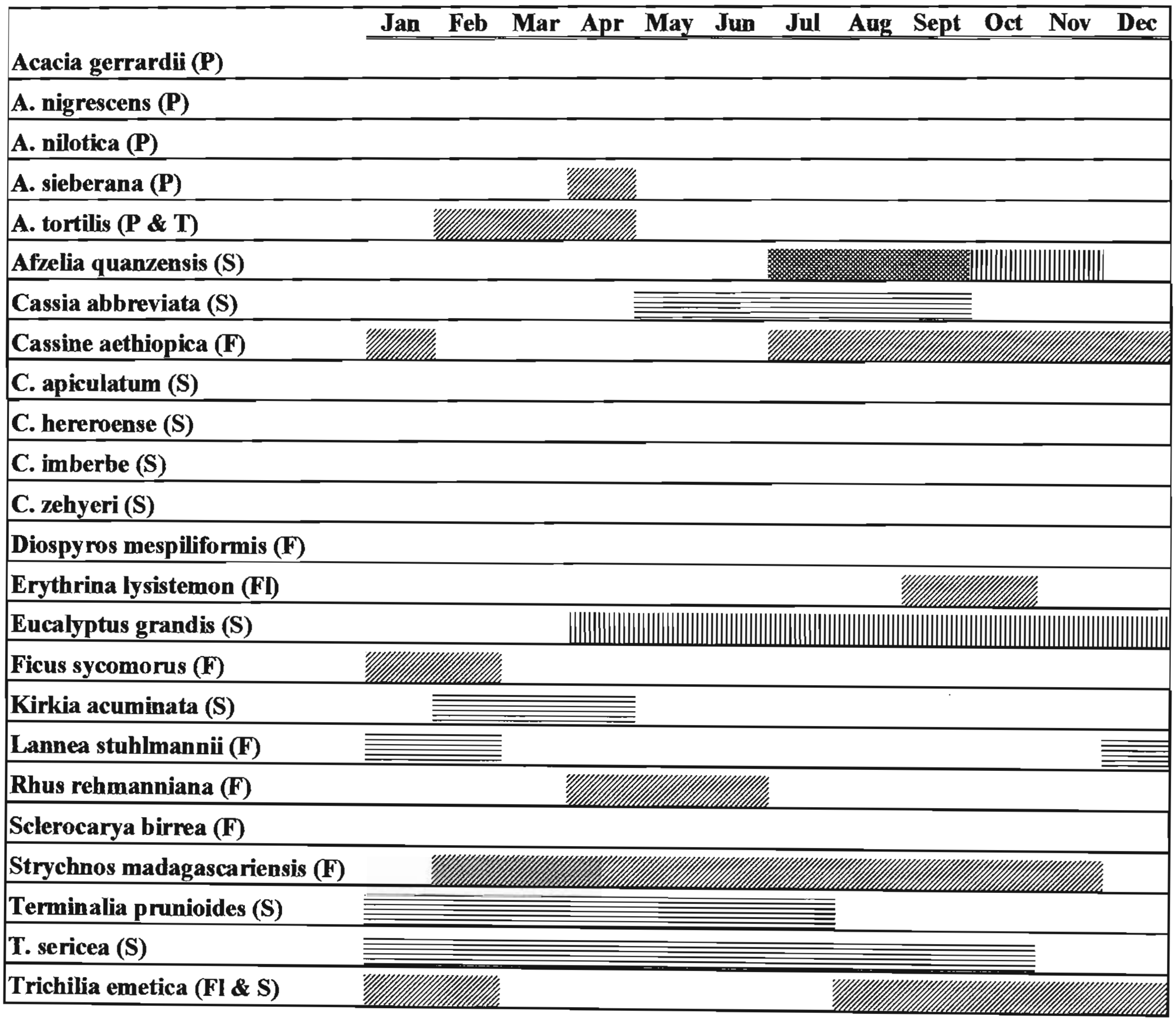

Figure 3.3: Tree species and the parts utilised by Brown-headed Parrots. Horizontal bars denote Punda Maria, diagonal bars denote Pretoriuskop and vertical bars denote Mozanbique. The solid fill denotes both Punda Maria and Pretoriuskop. The trellis fill denotes both Punda Maria and Mozanbique. F = fruit, Fl = flower, P = pod, S = seed and T = thorn.

Other fruits were discarded. The flowers of *Trichilia emetica* (Natal Mahogany) were eaten entire, however, the flowers of *Erythrina lysistemon* (Common Coral Tree) were removed and held in one foot. The nectary was squeezed in the bill and the flower discarded.

Acacia tortilis (Umbrella Thorn) has two types of thorn, hooked and straight thorns, arranged spirally around the branchlets. Only the long straight thorns were taken. In some instances, birds removed the thorn and chewed the base. In other instances the thorn was left on the branchlet. The bird applied the bill round the base and worked its way to the tip of the thorn without removing it from the branchlet. This behaviour remains puzzling but the birds were likely trapping and eating small ants or other insects. In January and February 1999, many of the Brown-headed Parrots in Pretoriuskop, were seen searching for, and eating cocooned caterpillars of an unknown species.

Three of the *Acacia* species and the four *Terminalia* species were available and eaten by Brown-headed Parrots at both KNP sites. Fruit items common to both sites, were *Diospyros mespiliformis* (Jackal Berry), *Ficus sycomoros* (Sycamore Fig) and *Scleocarya birrea* (Marula). Brown-headed Parrots utilised 16 tree species throughout the year at Punda Maria, of which 6 species were exclusive to this site. At Pretoriuskop they utilised 17 tree species, of which again 6 were exclusive to this site. Brown-headed Parrots at the Mozambique site were only seen to utilise 2 tree species for food. Brown-headed Parrots also fed on *Afzelia quanzensis* at Punda Maria although this species was only eaten for three months at Punda Maria in contrast with five months in Mozambique.

The decline in number of tree species utilised in Spring and early Summer and subsequent concentration on a relatively few species at both KNP sites is demonstrated in Figures 3.4 & 3.5, which show the relative percentage of time spent feeding on each species each month. Only tree species, which Parrots utilised > 10% of their total time feeding for any single month are shown.

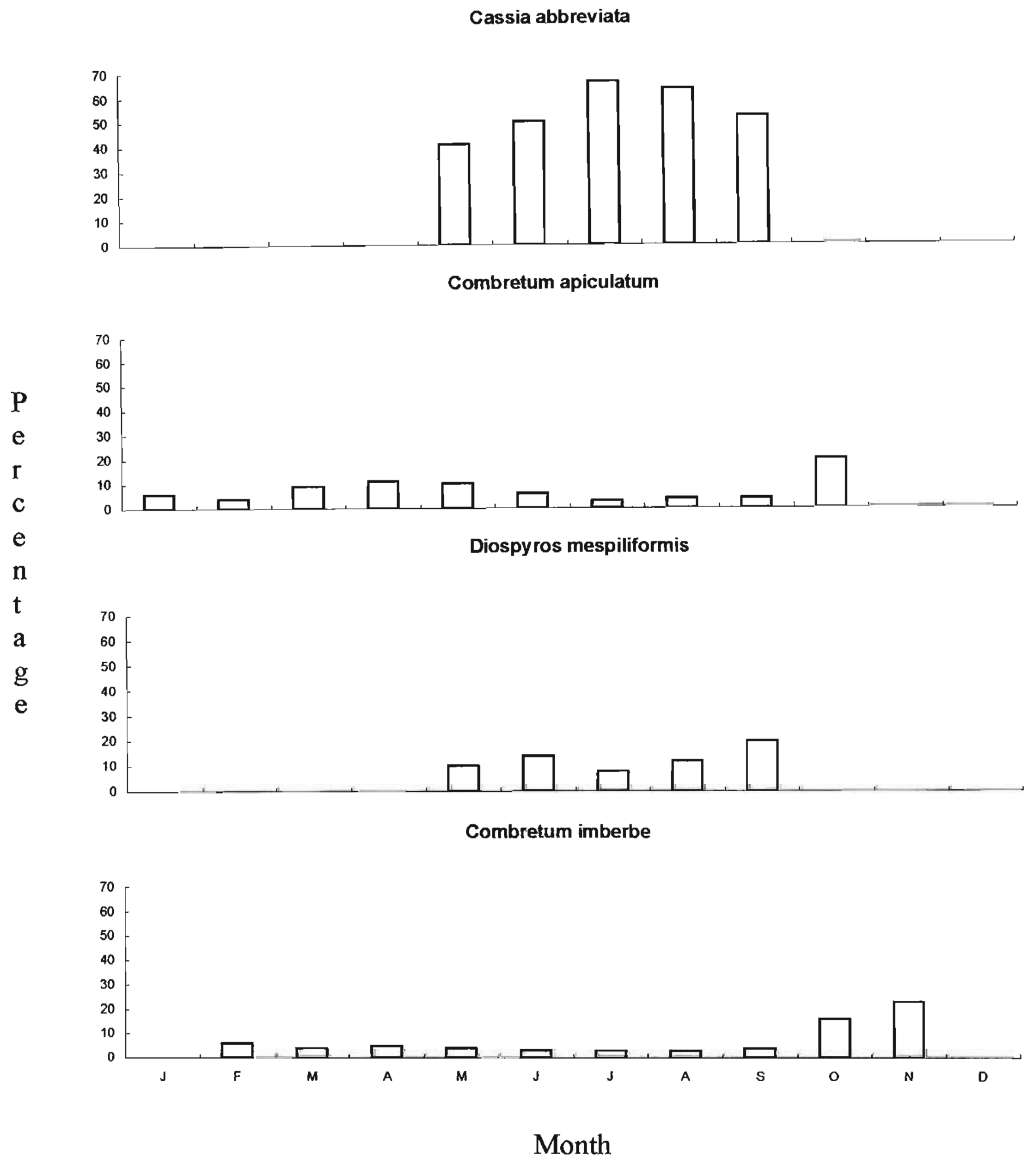

Figure 3.4a: Plant dietary preference (Δ10% of potential total food intake for at least a single month) of Brown-headed Parrots at Punda Maria, expressed as a percentage of total time observed feeding.

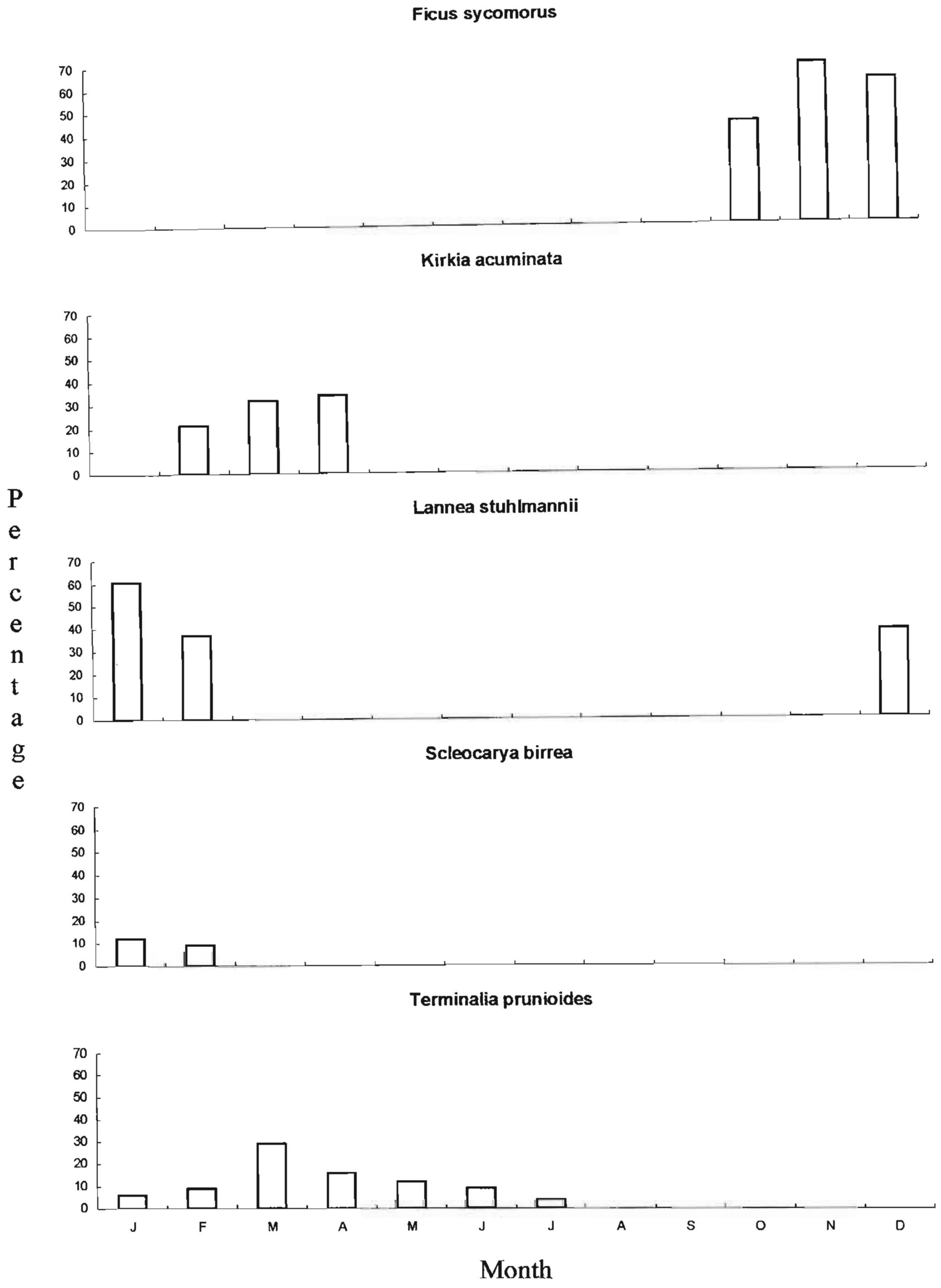

Figure 3.4b: Plant dietary preference (Δ10% of potential total food intake for at least a single month) of Brown-headed Parrots at Punda Maria, expressed as a percentage of total time observed feeding.

Therefore, although 16 species were eaten at Punda Maria only nine species comprised Δ 10% of the diet any single month (Figure 3.4). Of these nine species, the fruit *Scleocarya birrea,* formed a dietary constituent in January and February. But this species comprised relatively little of the entire dietary intake in each of those months, 12% and 9% respectively. The intake of *Diospyros mespiliformes* was > 10% of the entire diet for each month it was in season except July, where it dropped to 8% of the total. *Combretum apiculatum* and *C. imberbe* were also significant dietary items, the former species constituting Δ10% of the total diet in April, May and October, whilst the latter species formed Δ10% of the total diet in November and December. Similarly, *Terminalia prunioides* was utilised from January to July but only in March to May did this species constitute Δ10% of the total intake at Punda Maria (however, see below).

Of the nine species, which form Δ10% of the diet of Brown-headed Parrots in any one month, only four species formed the bulk of the annual diet, *Lannea stuhlmannii, Kirkia acuminata, Cassia abbreviata* and *Ficus sycomoros*. Of the 16 species utilised, 50% of these contributed < 5% of the annual intake (Figure 3.5).

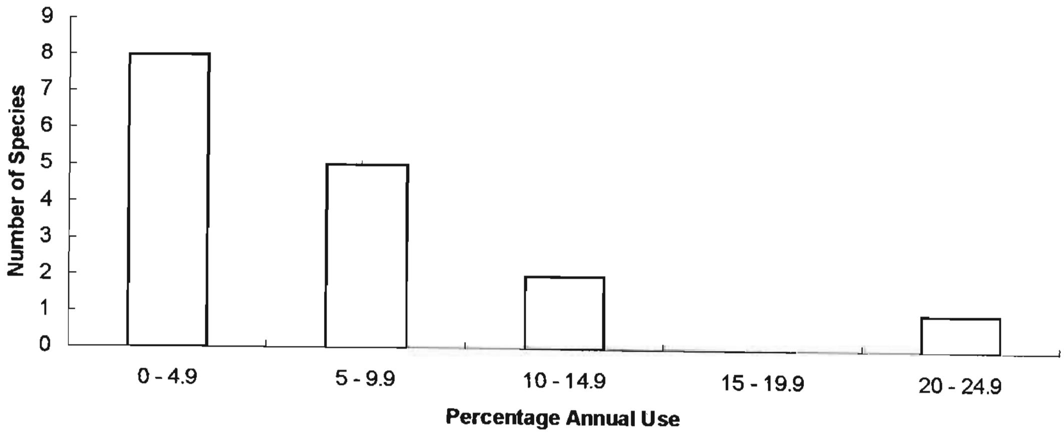

Figure 3.5: Number of tree species utilized by Brown-headed Parrots expressed as a percentage of their relative annual feeding regime at Punda Maria.

By far the most important species in the Punda Maria area was *Cassia abbreviata* (Figs. 3.4a & 3.5). This species was unique in that it constituted over 20% of the parrots relative annual feeding regime. The importance of this species is further illustrated in Figure 3.6, which details the monthly total sightings of Brown-headed Parrots in July, 1996. Of the 130 birds seen in that month, 112 of the sightings (86.15%) were made on five large *Cassia abbreviata* trees, which occupied an area 250m x 170m.

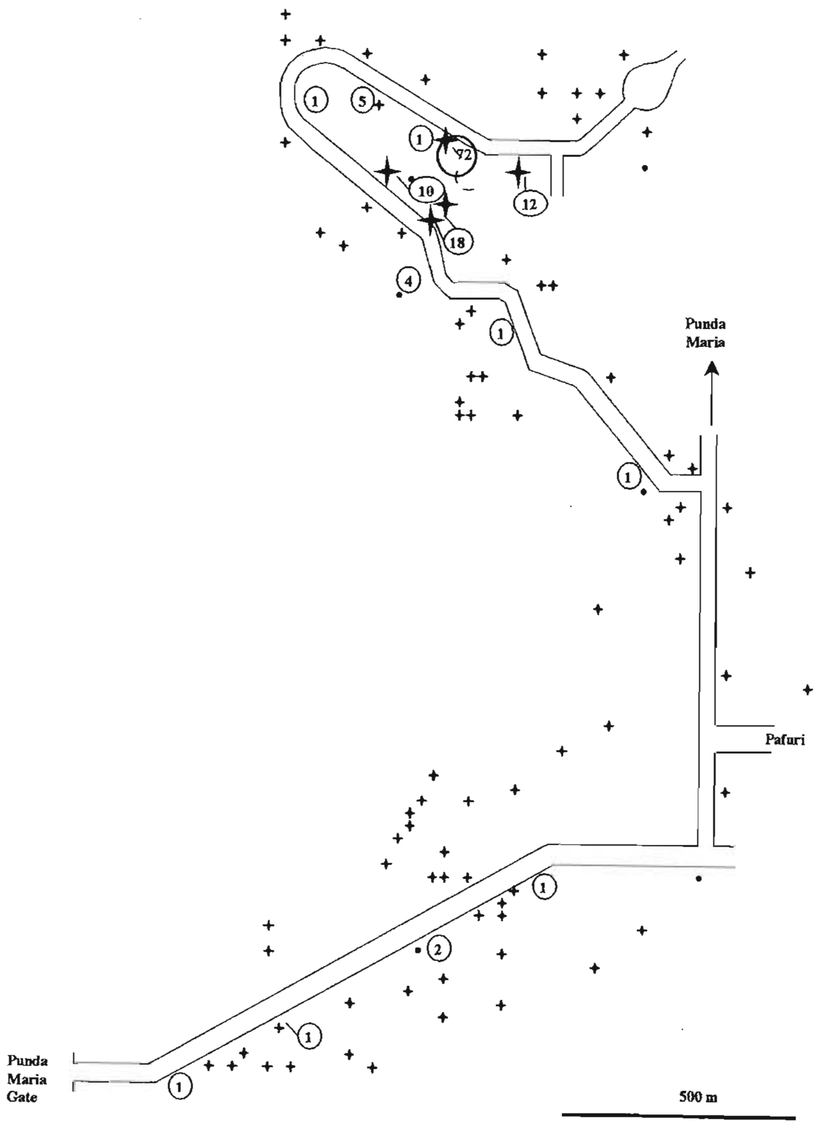

Figure 3.6: Brown-headed Parrot sightings in July 1996 on the Punda Maria transect feeding on *Cassia abbreviata*. Large stars represent trees above 5m in seed, smaller stars represent trees below 5m in seed. Dots represent trees not in seed.

At Pretoriuskop, seven species formed < 10% of the diet in any single month and ten species constituted < 5% of the relative annual feeding regime (Figure 3.7).

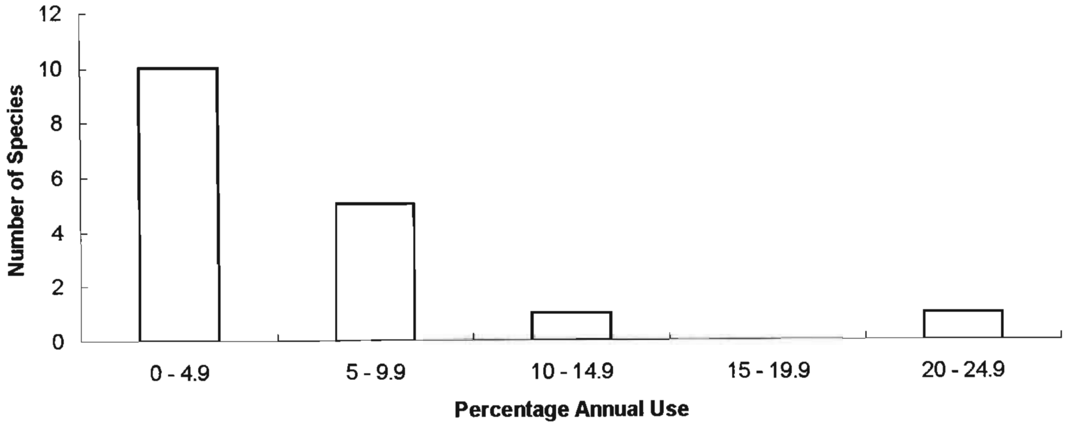

Figure 3.7: Number of tree species utilised by Brown-headed Parrots expressed as a percentage of their relative annual feeding regime at Pretoriuskop.

The seeds of *Trichilia emetica* constituted Δ 59% of the diet in January and February (Figure 3.8b). Like *Cassia abbreviata* at Punda Maria, *Trichilia emetica* was the major source of food for Brown-headed Parrots at Pretoriuskop constituting > 20% of the annual feeding regime. Throughout autumn and winter, *Acacia gerrardii, Cassine aethiopica, Combretum apiculdulatum, C. hereroense, C. imberbe, C. zehyeri, Diospyros mespiliformes* and the flowers of *Trichilia emetica* formed > 10% of the diet for at least one month (Figs. 3.8a & 3.8b). Only in September and October did the parrots concentrate their feeding efforts on a single species, *Erythrina lysistemon.* In December they returned to the seeds of *Trichilia emetica,* which constituted 63% of their diet in that month.

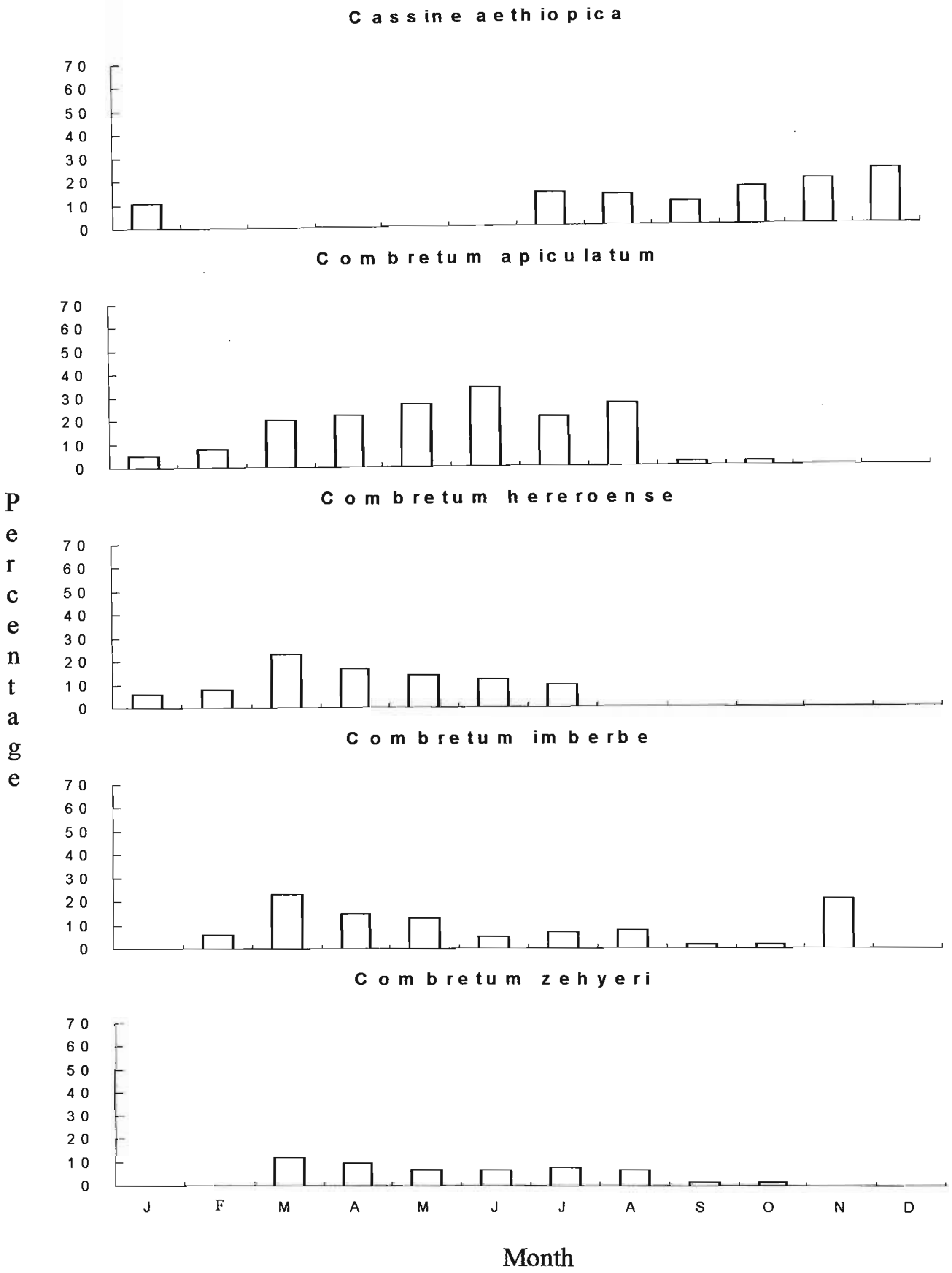

Figure 3.8a: Plant dietary preference (Δ 10% of potential total food intake for at least a single month) of Brown-headed Parrots at Pretoriuskop, expressed as a percentage of total time observed feeding.

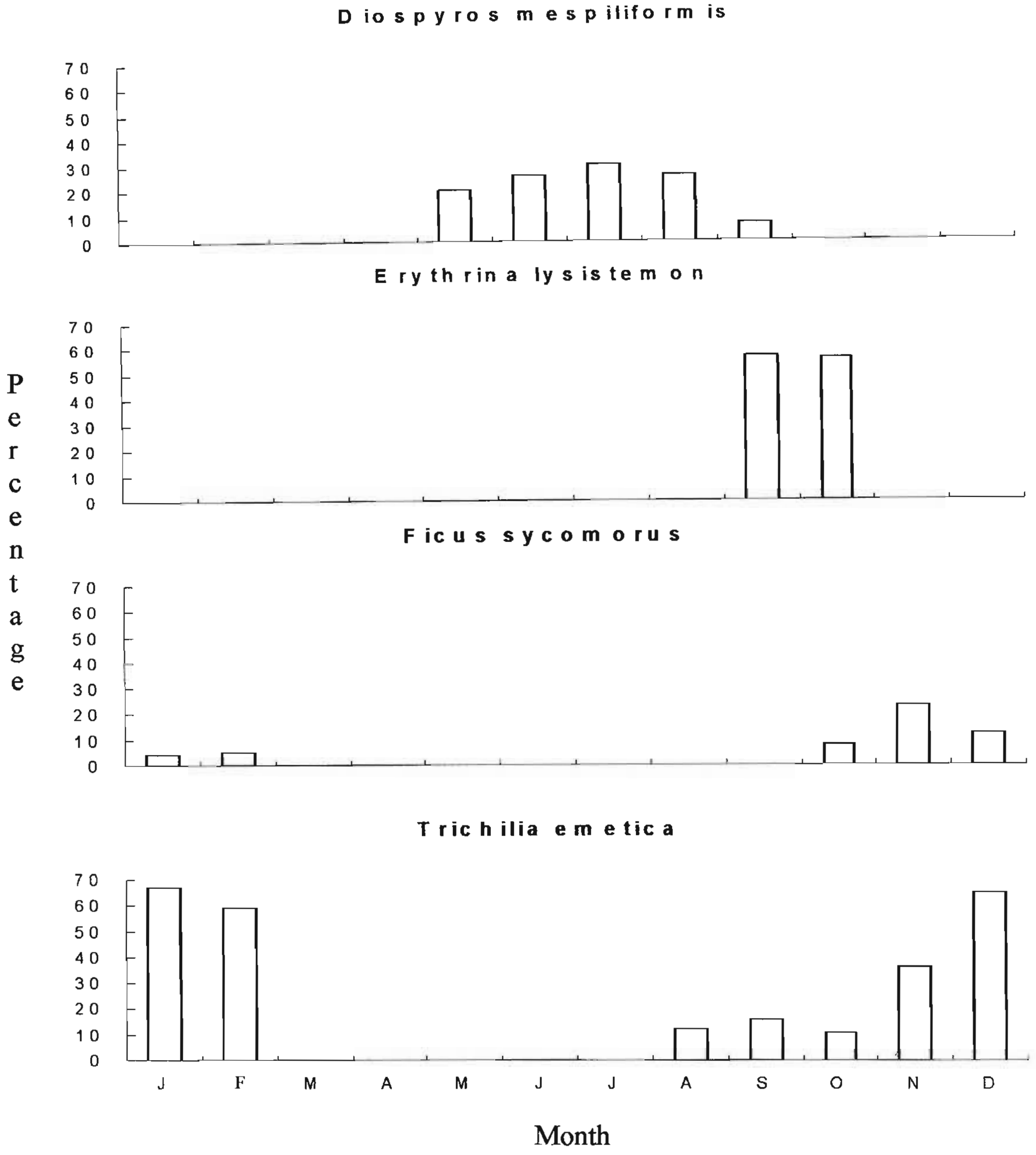

Figure 3.8b: Plant dietary preference (Δ than 10% of potential total food intake for at least a single month) of Brown-headed Parrots at Pretoriuskop, expressed as a percentage of total time observed feeding.

The seeds of *Eucalyptus grandis* were the most common item in the diet of the parrots in Mozambique. The only other food item seen to be taken was *Afzelia quanzensis* (Pod Mahogany). The seeds of this species are contained within a thick woody pod. The pod opens naturally by dehiscence. However, as mentioned earlier, area access was limited to the east of the *Eucalyptus* plantations. Birds seen foraging on the transect, were always moving in a general easterly direction.

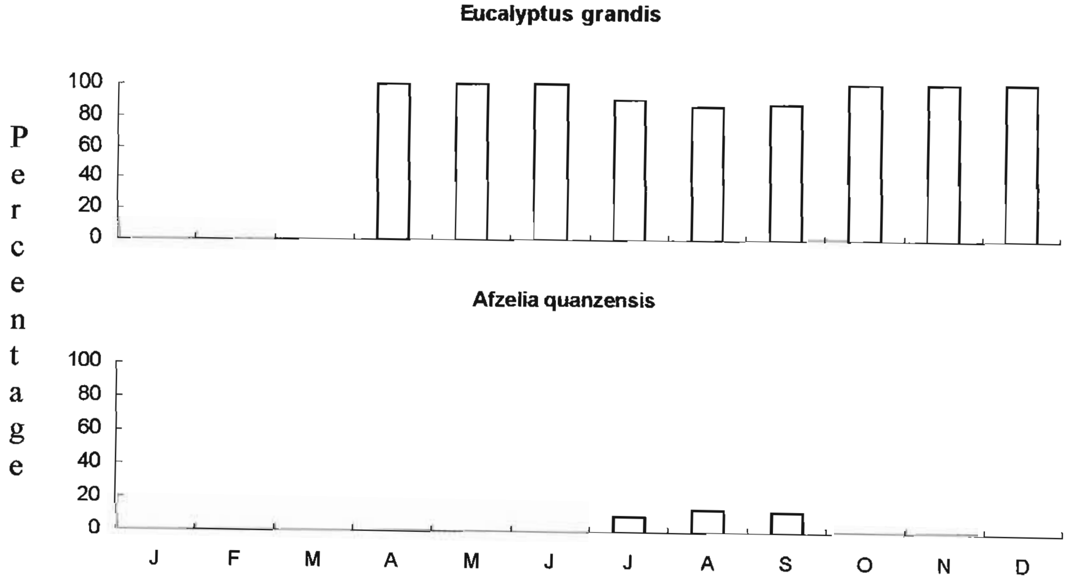

Figure 3.9: Potential food intake of Brown-headed Parrots at Mozambique, expressed as a percentage of total time observed feeding.

Drinking

Like all parrots, the Brown-headed Parrot drinks by immersing the beak and sucking the water up (Forshaw 1989). A mean of 15 immersions was made per drinking occasion (S.D. = 2, n = 237) and birds drank just after sunrise and just before sunset. The parrots in the three study areas used any source of water, small areas of veld water, dams and the artificial water troughs in the Kruger

National Park, which were implemented in the 1960's to provision large mammals during water shortages. They also drank from the small pools, which form under the taps in the tourist rest camps.

Discussion

Brown-headed Parrots are opportunistic, generalist feeders. An example of their opportunism being the utilization of Eucalyptus seeds in Mozambique, which has only been available to them in the last few decades. Across all the study sites no particular tree species seems to be crucial to the species' survival. At Punda Maria, *Cassia abbreviata* was the most utilised species, yet this was during the winter months, when *Combretum apiculatum, C. imberbe* and *Diospyros mespiliformes* formed the bulk of the diet of Parrots in Pretoriuskop. All three of these species were available and indeed were utilised to some extent by the parrots in Punda Maria. Therefore *Cassia abbreviata* is not an essential dietary element. Likewise, at Pretoriuskop, the most utilised species was *Trichilia emetica* during the early summer, when the parrots at Punda Maria concentrated on *Ficus sycomorus*, which again was available and being utilised at Pretoriuskop. However, by the end of the year the figs had disappeared and in January and February, the Parrots at Punda Maria concentrated on the fruits of *Lannea stuhlmannii*. This option was not available to the parrots at Pretoriuskop, which does not lie within the distribution of *L. stuhlmannii*, therefore the presence of *Trichilia emitica* during those months may be vital for the survival of Brown-headed Parrots in the Pretoriuskop area.

The generalistic nature and seasonality of the diet is similar to that reported for Orange-bellied Parrots (Poicephalus rufiventris) in Tanzania (Massa 1995) and Rüppell's Parrots (*P. rueppellii*) in Namibia (Selman *et al.* 2000). No species seems to be critically important with Rüppell's Parrots moving from one suite of species to another as and when those species become available. However, the only other *Poicephalus* Parrot, which has been studied, the Cape Parrot

(*Poicephalus robustus*), tends towards specialism on *Podocarpus* species (Wirminghaus *et al.*, 2002).

Relatively little is known about the diet of other African parrot species in the wild, although studies, which have been completed, indicate that each species includes an extremely varied range and number of food items. Brown-headed Parrots utilised 16 tree species for food at Punda Maria and 17 species at Pretoriuskop, whilst Selman *et al.* (2000) reported R✦ppell's Parrots feeding at 37 plant species. The Ground Parrot (*Pezoporus wallicus wallicus*) in Tasmania is granivorous and utilises at least 49 species (McFarland 1991), whilst the Scaly-headed Parrot (*Pionus maximiliani*) in southeastern Brazil is a generalist utilising 38 species (Galetti 1993). The greater diversity of the diet of these species compared with Brown-headed Parrots, is probably a function of greater habitat diversity. Phenological data in the latter study estimated 265 available tree species. Toyne & Flanagan (1997) noted Red-faced Parrots (*Hapalopsittaca pyrrhops*) feeding on 14 species, however, this was based on only 3 months observation.

In early 1999, Brown-headed Parrots at Pretoriuskop, were observed eating cocooned caterpillars and almost certainly eating other insects at other times of the year. The consumption of live animal material by parrots is probably widespread (Munn 1988; Sazima 1989; Forshaw 1989; Galetti 1993; Selman *et al.* 2000), and offers a supplemental source of protein at times when the only other nutritional source is fruit.

However, in many avian and mammalian species it has been demonstrated that switches in diet from insects to fruit consumption or from seeds to fruit may impose ecological constraints, involving phenotypic changes in gut retention rate, digestive efficiency and hence feeding rate (Levey & Karasov 1989). For instance, American Robins (*Turdus migratorius*), feeding on fruit take 3 days to increase their digestive efficiency, when switching to insects (Levey & Karasov 1992). Brown-headed Parrots were observed to switch through a mosaic of fruit, seeds and insects in one day. A future profitable line of enquiry will be consideration of the physiological adaptations, which allow parrots to make such rapid dietary switches.

Brown-headed Parrots are a major predator of the flowers of *Erythrina lysistemon*, which was a major seed source in its diet as the season progressed. This apparent contradiction was also reported from Scaly-headed Parrots, which utilise *Inga* spp. in the same way (Galetti 1993). In November and December 1996 at least 60% of the diet of Brown-headed Parrots at Punda Maria consisted of the fruits of *Ficus sycomoros*, yet Janzen (1981) has argued that the seeds of these fruits are destroyed in parrot's guts. The role of Psittacids as seed predators (Howe 1980; Galetti & Rodriqez 1992) and seed dispersers (Hopkins & Hopkins 1983) has been emphasised in South America, however, although the results presented here and elsewhere (Wirminghaus *et al.* 2002; Selman *et al.* 2000) implicate African Parrots as major seed predators, their role as seed dispersers is unknown and they may play a pivotal role in woodland ecology.

The results presented here detail the dietary preferences of the Brown-headed Parrot, however, it must be pointed out that the observations cover specific years and that the plant species may undergo dietary shifts between years. It may be that the patterns outlined are unique to the years reported (Block & Brennan 1993). It is probable that influences such as weather, conspecific density and plant phenology produce fluctuations in the relative and absolute utilisation of certain species between years. Further, it is possible that some species, which parrots did not utilise during the time of this study, may, nevertheless, be important dietary items at other times. This phenomenon was observed at Punda Maria between 1996 and 1997 in relation to *Cassia abbreviata*. In 1996, this species constituted over 20% of the annual food requirement of the parrots. Yet in 1997, the fruits of this tree did not develop. The Brown-headed Parrots simply turned to other species, which had ripening fruit.

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Chapter 4

Are Brown-headed Parrots Constrained by Temporal or Spatial Food Availability?

Introduction

Most species of parrots use their capacity of flight to procure digestible and nutritious food items, some migrating over large distances to ensure sufficient dietary items (Forshaw 1989). For instance the Cape Parrot (*Poicephalus robustus*) may travel 100 km per day to seek out nutritious food (Skead 1964, 1971; Wirminghaus *et al.* 2002). Such a strategy has a high energetic cost, therefore other species have adopted a more sedentary life-style.

The adoption of such a strategy is possible only if the predator species has evolved the ability to procure and digest the food available coupled with temporal accessibility of prey species (Block & Brennan 1993). In mixed woodland in the tropics, the availability of berries, seeds and fruits may vary both seasonally and from year to year (Janzen 1980; Karr 1990); the availability of food may be highly unpredictable (Lawes *et al.* 1990; Holmes 1990; Koen 1992); and therefore, predators experience competition for food items both from conspecifics and other species (Wright *et al.* 1999).

Although, some authors report local migration in Brown-headed Parrots (e.g. Rowan 1983; Juniper & Parr 1998), they do not migrate or move long distances (pers. obs.). In Chapter 3, I described the diet of the Brown-headed Parrot in terms of their utilization of species. In this chapter I consider the species utilized by the Parrots in terms of the energy and protein content, in turn relating this to the speed at which the birds can consume these items. I also consider the amount and type of interactions that Brown-headed Parrots may have with other species, which may be foraging on the same species. The hypothesis under test is that Brown-headed Parrot populations are not constrained by seasonal nutritional availability.

Methods

Detailed descriptions of the study areas and transects are given in chapter 2. At least three transect runs were attempted each day, two in the morning and one in the afternoon, with the first run beginning between 6 and 7 am, depending on season. The length of time of each run was dictated by events on the run. When seen, parrots were observed until they flew away, a transect run with no sightings lasted less than 30 minutes. A total of 1360 transect runs were made (Table 4.1).

Site	No. of Runs	Date	Min. Time	Max. Time	Mean Time
Punda Maria	368	2nd June 1996 – 12th Apr. 1997	28	217	163
Mozambique	217	15th June – 24th Dec. 1997	33	104	71
Pretoriuskop	749	1st Mar. 1998 – 2nd April 1999	37	241	174

Table 4.1: Number of transect runs made and the period of time spent at each site. The minimum and maximum time taken to complete each run and the mean time is given in minutes.

Any feeding behaviour of individuals or groups was recorded as and when observed. The species of each dietary item was noted as was the date. Which part of the prey species being consumed was also recorded and the number of items consumed in a continuous feeding bout of 10 minutes. Feeding bouts lasting less than 10 minutes were discounted. The mean handling times for each item was then calculated. Other species seen feeding on the same prey item were also noted in a similar manner. Representative specimens of each food item were collected. These were weighed to the nearest gram and stored at –25° C.

These specimens were later analysed for water content, crude protein, gross energy and calcium and phosphorus at the Department of Animal and Poultry Science at the University of Natal, following the methods of Helrich (1990). Samples were placed in a drying oven at 60°C until constant weight was achieved. The percentage water was then calculated and subsequently the water kg^{-1} sample. The nitrogen content was measured in a LECO FP20000 nitrogen analyser using the Dumas combustion method. This was converted to the equivalent crude protein content by a numeric factor (968.06 AOAC 1990). The gross energy was calculated from the energy released from combustion in an isothermal caloric bomb calorimeter.

Results

A summary of the nutritional content of the food items utilised by Brown-headed Parrots is given as Table 4.2. Little variation exists in the energy content of the food items (mean = 16.97 kJ g^{-1}, S.D. = 1.03), with much more variation in the protein content.

							Potential intake in 10 minutes			
	E	**P**	**M**	**H**	**S.D.**	**n**	***E***	***S.D.***	***Protein***	***S.D.***
Acacia gerrardii	17.80	11.61	5.06	39.18	22.96	137	32.80	19.22	4760.3	3001.3
A. nigrescens	17.76	11.79	11.60	47.39	28.57	193	66.48	40.08	9797.1	6112.3
A. nilotica	17.43	11.92	6.20	50.25	30.20	160	28.14	16.91	4193.3	2619.2
A. sieberana	17.66	12.14	13.70	44.25	24.87	75	50.07	28.14	7597.6	4863.9
A. tortilis	17.77	12.37	4.70	47.77	29.27	104	10.90	6.68	1686.1	1045.5
Afzelia quanzensis	15.83	15.91	7.29	134.09	26.82	136	22.37	4.47	4448.0	3706.6
Cassia abbreviata	17.20	18.49	0.52	11.75	1.96	209	9.09	1.52	2101.6	1801.1
Cassine aethiopica	15.78	1.31	1.13	27.21	3.76	218	5.13	0.71	83.9	73.8
Combretum apiculatum	17.61	10.41	0.27	16.78	1.60	209	5.50	0.52	716.2	653.9
C. hereroense	18.00	10.88	0.23	16.83	1.62	219	4.57	0.44	620.9	566.4
C. imberbe	17.73	10.96	0.26	16.75	1.59	236	5.02	0.48	687.8	628.2
C. zehyeri	17.45	7.58	0.48	33.25	6.41	196	6.18	1.19	585.5	490.9
Diospyros mespiliformis	15.49	1.28	1.45	26.85	7.23	128	5.72	1.54	91.5	72.1
Eucalyptus nigra	14.68	15.84	2.62	25.68	5.04	220	40.91	8.03	8100.6	6771.6
Ficus sycomorus	16.32	4.56	6.06	34.28	8.45	137	47.99	11.83	2735.7	2194.7
Kirkia acuminata	15.29	1.27	1.84	23.76	3.99	212	6.26	1.05	99.2	84.9
Lannea stuhlmannii	17.31	7.29	0.38	4.75	0.81	226	9.31	1.59	848.1	724.5
Rhus rehmanniana	16.07	6.38	0.34	1.00	0	93	48.44	0	3862.9	0
Scleocarya birrea	16.44	1.77	17.60	16.00	7.62	91	187.65	89.37	4151.8	2812.4
Strychnos madagascariensis	18.80	3.56	18.60	57.71	16.22	45	81.84	23.00	3641.8	2842.8
Terminalia prunioides	17.21	10.49	0.24	17.90	1.92	200	4.46	0.48	584.7	528.1
T. sericea	17.37	10.73	0.23	15.82	2.67	216	4.60	0.78	616.6	527.6
Trichilia emetica	17.42	16.47	4.14	4.92	1.41	214	295.97	84.82	60932.0	47359.5

Table 4.2: Summary of the nutritional value of the food observed to be consumed by Brown-headed Parrots. The total energy (E) (kJ g^{-1DW}) per gram of the dry weight of food items. The protein (P) (mg g^{-1DW}) per gram of the dry weight of food items. The mass (M) of the item is in grams. The mean handling time (H) in seconds and standard deviation of the mean. The mean intake of energy and protein standardised for 10 minutes feeding and the standard deviations is also shown (see text for detailed description).

Further sources of variance are the handling time for each item (mean = 29.86 s, S.D. = 27.46) and the mass of each item (4.56 g, S.D. = 5.67). Therefore for meaningful comparison, Table 4.2 also presents the energy and protein values after standardisation for the mass of each item and the number of items an individual was able to consume in 10 minutes of continuous feeding. Therefore a Parrot continuously eating *Combretum hereroense* for 10 minutes acquires 4.57 (± 0.44) kJ of energy. Eating the seeds of *Trichilia emetica* for the same amount of time, potentially, yields 295.97 (± 84.82) kJ of energy. Similarly, an individual eating *Diospyros mespiliformes* for 10 minutes acquires 91.5 (± 72.1) mg. protein, whilst the same amount of time spent feeding on *Rhus rehmanniana* accumulates 3862.9 mg. protein (*Rhus rehmanniana* was swallowed whole, no S.D. was measured).

No significant difference exists between the handling times of the *Combretum* spp, with the exception of *C. zeyheri* which is much larger, (ANOVA, $f_{(663,2)} = 0.16$, $p = 0.852$). Similarly, no statistical difference exists between the three species in terms of their nutritional value (Kruskal-Wallis, $H = 4.57$, $p = 0.470$, $df = 5$) (Table 4.3).

	Protein mg day^{-1}	**Energy (kJ g^{-1})**
C. apiculatum	**716.2**	**17.612**
C. hereroense	**620.9**	**17.998**
C. imberbe	**687.8**	**17.732**

Table 4.3: Nutrient value of three species of *Combretum* spp. eaten by Brown-headed Parrots

In terms of the similarity of handling times and nutritional content, the suite of *Combretum* spp., can be thought of as a single species (Table 4.3). Their accumulated utilisation over an annual cycle is shown as Figure 4.1, indicating their importance, especially at Pretoriuskop, where the three species constitute over 50% of the diet between March and June.

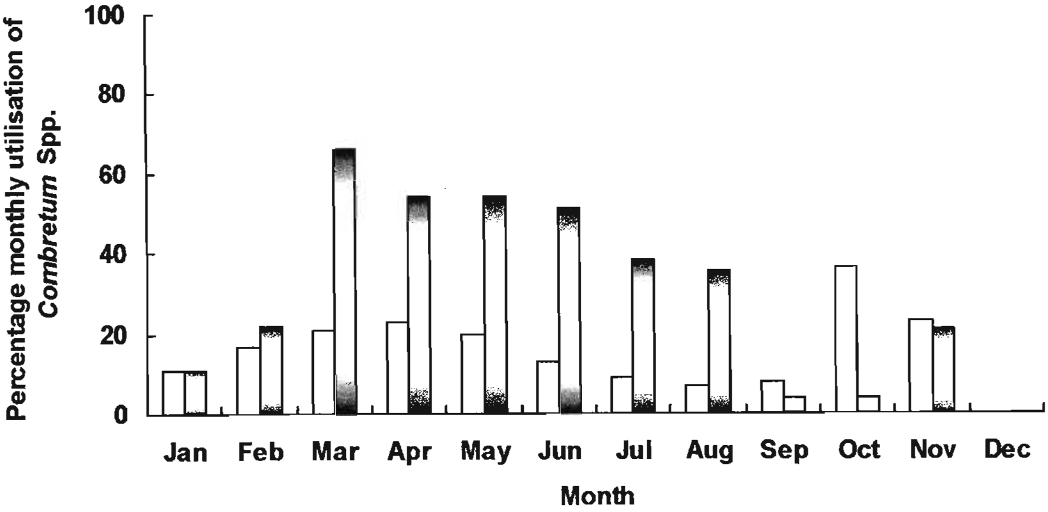

Figure 4.1; Percentage utilisation by Brown-headed Parrots of *Combretum* spp. in KNP, expressed as a percentage of total time observed feeding. Pretoriuskop is shaded.

In order to compare the seasonality of the nutritional content of the diet, the energy and protein content was calculated using the data from the previous chapter. Winter was defined as March to September. At Punda Maria, although the energy content of the summer diet is appreciably more than the winter diet the difference is not significant (Mann-Whitney, $U = 23$, $p = 0.093$). Similarly, no significant difference exists comparing the summer and winter protein content of the diet (Mann-Whitney, $U = 36$, $p = 0.156$), though there is increased protein intake during the winter. A significant difference exists between the calorific content of the winter and summer diet at Pretoriuskop (Mann-Whitney, $U = 15$, $p = 0.0369$) but no seasonal difference in the protein content of the diet (Mann-Whitney, $U = 19$, $p = 0.371$).

The total potential energy and protein intake of Brown-headed Parrots at each study site is given as Figures 4.2 & 4.3 respectively. The Figures are standardised and represent the sum of the nutritional content.

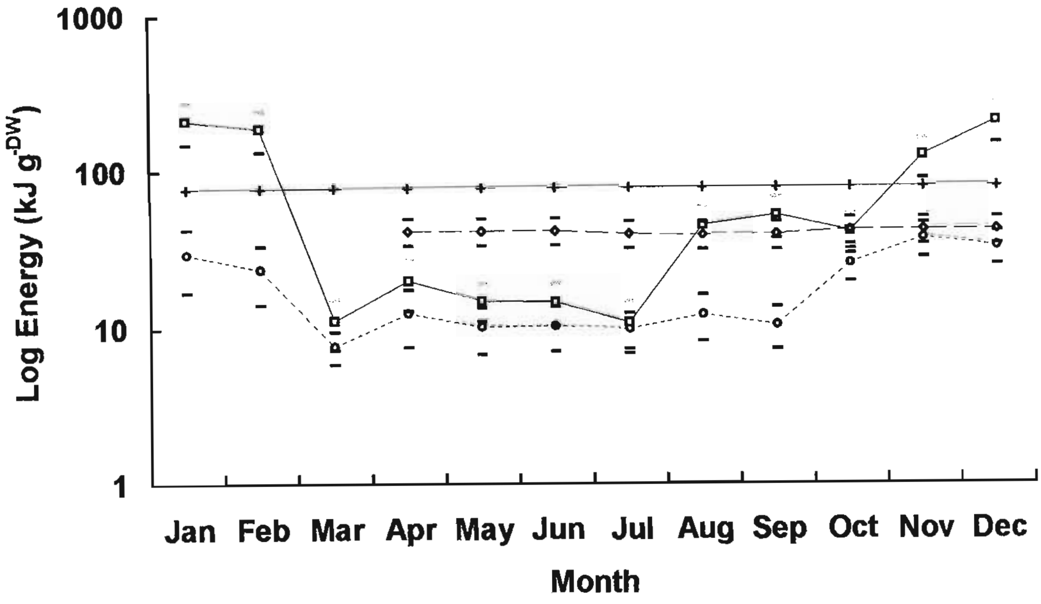

Figure 4.2: Log of the sum of the energy content, the relative monthly use of the dietary items and the total handling time of each item eaten by Brown-headed Parrots continuously eating for 10 minutes. The circles represent Punda Maria, the squares Pretoriuskop and the diamonds, Ponta Malongane. One standard deviation is shown in each case. The horizontal line represents the daily energetic basal metabolic requirement calculated from the allometric equation of Klasing (1998).

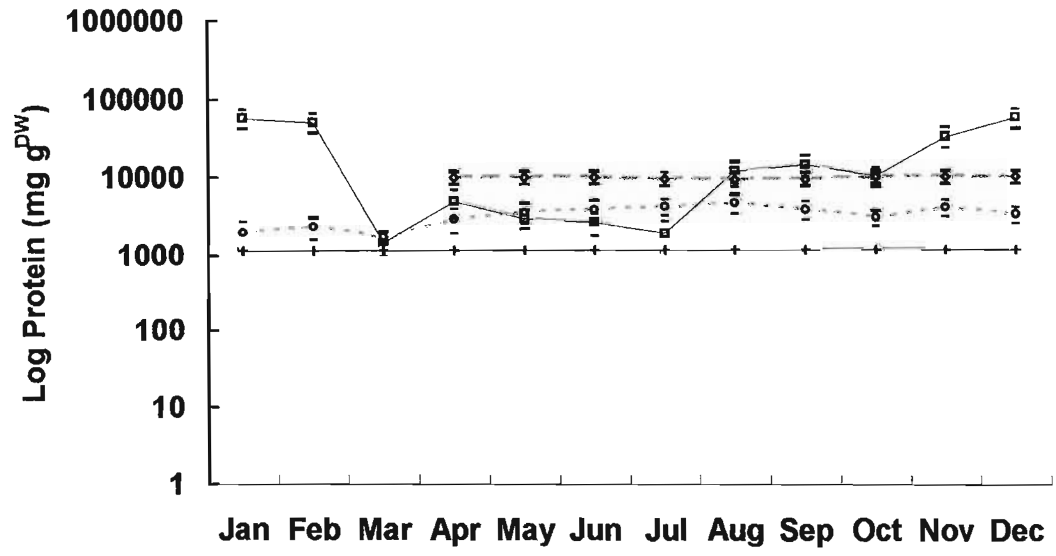

Figure 4.3: Log of the sum of the protein content, the relative monthly use of the dietary items and the total handling time of each item eaten by Brown-headed Parrots continuously eating for 10 minutes. The circles represent Punda Maria, the squares Pretoriuskop and the diamonds, Ponta Malongane. One standard deviation is shown in each case. The horizontal line represents the daily protein basal metabolic requirement calculated from the allometric equation of Klasing (1998).

Interaction with Other Species

At Ponta Malongane, as the pods of *Afzelia quanzensis* opened they were sought after by Samango Monkeys (*Cercopithecus mitis erythrarchus*), and Vervet Monkeys (*C. pygerythrus*). No other animals seemed to feed on *Eucalyptus* seeds.

Competition at Punda Maria and Pretoriuskop was of two distinct types, non-selective competition from large mammalian herbivores, elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*) and kudu (*Tragelaphus strepsiceros*) and selective competition from small mammals and bird species. The Bush Squirrel (*Paraxerus cepapi*) and nocturnal, arboreal rodents undoubtedly competed directly with Brown-headed Parrots for fruit. However, more sustained competition for fruit came from Green Pigeons (*Treron australis*). As mentioned earlier, the parrots manipulated the larger fruit items in their feet before eating, however, Green Pigeons were able to swallow these items whole. As such handling time for the fruit was appreciably less than those of the parrots (Table 4.4).

	Part Eaten	Handling Time	S.D.	*n*
Cassine aethiopica	Fruit	4.03	0.85	194
Diospyros mespiliformis	Fruit	3.89	0.80	183
Ficus sycomorus	Fruit	3.92	0.82	203
Lannea stuhlmannii	Fruit	4.04	0.81	188

Table 4.4: The mean handling time (seconds) and standard deviation for a Green Pigeon (*Treron australis*) to consume a food item after detection and the number of observations (n).

Grey Louries (*Corythaixoides concolor*) and three species of Hornbill (*Tockus nasutus, T. erythrorynchus* and *T. flavirostris*) also ate the fruit. Their handling times were slower than those of the parrots and as a result of their body size, procurement was limited in the vegetation. No other sustained competition was noted. The pods of *Cassia abbreviata* were eaten by Crested Barbets (*Trachyphonus vaillantii*) and Glossy Starlings (*Lamprotornis nitens*). They made no attempts to break into pods and were confined to eating the contents of older open pods, which the parrots ignored. Interestingly, both Bennett's (*Campethera bennettii*) and Goldentailed (*C. abingoni*) Woodpeckers, described as insectivorous by Maclean (1993), bored holes into the pods and extracted parts of the seeds. The hole made by the woodpecker significantly improved the parrots foraging efficiency (t-test comparing the opening of a virgin pod when the parrot made the initial opening to when a woodpecker made the initial opening, $t = -7.15$, $df = 35$, $p > 0.001$).

Brown-headed Parrots are sympatric with Grey-headed Parrots (*Poicephalus fuscicollis suahelicus*) in the Punda Maria area. Only five pairs of this much larger parrot were evident apart from January 1997, when a flock of some 70 birds entered the area. The two species segregated, with the larger species specialising on the fruits of *Scleocarya birrea* (Marula) and the Brown-headed Parrots feeding on *Lannea stuhlmannii* (False Marula). This flock left the area when the fruiting season ended.

Discussion

The composition of a species' diet is influenced by many factors. Broadly, the potential diet is governed by the physiological features of the species for food digestion, morphological features for food procurement and the life-cycle and morphology of the potential prey species (Klasing 1998). It is therefore, impossible to calculate the total calorific, protein or mineral content of a prey species in the wild from sample data (Dasilva 1992). Nevertheless, the results allow a number of general conclusions to be made.

From the previous chapter it can be seen that the suite of *Combretum* spp. are available and eaten for 11 months of the year. The similarities between three of these species (*C. apiculatum, C. herereonse*, and *C. imberbe*), in energy, protein content and seed size, means that they can be treated as one species in terms of the potential nutrition they provide for Brown-headed Parrots. From allometric equations the energetic basal metabolic rate for a non-passerine bird with a mass of 150g, is 77.1 kJ day^{-1} and the protein requirement for maintenance is 1161 mg day^{-1} (Klasing 1998). Although, the exact equation used to calculate these figures may be disputed (Laswieski & Dawson; Nagy 1987; Bennett & Harvey 1987; Dann *et al.* 1990), Table 4.3 indicates that in a few minutes, Brown-headed Parrots can extract enough nutrients from the *Combretum* spp. to meet their daily requirements. However, for most of the year, the Parrots at Punda Maria and Pretoriuskop forage on species other than *Combretum* spp., and Table 4.2 shows that these species either have a greater protein or energy content or are less time consuming to handle. *Combretum* spp. are not available to the Parrots at Ponta Malongane but the species available also provide the energy and protein requirement in a few minutes of concerted foraging.

Of course, the allometric equations used to calculate the basal metabolic rate omit a number of crucial factors, for example, the high energetic cost of flight (Maurer 1996) and digestion (Belovsky 1986). Furthermore, at various times of the year Brown-headed Parrots were eating the fruits of *Strychnos Madagascariensis* and pods of *Acacia sieberana*, both of these species contain toxins (Palgrave 1977). The energetic cost of detoxification may be significant for Colobine Monkeys (Dasilva 1992). Additionally, the total energy content of food items, as measured from chemical analysis is not available to the birds, as some 15% of the energy is excreted (Dasilva 1992, Karasov 1996). A further factor, which may constrain the food intake of the Parrots is competition from other species, however, Table 4.4 shows that this is negligible at least and at best interspecific interaction from Woodpeckers may be beneficial to Parrots foraging on some species at certain times of the year.

All of these costs must be met each day. However, an annual metabolic cost which must be circumvented if a species is to complete its annual life-cycle is the cost of reproduction. In avian species reproduction coincides with the availability of dietary items high in protein as in almost all species of birds protein requirement is highest at hatching and gradually declines as the bird reaches adult weight (Baker *et al.* 1996). A second peak of protein demand is reached with the onset of breeding by the female. Many species mobilise the protein requirement from body tissue, whilst other species increase the protein content of their diet (Bell 1980; Drent & Daan 1980; Alisauskas & Ankney 1992; Brice 1992).

As will be pointed out in Chapter 5, the breeding season of Brown-headed Parrots begins in April and continues until September, the winter months in South Africa. There is evidence that the Parrots switch from a diet high in energy during the summer to higher protein content in the winter. This switch seems to be an active choice as during the summer, higher protein foods are available than the ones utilized. These items are browsed at low volumes in summer and higher volumes in winter. This switch is not, however, explicit. The seeds of *Trichilia emetica*, which forms the bulk of the summer diet at Pretoriuskop, contain a very high protein content, as well as the highest energy content of any of the food items taken by Brown-headed Parrots.

Out with the breeding season, the parrots at both KNP sites forage on a few species, two at Punda Maria and three at Pretoriuskop, however, during the breeding season, between April and September this number rose to nine or ten at Pretoriuskop and up to thirteen at Punda Maria. There could be two reasons for this. First, that the species foraged reflect the number of species available. However, this was not the case as the suite of *Combretum* spp. was available and being eaten, although only forming a restricted percentage of the diet. A further explanation for the diversity of plant species utilised during the breeding season is that although the calorific and protein and content of the diet has been considered, there are many trace minerals and dietary constituents which are essential for healthy growth of the chick (Earl & Clarke 1991; Shafey 1993; Roudybush 1996). It is possible that a diet composed of a few species may not supply these essential elements.

With a paucity of species to choose from, birds in the Mozambique study site may, therefore, endure a reproductive bottleneck. The increased protein demands of breeding are unlikely to be met, unless some dietary switch takes place.

However, after consideration of all of these factors, Figures 4.2 and 4.3 indicate that Brown-headed Parrots feeding continuously for 10 minutes in any month will be able to reach their daily basal metabolic protein requirement and feeding for 30 minutes will be sufficient to realize their daily basal energy requirement. Considering, that they can potentially forage for 10 hours in winter and 12 hours in summer, the hypothesis that Brown-headed Parrots are not constrained by seasonal nutritional availability is accepted.

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Chapter 5

Associations of Individual Brown-headed Parrots

Introduction

Intraspecific association, the frequency with which two individuals of the same species are present in the same social group at the same time, intensely influences the behavioural characteristics of individuals, thereby underpinning all other aspects of their social and behavioural interactions (Myers 1983; Cairns & Schwager 1987). For example, individuals of many species occur in groups with interchangeable group members, the fission/fusion model (van Schaik 1989). This type of social organization is characterized by having members who may show no specific predilection for other members of the group. These individuals will therefore join or leave the group at random (Conradt & Roper 2000). Simultaneously, indivisible subunits may exist within the group through pair or genetic relationships. Such individuals will likely join or leave the larger group in conjunction with their affiliates (van Scaik 1989).

Despite the evolutionary and behavioural significance of group membership, little explicit research has been carried out on the spatial, temporal and structural composition of parrot assemblages. This has resulted in subjective impressions of group membership which have emerged from either investigations focused on other aspects of animal behaviour or from anecdotal perceptions (Ficken *et al.* 1981; Cairns & Schwager 1987).

Summer feeding flocks of Brown-headed Parrots are conspicuous because of the noise that they make (pers. obs.). Congregations of up to 100 individuals may be found at a good food source. Yet in early winter, birds are seen in much smaller groups or pairs. This has led to the widely held and often repeated view that Brown-headed Parrots are seasonal flock-formers, which form pairs just prior to the breeding season (Forshaw 1989; Maclean 1993). This synopsis is sustained in popular literature although no verifying research has been carried out to support this claim or that the vast majority of parrot species form a life-long or long-term pair bond (Forshaw 1989).

Therefore in this chapter, I test the hypothesis that associations amongst individual Brown-headed Parrots are random and if they are non-random, consider which factors influence these associations.

Methods

Parrot sightings were made whilst travelling along the transects of the three study sites described in detail in Chapter 2. Each sighting consisted of recording an encounter where the number of Brown-headed Parrots ≥ 1. Immediately after the sighting an instantaneous count was made of the total number of individuals encountered and any individuals with distinguishing features (Chapter 2). Cairns & Schwager (1987) have pointed out two potential spheres of bias in such counts. Individuals arriving or leaving groups whilst the count is being conducted result in uncertainty about the status of the individual as regards the group and temporal proximity of counts may result in counts which lack independence as the associations of the second sighting may be predicted from the associations of the first sighting. Therefore, as far as possible immigrations or emigrations from the sighting were ignored whilst the count was conducted and counts were made once per day to allow some degree of mixing amongst the total population of the area. A sighting is therefore defined as an encounter with at least one Brown-headed Parrot, *and* any other conspecifics, that were observed from that vantage point on a particular day.

In addition, preening behaviour was noted that occurred between any of the idvidually distinct birds.

Two indices of association were derived from the counts of distinct individuals as each index introduces some bias in the degree of association of individuals.

The Half-Weight Index has been used in a number of studies on a wide variety of subjects, for example Elk (Knight, 1970), Lion (Schaller, 1972), Giraffe

(Leuthold, 1979) and the Vampire Bat (Wilkinson, 1985) and has also been referred to as the Coherence Index. The index yields a probable association between two individuals, *a* and *b* of;

$$P = \frac{x}{x + y_{ab} + \frac{1}{2}(y_a + y_b)} \qquad (1)$$

Here x represents the total number of sightings where a and b are located together, y_a represents the number of sightings where only individual a is located and y_b represents the number of sightings where only individual b is located. The notation y_{ab} represents the total number of sightings, where both a and b are located separately. However, in this study, because instantaneous counts of sightings were taken, it was, therefore, impossible for a and b to be located in separate sightings contemporaneously. Therefore in this study y_{ab} always = 0. The index underemphasises the weighting of y_a and y_b on the premise that if individuals associate in large groups, they are more likely to be encountered together than separately.

The Simple Ratio Index has been used to describe associations amongst Red-Deer (Guiness *et al.*, 1979) and uses similar notation to the Half Weight Index, except that the influence of sightings of a or b without b or a is magnified, resulting in weaker association probabilities.

$$P = \frac{x}{x + y_{ab} + y_a + y_b} \qquad (2)$$

Again, in this study $y_{ab} = 0$. This index weighs each sighting identically and presents an exact association probability if the sample is equal to the population. Association matrices were then drawn up for each study site for the duration of time spent at each site. Additionally, association matrices were computed on a monthly basis for pairs of individually identifiable individuals.

Results

The numbers of individuals counted in group sightings varied considerably over time, although the same basic trend was observed at both Punda Maria and

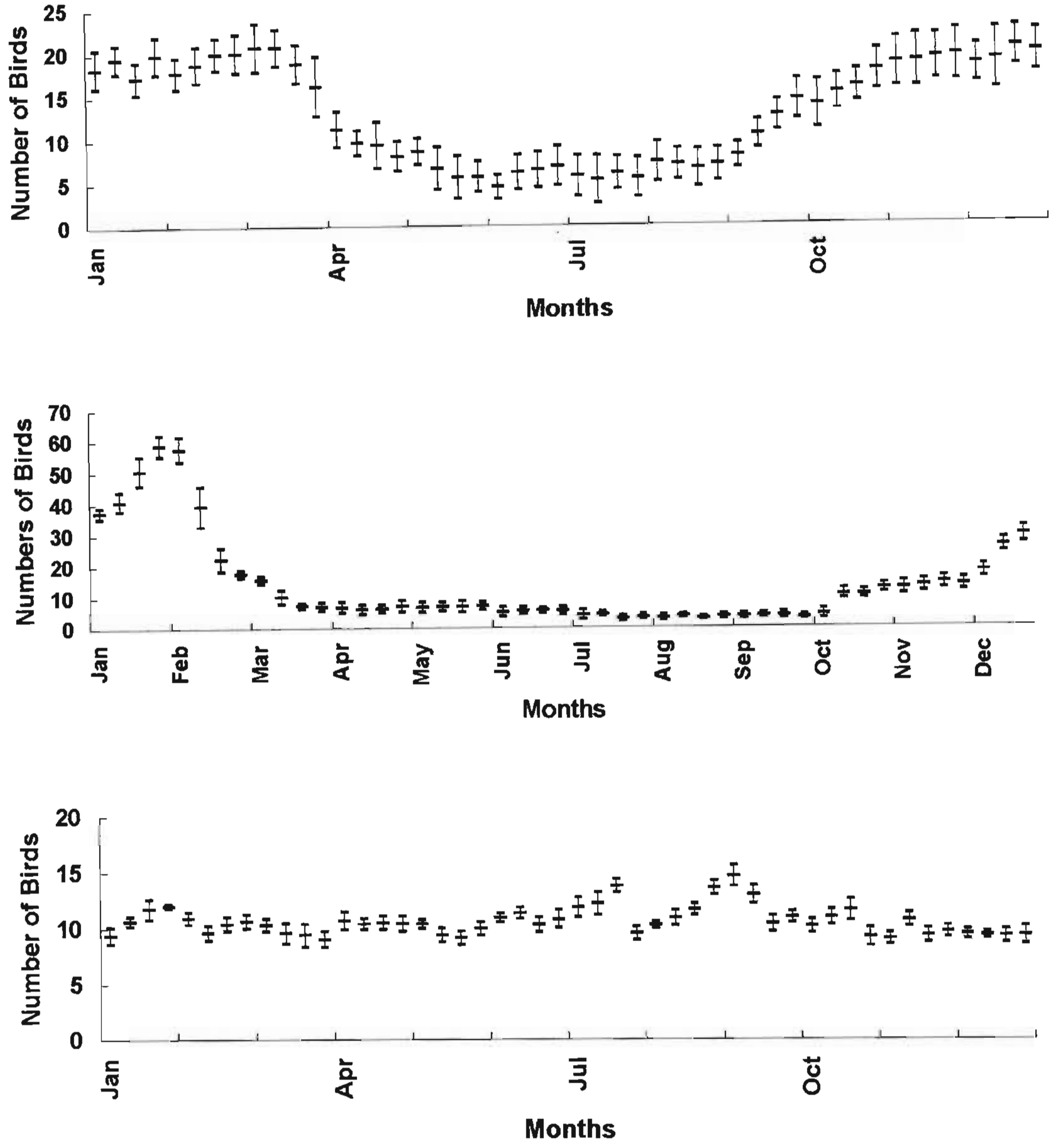

Figure 5.1: Mean number of individual Brown-headed Parrots congregations per week at Punda Maria (top), Pretoriuskop (middle) and Ponta Malongane (bottom).

Pretoriuskop. The numbers of individuals comprising a sighting peaked in the summer months before falling steeply around March. Numbers began to rise again in October (Figure 5.1). At Ponta Malongane the number of individuals comprising a sighting hardly changed per month. Within these group sightings, 24 visually distinctive individuals were recognised at Punda Maria, 20 at Pretoriuskop and 20 at Ponta Malongane. How these individuals associated with each other is illustrated in Tables 5.1 to 5.3 (n values are given as appendix 1).

Bird	1	2	3	4	5	6	7	8	9	10	11	12
1		**0.945**	0.430	0.446	0.335	0.370	0.411	0.384	0.294	0.292	0.054	0.263
2	**0.897**		0.404	0.414	0.321	0.357	0.395	0.373	0.294	0.285	0.042	0.259
3	0.274	0.253		**0.923**	0.416	0.407	0.438	0.412	0.266	0.239	0.081	0.307
4	0.287	0.261	**0.857**		0.447	0.424	0.440	0.420	0.272	0.262	0.077	0.294
5	0.201	0.191	0.263	0.288		**0.915**	0.502	0.457	0.307	0.306	0.056	0.270
6	0.227	0.217	0.256	0.269	**0.844**		0.500	0.449	0.284	0.289	0.055	0.280
7	0.259	0.246	0.280	0.282	0.335	0.333		**0.939**	0.383	0.351	0.086	0.345
8	0.238	0.230	0.259	0.266	0.296	0.289	**0.885**		0.395	0.362	0.068	0.350
9	0.172	0.173	0.153	0.158	0.181	0.165	0.237	0.246		**0.905**	0.071	0.363
10	0.171	0.166	0.136	0.151	0.181	0.169	0.213	0.221	**0.826**		0.078	0.318
11	0.028	0.022	0.042	0.040	0.029	0.028	0.045	0.035	0.037	0.040		0.237
12	0.152	0.149	0.181	0.173	0.156	0.163	0.209	0.212	0.221	0.189	0.135	
13	0.152	0.150	0.146	0.140	0.129	0.135	0.190	0.193	0.191	0.158	0.137	**0.833**
14	0.110	0.099	0.104	0.113	0.114	0.106	0.125	0.145	0.140	0.127	0.000	0.421
15	0.154	0.147	0.098	0.114	0.095	0.105	0.174	0.191	0.207	0.207	0.036	0.172
16	0.095	0.083	0.052	0.070	0.054	0.039	0.094	0.105	0.100	0.101	0.033	0.263
17	0.101	0.089	0.052	0.069	0.060	0.046	0.105	0.104	0.106	0.108	0.100	0.276
18	0.094	0.090	0.039	0.055	0.117	0.123	0.127	0.115	0.060	0.057	0.038	0.067
19	0.094	0.090	0.045	0.066	0.110	0.116	0.132	0.126	0.065	0.064	0.037	0.054
20	0.050	0.051	0.066	0.069	0.090	0.090	0.118	0.118	0.098	0.105	0.026	0.081
21	0.045	0.046	0.077	0.080	0.096	0.090	0.118	0.118	0.098	0.105	0.039	0.091
22	0.074	0.076	0.074	0.077	0.020	0.020	0.095	0.120	0.056	0.045	0.160	0.207
23	0.175	0.174	0.138	0.133	0.149	0.158	0.191	0.198	0.197	0.164	0.000	0.123
24	0.161	0.170	0.133	0.129	0.145	0.159	0.174	0.185	0.198	0.171	0.000	0.136

Table 5.1: Association matrix based on individual, identifiable Brown-headed Parrots seen in company with other identifiable Brown-headed Parrots at Punda Maria. Probabilities in bold represent associations of more than 0.800. Probabilities above the line represent associations calculated using a half weight index; those below the line are calculated using a simple ratio. See text for details.

	13	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
1	0.265	0.199	0.267	0.173	0.183	0.172	0.171	0.095	0.086	0.138	0.298	0.277
2	0.261	0.181	0.256	0.153	0.164	0.166	0.165	0.098	0.088	0.142	0.296	0.290
3	0.255	0.188	0.179	0.099	0.098	0.076	0.086	0.124	0.144	0.138	0.242	0.234
4	0.245	0.202	0.205	0.130	0.129	0.104	0.124	0.129	0.147	0.144	0.235	0.228
5	0.228	0.205	0.174	0.102	0.113	0.210	0.198	0.166	0.176	0.039	0.260	0.253
6	0.238	0.192	0.189	0.076	0.088	0.220	0.209	0.165	0.165	0.038	0.273	0.274
7	0.320	0.222	0.297	0.172	0.190	0.225	0.233	0.211	0.211	0.173	0.321	0.297
8	0.324	0.253	0.321	0.190	0.188	0.0207	0.224	0.211	0.211	0.214	0.330	0.312
9	0.320	0.245	0.343	0.182	0.192	0.112	0.123	0.178	0.178	0.105	0.328	0.331
10	0.272	0.225	0.344	0.183	0.194	0.108	0.120	0.189	0.189	0.086	0.282	0.291
11	0.241	0.000	0.069	0.065	0.182	0.073	0.071	0.051	0.076	0.276	0.000	0.000
12	**0.909**	0.593	0.293	0.417	0.432	0.125	0.103	0.150	0.167	0.343	0.219	0.239
13		0.525	0.282	0.394	0.466	0.147	0.125	0.134	0.151	0.348	0.209	0.230
14	0.356		0.188	0.679	0.618	0.182	0.205	0.040	0.040	0.275	0.173	0.170
15	0.164	0.104		0.186	0.183	0.105	0.117	0.158	0.147	0.110	0.265	0.274
16	0.246	0.514	0.103		**0.913**	0.206	0.232	0.087	0.087	0.190	0.146	0.154
17	0.304	0.447	0.101	**0.840**		0.257	0.282	0.085	0.085	0.182	0.133	0.139
18	0.080	0.100	0.055	0.115	0.148		**0.903**	0.172	0.172	0.121	0.181	0.178
19	0.067	0.114	0.062	0.131	0.164	**0.824**		0.188	0.171	0.179	0.190	0.177
20	0.072	0.020	0.086	0.045	0.044	0.094	0.104		**0.971**	0.133	0.198	0.196
21	0.082	0.020	0.079	0.045	0.044	0.094	0.093	**0.944**		0.156	0.198	0.206
22	0.211	0.159	0.058	0.105	0.100	0.065	0.098	0.071	0.084		0.185	0.169
23	0.117	0.095	0.153	0.079	0.071	0.099	0.105	0.110	0.110	0.102		**0.920**
24	0.130	0.093	0.159	0.083	0.075	0.098	0.097	0.109	0.115	0.092	**0.852**	

Table 5.1 ***cont.***

Bird	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1		**0.910**	0.589	0.541	0.485	0.483	0.436	0.451	0.535	0.563	0.403	0.516
2	**0.835**		0.482	0.535	0.441	0.361	0.300	0.452	0.540	0.522	0.524	0.399
3	0.417	0.317		**0.915**	0.388	0.324	0.309	0.295	0.358	0.236	0.318	0.411
4	0.371	0.365	**0.843**		0.413	0.319	0.465	0.378	0.413	0.439	0.485	0.326
5	0.320	0.283	0.241	0.260		0.379	0.440	0.467	0.433	0.483	0.423	0.449
6	0.318	0.220	0.193	0.190	0.234		0.272	0.340	0.534	0.437	0.428	0.339
7	0.279	0.177	0.183	0.303	0.282	0.158		**0.864**	0.273	0.335	0.419	0.444
8	0.291	0.292	0.173	0.233	0.305	0.205	**0.761**		0.359	0.321	0.482	0.259
9	0.366	0.369	0.218	0.260	0.276	0.364	0.158	0.219		**0.912**	0.313	0.411
10	0.392	0.353	0.134	0.282	0.318	0.280	0.201	0.191	**0.839**		0.382	0.268
11	0.252	0.355	0.189	0.320	0.269	0.272	0.265	0.317	0.185	0.236		0.262
12	0.348	0.249	0.259	0.194	0.289	0.204	0.286	0.149	0.259	0.155	0.151	
13	0.383	0.203	0.278	0.289	0.280	0.194	0.219	0.212	0.227	0.218	0.224	**0.824**
14	0.293	0.234	0.268	0.315	0.245	0.218	0.295	0.378	0.230	0.294	0.191	0.187
15	0.292	0.251	0.324	0.264	0.281	0.273	0.202	0.291	0.303	0.263	0.299	0.184
16	0.313	0.263	0.171	0.270	0.308	0.261	0.283	0.347	0.296	0.259	0.300	0.290
17	0.274	0.280	0.228	0.284	0.283	0.365	0.323	0.369	0.311	0.274	0.213	0.269
18	0.232	0.274	0.281	0.249	0.321	0.221	0.284	0.196	0.277	0.334	0.226	0.236
19	0.185	0.262	0.237	0.303	0.380	0.328	0.307	0.306	0.287	0.175	0.160	0.263
20	0.188	0.330	0.282	0.326	0.199	0.182	0.275	0.319	0.229	0.240	0.317	0.250

Table 5.2: Association matrix based on individual, identifiable Brown-headed Parrots seen in company with other identifiable Brown-headed Parrots at Pretoriuskop. Probabilities in bold represent associations of more than 0.750. Probabilities above the line represent associations calculated using a half weight index; those below the line are calculated using a simple ratio. See text for details.

Bird	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
1	0.554	0.453	0.451	0.477	0.430	0.377	0.313	0.316
2	0.338	0.379	0.401	0.416	0.438	0.430	0.415	0.496
3	0.435	0.423	0.490	0.292	0.372	0.439	0.383	0.440
4	0.448	0.479	0.418	0.425	0.442	0.398	0.465	0.491
5	0.438	0.394	0.439	0.471	0.442	0.486	0.551	0.332
6	0.325	0.358	0.429	0.413	0.534	0.362	0.494	0.309
7	0.360	0.456	0.336	0.441	0.488	0.442	0.469	0.431
8	0.349	0.549	0.451	0.515	0.539	0.328	0.469	0.484
9	0.370	0.374	0.465	0.457	0.475	0.434	0.447	0.372
10	0.358	0.455	0.417	0.411	0.430	0.501	0.297	0.387
11	0.366	0.321	0.460	0.462	0.351	0.368	0.275	0.481
12	**0.904**	0.315	0.310	0.450	0.423	0.382	0.417	0.400
13		0.310	0.389	0.417	0.441	0.509	0.545	0.482
14	0.183		**0.907**	0.343	0.265	0.328	0.470	0.459
15	0.242	**0.831**		0.441	0.339	0.369	0.462	0.442
16	0.264	0.207	0.283		**0.902**	0.278	0.381	0.369
17	0.283	0.153	0.204	**0.821**		0.277	0.405	0.438
18	0.342	0.196	0.226	0.161	0.161		**0.887**	0.289
19	0.294	0.307	0.300	0.235	0.254	**0.797**		0.365
20	0.318	0.297	0.284	0.226	0.280	0.169	0.223	

Table 5.2 ***cont.***

Bird	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1		**0.962**	0.254	0.205	0.197	0.156	0.149	0.106	0.206	0.193	0.134	0.038
2	**0.927**		0.244	0.196	0.188	0.155	0.155	0.122	0.191	0.177	0.133	0.056
3	0.145	0.139		0.264	0.254	0.178	0.162	0.088	0.204	0.205	0.079	0.108
4	0.114	0.109	0.152		**0.961**	0.141	0.142	0.151	0.233	0.226	0.131	0.058
5	0.109	0.104	0.156	**0.926**		0.149	0.149	0.150	0.232	0.225	0.141	0.069
6	0.085	0.084	0.098	0.076	0.081		**0.948**	0.195	0.112	0.113	0.167	0.110
7	0.081	0.084	0.088	0.076	0.081	**0.901**		0.186	0.105	0.105	0.178	0.111
8	0.056	0.065	0.046	0.081	0.081	0.108	0.102		0.144	0.135	0.146	0.063
9	0.115	0.105	0.114	0.132	0.131	0.060	0.055	0.078		**0.988**	0.188	0.089
10	0.107	0.097	0.114	0.127	0.127	0.060	0.056	0.072	**0.976**		0.168	0.089
11	0.072	0.071	0.041	0.070	0.076	0.091	0.098	0.079	0.104	0.092		0.081
12	0.019	0.029	0.057	0.030	0.036	0.058	0.059	0.033	0.047	0.047	0.042	
13	0.041	0.041	0.033	0.052	0.052	0.030	0.030	0.055	0.030	0.030	0.076	0.041
14	0.097	0.089	0.038	0.077	0.068	0.072	0.072	0.000	0.057	0.058	0.034	0.000
15	0.069	0.062	0.085	0.090	0.089	0.099	0.100	0.020	0.100	0.093	0.090	0.024
16	0.060	0.053	0.074	0.063	0.063	0.099	0.109	0.011	0.510	0.052	0.024	0.014
17	0.110	0.103	0.066	0.119	0.110	0.089	0.090	0.022	0.060	0.054	0.041	0.011

Table 5.3: Association matrix based on individual, identifiable Brown-headed Parrots seen in company with other identifiable Brown-headed Parrots at Ponta Malongane. Probabilities in bold represent associations of more than 0.750. Probabilities above the line represent associations calculated using a half weight index; those below the line are calculated using a simple ratio. See text for details.

Bird	13	14	15	16	17
1	0.079	0.177	0.128	0.114	0.199
2	0.078	0.164	0.116	0.101	0.187
3	0.064	0.074	0.156	0.138	0.124
4	0.099	0.143	0.164	0.119	0.213
5	0.098	0.128	0.163	0.118	0.119
6	0.058	0.134	0.181	0.181	0.164
7	0.059	0.135	0.182	0.196	0.165
8	0.103	0.000	0.040	0.022	0.038
9	0.059	0.108	0.182	0.098	0.114
10	0.059	0.109	0.170	0.099	0.102
11	0.142	0.066	0.165	0.047	0.079
12	0.078	0.000	0.047	0.027	0.022
13		0.057	0.053	0.123	0.100
14	0.029		0.222	0.279	0.414
15	0.027	0.125		0.204	0.219
16	0.066	0.162	0.114		0.302
17	0.053	0.261	0.123	0.178	

Table 5.3 ***cont.***

It can be seen that the probability of encountering, for example, bird 1 at Punda Maria with bird 2 at Punda Maria is far greater than encountering bird 1 with any other individual at Punda Maria. In fact the majority of association probabilities between individuals lie between 0.1 and 0.3 at both Punda Maria and Ponta Malongane and between 0.3 and 0.5 at Pretoriuskop (Figure 5.2).

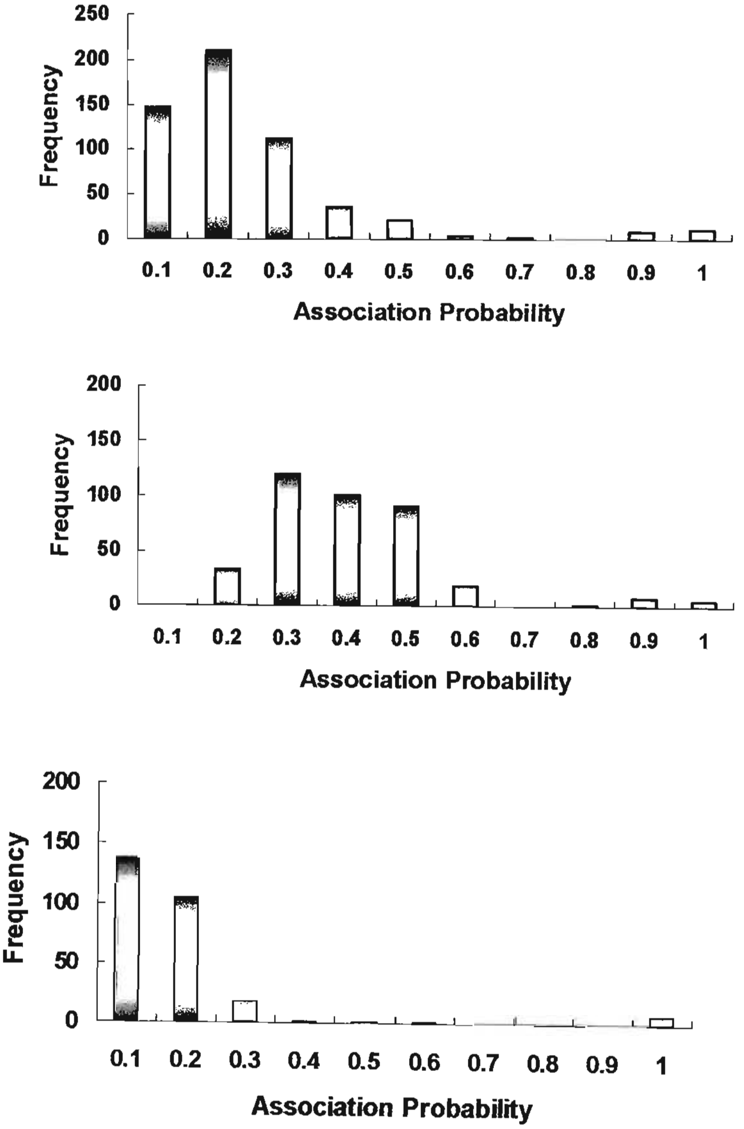

Figure 5.2: Histograms showing the frequency of association probabilities of Brown-headed Parrots at Punda Maria, Pretoriuskop and Ponta Malongane, respectively.

Individuals realising significantly greater probabilities are those specified in bold in Tables 5.1 to 5.3. These greater probabilities are summarised in Table 5.4 with related data on preening behaviour and here it can be seen that allopreening *only* occurs between these individuals.

		Association Index			
	Birds	Half-Weight	Simple Ratio	Preening Between	Preening to Others
Punda Maria	1 & 2	0.945	0.897	Yes	No
	3 & 4	0.923	0.857	Yes	No
	5 & 6	0.915	0.844	Yes	No
	7 & 8	0.939	0.885	Yes	No
	9 & 10	0.905	0.826	Yes	No
	12 & 13	0.909	0.833	Yes	No
	16 & 17	0.913	0.840	Yes	No
	18 & 19	0.903	0.824	Yes	No
	20 & 21	0.971	0.944	Yes	No
	23 & 24	0.920	0.852	Yes	No
Pretoriuskop	1 & 2	0.910	0.835	Yes	No
	3 & 4	0.915	0.843	Yes	No
	7 & 8	0.864	0.761	Yes	No
	10 & 11	0.912	0.839	Yes	No
	12 & 13	0.904	0.824	Yes	No
	14 & 15	0.907	0.831	Yes	No
	16 & 17	0.902	0.821	Yes	No
	18 & 19	0.887	0.797	Yes	No
Ponta Malongane	1 & 2	0.962	0.927	Yes	No
	4 & 5	0.961	0.926	Yes	No
	6 & 7	0.948	0.901	Yes	No
	9 & 10	0.988	0.976	Yes	No

Table 5.4: Summary of association indices of probabilities greater than 0.750 correlated with observed allopreening by Brown-headed Parrots. "Preening between" denotes preening observed between the two individual Parrots named in column 2, whilst "preening to others" denotes incidences where one of the Parrots named in column 2 was observed preening a Parrot not named in column 2.

Four of the pairs from Table 5.5 were located frequently on the transect at Punda Maria and were also observed tending nests and feeding young together. The incidence of association between these individuals per month is shown as Figure 5.3. It is clear that for most of the year the association between these individuals is very close to 1, or put another way, the probability of locating one of the individuals without the other is very small. However, the probability of locating one of the individuals on its own increased slightly in July and more so in August and September.

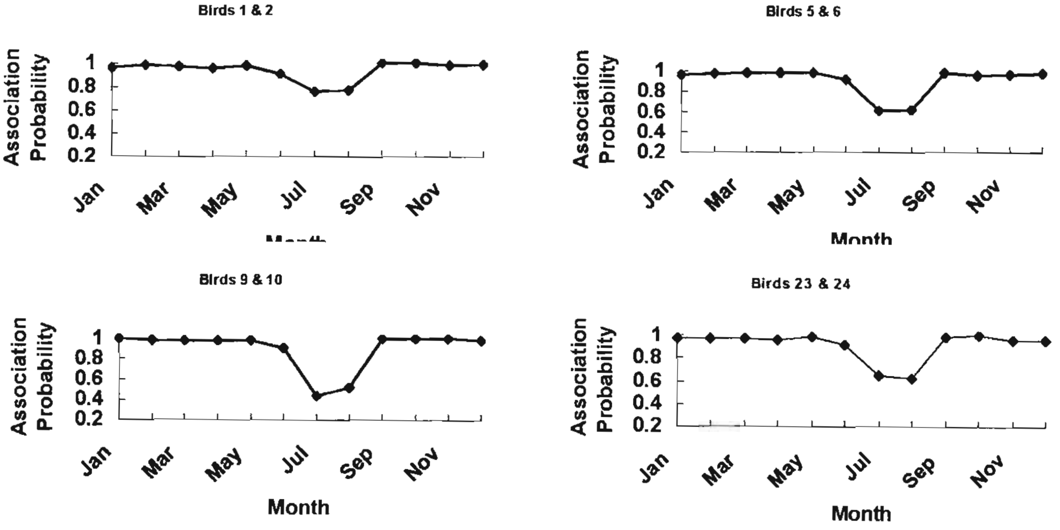

Figure 5.3: Association probabilities over 12 months of 4 pairs of identifiable Brown-headed Parrots at Punda Maria calculated from half weight index.

Discussion

The results show that certain individual parrots have higher associations with certain other individuals, both in terms of the amount of time that they spend with each other (Tables 5.2 to 5.3) and in physical contact (Table 5.4). When this association is analysed on a monthly basis, it is clear that this affinity extends throughout the year (Figure 5.3). It is difficult, therefore, not to conclude that the individuals detailed in Table 5.4 are in fact paired individuals and that the relationship between the individuals is not ephemeral, but a long-term one lasting at least through the non-breeding season (Figure 5.3). In July and August, the association seems to be less strong. However, it will be shown in Chapter 6 that those months represent the breeding season of Brown-headed Parrots and that the female spends most of her time brooding the eggs. The apparent reduction of association in those months provides further evidence that, far from pairing up just prior to breeding, these individuals are long-term, breeding pairs. The species can therefore be described as a monogamous flock former (Robertson 1996), the flocking being a function of food availability and the pair sub-units showing no especial affiliation to other members of the group; a classical fission/fusion model (van Schaik, 1997). Rowley (1990) and Rowley & Chapman (1991) found a similar arrangement existing in the Galah (*Eolophus roseicapillus*) and Major Mitchell Cockatoo (*Cacatua leadbeateri*), respectively. However, in the earlier study, 29% of the identified pairs only lasted one year after tagging. Rowley (1990) suggested that the transient nature of the pair bond was more a function of heavy mortality in individuals rather than "divorce".

The selection pressures involved in monogamy have been reviewed by Trivers (1972), whilst Krebs & Davis (1993) have emphasised the role of life history constraints and ecological factors on the costs and benefits of mating systems and parental care. It is clear from these discussions that where one parent exclusively incubates the eggs, the reproductive success of both parents depends on that parent being fed by the other parent (Ligon 1993). Further, if the chicks are totally reliant on the parents at hatching and early life, then the reproductive success of the parents can only be maximised by both parents participating in nurturing the young to independent adulthood (Ricklefs 1979; Walters 1984; Beletsky *et al.* 1995).

As shall be pointed out, captive breeding studies of Brown-headed Parrots have demonstrated that only the female incubates the chicks and is totally dependant on the male feeding her at the nest (Chapter 6). Second, like all parrots, Brown-headed Parrot chicks are altricial, born with sparse down and therefore totally dependent on their parents for temperature regulation and for food (Chapter 6). It is hardly surprising then that Brown-headed Parrots are monogamous.

The question of whether a species is monogamous or not is important in other ways as it encroaches upon a variety of behavioural and ecological aspects of the species' life history (Lack 1968; Orians 1969; Van Rhijn 1984; Handford & Mares 1985). For example, whilst many non-monogamous birds evolved complex and intricate ways to attract a mate, many monogamous birds, which form life long pair bonds, are sexually monomorphic (Maclean 1990). The formation of such a bond, precludes searching for a mate and thus the evolution of behaviours used exclusively in sexual contexts (Rowley 1974). Evidence to support this assertion has been found in two Australian parrots, the Galah (Pidgeon 1981) and the Short-billed White-tailed Black Cockatoo (Saunders 1983). Both these species are largely monomorphic and possess a paucity of sexually related vocalizations, the vast majority of vocalizations being used for group maintenance and cohesion. In a later chapter it will be shown that the same situation exists in the Brown-headed Parrot.

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Chapter 6

Breeding Biology of the Brown-headed Parrot.

Introduction

Of the 330 species of parrots which presently exist on the Earth, 90 are recognized as being at risk of extinction, whilst many more are thought to be endangered (Collar *et al.* 1994). One of the chief reasons for this situation is the exploitation of parrots in the avicultural trade (Mulliken 1995). Human interest in parrots is mirrored by the vast amount of popular literature, especially magazines solely devoted to the keeping and rearing of parrot species. Many of the articles appearing in these magazines offer advice on the breeding and rearing of parrots yet little is published on the growth process or rate of growth of the parrot chicks. Chick growth rate models of various avian species have been used to investigate subjects as diverse as: the detrimental effects of the dietary contaminant, *polychlorinated biphenyl*, on the growth of waterfowl chicks (Brisbin *et al.* 1986a), the effects of the El Nino-Southern oscillation on nestling growth in the Dark-rumped Petrel (*Pterodroma phaeopygia*) (Cruz & Cruz 1990), geographical variation in growth rates of Yellow-eyed Penguin chicks (*Megadyptes antipodes*) (van Heezik 1990), temporal variation in the growth rates of Lesser Snow Geese chicks (*Anser caerulescens*) (Cooch *et al.* 1991), parental feeding efficiency in Roseate Terns (*Sterna dougallii*) (Nisbet *et al.* 1995) and food requirement flexibility in captive Barn Owl chicks (*Tyto alba*) (Durant & Handrich 1998). It would therefore seem surprising that parrot breeders seem indifferent to chick growth rate as a species-specific knowledge of the characteristics of growth could serve as a general indicative template of chick health (Fendley & Brisbin 1977; Brisbin *et al.* 1986a; Brisbin *et al.* 1986b).

Until comparatively recently, growth curves have utilised some type of linear approximation to a portion of the curve as the sigmoidal nature of the full growth curve has been considered to require complex mathematical modeling procedures (Brisbin *et al.* 1986b). This was in part solved by Ricklefs (1967), however, the method was unable to draw comparable statistical inferences as one particular curve shape (e.g. logistic, Gompertz, monomolecular, von Bertalanffy, etc.) was used to fit different situations (Brisbin *et al.*, 1986b).

More recent attempts to describe biological growth processes have been based on a reparameterised Richards growth model (Richards 1959; White & Brisbin 1980; Brisbin *et al.* 1986a; Brisbin *et al.* 1986b). This model incorporates, among other parameters, a shape parameter (m). If the value m is set then the growth curve becomes the logistic curve ($m = 2.0$), the von Bertalanffy curve ($m = 0.67$) or the monomolecular curve ($m = 0$) (Brisbin *et al.*, 1986a).

The objectives of this chapter are twofold. First, I describe the general breeding biology of the Brown-headed Parrot in the wild. Second, I use a data set of body mass from captive bred Brown-headed Parrot chicks to generate a generalised growth curve. The aim being to produce a curve with suitable confidence limits which graphically illustrates the growth of a healthy chick, which can be used to anticipate malnutrition or disease. I also report on the timing of critical growth phases.

Methods

In the Field

Brown-headed Parrot nests were located at Punda Maria and Pretoriuskop in June and July 1997 and 1999, respectively. Nests were located by finding individuals feeding and following them by vehicle. Nest sites were observed using a Kowa telescope fitted with a 20-60x zoom lens. Extensive observations of nests were only made if the nest site had vehicular access to within 50m. These nest sites were observed either from 06:30 – 12:00 or 12:30 – 17:30. Which nest to observe on any particular day was chosen at random. The tree species was noted and the height above ground of the cavity and cavity entrance diameter were measured using a series of extendable poles. The aspect of the cavity entrance was noted using a compass. Where $n < 30$ the statistical package Minitab V.13

was used to estimate the median with 95% confidence limits using a one-way Wilcoxon signed rank test.

In Captivity

In captivity Brown-headed Parrot eggs were removed from their parents but kept in their respective clutches. Chicks were weighed at first hatching to the nearest 0.1g and thereafter, where possible, weighed everyday for the following 70 days. The chicks were initially kept at a temperature of 37°C until pinfeather eruption when the temperature was gradually reduced to around 27°C (for detailed information regarding chick maintenance see Chapter 2).

The data were then fitted to a reparameterised Richards growth model, in SAS statistics package, using the following formula:

$$\frac{W_{i+1} - W_i}{t_{i+1} - t_i} = \frac{2(m+1)}{T(1-m)}(W^{1-m} W_i^m - W_i) + e_i \qquad (1)$$

where W_i is the value of the growth variable (mass) at time t_i, W is the asymptotic value of the variable under study, T is the overall growing time indicative of growth rate, m is the Richards shape parameter and e_i is the stochastic error at time t_i. Each of these parameters was calculated using a non-linear least squares iterative process until convergence was met (White & Brisbin 1980). Any chick dying before fledging were not included in the analysis.

Results

Breeding Season

Brown-headed Parrots are monogamous flock-formers during the summer, with the flock sizes becoming smaller as winter approaches (see chapter 5 for more detailed information). Although no copulation attempts were observed, the incidence of allopreening and feeding between pairs increased beginning in April. This was coupled with less interaction with birds outside the pair bond.

Nest-site and nest cavity characteristics

Eleven nests were located, six at Punda Maria and four at Pretoriuskop. The remaining nest was found by chance near Satara campsite in the central KNP. Of these, four nests at Punda Maria and two nests at Pretoriuskop met the criteria for extended observation. The dimensions of each nest-site are given as Table 6.1. Seven species of tree were used for nesting. The median height above ground of the cavity is 9.50m (95% C.L. = 7.50m, 11.50m, n = 11), whilst the cavity opening is almost spherical (median width = 7.0cm, 95% C.L. = 6.50cm,

				Cavity	
Location	Tree Species	Hag (m)	Aspect	Width (cm)	Height (cm)
PM^1	*Adansonia digitata*	14	NE^B	6	8
PM^2	*Adansonia digitata*	12	NE^B	8	9
PM^3	*Colophospermum mopane*	9	N^T	6	6
PM^4	*Colophospermum mopane*	7	N^T	6	7
PM^5	*Entandrophragma caudatum*	11	E^B	9	8
PM^6	*Entandrophragma caudatum*	13	NE^B	8	9
PRET^1	*Acacia sieberiana*	8	N^T	7	7
PRET^2	*Celtis africana*	9	NE^T	7	8
PRET^3	*Celtis africana*	7	N^T	8	7
PRET^4	*Erythrina lysistemon*	8	N^T	7	8
SAT	*Acacia nigrescens*	6	N^T	6	6

Table 6.1: Morphological features, locations and tree species utilised by nesting Brown-headed Parrots. PM = Punda Maria, PRET = Pretoriuskop, SAT = Satara, Hag = Height above ground. NE or N being northeast or north respectively, the superscript refers to whether the cavity was situated on the branch or trunk.

8.00cm, n = 11: median height = 7.50cm, 95% C.L. = 7.00cm, 8.50cm, n = 11). All nest-sites found faced north or northeast, suggesting that this aspect has some importance. Additionally, all nest-sites had small branches close to the cavity entrance. This was especially true for nest-sites in trunks. All of these nest-sites had the entrance below the branch. The adults perched briefly on these small branches before flying up and flipping upside down before gripping the bottom of the entrance. The adult then had enough purchase to lever itself into the cavity. All active nest-sites had signs of fresh scraping on the bottom of the cavity entrance from adults gaining access in this way.

General adult breeding behaviour

It was not possible to gain access to any nests directly for reasons already explained, therefore the behaviour of chicks prior to fledging cannot be described or commented on, although inferences are made from observations of captive breeding pairs. A total of 1287 hours were spent at the 6 nest-sites where extended observations were possible. Once a nest had been detected it was impossible to know how long it had been active. However, for extended periods at the beginning of the nesting period the behaviours observed were duplicated at each site.

A single bird arrived on a perch close to the nest just after sunrise between 6h30 and 7h00 and vocalized. From knowledge of captive breeding birds, this was certainly the male (pers. obs.). Within a few seconds the female appeared at the cavity entrance and both flew to the nearest standing water to drink. Upon returning both adults occupied the small branches close to the nest and allopreened (mean occupancy = 858s, S.E. = 23s, n = 111; mean allopreening bout = 6.5s, S.E. = 0.4s, n = 563), before the female returned to the nest and the male flew off. This behaviour, with the exception of the female leaving, occurred 3 to 4 times per day. However, the male also regurgitated food to the female prior to the bout of allopreening. Around 17h00, approximately 30 minutes before sunset, the early morning behaviour was repeated, with the female returning to the nest for the evening and the male flying off to roost.

After the chicks hatched, this behaviour altered slightly. When the adults flew off to drink they did not return immediately. Parents returned to the nest-site separately or together, again for 3 or 4 times daily. If they arrived separately, the first to arrive vocalized until the absent partner arrived. If that partner did not arrive, then the other adult flew off and did not enter the nest. This occurred 9 times in 298 observations. On the remaining occasions both parents arrived and occupied the branches close to the nest-site. One adult entered the nest, presumably to feed the chicks (time in nest = 3.2s, S.E. = 0.4s, n = 963). On leaving the nest-site, it flew down to its waiting partner where regurgitation took place between them. Adult-to-adult regurgitation took place more than once at each visit. Therefore only one adult fed the chicks. From captive breeding birds, this was certainly the male (pers. obs.). Upon conclusion of feeding, the adult, which had not yet accessed the nest, (female) flew up into the nest. From telescopic observation and inspection of the ground below the nest after the adults had left, the female had obviously cleaned the nest of debris and excrement. The adults then spent time (mean = 595s, S.E. = 65s, n = 289) on their perches sleeping, allopreening or self-preening, before flying off either together or in separate directions.

Four to five days before the chicks fledged, four of the nests were visited by bush squirrels (*Paraxerus cepapi*) and/or Grey Hornbills (*Tockus nasutus*). These visitors entered the nest for a few seconds and left. If the adult parrots were in attendance, they did not pay any attention to these visitors. At one nest (PM5, table 6.1), squirrels moved nesting material into a cavity within 20 minutes of the fledglings leaving.

Post-fledgling Behaviour

Upon leaving the nest-site, the fledgling parrots were escorted by their parents to a "nursery area". These areas were characterized by having a number of heavily foliated trees surrounding or close to standing water. Each family occupied a separate tree, although chicks moved from tree to tree when alarmed. Whilst the parents were foraging the chicks remained silent and motionless. After 10 days occupancy chicks began to explore the tree and after 14 days the chicks began to forage with their parents. Chicks were dependant on their parents for a further 28 days, when they became fully independent.

Chick Growth In Captivity

Brown-headed Parrots exhibit asynchronous egg laying. In captivity the median time that the second chick hatched after the first was 93.3 hours (95% C.L. = 74.0h, 107.5h, n = 8), whilst the third chick hatched 52.5 hours (95% C.L. = 49.0h, 57.0h, n = 7) after the second. The chicks hatched blind and were covered with long, off-white down. The median time before the eyes opened was 231.5 hours (95% C.L. = 205.5h, 248.5h n = 6). Pinfeathers began to develop around day 17 and after 24 days the chicks began to develop green feathers on the wings, back and chest. Chicks left the nest around the 65th day after hatching. Their upper beaks were horn coloured with a slight tinge of red and the iris was very dark and indistinguishable from the pupil. Over the next 6 months the beak gradually darkened to the adult grey colour, however, it took 12 months before the eyes lightened. The under-wing colouration was more dilute in the chicks and the borders of yellow were not sharply defined as in adults (Taylor & Horsfield, 2001).

The actual growth rate is shown as Figure 6.1. As is typical of birds, the growth rate was initially slow. Growth rate began to increase at day 10; thereafter chicks gained mass rapidly until day 32 when they reached an asymptote. After day 52 there was a slight decrease in mass before fledging at around day 65.

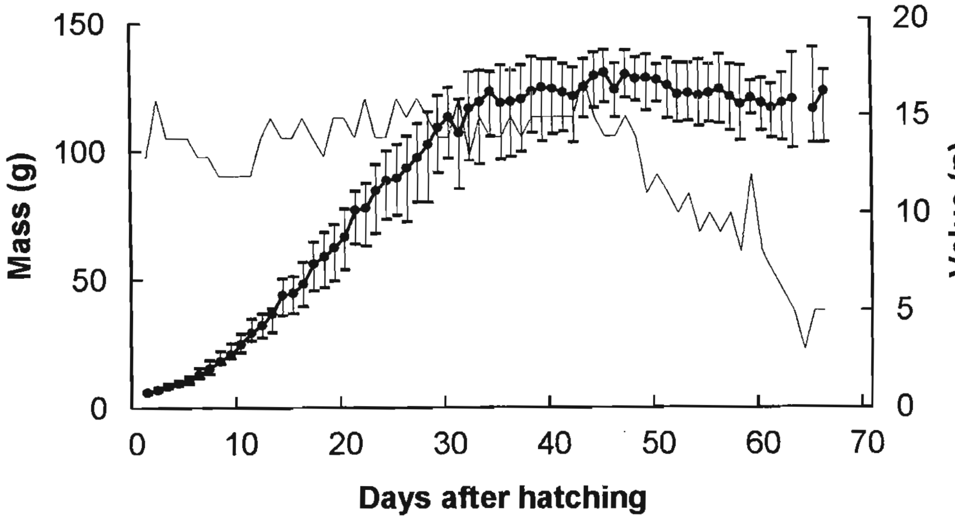

Figure 6.1: Median daily body mass accumulation of Brown-headed Parrots chicks with 95% confidence limits of the mass. As the value of n fluctuated, the values are also shown on the graph as a solid line. On day 65 the value of n was 3, therefore the corresponding mass is omitted in the figure.

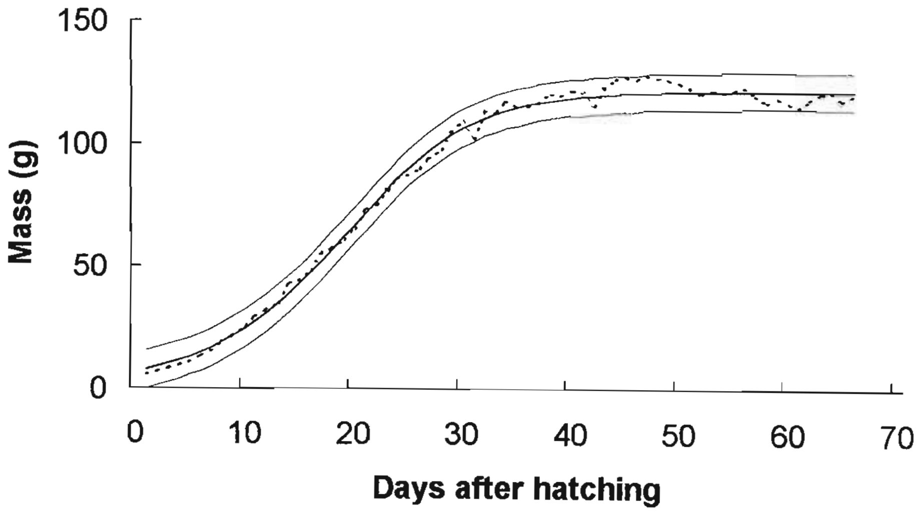

Figure 6.2: Richards growth model of daily body mass accumulation of Brown-headed Parrot chicks. The solid lines represent the curves generated from the model with attendant 95% confidence limits. The dotted line equals the medial chick mass accumulation per day from figure 6.1.

Parameter	Estimate	Std. Error	Lower 95% Confidence	Upper 95% Confidence
Asymptotic mass (g)	121.466	0.741	119.985	122.947
Growing period (days)	36.379	1.119	34.143	38.616
Shape parameter	2.399	0.277	1.846	2.951

Table 6.2: Asymptotic mass, the growing period and the shape parameter estimates, standard error and 95% confidence limits generated from the Richards growth model of Brown-headed Parrot chicks.

The parameter estimates resulting from the Richards growth model are given as Table 6.2. The actual model with 95% confidence limit is shown as Figure 6.2. The model shows a very good fit to the observed growth rates and does not transgress out with the 95% confidence limits. This goodness of fit is also shown in the randomness of the signs of the residual errors (Figure 6.3). According to the model the asymptotic mass is reached after 36.38 days (Table 6.2) and mass accumulation was most rapid up to day 19, when daily mass accumulation began to slow (Figure 6.4). From the model an inverse measure of growth rate, $t_{(10\text{-}90)}$, the time in days to grow from 10% to 90% of the asymptotic mass can be calculated as 27.5 days.

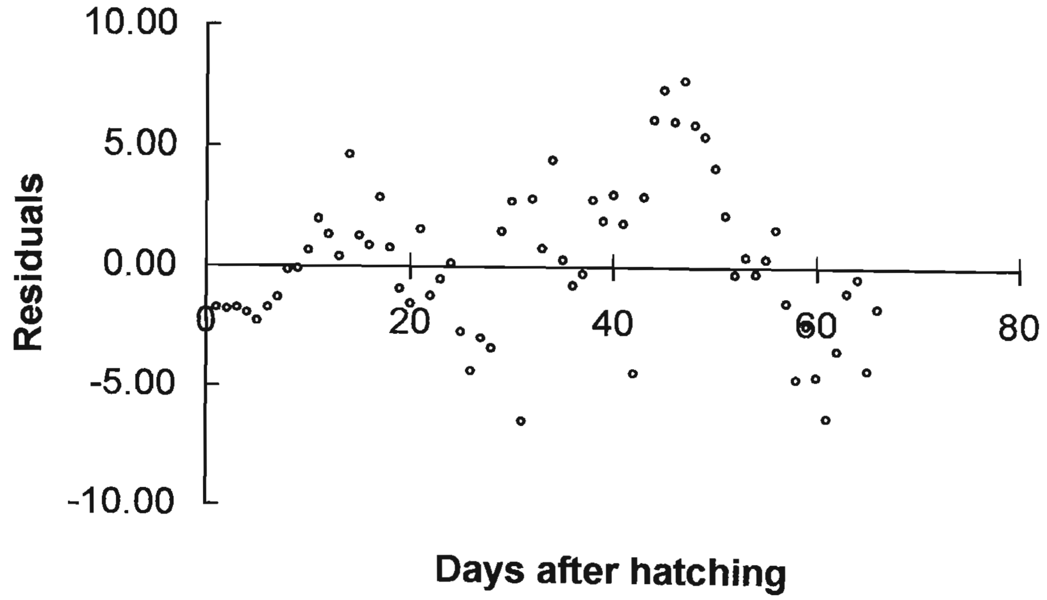

Figure 6.3: Residual errors for the Richards growth model plotted against days after hatching for Brown-headed Parrot chick mass accumulation.

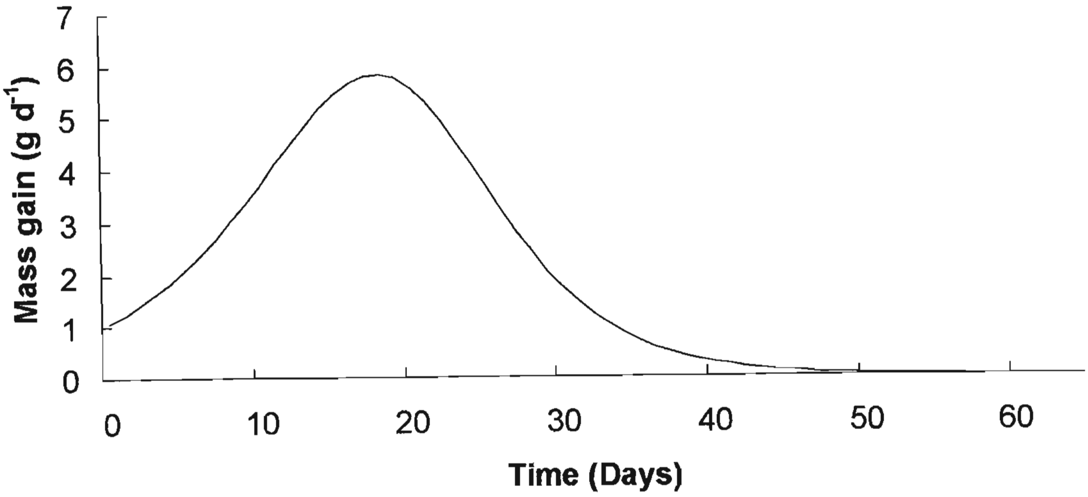

Figure 6.4: The daily mass gain in Brown-headed Parrot chicks from the Richards growth model showing the point of inflection at 19 days.

Discussion

Like many parrot species, Brown-headed Parrots nest in naturally occurring cavities in either the trunk or branch of a large tree. The ideal cavity seems to have a northerly orientation (Table 6.1). Many authors have commented on the apparent non-randomness of nest-site orientations in cavity nesting birds (e.g. Peterson & Grubb 1983; Korol & Hutto 1984). Most of these studies have shown that the general preferred orientation is south and this was also the case in a study of the nest-sites of Puerto Rican Parrots (*Amazona vittata*) (Rodriguez-Vidal 1959). However, a more recent study of the latter species has indicated a nest-site orientation not significantly different from random (Snyder *et al.* 1987). In this study, all nest-sites, apart from one, faced north or north-east. It is unlikely that this is coincidence. Of 243 Galah (*Eolophus roseicapillus*) nests found by Rowley (1990) 111 had a northerly aspect. Although, he makes no further comment, he agrees with Saunders (1979) and Saunders *et al.* (1982) that the cavity aspect is a function of cavity availability and not an intrinsic choice by the breeding pair. However, the trees where nest-sites PM1 and PM5 were situated had at least four other cavities yet squirrels and hornbills did not visit or use these. And by reason of their occupancy the Brown-headed Parrots did not use them either. The numbers of potential colonisers of existing Brown-headed Parrot nests and the speed with which they were occupied after the Parrots left substantiates that the geographical aspect has some importance. Of course, the cavities may not have been suitable for other unknown reasons, for example height above ground or cavity depth, but further study of the circumstances of cavity suitability would be a profitable area for avian conservation.

Popular ornithological field guides have suggested that Brown-headed Parrots prefer *Adansonia digitata* as nesting trees (e.g. Maclean 1993) but the tree species is not critical (Table 6.1). First the southerly limit of *Adansonia digitata* distribution is slightly south of the Punda Maria area, with a few individuals occurring north of Tshokwane (Gertenbach 1983). Brown-headed Parrots extend to the extreme south of the KNP, beyond the southerly limit of *Adansonia digitata*. However, the defining factors of the archetypal nest-site are probably only met in larger trees. This important conservation issue is discussed in the final chapter, however, it is worth mentioning that, as other cavities were available, the specific nest-site criteria may mean that suitable nest-site availability is a constraining variable on the breeding biology of the species.

The use of creches has been described for the Galah (Rowley 1990). However, Brown-headed Parrot and Galah crèches exhibit functional differences. In the latter case, the crèche is a site where recent fledglings gather to practice flying, independent of parental influence. After flight is mastered the family moves to a crèche closer to the foraging areas. At this time, the crèche functions in a manner strikingly similar to Brown-headed Parrot "nursery areas". In both arrangements the dependent young spend their time in the shade of the tree canopy silent and motionless and are fed by their parents who return periodically. In both cases the young erupt into food begging calls when they hear the approach of their parents.

Various hypotheses to explain the costs and benefits of living in groups have been reviewed by Krebs & Davies (1993), however, it is difficult to harmonize any of these hypotheses with reasons why Brown-headed Parrot chicks should congregate in nursery areas. The chicks are, as has been stated, not fully independent, therefore such congregations may attract predators, risking a concomitant increase in fledgling mortality, without any obvious benefit towards fledgling survival. Whilst the fledglings remain silent for most of their occupancy and are well camouflaged, the outburst of food begging calls, when their parents arrive, would seem to obviate their otherwise cryptic behaviour. It therefore seems plausible that there should be selection pressure for them to remain in the nest until they are independent. Therefore, the underlying reason for the use of "nursery areas" may be correlated with the lack of suitable cavities mentioned above.

I suggest that the cost of the chicks remaining in the nest is that the number of potential nest site occupants calls attention to the cavity. The *entire* clutch of fledglings is, therefore, in increased danger of predation. It would therefore be beneficial to move the chicks to a less conspicuous locality where the parents can locate them. Additionally, the dispersion of the clutch throughout the tree safeguards against the whole clutch being predated.

Linked to the idea of conspicuity of the nest is the question why one adult does not enter the nest if the other parent does not arrive. The female does not feed the chicks directly (see below) and so this would therefore preclude her from entering the nest. The male arriving alone faces a trade-off. Entering the nest draws attention to the cavity, thereby increasing the risk of predation on the chicks. The benefit is that he can feed the chicks. Clearly, on his own, with a reduced food load and no likelihood of gaining food from the absent female, the cost of entering the nest outweighs the benefit accruing.

Armstrong & Juritz (1996) have suggested that Brown-headed Parrots may be regular cooperative breeders, however, no evidence was collected to support this claim. From studies of captive breeding, it is known that the female incubates the eggs and is fed by the male at this time, although in cage breeding the female will leave the eggs to feed herself (Taylor & Horsfield 2001). Exclusive access to incubation by the female has also been recorded in the Green-Rumped Parrotlet (*Forpus passerinus*), whilst the sexes share incubation in the Major Mitchell Cockatoo (*Cacatua leadbeateri*) (Waltman & Beissinger 1992; Rowley & Chapman 1991, respectively). After fledging Brown-headed Parrot chicks are fed by the male.

The Richards growth model fits the data from the captive bred chicks well, with the 95% confidence limits of the mass of the chicks remaining inside the growth model parameters. The model is flexible and the 95% confidence limit of the shape parameter includes the value of 2.0 (Table 6.2). This suggests that in this case the curve is an approximation of the logistic growth model. This latter curve has been used in studies of other parrot species (Bucher 1983; Navarro & Bucher 1990; Waltman & Beissinger 1991) and like them it is found that the initial nestling growth rate is slow, in this case until day 10 (Figures 6.1 and 6.2). Ricklefs (1967) has pointed out that the inverse measure of growth rate, $t_{(10-90)}$, can be used to meaningfully compare growth rates amongst species where the growth curves are fitted using different equations. In this study, $t_{(10-90)} = 27.5$ days, whilst in a study of the similarly sized Monk Parakeet (*Myiopsitta monachus*) (Navarro & Bucher 1990) the pooled value of $t_{(10-90)} = 18.0$ days, indicating that the absolute growth rate of Brown-headed Parrot chicks is considerably slower than in the former species. This relatively slow growth is also confirmed by two Australian Parrots, which are also secondary cavity nesters and attain a similar adult body mass. The chicks of the Red-Winged Parrot (*Aprosmictus erythropterus*) (mean adult mass 156g) and the Regent Parrot (*Polyelis swainsonii*) (mean adult mass 149g) spend only 35 and 40 days, respectively, in the nest after hatching, as opposed to the 65 days of Brown-headed Parrot chicks in captivity (Saunders *et al.* 1984). Teather (1996) has pointed out that environmental quality strongly influences the growth of many avian species and may be an important indicator of environmental stress adversely affecting growth. All of the Brown-headed Parrot chicks in this study were hand fed and kept at optimum environmental conditions. Therefore, although the model offers a robust mathematical solution to show graphically the limits of daily growth of healthy Brown-headed Parrot chicks, it also indicates that the growth of Brown-headed Parrot chicks is at odds with the linear relationship between body mass and nestling period proposed by Saunders *et al* (1984).

Brown-headed Parrot chicks exhibited a growth overshoot, which began around day 45, followed by a steady decline in mass until fledging. This is consistent with other studies (e.g. Lancombe *et al.* 1994; Nisbet *et al.* 1995). Ricklefs & Schew (1994) have suggested that the reason for this overshoot is an accumulation of adipose tissue as insurance against times when there is a food shortage.

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Chapter 7

Do Adaptive Hatching Hypotheses Explain Asynchronous Hatching in Brown-Headed Parrots?

Introduction

Egg incubation before the clutch is complete is ubiquitous amongst altricial and semi-altricial birds (Stenning 1996) and produces siblings, whose age may vary by a few hours or days (Stokland & Amundsen 1988). However, the disparity of age produces a disparity in relative size, which often leads to the death of the younger, weaker chick through siblicide or starvation. Further, the parents will remain passive and not intervene in conflicts or attempt to increase their provisioning effort towards weaker chicks (Stenning 1996). This method of parental care seems to be inconsistent with evolutionary thought, as it does not seem to maximise the parent's reproductive success.

Many hypotheses have been proposed to explain the adaptive significance of asynchronous hatching (Vinuela 2000). The most widespread and oldest explanation for this behaviour is the brood reduction hypothesis (Lack 1947, 1954). Briefly, the brood reduction hypothesis holds that the parents produce the maximum number of eggs, which can be provisioned by them in ideal conditions. As food availability is ephemeral and unpredictable, the parents adjust the number of chicks they can provision on a *post hoc* basis so that the smallest, last-hatched chick will quickly starve as a result of sibling competition or die as a result of sibling aggression. This reduction increases the survival chances of the remaining chicks (Lack 1954). Conversely, if all the chicks have been hatched synchronously, then in the event of food availability becoming constraining, complete breeding failure would occur.

Like the brood reduction hypothesis, many of the other explanations of asynchronous hatching are based on the view that the chick size has some adaptive importance (Stoleson & Beissinger 1997). However, a commonality of all these hypotheses is the implication that in an ideal situation, with food being available *ad libiditum*, every chick in the brood has an equal chance of surviving and reaching optimal adult size.

As was pointed out in the previous chapter, Brown-headed Parrots are typical altricial birds whose eggs hatch asynchronously over a period of a few days. Therefore, it would be expected that if any of the adaptive hatching hypotheses (Stoleson & Beissinger 1997) explain asynchronous hatching, then where the chicks are hand fed and food is not a constraint, all chicks should fit the general growth model and have an equal probability of survival.

Therefore, in this chapter, I test the hypothesis that adaptive hatching hypotheses, as an adaptation to food availability constraints, do not offer an explanation for asynchronous hatching in Brown-headed Parrots.

Methods

In captivity, Brown-headed Parrot eggs were removed from their parents and kept in their respective clutches. Newly hatched chicks were ringed by individual markers and weighed to the nearest 0.1g. Thereafter the chicks were weighed every day for the following 70 days. The chicks were initially kept at a temperature of 37°C until pinfeather eruption when the temperature was gradually reduced to around 27°C.

The average weights of first, second and third hatched chicks were calculated. These averages were fitted to a reparameterised Richards growth model, (SAS statistics package), using the following formula:

$$\frac{W_{i+1}-W_i}{t_{i+1}-t_i}=\frac{2(m+1)}{T(1-m)}(W^{1-m}W_i^m-W_i)+e_i \qquad (1)$$

where W_i = the growth variable (mass) at time t_i, W = asymptotic value of the variable under study, T = overall growing time indicative of growth rate, m = the Richards shape parameter and e_i = the stochastic error at time t_i. Each of these parameters was calculated using a non-linear least squares iterative process until convergence was met (White & Brisbin 1980).

Results

The growth parameter estimates from each fitted model are presented in Table 7.1, where n = 5 in all cases. The asymptotic weight estimate (*W*) is greater across the hatching order and no overlap exists between the 95% confidence intervals of the three cohorts, indicating that the weight difference is a significant one. Comparing the weight of the chicks from day 30 to day 60 shows that the asymptotic weight of the third hatched chick is significantly lower than either the first or the second (*One-Way ANOVA*, $f_{(2,87)} = 170.51$, $p < 0.001$).

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95% Confidence Interval	
			Lower	Upper
			First Hatched	
W	134.037	0.451	133.14	134.94
T	37.47	0.585	36.30	38.64
M	2.30	0.134	2.03	2.57
			Second Hatched	
W	130.85	0.73	129.39	132.30
T	33.14	1.02	31.09	35.18
m	2.84	0.33	2.19	3.50
			Third Hatched	
W	118.00	0.79	116.42	119.59
T	29.36	1.15	27.06	31.66
m	2.41	0.34	1.74	3.09

Table 7.1: The asymptotic weight estimate (*W*), the overall growing period (*T*) and the shape parameter (*m*) from the Richards Growth Model fitted to the average growths of first, second and third hatched Brown-headed Parrots in captivity.

The overall growing period (*T*) is also greater across the hatching order and no overlap exists between the 95% confidence intervals of the first and second hatched cohorts, again indicating that the overall growing period is significantly longer for the first hatched chick. However, the overlap of the 95% confidence interval indicates that no significant difference exists between the overall growth period of the second and third chicks. The shape parameter (*m*) does not show any significant difference across the three chick cohorts. This is summarised in Figure 7.2 to 7.4, whilst the growth model residuals for each cohort are given as Figure 7.5. The growth inflection points of the second and third hatched chicks are similar but occur earlier in the growth period and are greater than the first hatched chick, indicating that the second and third hatched chicks gained weight more quickly than the first hatched chick and have the capability of gaining more weight per day (Figure 7.1).

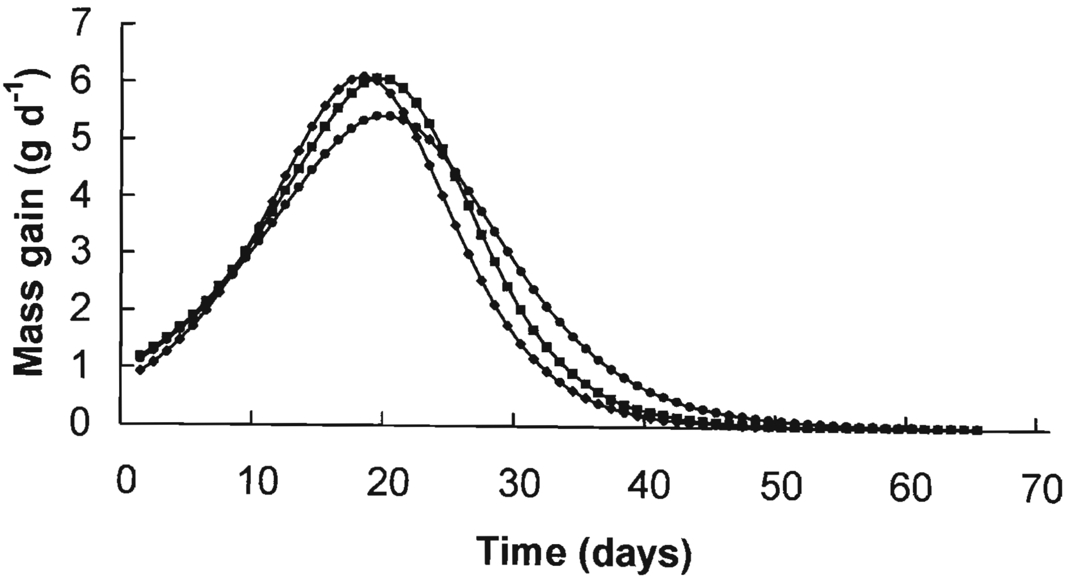


Figure 7.1: The growth inflection points of the three Brown-headed Parrot chick cohorts. The circles indicate the first hatched, the squares are the second hatched and the diamonds are the third hatched.

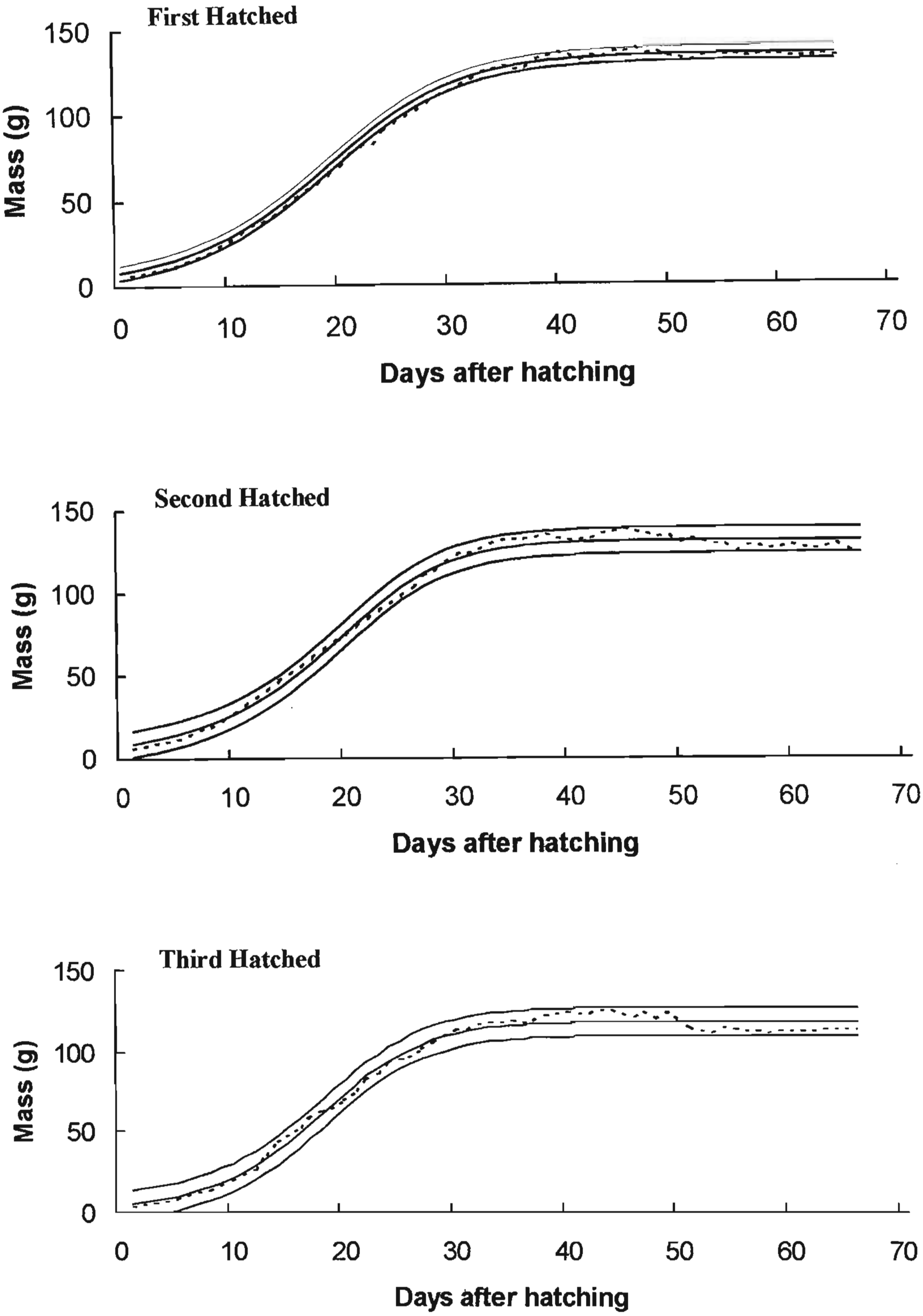


Figure 7.2: Growth models of first, second and third hatched Brown-headed Parrot chicks, showing the actual growth as a dotted line, with the Richards growth model and 95% confidence intervals.

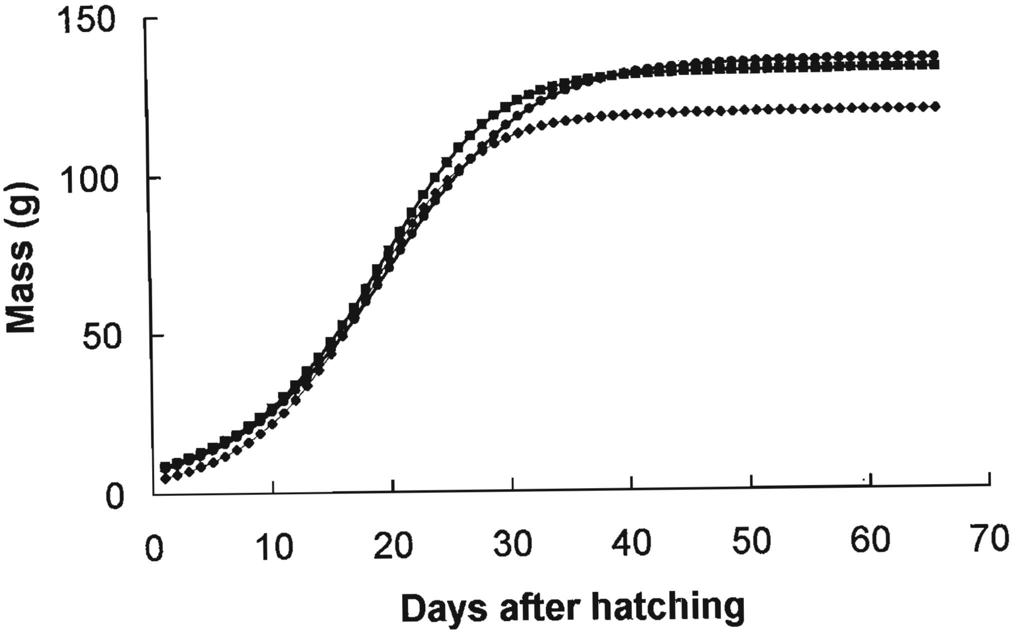


Figure 7.3: Comparison of the mean mass of the three Brown-headed Parrots chick cohorts from the Richards Growth model. The circles indicate the first hatched, the squares are the second hatched and the diamonds are the third hatched.

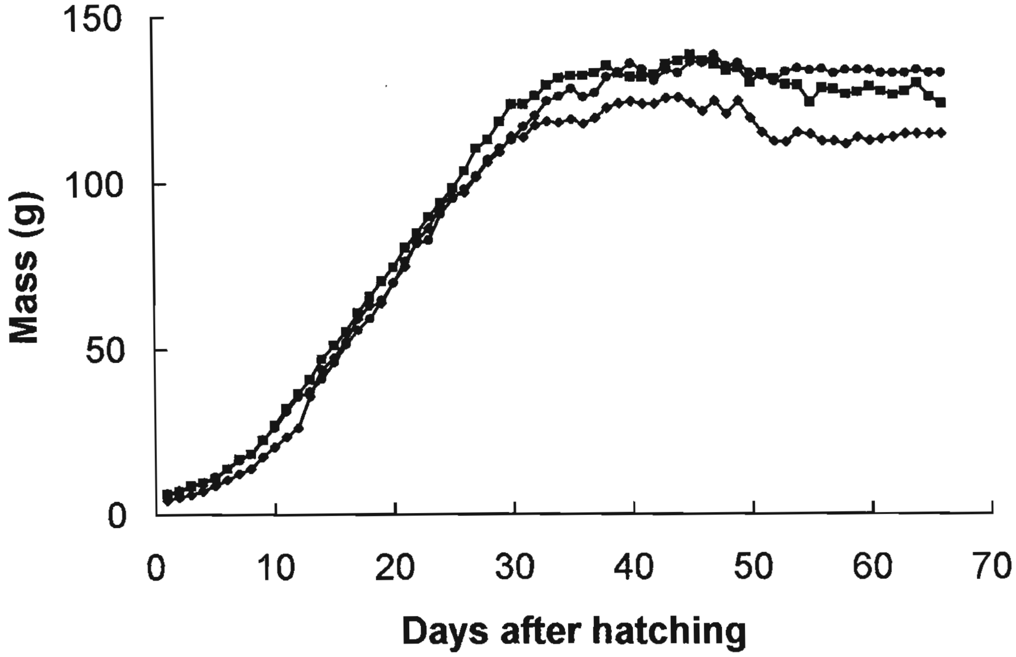
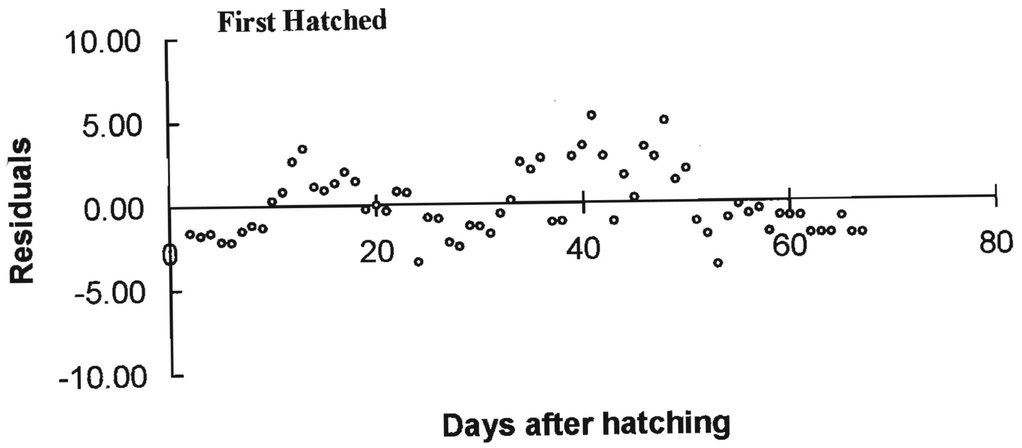
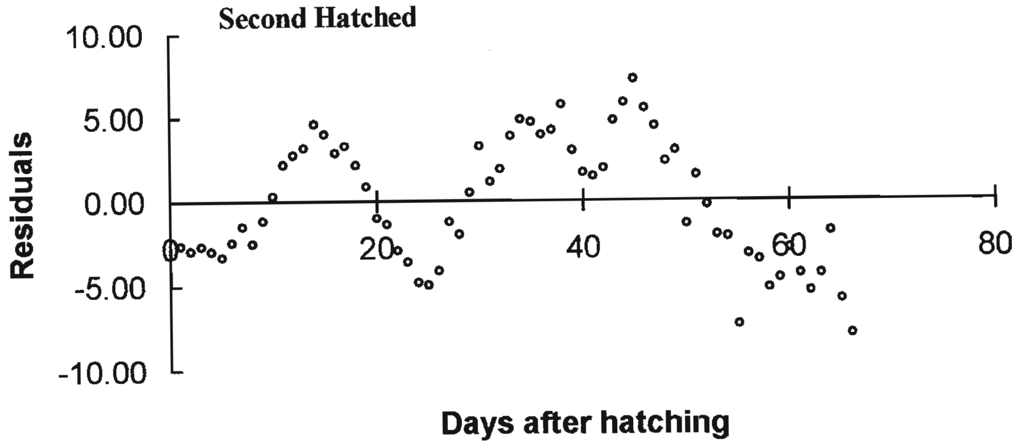


Figure 7.4: Comparison of the actual mean mass of the three Brown-headed Parrots chick cohorts. The circles indicate the first hatched, the squares are the second hatched and the diamonds are the third hatched.





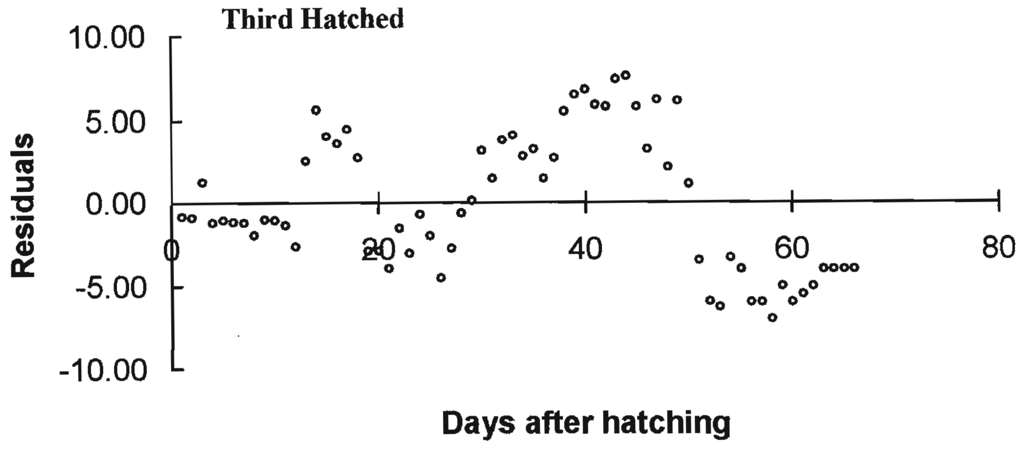


Figure 7.5: Residuals from the Richards growth model for the weight gain of the first, second and third hatched Brown-headed Parrot chicks.

Discussion

The suite of hypotheses, which have been advanced to explain the advantages of asynchronous hatching can be collectively referred to as adaptive hatching hypotheses (Stoleson & Beissinger 1997). All of these hypotheses have, at their core, food dependence as their central criterion. The Brood Reduction hypothesis asserts that parents lay the maximum number of eggs that they can raise under ideal conditions but if these conditions change then loss of the youngest chick(s) will increase the survivorship potential of the eldest (Lack 1954; Rickels 1965; Mock 1994). The Peak Load hypothesis posits that hatching asynchrony produces a chick size hierarchy, which temporally offsets the peak of food demand, thus smoothing out the parental effort (Hussell 1972; Mock & Schwagmeyer 1990). The Dietary Diversity Hypothesis similarly places an emphasis on parental effort but predicts that a particular limiting food resource is the constraint (Magrath 1990). The Hurry-up hypothesis holds that later hatched chicks may be sacrificed and the first chicks development accelerated in the face of a diminishing food resource (Hussell 1985). The Sex Ratio Manipulation hypothesis proposes that later hatched chicks of the more resource demanding sex may be sacrificed (Slagsvold 1990). However, each of these hypotheses has a major underlying assumption, that where food does not become limiting, all of the brood have an equal chance of survival to complete development.

The results presented here do not support this assumption. The asymptotic weight of the last hatched chick is consistently and significantly lower than the first or second hatched chick, yet food availability is not a limiting factor. This trend of asynchronous hatching resulting in reduced growth has been reported many times in the wild (Greg-Smith 1985; Bryant & Tatner 1990; Stouffer & Power 1990; Veiga 1990; Ostreiher 1997) and where food was not limited (Bryant 1978; Werschkul 1979; Amundsen & Stokland 1988; Wiebe & Bortolotti 1995; Nilsson & Svensson 1996; Stoleson & Beissinger 1997). For example early hatched Tree Swallows (*Iridoprocne bicolor*) grow better than late hatched chicks (Zach 1982). Similarly, White & Brisbin (1980) compared the growth of a cohort of Barn Owl chicks (*Tyto alba*) using a Richards Growth model. They found that although the shape parameter of the growth model was not dissimilar for each cohort, the asymptotic weight was significantly different, with the fourth hatched chicks reaching an asymptote over 200g (> 33%) less than the first born. Their tentative suggestion was that the way that the chick grows is under genetic control and is therefore largely immutable. The asymptotic weight, on the other hand, is under environmental control so that asynchronous hatching places subsequently hatched young at different strengths of sibling competition.

Although asynchronously hatching Crimson Rosellas (*Platycercus elegans*) do not suffer from reduced growth of the last hatched chick (Krebs 1999), this seems to be an exception and adaptive hatching hypotheses cannot be thought of as a reasonable explanation for asynchronous hatching, especially considering the results reported here.

Over the last ten years, it has been agreed that birds may have evolved asynchronous hatching for one of a variety of reasons (Stenning 1996) and some studies have led to conclusions, which contest the idea of adaptive hatching hypotheses entirely. One such study, of Green-rumped Parrotlets (*Forpus passerinus*) concludes that the evolution of asynchronous hatching is a result of limited breeding opportunities (Beissinger & Waltman 1991). The authors argue that where nesting opportunities are limiting, through competition, pairs which obtain a nesting site should invest heavily in reproductive effort and nest defence, leading to large clutch sizes, which fledge successfully.

I propose that, to an extent, the Limited Breeding Opportunity hypothesis explains the asynchronicity of Brown-headed Parrots. I have shown in the previous chapter that the nest cavity suffers interspecific visits towards the end of the nestling period and suggested that this forces the parents to vacate the nest site along with the chicks to avoid potential eviction or maybe chick predation. Interspecific pressure would therefore produce a time span over which Brown-headed Parrots must begin and complete their breeding season. Therefore, the female lays the first egg at the earliest opportunity and begins to incubate. The last hatched chick, which leaves the nest at the same time as its older siblings has therefore spent less time developing and weighs less. If this system of parental control is adaptive then there is a selective advantage in producing two healthy chicks and one lighter one, which may survive.

The long-term survivorship of Brown-headed Parrot chicks cannot be commented on, but any future study of the conservation of this species must address this issue. One way of conserving this species in the wild may be to remove the third hatched chick from nests for captive rearing, thereby ensuring its survival and satisfying the demands of the avicultural trade (Stoleson & Beissinger 1997).

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Chapter 8

The Vocalizations of the Brown-headed Parrot; Their General Form and Ecological Context.

Introduction

Amongst the varied sensory channels open to birds for communication, sight and sound are by far the most "important". Although visual communication is crucial for many species (Miller & Emlen 1975; Stoddard & Beecher 1983; Whitfield 1986, 1987), as demonstrated by their elaborate plumage and colouration, visual signals have several disadvantages. Darkness, poor light, dense foliage or physical obstructions all produce events when the individual can be partially or wholly hidden from view (Hailman 1977, 1979; Endler 1990, 1992, 1993). Clearly this is inadequate if the bird's "intention" is communication. Sound travels over long distances, can be heard at all times of the day and can penetrate dense foliage (Richards & Wiley 1980; Wiley & Richards 1982). A further advantage is its non-permanency. Vocalisations can be produced only when required with large amounts of information being transmitted quickly and efficiently (Catchpole & Slater 1995). Avian vocalisations can be separated into songs and calls, although this differentiation should not be seen as definitive. Bird song has been defined by Catchpole & Slater (1995) as "tending to be long, complex vocalisations produced by males during the breeding season", whilst "calls tend to be shorter, simpler and produced by both sexes throughout the year".

By and large vocalisation studies have concentrated on passerines, especially oscines and relatively little work has been conducted on calling species (Bretagnolle 1996). Whichever species has been studied, a first and necessary step is to describe the singing or calling repertoire of the species correlating this information with its life history, habitat and behaviour (Bertram 1970; Beightol & Samuel 1973; Miller & Gottlieb 1976; Barklow 1979; Hausberger *et al.* 1994).

This descriptive phase facilitates a transition towards hypothesis testing and question generation, such as those regarding parent offspring recognition or individual recognition amongst adults (Bailey 1978; Pidgeon 1981; Falls 1982; Storey 1984; Wooller *et al.* 1984). However, the descriptive phase should not just be seen as a means to an end. Kroodsma *et al.* (1996) have emphasised the importance of this phase, especially in species which a) have not been previously studied and b) are experiencing declines in overall abundance. This scenario exists in most of the world's parrot species, which remain the least studied of all vertebrate families (Collar & Juniper 1991).

Not surprisingly no study exists on the vocal communication of the Brown-headed Parrot, published information being restricted to onomatopoeic descriptions in field guides (e.g. Maclean 1993; Sinclair *et al.* 1993). Maclean (1997) describes two calls a "strident *chree-oo* and a sharp *Kreek*", whilst Mackworth-Praed and Grant (1952) report that feeding is accompanied by "conversational chattering". No attempt has been made in the past to consider the ecological context of the calls or analyse the calls in a critical manner.

The first section of this chapter remedies this situation by presenting sonograms of typical calls of the species and the behavioural context in which these calls are produced. Behaviour can be defined as an evolutionary adaptive response to specific requirements of an organism's environment (Maclean 1990). It can involve more than one individual i.e. flocking, more than one species, i.e. feeding or be a process applied by an individual to itself i.e., preening, but each behavioural activity produces a beneficial reward greater than the cost of the behaviour (Miller 1988). As such, behaviours determine the time budgets of species and individuals. However, a corollary of avian behaviour includes a species' repertoire of songs or calls. Therefore, as well as outlining a generalised ethogram of Brown-headed Parrots, describing, with accompanying illustrations, maintenance activity and feeding, agonostic, epigamic, etepimeletic, exploratory and play behaviours, I correlate these processes with accompanying vocalisations. Although necessarily descriptive, it provides a template upon which the rest of the study is based.

Methodology

All recordings were made in the Kruger National Park at a distance of 2 - 5 m from the bird.

All recordings detailed here were recorded using a TASCAM DA-P1 DAT-Recorder. This was fitted with a super-cardioid Sennheiser ME67 shotgun microphone and a Sennheiser K6 windshield. The tape recorder was set at a sampling rate of 48 kHz for all recordings, allowing the microphone to operate at its fullest frequency response of 50 to 20,0000 Hz.

All recordings were transferred to computer using the sound analysis program, Avisoft-SASLab Pro, Ver. 3.95f (Raimund Specht, Berlin). This software is a real-time sound analysis system for use with IBM compatible computers. The software generates real-time displays of spectrogams and power spectra.

The sound files were transferred to a writeable CD, using a HP CD-Writer 7500 series. This allowed for permanent storage of the sound files.

Spectrograms were produced using the analysis program Avisoft-SASLab, using a Hamming evaluation window in all cases. A free reticule cursor was used to compute all measurements. For printing, an FFT-length of 256 was used, which returned a bandwidth of 244Hz, an inverse bandwidth of 4.103ms, and gave a final frequency resolution of 187Hz and a temporal resolution of 2.6667ms. For the time domain analysis an FFT-length of 64 was used, decreasing temporal inverse bandwidth to 1.026ms and yielding an increased temporal resolution of 0.6667ms at the expense of a frequency resolution of 750Hz. For frequency analysis an FFT-length of 1024 was chosen, which decreased the bandwidth to 61Hz and gave an increased frequency resolution of 46Hz and a decreased temporal resolution of 10.7ms. Spectrograms were then produced using a Fast Fourier Transformation (FFT) length of 512 and a Hanning time window. Undesired artifacts of the sound files (wind etc.) and extraneous sound were then attenuated using a Butterworth filter. This has a maximally flat frequency response in the range of frequencies, which should not be attenuated by the filter. Typically this was set to remove frequencies below 500 Hz. No filter was used on the upper level of the signal.

Minitab Ver. 13 (Minitab Inc., Pa.) was used to calculate descriptive statistics.

Results

A range of general calls were recorded. Each of these is described and the related behavioural scenario is described.

Chick *Double Food Begging* Call

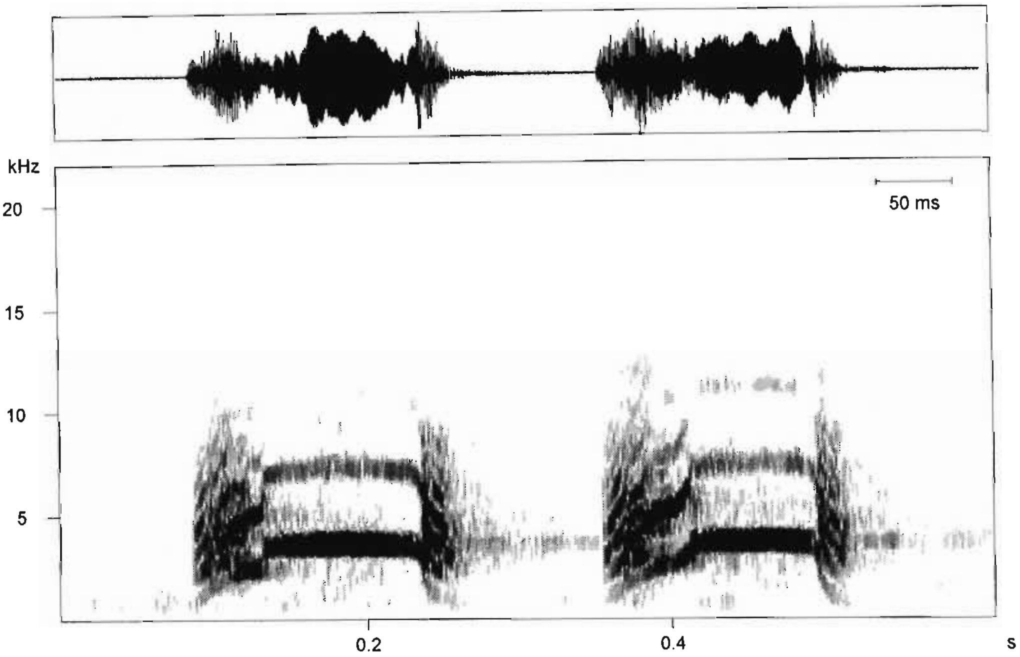

Figure 8.1: Power spectrum and spectrograph of the typical *double food begging* call of a Brown-headed Parrot chick.

In late August the chicks leave the nest and are left by the parents in "nursery areas" (Chapter 6). These areas are characterised by having a number of heavily foliated trees surrounding standing water. Here the chicks remain silent and motionless until the parents return to feed them. As the parents fly in the chicks begin to call. The *double food begging* call (Figure 8.1) elicits feeding from the parent (Figure 8.2). If the call is not made then the chick is ignored by the parents. 1207 *double food begging* calls were recorded from 27 chicks.

The mean call rate is 25 calls per minute, however, this rate is dependent on the degree of excitement of the chick. At the initial arrival of the parents, the chick call rate approaches a mean of 60 per minute. The mean length of the total call is 0.463s (n = 1207, S.D. = 0.013s) and the silence between elements is 0.0812s (n = 1207, S.D. = 0.010s).

The call features two elements separated by silence. Each element begins with a rising frequency modulation. This is followed by a tone with one or more harmonics. The elements conclude with a descending frequency modulation. The mean duration of each part of the call, their frequency ranges and associated standard deviations is shown as Table 8.1.

	Parameter Description	**Mean**	**S.D.**
First Element	**Duration of Element**	**0.173**	**0.017**
	Duration of Rising Frequency Modulation	**0.048**	**0.009**
	Duration of Fundamental Harmonic	**0.100**	**0.021**
	Duration of Descending Frequency Modulation	**0.023**	**0.005**
	Lowest Frequency of the Fundamental Band	**3010**	**68.5**
	Highest Frequency of the Fundamental Band	**4220**	**76.2**
	Lowest Frequency of the Harmonic Band	**6800**	**90.7**
	Highest Frequency of the Harmonic Band	**7830**	**76.6**
Second Element	**Duration of Element**	**0.165**	**0.022**
	Duration of Rising Frequency Modulation	**0.062**	**0.018**
	Duration of Fundamental Harmonic	**0.077**	**0.023**
	Duration of Descending Frequency Modulation	**0.022**	**0.004**
	Lowest Frequency of the Fundamental Band	**3180**	**72.1**
	Highest Frequency of the Fundamental Band	**4300**	**84.2**
	Lowest Frequency of the Harmonic Band	**7060**	**81.4**
	Highest Frequency of the Harmonic Band	**8010**	**89.5**

Table 8.1: The temporal and frequency parameters of the *double food begging* call of Brown-headed Parrot chicks, n = 1207. All time measurements are in seconds. All frequency measurements are in Hz.

Apart from the *alarm growl* (Figure 8.12) this call type is the only call made by the young until 14 days after leaving the nest, apart from the triple food begging call (Figure 8.4). Over time the call develops into the adult *double chip* call (Figure 8.5).

Chicks in the act of being fed (Figure 8.2) continue to utter a *double* or *triple food begging* call, as did chicks being preened by their parents (Figure 8.3). However it is doubtful, that the connotation of the call changed as food begging always indicated the presence of at least one parent.

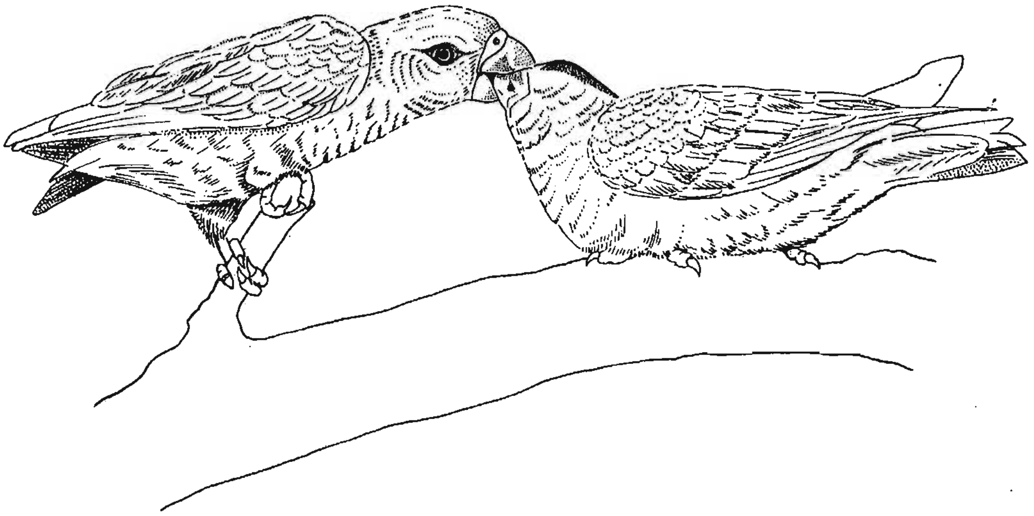

Figure 8.2: Brown-headed Parrot parent feeding chick. Although the parent's beak is forced into the chick's mouth, the chick continues to make *double food begging* calls.

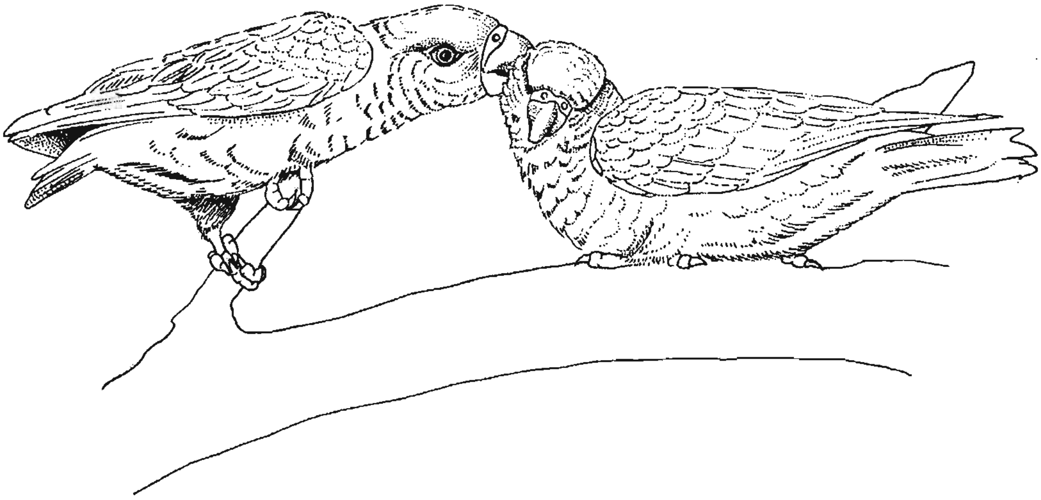

Figure 8.3: Brown-headed Parrot parent preening chick. This succeeds feeding, however the chick continues to make *double food begging* calls.

Chick *Triple Food Begging* Call

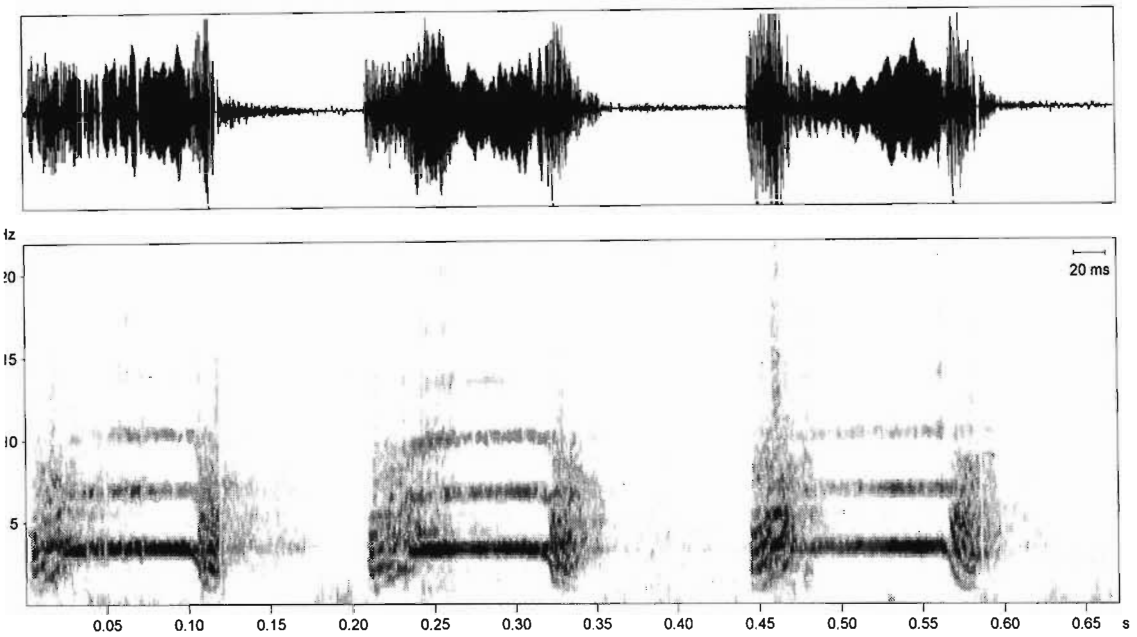

Figure 8.4: Power spectrum and spectrograph of the triple "food begging" call of a Brown-headed Parrot chick.

The chick *triple food begging* call (Figure 8.4) was only heard upon the immediate arrival of parents before first feeding. It can therefore be thought of as a highly excited version of the *double food begging* call and indeed these calls were often heard in the same calling bout (Figure 8.5).

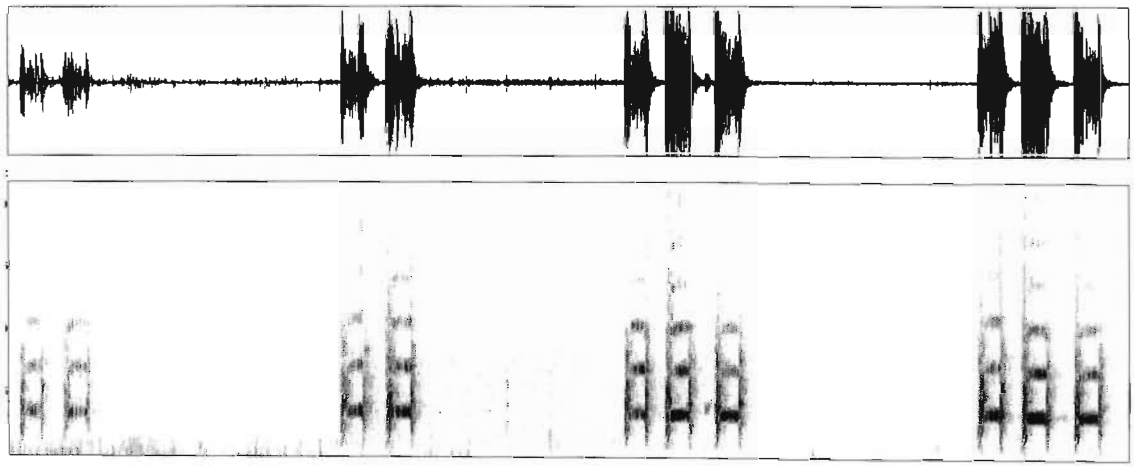

Figure 8.5: Power spectrum and spectrograph of part of a calling bout of a Brown-headed Parrot chick showing mixed *double* and *triple food begging* calls.

The frequency modulation pattern of each of the three elements is equivalent to the elements of the *double food begging* call, however, the total length of the call is longer (mean = 0.06019s, S.D. = 0.013s, n = 45). Descriptions of the 3 elements are shown in Table 8.2.

	Parameter Description	**Mean**	**S.D.**
First Element	**Duration of Element**	**0.136**	**0.003**
	Duration of Rising Frequency Modulation	**0.035**	**0.002**
	Duration of Fundamental Harmonic	**0.067**	**0.001**
	Duration of Descending Frequency Modulation	**0.034**	**0.003**
	Lowest Frequency of the Fundamental Band	**3100**	**54.7**
	Highest Frequency of the Fundamental Band	**3900**	**48.0**
	Lowest Frequency of the Harmonic Band	**6500**	**58.6**
	Highest Frequency of the Harmonic Band	**7700**	**41.2**
Second Element	**Duration of Element**	**0.137**	**0.002**
	Duration of Rising Frequency Modulation	**0.033**	**0.003**
	Duration of Fundamental Harmonic	**0.088**	**0.004**
	Duration of Descending Frequency Modulation	**0.035**	**0.002**
	Lowest Frequency of the Fundamental Band	**2900**	**60.2**
	Highest Frequency of the Fundamental Band	**3900**	**51.4**
	Lowest Frequency of the Harmonic Band	**6300**	**39.5**
	Highest Frequency of the Harmonic Band	**7400**	**34.2**
Third Element	**Duration of Element**	**0.145**	**0.004**
	Duration of Rising Frequency Modulation	**0.032**	**0.002**
	Duration of Fundamental Harmonic	**0.084**	**0.004**
	Duration of Descending Frequency Modulation	**0.034**	**0.002**
	Lowest Frequency of the Fundamental Band	**2900**	**62.8**
	Highest Frequency of the Fundamental Band	**3900**	**59.6**
	Lowest Frequency of the Harmonic Band	**6300**	**40.0**
	Highest Frequency of the Harmonic Band	**7400**	**27.8**

Table 8.2: The temporal and frequency parameters of the *triple food begging* call of Brown-headed Parrot chicks, n = 45. All time measurements are in seconds. All frequency measurements are in Hz.

Chick *Transition* Call

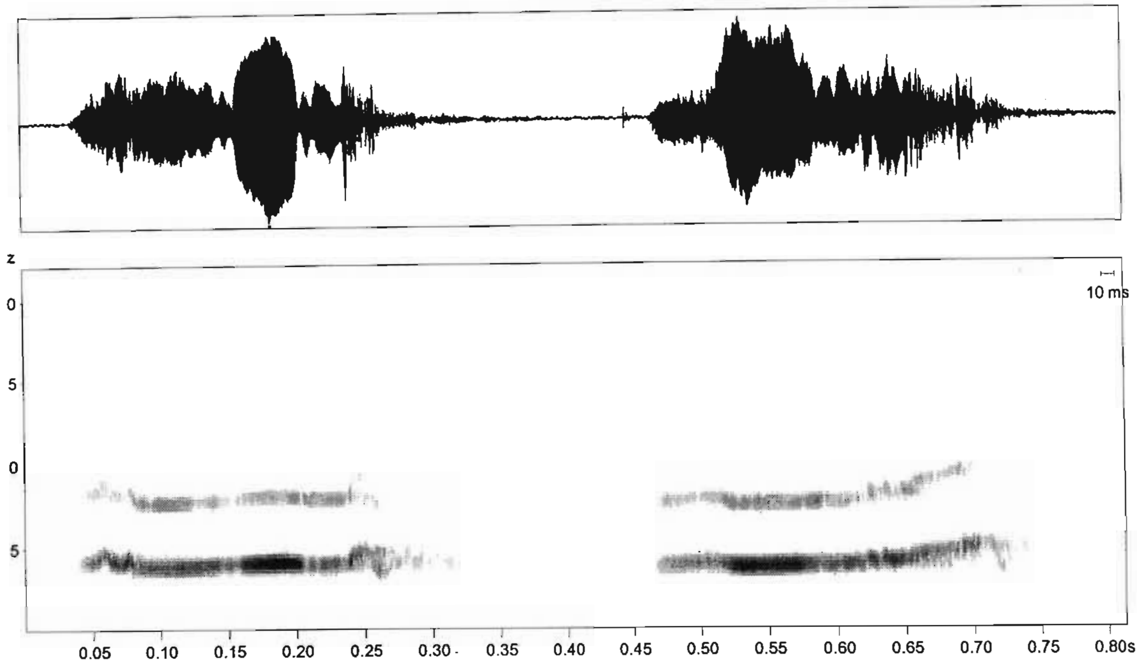

Figure 8.6: Power spectrum and spectrograph of the transition call of a Brown-headed Parrot.

The chick *double food begging* call is not lost as the chick becomes an adult but is transformed by way of a *transition* call (Figure 8.6) into the adult *double chip* contact call (Figure 8.7). It is unclear how long this transformation takes, however, only three individuals were ever recorded during this transition, therefore it is presumed that the transition happens over a very short time span, perhaps only a few days.

The transition call is far longer than the *double food begging* call, even exceeding the *triple food begging* call in duration (mean = 0.6873, S.D. = 0.131, n = 16) and shows the most temporal variation of any of the calls of the Brown-headed Parrot. This is also true of the silence between the elements (mean = 0.205, S.D. = 0.061, n = 16). The call shows little of the frequency modulations which introduces each element of the *double food begging* call and was never tripled, although this cannot be excluded (Figure 8.8). Towards the end of each element of the call a sudden frequency modulation occurs suggesting the almost instantaneous frequency modulation, which is evident in the *double chip* call of the adult (Fig 8.6).

	Parameter Description	Mean	S.D.
First Element	Duration of Element	0.220	0.023
	Duration of First Frequency Modulation	0.042	0.010
	Duration of Fundamental Harmonic	0.156	0.018
	Duration of Second Frequency Modulation	0.022	0.004
	Lowest Frequency of the Fundamental Band	3100	101.6
	Highest Frequency of the Fundamental Band	4500	120.7
	Lowest Frequency of the Harmonic Band	7300	92.1
	Highest Frequency of the Harmonic Band	8400	111.7
Second Element	Duration of Element	0.258	0.023
	Duration of First Frequency Modulation	N/A	N/A
	Duration of Fundamental Harmonic	N/A	N/A
	Duration of Second Frequency Modulation	N/A	N/A
	Lowest Frequency of the Fundamental Band	3110	125.3
	Highest Frequency of the Fundamental Band	4500	113.8
	Lowest Frequency of the Harmonic Band	6900	99.6
	Highest Frequency of the Harmonic Band	8200	85.4

Table 8.3: The temporal and frequency parameters of the *transition* call of Brown-headed Parrot, n = 16. All time measurements are in seconds. All frequency measurements are in Hz. The durations of the separations of the second element are not clear and were not measured.

Adult *Double Chip* Contact Call

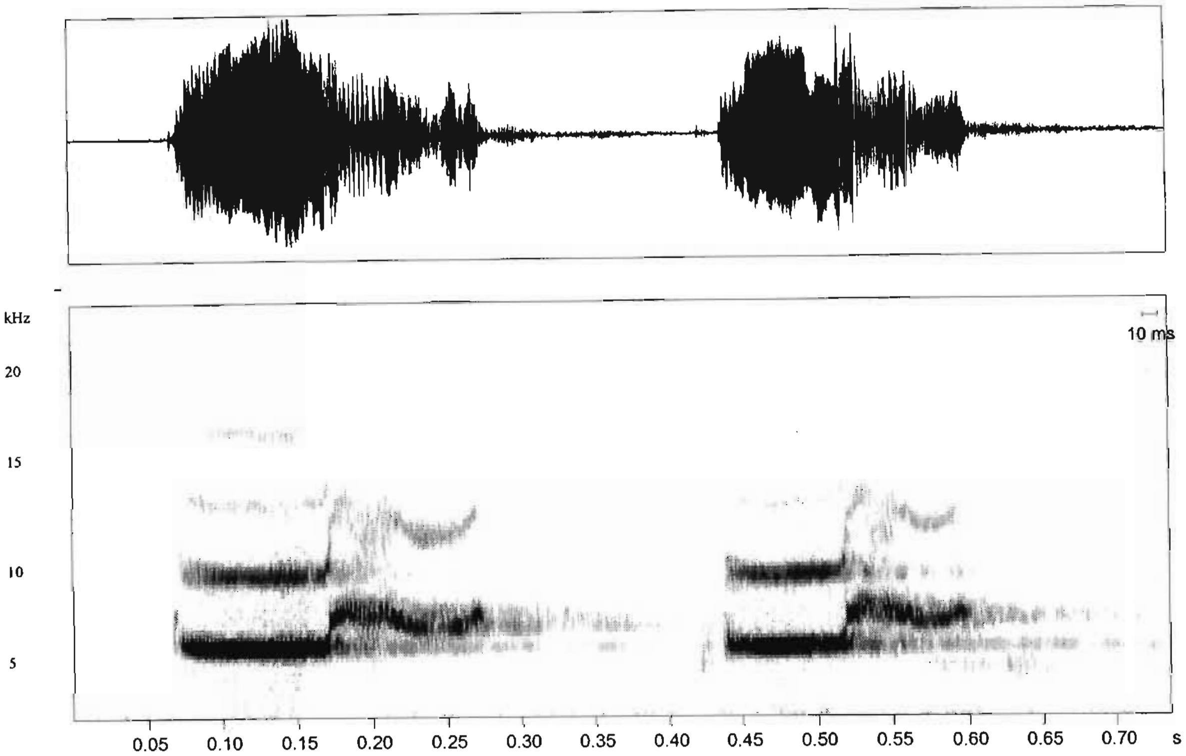

Figure 8.7: Power spectrum and spectrogram of the *double chip* contact call of the Brown-headed parrot.

The adult *double chip* contact call (Figure 8.7) derives from the *double food begging* call of the chick by way of the *transition* call. This purpose of this call is to establish contact between individuals and, once contact has been made, maintain group cohesion. As such the call can be made by a solitary bird either feeding or resting or be made by birds feeding in a flock. In both cases the call can illicit an answering *kreek* (Figure 8.9) from conspecifics.

The call is in two separate but very similar elements. Each element opens with a fundamental tone, with accompanying harmonics, very similar to the middle portions of the chick *double food begging* call. This is followed by an almost instantaneous frequency modulation. The elements end with a frequency modulated tone and an accompanying harmonic, however, the fundamental and its harmonic continue through. Mean total duration of the call is 0.535s (S.D. = 0.115, n = 389) and the silence between elements lasts 0.179s (S.D. = 0.010, n = 389).

Thirty-four known individuals were recorded. *Double chip* contact calls were also recorded from birds with no individual markings but these were not included in the details of the call parameters, which is shown as Table 8.4.

	Parameter Description	**Mean**	**S.D.**
First Element	**Duration of Element**	**0.101**	**0.003**
	Duration of 1st Fundamental	**0.070**	**0.002**
	Duration of 2nd Fundamental	**0.032**	**0.001**
	Difference Between 1st Fundamental and Harmonic	**3510**	**108.6**
	Difference Between 2nd Fundamental and Harmonic	**1330**	**81.82**
Second Element	**Duration of Element**	**0.093**	**0.004**
	Duration of 1st Fundamental	**0.068**	**0.002**
	Duration of 2nd Fundamental	**0.026**	**0.003**
	Difference Between 1st Fundamental and Harmonic	**3940**	**114.89**
	Difference Between 2nd Fundamental and Harmonic	**1660**	**117.50**

Table 8.4: The temporal and frequency parameters of the *double chip* contact call of Brown-headed Parrot adults. All time measurements are in seconds. All frequency measurements are in Hz. First and second fundamentals refer to the section of each element preceding and succeeding the rapid frequency modulation at the centre of each element.

Adult *Triple Chip* Call

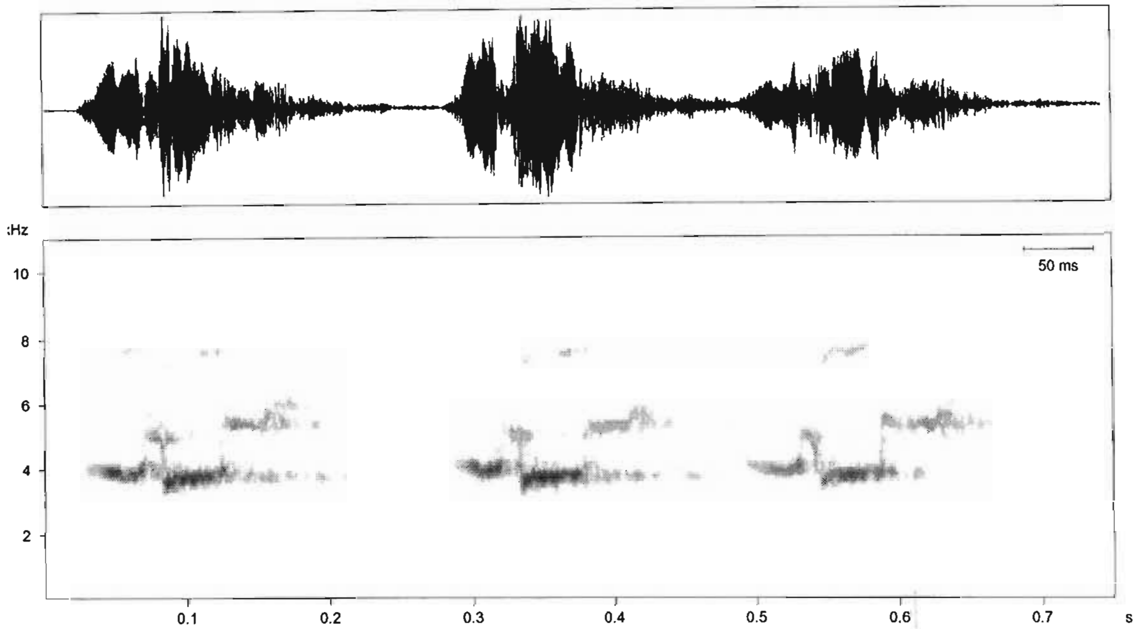

Figure 8.8: Power spectrum and spectrogram of the *triple chip* call of an adult Brown-headed Parrot.

The adult *triple chip* call (Figure 8.8) of the Brown-headed Parrot is difficult to interpret and somewhat of a mystery. The call was recorded at both Punda Maria and Pretoriuskop but only on six occasions. None of the birds making this call were identified and I was unable to estimate their emotional state. The call may be similar to the chick *triple food begging* call and may be uttered by an individual in extreme excitement. Alternatively, the call may be an experimental call (Figure 8.13). As a result of the paucity of recorded calls no descriptive statistics are given.

Equally unexplained is a *quadruple chip* call uttered, but not recorded, by one individual in the Pafuri area, 60km north of Punda Maria.

Adult *Kreek* Call

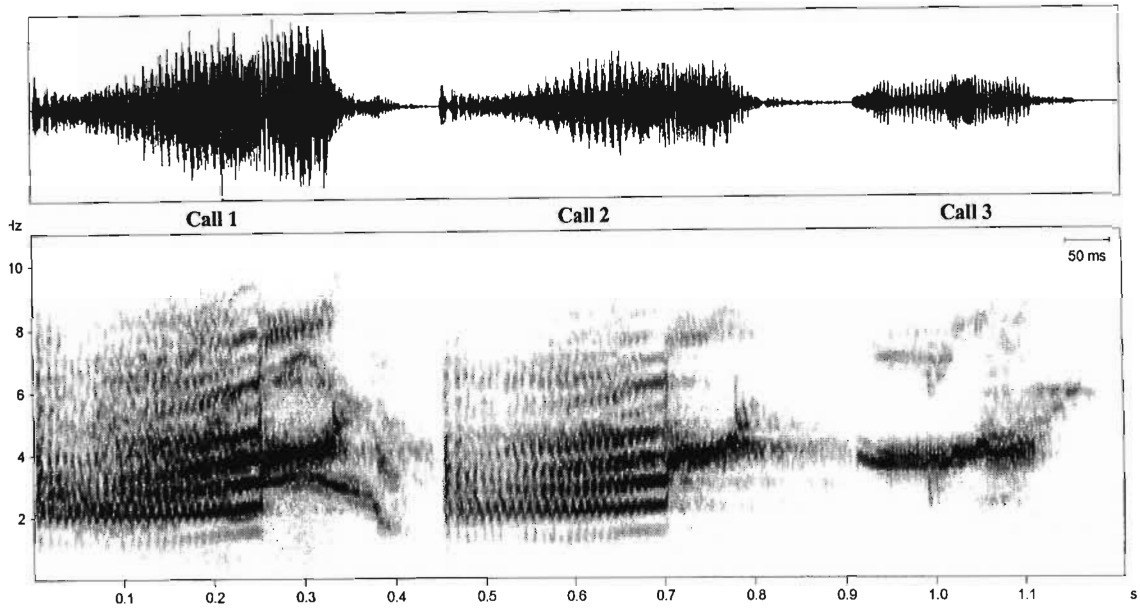

Figure 8.9: Power spectrum and spectrogram of the *kreek* calls of adult Brown-headed Parrots. Calls 1 and 2 are from the same individual, whilst call 3 is from a second individual.

The *kreek* call (Figure 8.9) is a common call made by the species and is the first of three call types, which are simultaneously easily identifiable yet highly variable amongst and between individuals. It is often used by an individual in response to an adult *double chip* contact call from a distant bird and is always used in flight. As a response the call is always made as a single call. In flight the call is repeated and mixed with the *chreeo* call (Figure 8.10). *Kreek* calls and the succeeding *chreeo* calls are always made whilst foraging, however, *kreeks* seem to be associated with pleasure. The call is often given by an individual being preened or when eating, when the pupils will dilate and the head feathers are erected (Fig 8.10).

The variability within the *kreek* call is shown in Figure 8.9, which shows the power spectra and sonograms of 2 *kreek* calls recorded from a single bird within a period of 16 seconds and, for comparison, a *kreek* from a different individual. The power spectra of the first call shows that much more energy has been expended in this call, rather than the second. Also the first call has a much more complicated ending, with frequency modulations simultaneously descending and ascending, suggesting double voicing, however, given the variability, certain elements remain fixed. The effect to the human ear is that the call sounds extremely harsh and abrasive.

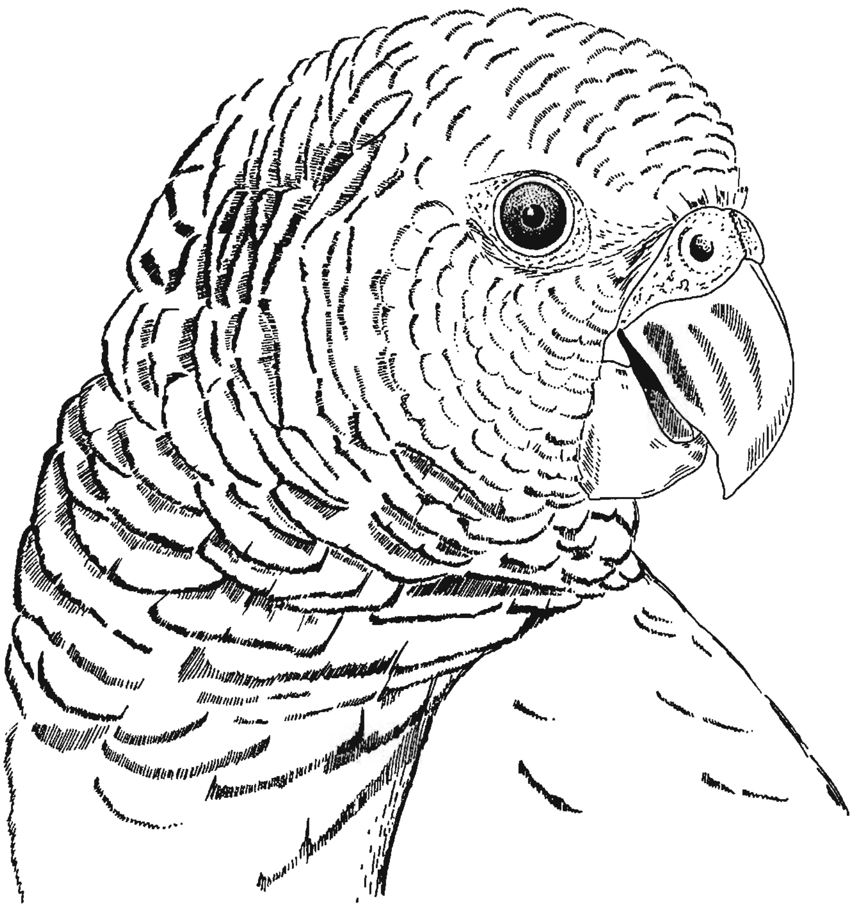

Figure 8.10: Head of an adult Brown-headed Parrot showing erect head feathers and dilated pupil, often associated with a *kreek* call.

Adult *Chreeo* Call

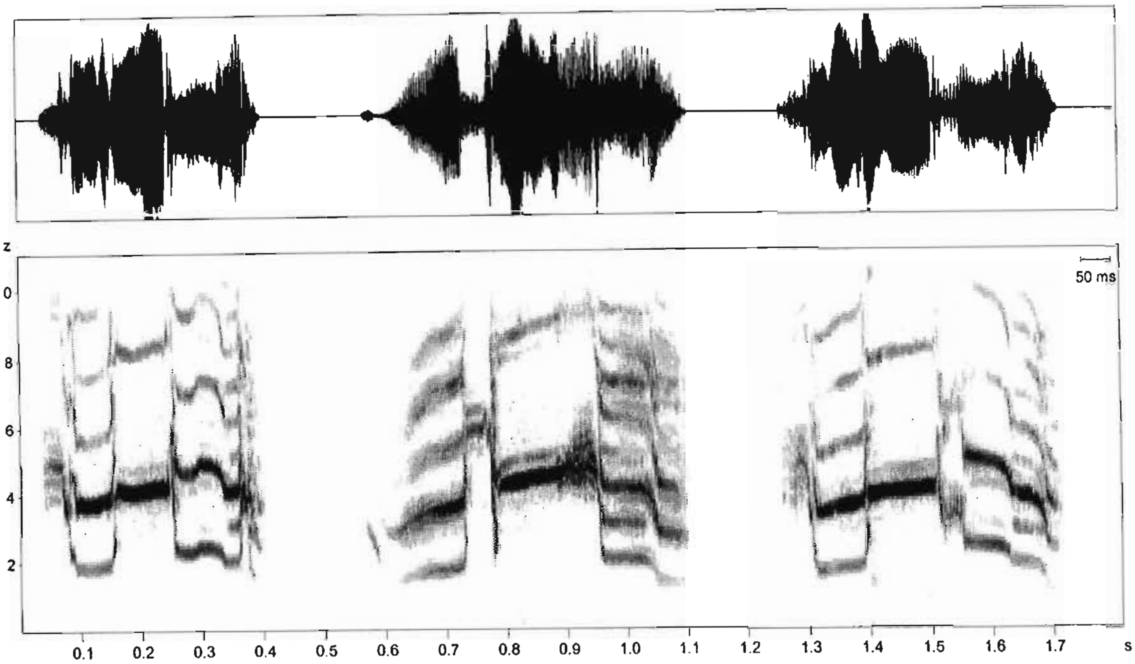

Figure 8.11: Power spectrum and spectrogram of three *chreeo* calls of adult Brown-headed Parrots. All calls are from the same individual.

The adult *chreeo* call (Figure 8.11) is another common call of the Brown-headed Parrot, which is easily identifiable yet is extremely variable both amongst individuals and between individuals. The three calls shown in Figure 8.11 are an example of the variation and all come from a single individual and were recorded within 48 seconds of each other. The first and third calls are similar, with a frequency modulation followed by five harmonics, with the energy being carried on the second. After a further frequency modulation, the second and fourth harmonic carries through to another modulation. Whilst each call ends with four sidebanded harmonics, the two calls become completely different. The wave pattern of the first call is sinusoidal, whilst the second descends over two modulations. The second call does not begin on a modulation but with the five harmonics. After these have modulated, a section appears which is absent from calls 1 and 3. This section is carried through by the third harmonic. The rest of the call is similar to call 3.

This call and the *kreek* call are often associated with feeding, however, the *chreeo* call tends to be associated with looking for foraging and food manipulation and are often interspersed with *double chip* contact calls (figure 8.12).

Figure 8.12: An adult Brown-headed Parrot searching for food. These investigations are often accompanied with the *chreeo* call interspersed with the *double chip* contact call of the species.

Adult *Zzweet* Call

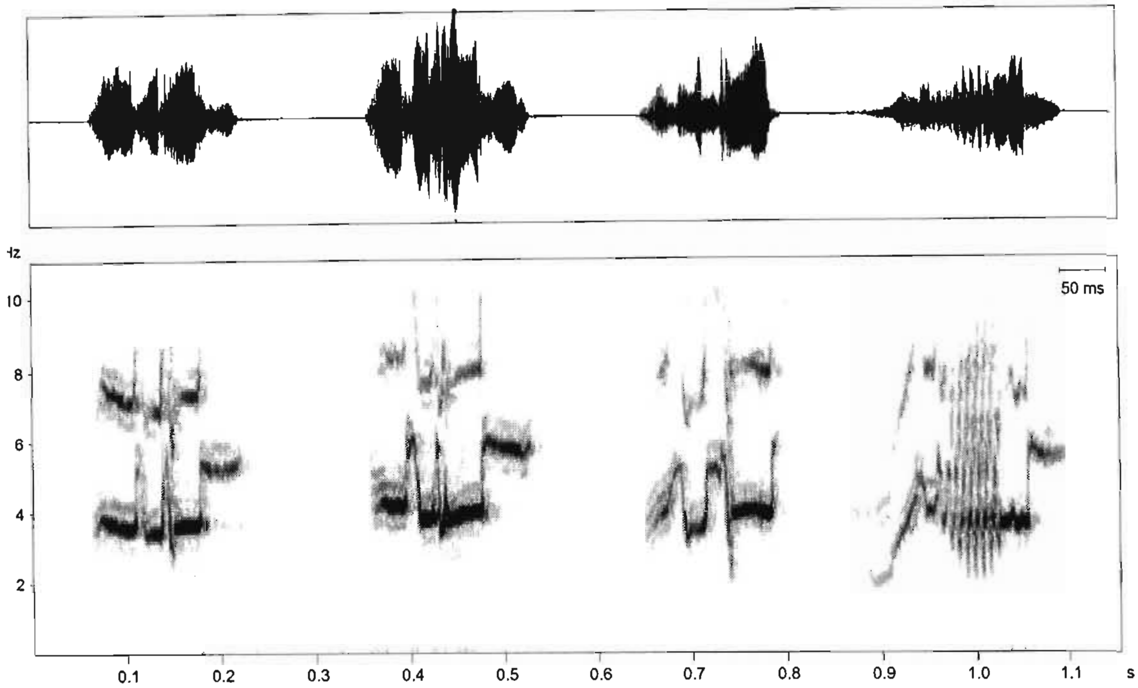

Figure 8.13: Power spectrum and spectrogram of four *zzweet* calls made by the same adult Brown-headed Parrot.

The adult *zzweet* call (Figure 8.13) is by far the most common call made by the species. However, its function, if it has one, is unknown. Adults make these sounds in all situations apart from alarm. The vocal dexterity of Brown-headed Parrots is nowhere better shown than in *zzweet* calls. Again these calls are recognizable yet highly variable. Although calls 1 and 2 are similar, the entire call 2 is on average pitched 500 Hz. higher than call 1. Call 3 is, again similar to the others but is introduced by an ascending frequency modulation, whilst the introduction in calls 1 and 2 is by way of a sidebanded tone with a harmonic. Similarly, call 4 is introduced by an ascending frequency modulation, but whilst the bird holds the energy in the first harmonic, it introduces a *trill* throughout the entire middle section. This is, probably, produced by allowing the tongue to vibrate against a mandible.

Alarm or *Threat* Call

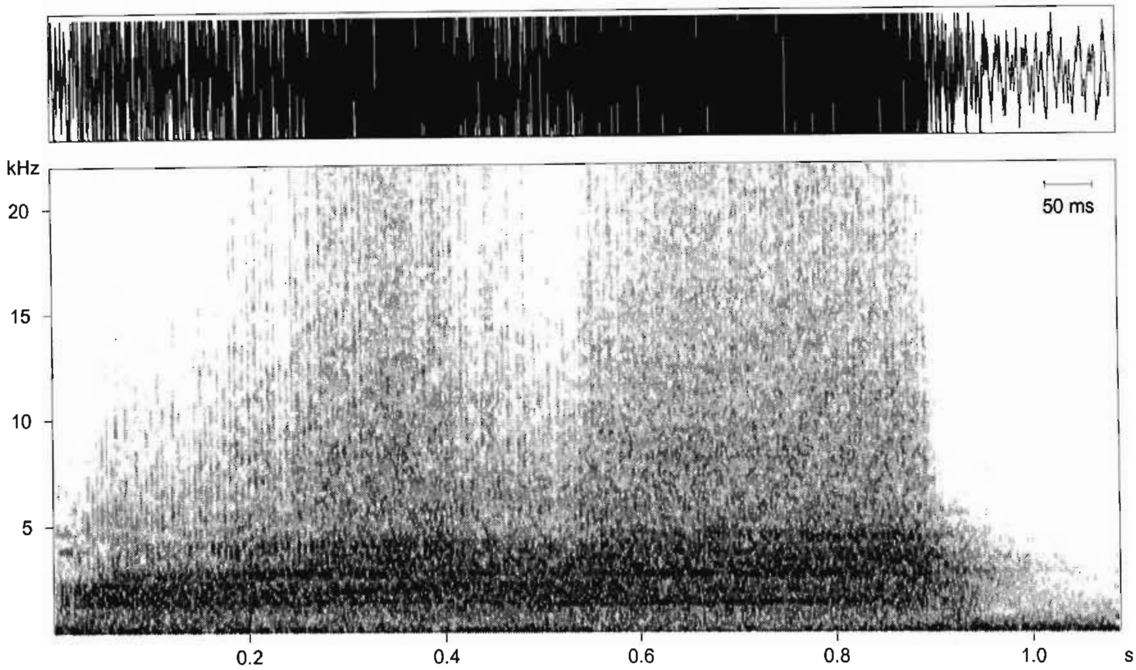

Figure 8.14: Power spectrum and spectrogram of the alarm call of the Brown-headed Parrot. Note: The figure is unfiltered.

This call (Figure 8.14) serves two purposes, signaling both alarm and threat. The call is a "structureless" growl of extremely high amplitude in a bandwidth between 1 and 5 kHz. (mean duration = 0.912s, S.D. 0.057s, n = 9). The call is produced by both adults and chicks and is made by the bird expelling air. I witnessed the call being used in two different scenarios.

Birds being pursued by avian predators will usually utter normal flight calls. Should the distance between the predator and prey reduce to a point where the prey feels threatened, the flight call is replaced by the *alarm* call. With increasing distance the flight call resumes. Non-flight birds also articulate *threat* calls in a variety of threat situations. In this scenario, the call is accompanied by a threatening posture (Figure 8.15). The body is lowered, the wings are held upright and the head pushed forward.

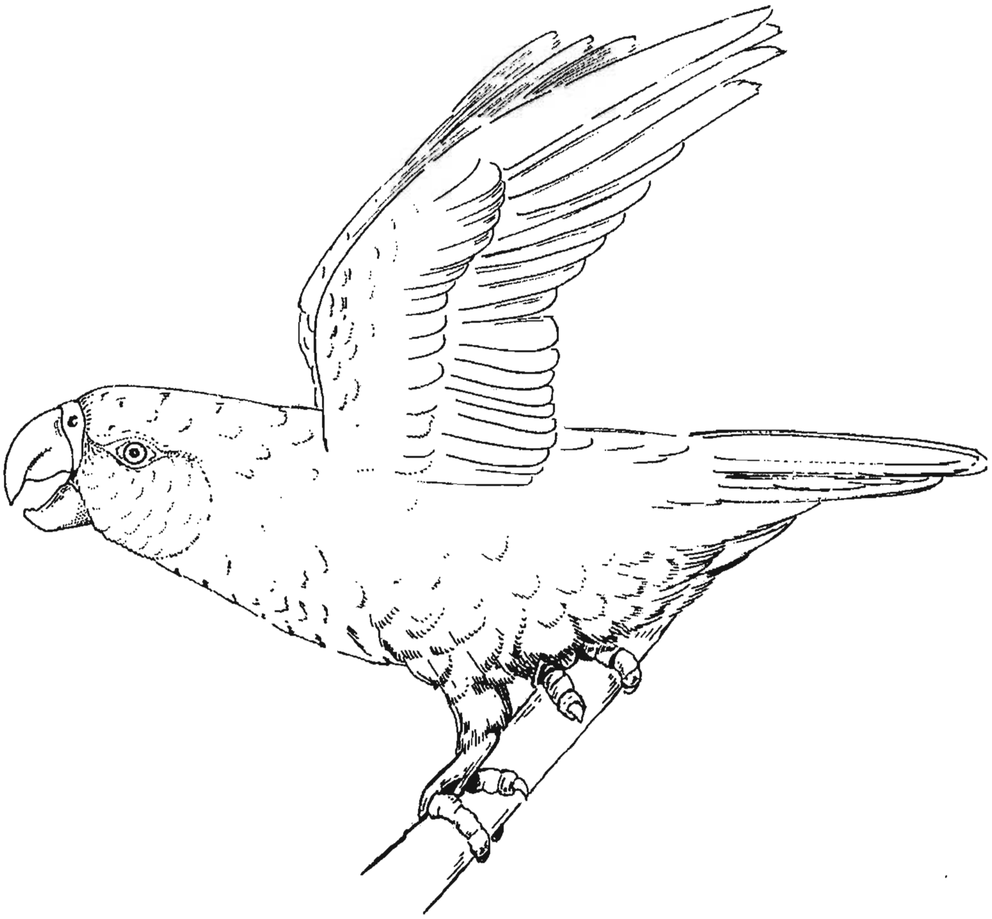

Figure 8.15: Threat Posture of an adult Brown-headed Parrot. This posture is usually accompanied with the *threat* call in which air is expelled through the open beak.

Adult *Conversational Chattering*

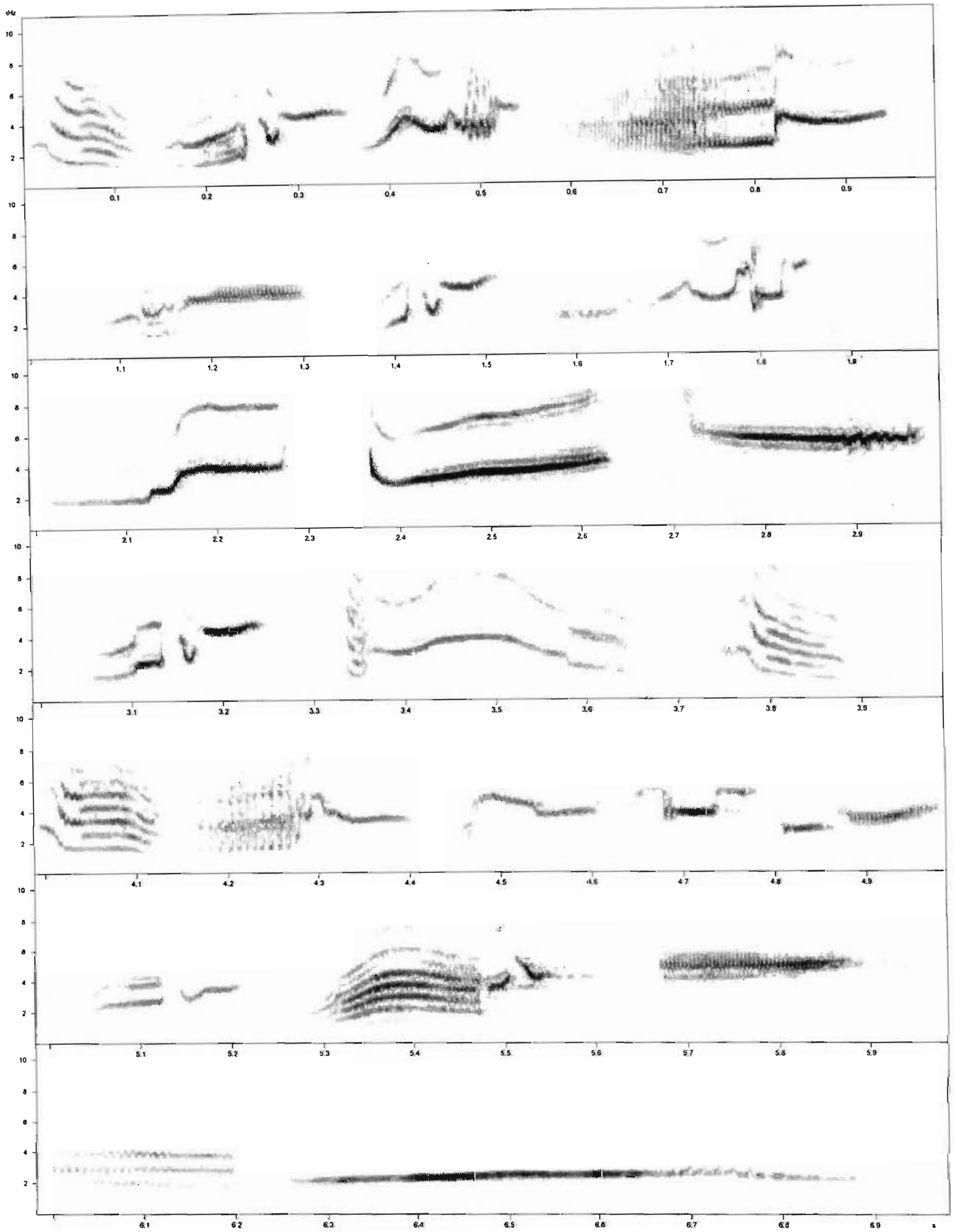

Figure 8.16: *Conversational Chattering* calls of adult Brown-headed Parrots. Twenty-three calls are shown representing various temporal lengths and frequency structures.

If these calls have a function it is either contentment or experimentation. The calls are often uttered when feeding, but always when an individual is resting or sleeping (Figure 8.17). A variety of calls are shown as Figure 8.16. The energy content of these calls is very low and they are sometimes barely audible. For this reason it is difficult to estimate how common these calls are, however, every bird which allowed close recording (2-3m) was found to be making these sounds.

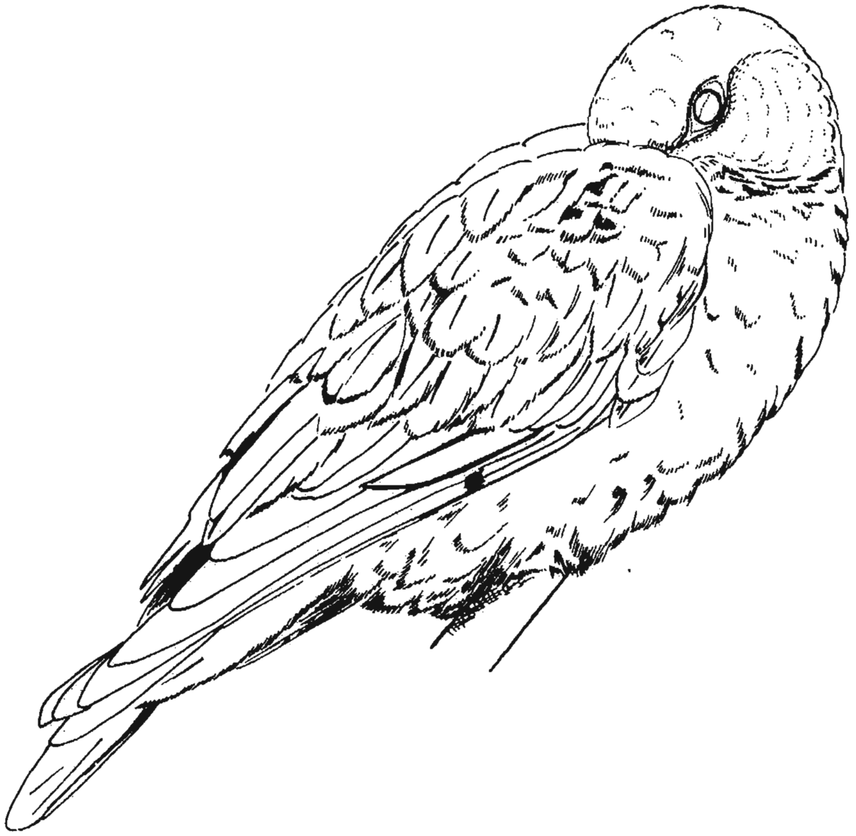

Figure 8.17: Many of the "conversational chattering" calls of Brown-headed Parrots are made whilst an individual is resting or sleeping.

Discussion

The results indicate that the Brown-headed Parrot has seven individual call types. Although, this includes the chick *double food begging* call, it does not include aberrant calls such as the chick *triple food begging* call or transitional calls. This is general agreement with other parrots, which have been studied.

Among the most studied, are the Australian parrots, where the Eastern Rosella (*Platycercus eximius*) has been found to have between 19 and 25 separate call types (Brereton 1963, 1971; Brereton & Pidgeon 1966). This is the largest vocabulary of any Australian parrot species, with the Cockateil (*Nymphicus hollandicus*) (Zann 1965), the Budgerigar (*Mellopsittacus undulates*) (Brockway 1964a & 1964b; Wyndham 1980) and the Galah (*Cacatua roseicapilla*) (Pidgeon 1981) having 7, 8 and 9 individual calls respectively. However, this paucity of individual call types may belie a deeper syntactic meaning and Saunders (1983) suggests that there is certainly a variation of each call within a single bird's repertoire. This variation may convey different meanings on the call depending on mood or situation.

A second reason for the paucity of separate call types may be as a result of parrot life history. Short-lived birds with ephemeral pair-bonds require elaborate courtship displays and in many species these include complex vocal signals to attract and keep a mate and to retain a viable territory (Catchpole & Slater 1995). This situation does not arise in most parrot species, which are relatively long-lived, retain a long-term pair bond throughout the non-breeding season and are largely non-territorial (Rowley 1974). In line with this view, and supporting the position put forward in chapters 5 and 6, I found no calls, which were purely associated with sexual situations or with territorial advertisement.

A number of other reasons for the lack of separate call types in parrots have been suggested. Brereton (1971) suggested a correlation between vocabulary, social organisation and habitat, proposing that parrots inhabiting more arid areas live in larger, looser social groups, which in turn requires a less complex vocal repertoire for group cohesion. Both Wyndham (1980) and Rowley (1990) submit that the number of apparent separate parrot call types is a result of researcher subjectivity and that parrot call types may be artificially increased or decreased by either the researcher identifying discrete sounds where none exist or not recognising differences, which may be important in parrot communication. It is difficult to make a judgement on these suggestions, as researcher fidelity probably influences all animal vocal investigations. Further, although Farabaugh & Dooling (1996) accept Brereton's *general* conclusions they point out that no rigorous testing of the theory has been carried out and that such a test would depend on the size of the repertoire which is learned.

Whilst the chick *double food begging* call of the Brown-headed Parrot is certainly innate, figure 8.6 suggests, that in common with other parrot species, the acquisition of an adult vocabulary is learned (Farabaugh *et al.* 1994; Farabaugh & Dooling 1996; Baptista 1996). However, acquiring an adult vocabulary does not indicate that this new language replaces the juvenile language. On two occasions in September 1998, two "adults" were recorded, whilst foraging. These "adults" had a complete repertoire of adult calls. Upon the approach of their parents, they immediately stopped foraging and reverted to chick *double food begging* calls and were fed by the parents. After the parents left the chicks reverted to adult calling and returned to foraging for themselves.

It is well known that parrots have an ability to mimic sounds throughout their lives, which in turn implies that they are continually learning new vocalizations. Although no plausible reason has been advanced for this ability I suggest that the number of *conversational chattering* calls, is a direct manifestation of this capacity, as are the call variations identified in figures 8.9, 8.11 and 8.13. As has been pointed out the simultaneous ascendancy and descendancy of the end of the *kreek* calls suggests double voicing, a peculiarity of the oscines, which have dual control of the syrinx during voice production (Greenewalt 1968), however, the psittacine syrinx is anatomically different from the oscines. Parrots are not capable of double voicing through that organ (Gaunt & Gaunt 1985) but it is possible that the sound is secondary production caused by vibration of the fleshy tongue against the mandible.

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Chapter 9

Parent Offspring Recognition in the Brown-Headed Parrot

Introduction

Apart from the case of co-operatively breeding species, natural selection will favour adults that care for their own progeny rather than young they have not sired (Burtt 1977). Therefore, where the young are mobile and able to intermingle with other broods, one would expect strong selection pressure to exist for recognition between parents and their young. This is especially true in the case of colonially breeding species. Indeed, Lack (1968) suggests that parent offspring recognition is a prerequisite for the evolution of the colonial breeding system.

Many studies have confirmed that in breeding colonies such recognition takes place by individual vocal signatures, facilitating either mutual recognition e.g. Adelie Penguin (*Pygoscelis adeliae*) (Jouventin & Roux 1979), recognition of the parents by the chick e.g. Laughing Gulls (*Larus atricilla*) (Beer 1969, 1970, 1975 & 1979), or recognition of the chick by the parents e.g. Royal Tern (*Sterna maxima maxima*) (Buckley & Buckley 1972). In some of these studies, an attempt was made to establish the timing at which recognition developed. In all cases it has been found that recognition develops just before the chicks are able to leave the nest area. However, the absolute timing of the development of recognition varies amongst species and may even be facultative and not species-specific (Falls 1982). For instance, Rautenfeld (1978) showed that for Herring Gulls (*L. argentatus*) nesting on cliffs, where intermingling is impossible, recognition was lacking until the chicks were 14 days old, whilst Tinbergen (1953) demonstrated that Herring Gulls nesting on the ground in close proximity to other nests, can recognise their chicks 5 days after hatching.

Further evidence to support the view that parent offspring recognition is a key adaptation to a colonial breeding system comes from studies of various Swallow species. Beecher *et al.* (1981a) showed that the adults of the highly colonial Bank Swallow (*Riparia riparia*) are capable of recognising their chicks 15 days after they hatched. Chicks were recognised by their call (Beecher *et al.* 1981a) and the ability develops in the adult at the time when the chicks are first able to leave the nest (Beecher *et al.* 1981b). In a further study, Beecher (1982), demonstrated that the more solitary Rough-winged Swallow (*Stelgidopteryx ruficollis*) was unable to discriminate between it's own chicks and Bank Swallow chicks. Suggesting that where the nest and the young are non-mobile, vocal recognition may not evolve and nest site recognition is sufficient for the parent to be reasonably sure that it is feeding its own chicks.

Apart from chick intermingling, a further situation in which parent offspring vocal recognition may arise is where the mobile young stray from the nest and parent and chick loose sight of each other. Such a situation is described in Laughing Gull colonies where visual contact is lost merely as a consequence of the small size of the chick and the vegetation height and structure (Beer 1969).

As has been stated in Chapter 6, an analogous situation arises in the Brown-headed Parrot. Nest site recognition may be sufficient when the chicks are non-mobile, however, a recognition problem arises for returning parents in finding their own chicks in the "nursery area" when those chicks are mobile yet camouflaged. From observation of the "nursery area" it was noted that parents call as they fly into the area and these calls are answered by food eliciting calls from a set of chicks. Therefore playback experiments were performed to examine whether parent offspring vocal recognition exists in this species. Two experimental designs were used to investigate whether the chicks recognised the parents or vice versa.

Study Areas and Methodology

Independent trials took place at both Punda Maria and Pretoriouskop immediately after the chicks had left the nest for the nursery area (Chapter 6). As the parents flew in to feed their chicks, their flight call was recorded using a

Marantz CP230 tape recorder fitted with a UECM-83 directional microphone. Any individual wing patternation from either parent was also noted. This allowed the chicks to be matched to the parents. The arrival of the parents set off calling bouts by the chicks and these were also recorded. The parent and chick calls were then transferred onto a computer using Batsound (Pettersson Elektronik AB, Sweden). Family specific tapes were then made which comprised, the parent's flight call, the flight calls of two other sets of adults (foreign adults), the food begging call of the chicks and the food begging calls of two other sets of chicks (foreign chicks). All of the foreign calls were recorded in other areas of the KNP and to avoid pseudoreplication the same adult and chick foreign calls were used for each family tape. The three calls of adults were randomized on the tape with one minute silence between each, followed by the three calls of chicks, which were also randomized with one minute silence between each call. By then linking the wing patternation to each call, each family was allocated one tape. New experimental tapes were made every 3 to 4 days to avoid the possibility of voice maturation, especially in the chicks, yielding erroneous results.

An hour after the parents had returned to the foraging areas, the chicks were played back the tape of their parental flight call and the foreign adults. Replay was made using a Motorola speaker (Frequency response 500 – 20,000 Hz.) from a distance of ± 10 metres. Their response was noted as either passive (no response) or active (answer with food begging calls).

Adults were followed to the foraging areas and if it was possible to identify an adult from the wing patternation and if the adult was < 20m away, the tape of the food begging calls of its chick and the foreign chicks were played back. I accepted any response other than ignoring the call as a positive response. It should also be pointed out that for each experiment only one adult was used as the experimental animal. Where both sets of parents were individually identifiable, which was a rare occurrence, the most easily identifiable adult was used.

As has been pointed out elsewhere, the chicks spend ± 21 days in the nursery area, after which they begin to follow their parents when they forage.

Therefore, for the next 7 days, the experiment was continued for both parents and chicks if the parent could be positively identified.

Cochran's Q test was used to analyze the data (Zar 1996).

Results

Chick Recognition of Parents.

A total of 1115 (604 at Punda Maria and 511 at Pretoriuskop) experiments were conducted where chicks were played adult calls and the results of these experiments are summarized in Table 9.1 and Figure 9.1. For the first two weeks in the nursery area, all chicks responded positively to the calls of their parents ($p < 0.001$). Although occasionally, chicks did not respond, there were no occasions where chicks responded positively to the call of a foreign adult (Figure 9.1).

	Week 1		**Week 2**		**Week 3**		**Week 4**	
Family	*Q*	*N*	*Q*	*n*	*Q*	*n*	*Q*	*n*
PM1	42.89*	*27*	49.64*	*33*	13.86*	*14*	16.55*	*11*
PM2	27.26*	*19*	40.92*	*26*	15.60**	*15*	12.67**	*9*
PM3	30.33*	*18*	37.00*	*24*	12.18**	*11*	22.84*	*19*
PM4	37.00*	*24*	26.38*	*16*	7.00****	*6*	19.60*	*15*
PM5	44.86*	*28*	39.93*	*28*	22.57*	*21*	14.60*	*10*
PM6	21.50*	*16*	19.60*	*15*	12.15**	*13*	10.75**	*8*
PM7	35.04*	*23*	38.00*	*27*	10.40***	*10*	21.50*	*16*
PM8	51.60*	*34*	45.74*	*31*	19.18*	*17*	14.60*	*10*
Total		***189***		***200***		***107***		***98***
P1	38.00*	*27*	46.83*	*29*	7.00****	*8*	8.86****	*7*
P2	19.60*	*15*	20.46*	*13*	8.67****	*9*	16.55*	*11*
P3	18.50*	*12*	20.46*	*13*	7.00****	*6*	5.20	*5*
P4	36.08*	*26*	48.80*	*30*	8.86****	*7*	12.67**	*9*
P5	25.33*	*18*	27.26*	*19*	10.40***	*10*	8.86****	*7*
P6	17.71*	*14*	28.35*	*17*	8.67****	*9*	10.75**	*8*
P7	29.20*	*20*	27.26*	*19*	17.38*	*16*	24.40*	*15*
P8	25.33*	*18*	24.40*	*15*	8.67****	*9*	18.50*	*12*
P9	23.40*	*17*	27.26*	*19*	17.38*	*16*	26.38*	*16*
Total		***167***		***174***		***90***		***90***

Table 9.1: Cochran's Q-test of differential responses of Brown-headed Parrot chicks being played back recordings of adult calls, with the appropriate value of n, the number of play backs to which each family was subjected and the total numbers of experiments done in each week at each location. PM denotes Punda Maria and P denotes Pretoriuskop. Statistical significance is as follows: $^{*}p < 0.001$, $^{**}p < 0.005$, $^{***}p < 0.01$ and $^{****}p < 0.05$.

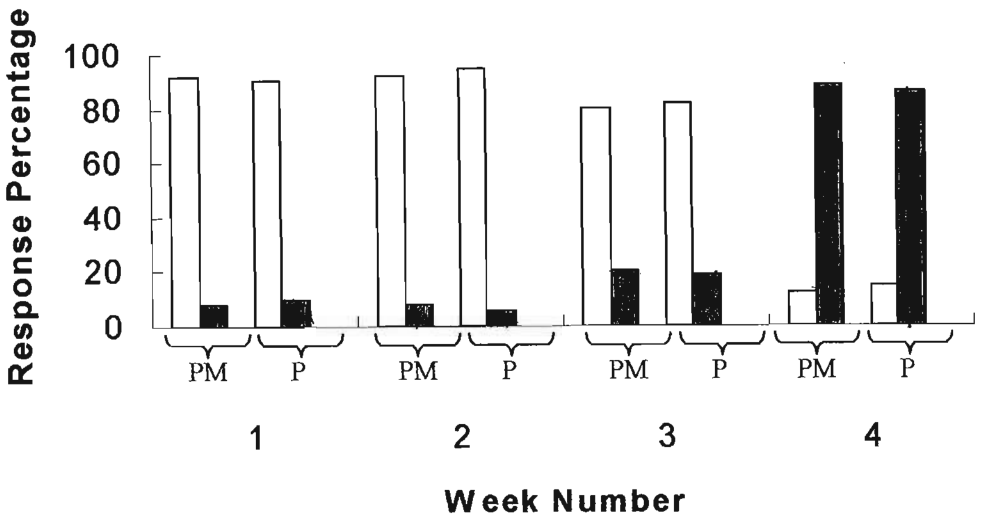

Figure 9.1: The percentage response of Brown-headed Parrot chicks being played back the flight calls of conspecific adults, where PM signifies Punda Maria and P signifies Pretoriuskop. The unshaded areas represent correct responses by the chicks to their parent's calls. The shaded areas represent occasions when the chick did not respond to any of the adult calls.

In the third week in the nursery area, although the positive response remained statistically significant, generally the level of significance was greatly reduced (Table 9.1). In the fourth week, when the chicks were foraging with their parents, the most common response was no response to the calls. For 14 of the 17 families tested, the lack of response was highly statistically significant (at least $p < 0.005$, Table 9.1).

Parent Recognition of Chicks.

A total of 409 (249 at Punda Maria and 160 at Pretoriuskop) experiments were conducted where adults were played chick calls and the results of these experiments are summarized as table 9.2 and figure 9.2.

	Week 1		Week 2		Week 3		Week 4	
Family	*Q*	*N*	*Q*	*n*	*Q*	*n*	*Q*	*n*
PM1	2.46	*13*	1.40	*9*	0.29	*7*	32.00*	*16*
PM2	2.00	*8*	1.00	*7*	1.00	*7*	30.00*	*15*
PM3	6.40	*21*	2.36	*12*	1.86	*14*	46.00*	*23*
PM4	2.00	*7*	8.50	*11*	0.67	*8*	32.00*	*16*
PM5	2.36	*12*	3.00	*6*	0.67	*9*	56.00*	*28*
Total		***61***		***45***		***45***		***98***
P1	1.00	*7*	1.60	*5*	0.50	*4*	8.00****	*24*
P2	1.00	*9*	3.25	*8*	0.500	*5*	10.00***	*21*
P3	3.00	*6*	1.00	*6*	0.50	*3*	6.00****	*31*
P4	3.00	*6*	1.60	*5*	1.60	*3*	6.00****	*17*
Total		***28***		***24***		***15***		***93***

Table 9.2: Cochran's Q-test of differential responses of Brown-headed Parrot adults being played back recordings of chick calls, with the appropriate value of *n*, the number of playbacks to which each family was subjected and the total numbers of experiments done in each week at each location. PM denotes Punda Maria and P denotes Pretoriuskop. Statistical significance is as follows: *p < 0.001, ***p < 0.01 and ****p < 0.05.

During the time that the adults foraged and returned to the chicks in the nursery area the most common response to the play back of chick calls was to ignore the stimulus. Although this was not statistically significant during that time, it became significant during the 4th week, when the adults were foraging accompanied by their chicks. The degree of significance was greater at Punda Maria, however, this may have been a function of the greater sample size at that site.

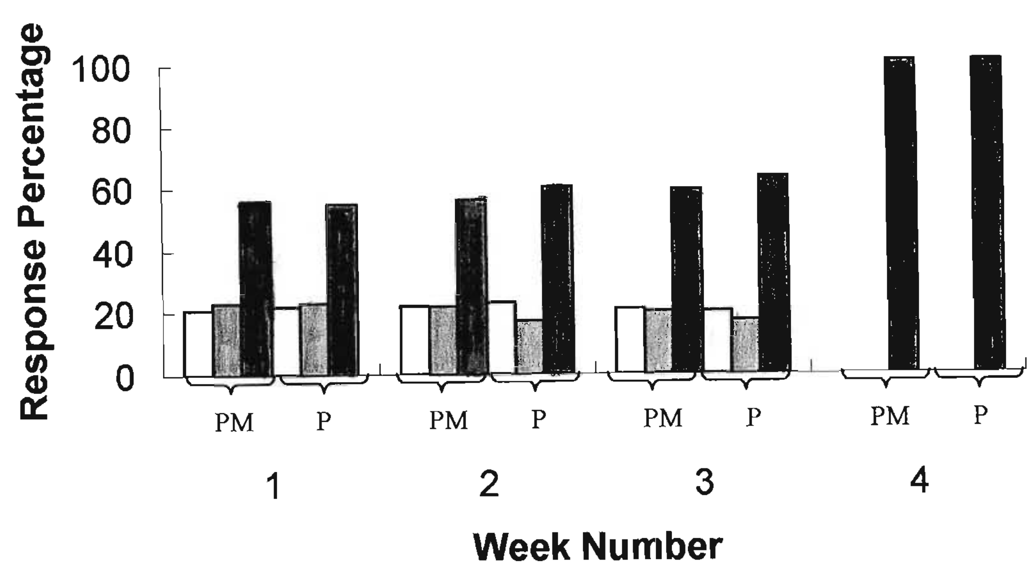

Figure 9.2: The percentage response of Brown-headed Parrot adults being played back the food begging calls of chicks, where PM signifies Punda Maria and P signifies Pretoriuskop. The unshaded areas represent correct responses by the adults to their chick's calls. The lightly shaded areas represent occasions when the adult responded to the calls of foreign chicks and the shaded areas represent occasions when the adult did not respond to any of the chick calls.

Discussion

The results indicate that Brown-headed Parrot chicks are able to vocally discriminate between at least one of their parents and the call of foreign individuals. At each study site the statistical significance is greater than 99.9% in the first 2 weeks of occupancy of the "nursery area". Occasionally the chicks did not respond to any of the calls played back to them (< 10%), however, they never responded to a call, which did not originate from their parents. Thereafter in week 3 of occupancy, in nearly all cases, the significance of vocal discrimination decreased dramatically (Table 9.1). Prior studies have demonstrated that in other avian species a chick's ability to recognize parental calls is highly correlated with an increase in chick mobility e.g. Common Murre (*Uria aalge*), (Tshantz 1968), Black-billed Gull (*Larus bulleri*), (Beer 1970), Black-billed Gull (*L. delawarensis*), (Evans 1970), Razorbill (*Alca torda*), (Ingold 1970), Arctic Tern (*Sterna paradisaea*), (Busse & Busse 1977), Laughing Gull (*L. atricilla*), (Beer 1979), Galah (*Cacatua roseicapilla*), Rowley 1980), Bank Swallow, (*Riparia riparia*), (Beecher *et al.* 1981a & b) and Budgerigar (*Melopsittacus undulatus*), (Powell 1993). In each of these studies, the authors have demonstrated relationships between the age of recognition development and the life history of the species. For altricial species such as the Common Murre, recognition has developed in the first few days of hatching (Tshantz 1968), whilst in the Galah, chicks begin to recognize their parent's calls around the 35th day after hatching. Recognition is complete by the 40th day, with the fledglings leaving the nest on the 49th day (Rowley 1980). Clearly, as vocal recognition is highly developed in the Brown-headed Parrot chicks from the first week of occupancy of the "nursery area", this ability must arise prior to the chick leaving the nest. Exactly when vocal recognition develops would be a fruitful area of study.

Conversely, Brown-headed Parrot parents seemed to show no discrimination of their own chicks by voice from those of foreign chicks as they fly into the area. However, in week 4, the principal response to all stimuli was to remain silent. Such one-way differentiation seems puzzling as it would not seem to be evolutionarily stable. If the parents do not recognise their chicks, it would be in the interests of all the chicks in the "nursery area" to begin food-begging calls, upon the arrival of any adult, in the hope that they could elicit a free meal. This situation was never observed. At no time did more than one set of chicks begin to call in response to the calls of arriving adults. Therefore, either some explanation for the parents not needing to recognize their chicks must be forthcoming or some kind of parent chick recognition must be in operation.

Falls (1982) suggested that adult birds may not be capable of identifying their own young from individual characteristics of their calls, but instead by the differential response of the young to their parents (Miller & Emlen 1975; Beer 1979; Conover *et al.* 1980; Hitchock *et al.* 1988). This has also been stressed by Beecher (1982). He has suggested that there are costs involved in learning the calls of other birds and that the cost for a chick not recognizing its parents is far higher than for the parent not recognizing its chicks, especially when the parent has other chicks to feed. Furthermore, Falls (1982) has pointed out that although the calls are stereotyped in adults, chick calls develop as the chick matures. A further learning constraint would occur to the parent of multiple offspring, which would have to learn the calls of all of its offspring, whilst the chick would have to, at the very least, only learn one of its parents calls. Additionally, parents would have to learn calls in each successful breeding season. Therefore, it would seem be less costly for the chicks to learn the parental call than vice versa.

A second explanation for the parents not responding to their chicks by voice is that the parent does indeed recognise the chick call but confirms the identity of the chick by individually distinct markings prior to feeding. Although I found it impossible to individually identify chicks, this would not preclude a parent's ability to do so. This would explain the results of the experiments where the chicks were foraging with their parents in week 4. Here no adult responded to any of the chick's calls and the chicks only responded to the calls of their parents in 12.2% of the trials at Punda Maria and 10.0% of the trials at Pretoriuskop. A reasonable explanation of this behaviour would be that if the parents are in sight of the chicks and vice versa then call recognition would become a secondary process in favour of sight recognition as cognitive capacity develops. Multiple recognition systems have been suggested in both the Cliff Swallow (*Hirundo pyrrhonota*) (Stoddard & Beecher 1983) and the Royal Tern (*Sterna maxima*) (Buckley & Buckley 1970, 1972). Both these species may utilise a dual recognition system based on voice characteristics and individual markings.

A second possibility is that the parent's do recognise their own chicks voice as has been suggested in the case of the Galah (Rowley, 1980) but that ability was masked because the playback experiment was done out of ecological context. Increased risk of predation or simply getting lost, will exert strong selection pressure on the chicks to stay within the "nursery area". In turn this would result in the evolution of vocal discrimination to allow parents to find their own chicks. Therefore, parents may not respond to chick calls out of that area. This could only be conclusively tested in an aviary. However, a prerequisite of such an identification system would be extreme vocal signature variability in the chick calls (Falls 1982). Such a stereotypical and individually distinct call has been demonstrated in the calls of pre-fledgling Budgerigars (Powell 1993) and whether this variability exists in young Brown-headed Parrots is the subject of the next chapter. A second corollary of these results is that if the chicks can recognise the parents then there should be strong intra-individual differences in the calls of the adults. This possibility is investigated in Chapter 10.

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Chapter 10

Individual Vocal Differences of the Brown-headed Parrot

Introduction

The adaptive advantages of using sound over other forms of sensory communication are that sound can be used at any time of the day, it can penetrate vegetation, it travels over long distances, it has a fast rate of change and it is reasonably locatable (Catchpole & Slater 1995). However, sound production carries with it a high-energy cost associated with each singing bout (Grieg-Smith 1983; Gottlander 1987; Eberhardt 1994). Therefore the information transmitted should be optimised to include both species specificity and individual specificity (Falls 1982). Marler (1960) first suggested that species specificity should be conveyed by invariant elements within the vocalization, whilst elements of the vocalizations which varied between individuals, were likely to carry information about the individual's identity. Knowledge of identity is particularly important in preventing individuals wasting time and energy during social interactions (Wilson 1975; Lambrechts & Dhondt 1995). This ability has been assumed to reduce costly fights between territorial neighbours (e.g. Brooks & Falls 1975; Falls & Brooks 1975; McGregor & Avery 1986; Brindley 1991; Godard 1991; Stoddard *et al.* 1991; McGregor & Westby 1992; McGregor 1993) or allow mates to find each other in colonies (e.g. White 1972; Brooke 1978; Jouventin *et al.* 1979; Spiers & Davis 1991; Lengagne *et al.* 1999). In fact, individual recognition amongst cooperatively breeding birds is so ubiquitous that to dispute its existence is now considered absurd (Stoddard 1996). Equally, parent offspring recognition has been shown to be fundamentally important in preventing parents mistakenly caring for young other than their own, in species where the chicks are mobile and the breeding season is synchronous (Beecher 1991; Chapter 9, this study).

The efficient operation of individual recognition makes two assumptions, that the vocalisations of the sender are individually distinct and that the recipient is able to decipher the vocalisation into something meaningful. Whilst the second assumption is out with the scope of this study, the first assumption contains the implicit functional dilemma of how the recognition signature is transmitted. This dilemma is further compounded when non-oscine, calling birds are considered. These species, by definition, have a relatively narrow vocabulary consisting of only a few calls, yet if individual recognition in these species exists, then variations within the call must also fulfil the purpose of species-recognition (Catchpole & Slater 1995), as well as in some cases, geographical dialects and sexual dimorphism (e.g. Baptista & Morton 1982).

For example, Hutchinson *et al.* (1968) and Berger & Ligon (1977) using calls of Sandwich Terns (*Sterna sandvicensis*) and Pinon Jays (*Gymmorhinus cyanocephalus*), respectively, both found that the coefficients of variation of certain parameters within the calls was greater than the coefficient of variation for the total length of the call and concluded that those parameters with low variability were species specific whilst those parameters with high variability were individually specific. Even more spectacularly, the Blue Petrel, (*Halobaena caerula*) has only one major call, yet temporal parameters towards the end of the call serve as individual signatures, syntactic parameters identify sexes and a combination of temporal and frequency parameters identify geographical dialects (Genevois & Bretagnolle 1994; Bretagnolle 1998).

In chapter 9, it was demonstrated that Brown-headed Parrots chicks, occupying the nursery area, are able to recognise their incoming parents by voice. Therefore, in this chapter I analyse the adult calls in the frequency and temporal domain to ascertain whether there are parameters, which are invariable thereby fulfilling the prediction of species recognition and whether there are parameters, which show greater variation, allowing individual voice distinctiveness.

It was shown in chapter 8 that one of the calls of the Brown-headed Parrot is the *double chip* contact call, whose purpose is group maintenance and contact between individuals. The call is relatively stable and easily recognised and was therefore used to test the hypothesis that the parameters of the contact calls of adult the Brown-headed Parrot are invariate across individuals in both the time and frequency domain and could therefore be used as a template towards individual recognition.

Methods

To avoid the possibility of dialect variations becoming an extraneous variable, vocalisations were collected at Pretoriuskop rest camp only (Chapter 2). Individual birds were approached to a distance of 3 - 5 m. A Sennheisser K6 microphone power module fitted with an ME67 long gun microphone capsule, which was in turn fitted with a wind baffle, was used for recording. This system returned a frequency response of 40 – 20,000 Hz at 2.5 dB. The recording unit was a TASCAM DA-P1 Digital Tape Recorder. The recorder was set at a sampling rate of 48,000 cycles per second, giving an effective recorded upper frequency of 24,000 Hz.

Entire calling bouts of individuals were recorded with the following proviso; as the length of the bout was not known the effective cut-off of recording was when the bout had included 25 double-chip contact calls.

Nine adults were recorded which featured enough contact calls for analysis. Each bout was then transferred to computer and then to compact disc. From each bout 10 contact calls were chosen at random from each individual. The parameters measured are shown as Figure 10.1 and the parameters used in the analysis are described in Table 10.1.

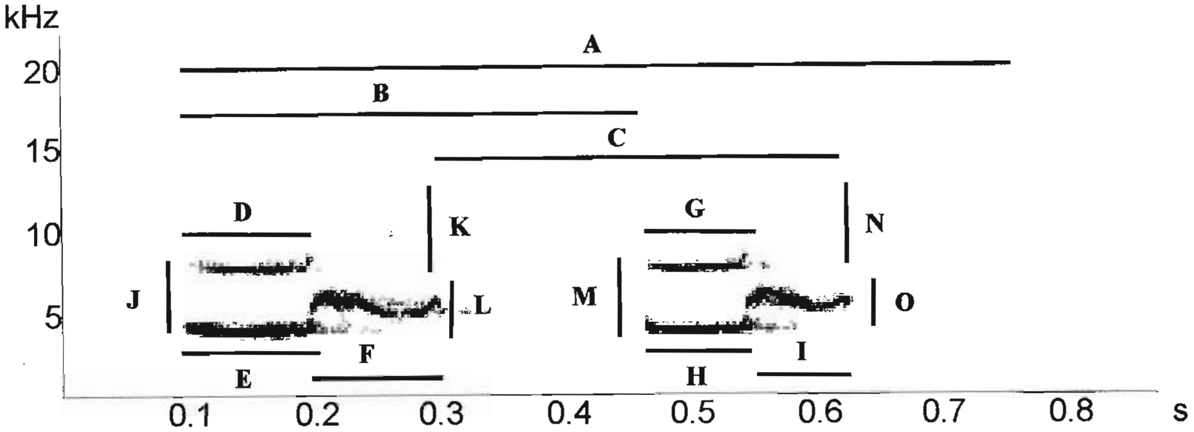


Figure 10.1: Typical spectrogram of the *double chip* contact call of an adult Brown-headed Parrot and the parameters measured to analyse the call. The key to the measurements is contained in table 10.1.

Temporal Parameters	Description
A	Total Length of the Call
B	Beginning of 1st Segment to Beginning of 2nd Segment
C	Beginning of 1st Segment to End of Peak Amplitude of 2nd Segment
D	Length Peak Amplitude 1st Part 1st Harmonic of 1st Segment
E	Length Peak Amplitude 1st Part Fundamental Harmonic of 1st Segment
F	Length of Peak Amplitude 2nd Part Fundamental Harmonic of 1st Segment
G	Length Peak Amplitude 1st Part 1st Harmonic of 2nd Segment
H	Length Peak Amplitude 1st Part Fundamental Harmonic of 2nd Segment
I	Length of Peak Amplitude 2nd Part Fundamental Harmonic of 2nd Segment
Frequency Parameters	
J	Difference Between Fundamental and 2nd Harmonic in 1st Segment
K	Difference in 2nd Part of Fundamental Harmonic in 1st Segment
L	Difference in 2nd Part in 2nd Harmonic of 1st Segment
M	Difference Between Fundamental and 2nd Harmonic in 2nd Segment
N	Difference in 2nd Part of Fundamental Harmonic in 2nd Segment
O	Difference in 2nd Part in 2nd Harmonic of 2nd Segment

Table 10.1: Definition of the parameters measured to analyse the spectrogram of the contact call of the Brown-headed Parrot.

Derived Variable	Origin	Description
P	B - C	Total Length of Silence Between the Segments
Q	E + F	Total Time Length of 1st Segment
R	H + I	Total Time Length of 2nd Segment
S	K + L	Total Frequency Range of 1st Segment
T	N + O	Total Frequency Range of 2nd Segment

Table 10.2: Origin and description of derived variables used in statistical analysis of adult Brown-headed Parrot *double chip* contact calls.

From the measured parameters, five further variables were derived as shown in Table 10.2, resulting in a total of 18 variables for each call.

Spectrograms were produced using the analysis program Avisoft-SASLab Pro Ver. 3.95f (Raimund Specht, Berlin), using a Hamming evaluation window in all cases. A free reticule cursor was used to compute all measurements. For printing, an FFT-length of 256 was used, which returned a bandwidth of 244Hz, an inverse bandwidth of 4.103ms, and gave a final frequency resolution of 187Hz and a temporal resolution of 2.6667ms. For the time domain analysis an FFT-length of 64 was used, decreasing temporal inverse bandwidth to 1.026ms and yielding an increased temporal resolution of 0.6667ms at the expense of a frequency resolution of 750Hz. For frequency analysis an FFT-length of 1024 was chosen, which decreased the bandwidth to 61Hz and gave an increased frequency resolution of 46Hz and a decreased temporal resolution of 10.7ms.

For statistical analysis the data were entered into Minitab Ver. 13 (Minitab Inc., Pa.) Each single bird was assigned a number (factor) and the relevant parameters for each of its 10 contact calls was entered. As the parameters were of a different magnitude the coefficient of variation (CV) was calculated as a measure of variation and the population CV to individual CV ratio was used to measure stereotypic elements of the calls (Hutchison *et al.* 1968; Jouventin 1982; Bretagnolle 1989). A discriminant function analysis was then conducted along with cluster analysis of the observations allowing the calculation of the classification success based on *a posteriori* predictions of group (ten calls for each individual) membership.

Results

The coefficients of variation for each of the measured and derived parameters are given as Table 10.3. The least variance occurring across the population is shown in the time parameters, with the most invariate being the

		Individual									
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**All**
Time Parameters	**A**	0.99	3.50	2.72	4.15	5.47	3.06	3.59	2.79	2.98	**0.34**
	B	2.00	11.55	3.35	15.56	7.02	7.12	10.74	7.46	0.55	**24.24**
	C	20.16	11.14	4.77	5.93	8.02	6.49	3.36	37.58	0.74	**30.85**
	D	9.50	14.95	7.70	5.83	32.59	20.41	4.44	5.22	5.72	**19.79**
	E	5.79	12.68	10.02	5.78	32.59	25.91	3.63	2.41	3.36	**18.88**
	F	3.53	24.18	7.10	25.84	11.39	24.81	13.73	4.78	0.70	**29.97**
	G	12.30	2.52	6.14	4.60	32.67	18.65	3.21	14.95	5.85	**21.09**
	H	13.71	4.66	6.96	6.03	32.67	24.32	2.41	18.88	4.70	**22.91**
	I	5.83	33.75	13.82	7.61	8.71	18.29	9.13	5.91	9.57	**25.64**
	P	29.51	7.53	7.45	10.87	14.91	17.75	7.25	15.74	3.97	**53.61**
	Q	3.37	10.07	6.98	10.28	24.17	13.22	5.00	1.20	1.87	**18.02**
	R	6.48	12.25	6.08	3.76	20.45	6.80	4.59	11.61	1.09	**16.33**
Frequency Parameters	**J**	2.98	3.85	4.80	6.72	35.82	10.56	3.23	6.52	0.46	**29.31**
	K	23.38	15.29	15.46	0.00	40.20	14.40	27.40	6.65	4.03	**58.19**
	L	11.87	1.35	17.09	8.21	16.59	18.90	2.40	5.92	2.23	**32.07**
	M	1.06	0.00	5.66	1.20	5.77	0.16	9.86	10.01	0.21	**27.64**
	N	6.75	0.05	16.96	10.82	22.28	7.04	23.64	10.38	15.82	**67.21**
	O	7.37	0.00	13.82	1.43	4.63	32.96	5.28	10.16	2.34	**36.90**
	S	8.28	1.95	15.66	4.81	13.05	14.35	8.61	3.66	1.10	**33.01**
	T	5.71	0.02	9.86	5.37	9.41	18.75	6.62	10.11	5.64	**42.70**

Table 10.3: The Coefficient of Variation ratio (ratio of mean to standard deviation x 100) calculated for each parameter for each individual and the total CV across the population of the nine Brown-headed Parrot individuals. The CVs are grouped according to whether they are time or frequency parameters.

total length of the call. In general, the frequency parameters show more variation across the population.

Therefore, it can be assumed that if any variation exists between the calls, it originates from either variability between individuals or variability between groups of calls, independent of the individuality of the caller.

The first discriminant analysis is carried out on the measured variables from Table 10.1. The high correlation between these variables and the derived variables from Table 10.2 means that analysis of the derived variables is done separately. The number of groups (group = 10 calls from each individual) was prespecified as nine; the number of individuals in the study. A linear discriminant function was used for analysis and the classification summary is given as Table 10.4.

TG / PG	1	2	3	4	5	6	7	8	9
1	**10**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
2	**0**	**10**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
3	**0**	**0**	**10**	**0**	**0**	**0**	**0**	**0**	**0**
4	**0**	**0**	**0**	**10**	**0**	**0**	**0**	**0**	**0**
5	**0**	**0**	**0**	**0**	**10**	**0**	**0**	**0**	**0**
6	**0**	**0**	**0**	**0**	**0**	**10**	**0**	**0**	**0**
7	**0**	**0**	**0**	**0**	**0**	**0**	**10**	**0**	**0**
8	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**10**	**0**
9	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**10**

Table 10.4: Discriminant function analysis of the variables given in Table 10.1 taken from 9 Brown-headed Parrots. TG = the true group of each factor, whilst PG = the predicted group after the analysis.

The nine true groups consisted of ten contact calls each and the analysis based on both measured temporal and measured frequency variables mirrors this circumstance (proportion correctly assigned = 100%).

The analysis, however, gives no indication of which type of variable discriminates the group, therefore discriminant analyses for the temporal and frequency variables alone is presented as Table 10.5 and 10.6 using the same discriminant function.

TG PG	1	2	3	4	5	6	7	8	9
1	10	0	0	0	0	0	0	0	0
2	0	9	0	0	0	0	0	0	0
3	0	0	10	0	0	0	0	0	0
4	0	0	0	10	0	0	0	0	0
5	0	0	0	0	10	0	0	0	0
6	0	0	0	0	0	10	0	0	0
7	0	0	0	0	0	0	8	0	0
8	0	0	0	0	0	0	2	10	0
9	0	1	0	0	0	0	0	0	10

Table 10.5: Discriminant function analysis of the temporal variables given in Table 10.1 taken from 9 Brown-headed Parrots. TG = the true group of each factor, whilst PG = the predicted group after the analysis.

TG PG	1	2	3	4	5	6	7	8	9
1	9	0	0	0	1	0	0	0	0
2	0	10	0	0	0	0	0	0	0
3	0	0	10	0	0	0	0	0	0
4	0	0	0	10	0	0	0	0	0
5	1	0	0	0	9	0	0	0	0
6	0	0	0	0	0	10	0	0	0
7	0	0	0	0	0	0	8	0	0
8	0	0	0	0	0	0	0	10	0
9	0	0	0	0	0	0	2	0	10

Table 10.6: Discriminant function analysis of the frequency variables given in Table 10.1 taken from 9 Brown-headed Parrots. TG = the true group of each factor, whilst PG = the predicted group after the analysis.

It is evident from Tables 10.5 and 10.6 that taken alone, the temporal and frequency variables reported in Table 10.1 do not reflect the equality of the true and predicted group as successfully as when they are considered together (proportion correctly assigned = 96.7% on measured temporal variables and 95.6% on measured frequency variables).

I then considered the derived variables from Table 10.2 in a similar manner.

TG PG	1	2	3	4	5	6	7	8	9
1	7	0	0	0	0	0	0	0	0
2	3	10	0	0	0	0	0	0	0
3	0	0	8	0	0	0	0	0	0
4	0	0	2	10	0	0	0	0	0
5	0	0	0	0	10	0	0	0	0
6	0	0	0	0	0	10	0	0	0
7	0	0	0	0	0	0	8	0	0
8	0	0	0	0	0	0	0	10	0
9	0	0	0	0	0	0	2	0	10

Table 10.7: Discriminant function analysis of the derived variables given in Table 10.2 taken from 9 Brown-headed Parrots. TG = the true group of each factor, whilst PG = the predicted group after the analysis.

TG PG	1	2	3	4	5	6	7	8	9
1	7	0	1	0	0	0	0	0	0
2	3	9	0	0	0	0	0	3	0
3	0	0	8	3	0	0	0	0	0
4	0	0	1	7	0	0	0	0	0
5	0	0	0	0	7	0	0	0	0
6	0	0	0	0	3	10	0	0	0
7	0	0	0	0	0	0	3	0	0
8	0	0	0	0	0	0	4	0	0
9	0	1	0	0	0	0	3	7	10

Table 10.8: Discriminant function analysis of the derived temporal variables given in Table 10.2 taken from 9 Brown-headed Parrots. TG = the true group of each factor, whilst PG = the predicted group after the analysis.

TG PG	1	2	3	4	5	6	7	8	9
1	8	0	0	0	3	0	0	0	0
2	1	10	0	0	0	0	0	0	0
3	0	0	7	0	0	0	0	0	0
4	0	0	2	10	0	0	0	0	0
5	1	0	0	0	4	0	6	0	0
6	0	0	0	0	0	10	0	0	0
7	0	0	0	0	2	0	2	0	0
8	0	0	1	0	0	0	0	10	0
9	0	0	0	0	1	0	2	0	10

Table 10.9: Discriminant function analysis of the derived frequency variables given in Table 10.2 taken from 9 Brown-headed Parrots. TG = the true group of each factor, whilst PG = the predicted group after the analysis.

The combined derived variables correctly assign 92.2% of the contact calls into their true groups, but taken separately, the derived temporal variables correctly assign only 67.8% whilst the derived frequency variables correctly assign 78.9% of the calls into their true groups.

The lack of accuracy associated with the derived variables may well be a function of the number of variables (15 from Table 10.1 v. 5 from Table 10.2), however, both the measured and derived variables indicate that consideration of the temporal *or* frequency elements of the calls alone yields considerably less accuracy than considering the temporal *and* frequency elements together.

A further discriminant analysis was carried out using the measured variables calculated from the fundamental frequency of the call (Figure 10.10).

TG PG	1	2	3	4	5	6	7	8	9
1	10	0	0	0	0	0	0	0	0
2	0	10	0	0	0	0	0	0	0
3	0	0	9	0	0	0	1	0	0
4	0	0	0	10	0	0	0	0	0
5	0	0	0	0	10	0	0	0	0
6	0	0	0	0	0	10	0	0	0
7	0	0	1	0	0	0	4	0	0
8	0	0	0	0	0	0	0	10	0
9	0	0	0	0	0	0	5	0	10

Table 10.9: Discriminant function analysis of the measured temporal and frequency variables of the fundamental frequency of the contact calls of 9 Brown-headed Parrots. The variables used are E, F, H, I, J, L, M and O from Table 10.2. TG = the true group of each factor, whilst PG = the predicted group after the analysis.

The discriminant analysis correctly assigns eight of the groups of calls to the same individual, but looses accuracy in individual 3 and especially in individual 7, where only four calls are correctly assigned and six calls are assigned to the wrong birds. The overall accuracy of the analysis using the fundamental frequency variables is 92.2%.

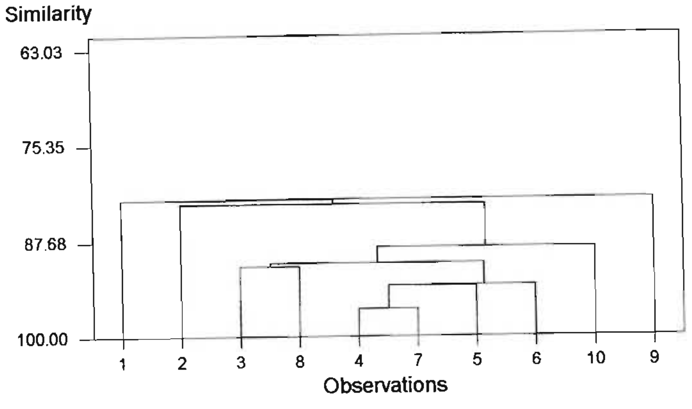
Confirmation that the predictions correspond with the true group was done by clustering the observations. The cluster analysis was carried out using a final partition of 9 clusters. This was based on the number of true groups and the analysis used a single linkage method and Euclidian distance for percentage similarities. The analysis package assigned a number to each call, so that observation 7 in figure 10.2 corresponds to the 7th call of the 1st individual, whilst observation 34 corresponds to the 4th call of the 4th individual.

The suite of calls from individual 1 are shown as cluster 1 in Figure 10.2. The figure indicates that these 10 calls are similar at a level above 80% and are sufficiently different from calls of other individuals to warrant a separate cluster of the observations. Clusters 2 and 3 in Figure 10.2 show the 10 calls from individual 2. Nine of these calls are clustered together again at a similarity greater than 80%. The 7th call from this individual is not sufficiently similar to be included in the 2nd cluster, however, it is sufficiently different from the calls of other individuals not to be clustered with them.

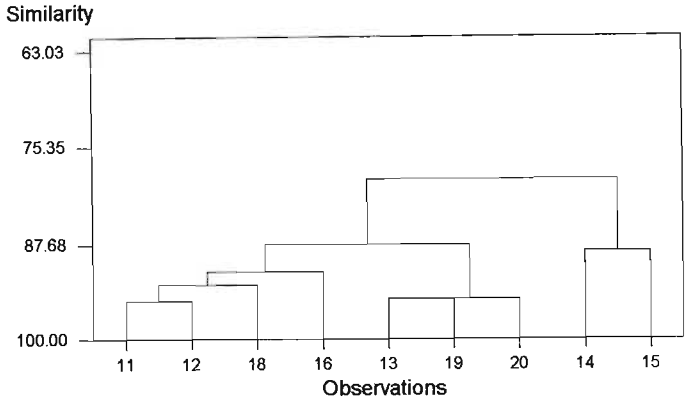
The calls of individuals 3 and 4 are sufficiently similar as to be shown in one cluster, cluster 4 of Figure 10.2. However it should be noted that, although they are similar the analysis has distinctly separated each suite, apart from call 31, the first call of fourth individual, which is more similar to the calls of the third individual.

The calls of the fifth individual have been clustered into two distinct groups, cluster 5 and 6, denoting that these calls are different but are not sufficiently similar to the calls of other individuals to be clustered with other individuals. An equivalent situation exists for the sixth individual, whose calls again occupy two separate clusters, clusters 7 and 8 of Figure 10.2. Calls 52 and 60 are identical in cluster 7.

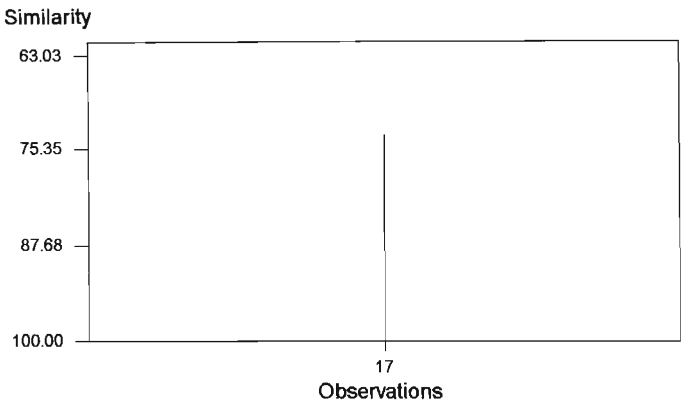
The seventh, eighth and ninth individuals have all been partitioned into a single cluster, cluster 9 of Figure 10.2, denoting similarities in their calls, yet the analysis retains their discrete individuality.



Cluster 1

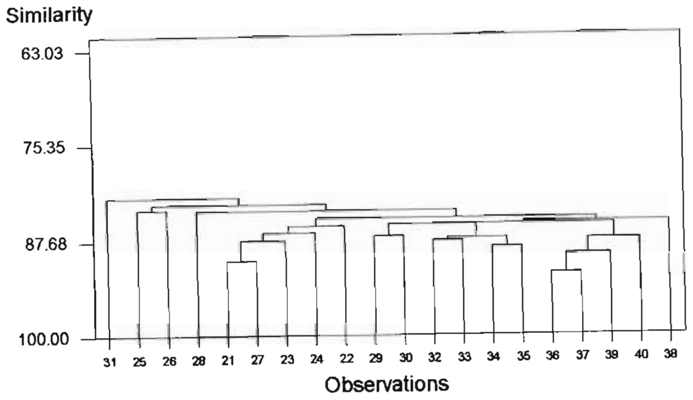


Cluster 2

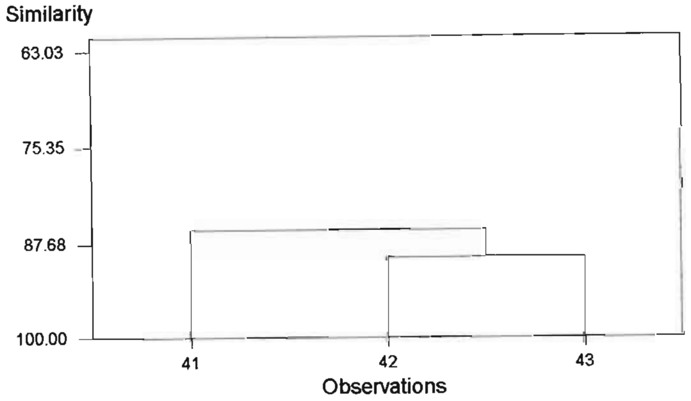


Cluster 3

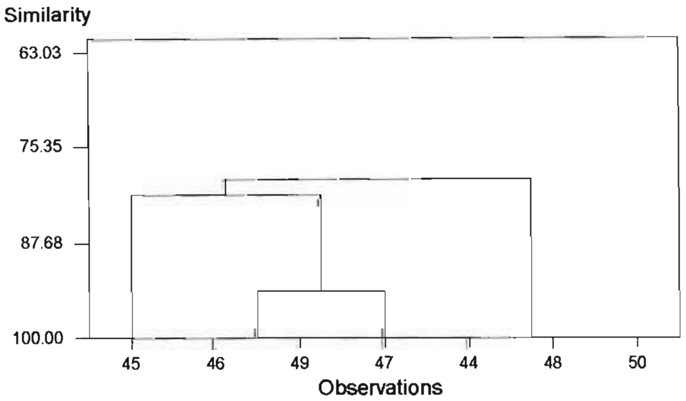
Figure 10.2: Clusters 1 to 3 of the multivariate cluster analysis of Brown-headed Parrot contact calls. The percentage of similarity is shown as the y axis. Observations correspond to numbered calls (See text for further details).



Cluster 4

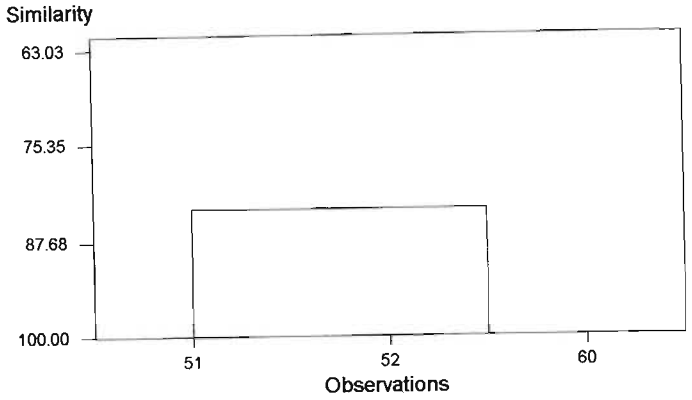


Cluster 5

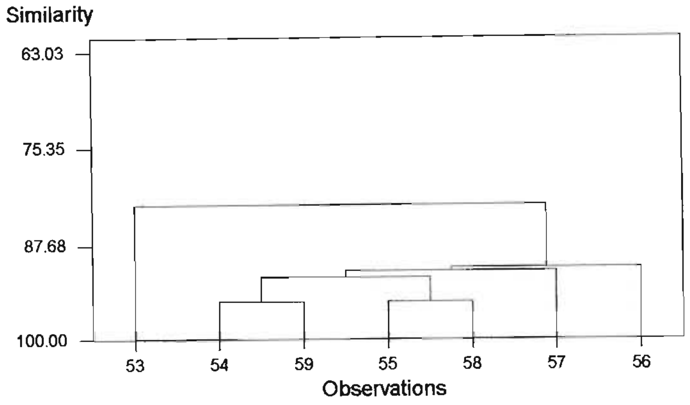


Cluster 6

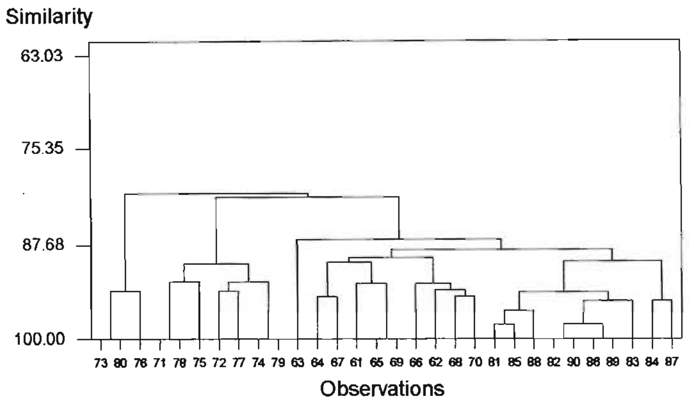
Figure 10.2 cont.: Clusters 4 to 6 of the multivariate cluster analysis of Brown-headed Parrot contact calls. The percentage of similarity is shown as the y axis. Observations correspond to numbered calls (See text for further details).



Cluster 7



Cluster 8



Cluster 9

Figure 10.2 cont.: Clusters 7 to 9 of the multivariate cluster analysis of Brown-headed Parrot contact calls. The percentage of similarity is shown as the y axis. Observations correspond to numbered calls (See text for further details).

Discussion

The coefficient of variation results show that across the time and frequency domains the *double chip* contact call of the Brown-headed Parrot is, in general, more stereotypical amongst individuals than between individuals. The exception is the total length of the call, which shows very little variation between individuals. Although this is of interest it is unlikely to throw any light on the question of individually identifiable carrier signatures without consideration of the content of the call.

The discriminant analysis taken in conjunction with the cluster analysis strongly suggests that individual Brown-headed Parrots can be distinguished on the sole basis of acoustic differences present in their contact calls. Taken in isolation, neither the frequency signatures nor temporal signatures assign the calls to individuals very accurately, however, when the frequency and temporal domains are considered together 100% assignment accuracy is obtained from the discriminant analysis. Furthermore, the greatest accuracy only accrues when the wide band is considered, i.e. inclusion of the second harmonic in the calculation. This is surprising for a number of reasons.

First, harmonics above the fundamental appear to degrade systematically as a function of distance (Wiley & Richards 1978). Whilst signal degradation is used by the receiver to judge the proximity of the sender (Morton 1998; Naguib 1998; Wiley 1998) if these harmonics are also carrying crucial identification signatures, then that information will be lost through distance modulation caused by temperature and wind fluctuations and broadcast height, as well as temporally stable factors such as scattering, absorption and deflection (Brown 1982). Second, wide-band calls are limited to carrying messages through amplitude changes, whereas the narrow band fundamental can carry messages through both amplitude and frequency modulations (Wiley & Richards 1978). Finally, many authors have recognised "sound windows", which allow minimum frequency attenuation depending on environmental conditions (Marten & Marler 1977;

Waser & Waser 1977; Wiley & Richards 1978; Richards & Wiley 1980). These "windows" lie between 200 to 3000Hz and calls within these frequency limits will travel further than calls out with the limits. As far as the results show, the information carried on the fundamental, the sound window harmonic, is not enough to discriminate one individual from another. It would therefore seem that carrying individual signatures on the harmonic is maladaptive. However, a second explanation presents itself.

Rooke & Knight (1977) studied avian discrimination in both frequency and temporal domains and concluded that although bird's and man's abilities to interpret threshold frequency changes was comparable, avian hearing is able to discriminate changes of as little as 0.5 ms, which is some 100x better than human hearing. Further, Park & Dooling (1985, 1986) have demonstrated that the Budgerigar (*Melopsittacus undulatus*) has the ability to detect and recognise con-specific contact calls based on extremely fine frequency modulations. Although the temporal resolution of the sonograms was 0.6667 ms, the possibility exists that this resolution was still too broad to chronicle subtle temporal and frequency inflections.

Unlike birdsong, calls have a much lower degree of structural complexity and a correspondingly lower information load for recognition potential (Lambrechts & Dhondt 1995). This has been demonstrated in a comparative study of the Cliff Swallow (*Hirundo pyrrhonota*) and the Barn Swallow (*H. rustica*). Although both species recognise their young from individual vocalizations, the young of the Cliff Swallow, joins a much larger crèche size (Stoddard & Beecher 1983; Beecher *et al.* 1985). Analysis of the food-begging call of young Cliff Swallows has shown that the call contains a significantly greater information capacity than the Barn Swallow (Medvin *et al.* 1992).

I therefore suggest that the *double chip* contact call of the Brown-headed Parrot does not provide enough information capacity in any particular spectral set to be the basis of individual recognition but that recognition is based on a combination of frequency and temporal elements as demonstrated by the discriminant analysis. This has been shown in other calling birds. For instance, Bailey (1978) found greater differences between individuals rather than within individuals in the duration and fundamental frequency of the separation call of the Bobwhite Quail (*Colinus virginianus*) and suggested that these parameters may form the basis of individual recognition in this species. Further work on this species has led to the suggestion that variability of the frequency characteristics also allows individual recognition in this species (Baker & Bailey 1987). The individually distinctive calls of the Snow Petrel (*Pagodroma nivea*) derive from differences in call duration, frequency parameters and temporal patterns (Barbraud *et al.* 2000)

A mixture of at least six frequency and temporal parameters has also been shown to yield significant inter individual differences in the contact call of the Spectacled Parrotlet (*Forpus conspicillatus*) (Wanker & Fischer 2001).

An advantage of vocal individuality, especially in hole-nesters where the male feeds the sitting female, is that she only needs to leave the eggs to be fed when she hears the males approach. Similarly, the nestlings need only approach the hole entrance and start to food beg is when they hear the parents approach. Thus the presence of a sitting female or nestlings in the cavity is concealed until the point where adults are close by to defend them (Saunders 1983).

A further advantage accrues to monogamous, flock-formers. Brown *et al.* (1988) have shown that Budgerigars will react to contact calls specific to their flock, whilst Ali *et al.* (1993) have demonstrated that Budgerigars more readily react to their mate's contact call than to the calls of other Budgerigars. Also, both Saunders (1983) and Rowley & Chapman (1986) have proposed that the flock members of some Australian parrots share a common, but unique, contact call. Furthermore, Wanker & Fischer (2001) have shown that established pairs of Spectacled Parrotlets have contact calls, which are very similar to each other and speculate that either call mixing occurs or one partner imitates the call of their mate. Farabaugh & Dooling (1996) have argued that these abilities allow birds to recognise both their own flock and their partner within the flock from a single call type. Whatever the reason, the mechanism requires the ability to learn calls through social interaction (Pepperberg 1985; Janik & Slater 1997).

The results of this study demonstrate that the *double chip* contact calls of the Brown-headed Parrot contain elements, which are specific to individuals, a prerequisite of individual voice recognition (Falls 1982). Whether these elements are indeed used to recognise conspecifics should be the subject of further study.

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Chapter 11

High Frequency Calls of Brown-headed Parrots; But Can They Hear Them?

Introduction

Of all avian species, it is probable that the Strigiformes have the most sensitive hearing at higher frequencies (Konishi 1973). However, this ability is certainly a corollary of their predatory lifestyle (Dooling 1992), and for all other birds the main purpose of song is to convey a variety of information to any potential receiver (Catchpole & Slater 1995). It would therefore be reasonable to expect that the songs or calls of birds would fall in a frequency band significantly lower than the upper threshold of their hearing. And if the purpose is communication, then it would be difficult to imagine selection for vocalisations outside the hearing potential of the sender or receiver.

Therefore, in a variety of studies a correlation has been shown between the frequencies at which a bird's hearing is most sensitive and the spectral characteristics of their songs or calls (Dooling 1992). In other words, although there is broad similarity in the hearing sensitivity over the avian class, the frequency of vocalisation appears to conform to the range of frequencies that a particular species can hear most efficiently (Dooling *et al.* 1970; Konishi 1970). For example, the Swamp Sparrow (*Geospiza georgiana*) and the Song Sparrow (*G. melodia*) have been shown to have distinct differences in the temporal organisation of their song (Marler & Peters 1989), which is reflected in differences in their auditory sensitivity (Okanoya & Dooling 1988). These differences aside, it is generally accepted that the more recently evolved Passeriformes are the most sensitive to higher frequencies with an upper threshold of 9.7 kHz, whilst the upper threshold of the non-Passeriformes (excluding Strigiformes) is 7.5 kHz. However, during the course of studies on the contact calls of the Brown-headed Parrot (*Poicephalus cryptoxanthus*), spectrograms clearly showed that the vocalizations of this species included elements, which far exceeded 10 kHz.

In view of the above assertions a series of experiments on both captive and wild birds was undertaken to test the hypothesis that Brown-headed Parrots could not hear these elements above 10 kHz and that the elements were functionless, artifacts of the calls. Although Konishi (1970) developed a neurophysiological method of determining the auditory range of birds, a behavioural approach was used here, as it allowed both captive and wild experiments and both methods give similar results (Konishi 1985).

Methods

A recording of a complete calling bout of a Brown-headed Parrot was made at Pretoriuskop Restcamp, KNP, using a TASCAM DA-P1 DAT recorder equipped with a Sennheiser ME67 directional microphone with a response range between 40 and 20,000 Hz. From this recording a *double chip* contact calls were chosen at random. The call was then imported using a PCI Audiomedia III into a PowerMacintosh computer, using the software Sound Designer II. The calls were then either left intact (Stimulus 1) or filtered using a low band pass (Stimulus 2) or a high band pass (Stimulus 3) at the 10 kHz level.

An experimental tape was then produced with each stimulus appearing at random 4 times. The total duration of the tape was 36 minutes (Table 11.1).

Start	4	ST1	2	ST2	2	ST3	4	ST3	2	ST2	2	ST1
4	ST2	2	ST1	2	ST3	4	ST1	2	ST3	2	ST2	**End**

Table 11.1: The randomised order of the experimental tape played to Brown-headed Parrots in both the captive and field experiment. Single numerals indicate periods of silence in minutes, ST indicates the respective stimulus played.

This tape was used in both the captive and wild bird experiments.

As the subject of this study was not the contact call of the species itself but rather whether Brown-headed Parrots can hear calls containing elements above 10 kHz, the experimental tape was played through the speakers to be

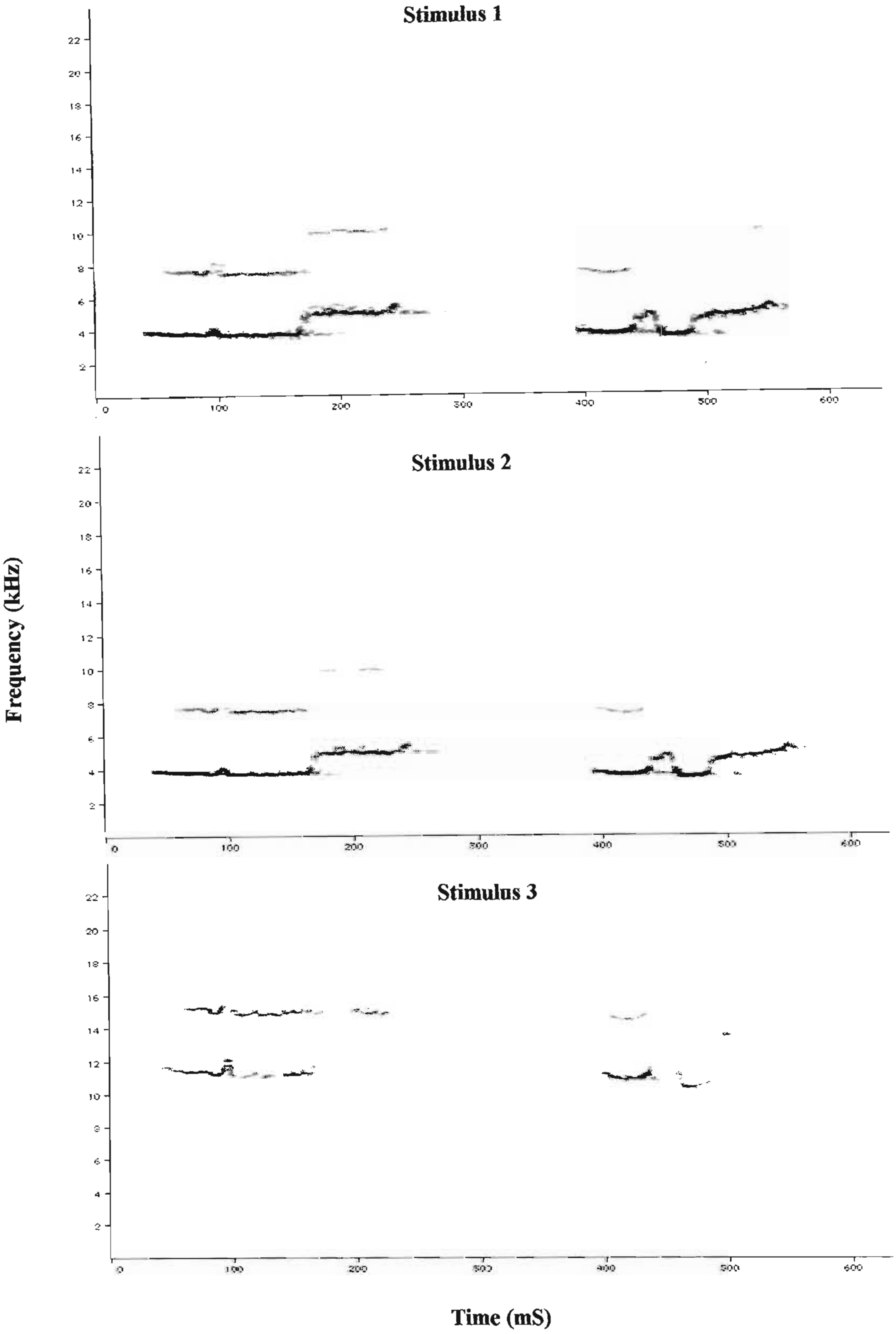

Figure 11.1: Sonograms of the three stimuli replayed to the Brown-headed Parrots both in the wild and captivity. The sonograms have been computed from recordings of the speaker playback.

used. Sonograms were produced of the frequency response of the speaker in the observation chamber for each of the three stimuli to confirm that the speakers were reproducing elements of the call above and below the 10 kHz level. These sonograms are shown as figure 11.1.

During the captive bird experiment, birds were placed in an observation cage and after 24 hours habituation, the tape was played to them. Their behaviour over the playback period was videotaped using a Sony CCD-TR820E. The videotape was then played back in the laboratory and different behaviours were noted. For details of captive maintenance see Chapter 2.

The number of behaviours performed in the 10 seconds before and the 10 seconds after the stimulus was played was recorded, these behaviours included feeding, moving, vocalization, sleeping and sneezing. The last action before the stimulus was played was noted and this was compared with the reaction of the parrot after the stimulus. Additionally, the number of times the bird moved its head in the 10 seconds before the stimuli was compared with the number of times it moved its head in the 10 seconds after the stimuli. The assumption being that an alert bird would keep its head still as movement would interfere with hearing.

In the field experiment, individuals that were feeding or preening on their own were approached to a distance of 3m or less and the same experimental tape was played to them. Although their response was noted, it was difficult to judge it in fine detail as in the laboratory. Therefore only three types of reaction were accepted, none (i.e. continuing the action already engaged in before the stimulus), vocalisation or stopping the immediate activity and remaining still.

As these data are nominal and independent a Chi-Squared test was used to test for significance.

Results

Twelve experiments were done on the captive birds and 24 on wild birds.

Comparing the total numbers of behaviours observed 10 seconds before and 10 seconds after each stimulus revealed a significant reduction in general activity after the parrots were played either the complete call or the stimulus where the only the high frequency elements remained (Table 11.2).

	Before	After	χ^2	Sig.
Stimulus 1	20	7	7.25	<0.01
Stimulus 2	27	15	2.88	N.S.
Stimulus 3	30	12	6.88	<0.01

Table 11.2: The total number of behaviours of Brown-headed Parrots 10 seconds before being played a stimulus compared with the number of activities 10 seconds after the stimulus.

When Stimulus 2 was played, that is, where the stimulus only included the frequencies below 10 kHz, there was no significant change in the level of activity.

Comparing the last action before the stimulus and the first action after it had been played showed that the most common reaction upon being played either stimulus was to stop that activity and not take up another positive activity (Figure 11.1).

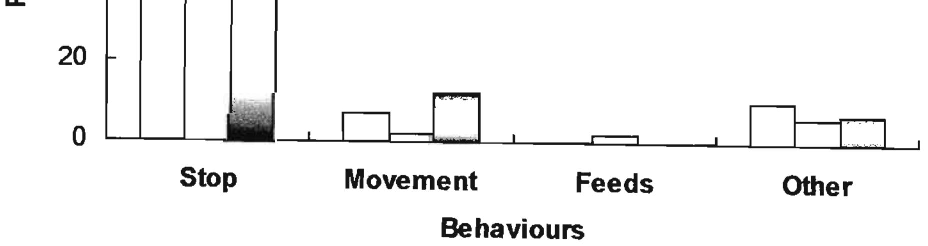

Figure 11.1: The first behavioural action after a stimulus had been played to the Brown-headed Parrots in captivity. The area with no shading represents stimulus 1, grey shading is stimulus 2 and heavy shading is stimulus 3.

Statistical analysis showed that this general trend of ceasing activity was significant for each stimulus played (Stimulus 1: $\chi^2 = 57.9$, df = 2, p <<0.001; Stimulus 2: $\chi^2 = 138.51$, df = 3, p <<0.001; Stimulus 3: $\chi^2 = 60.77$, df = 2, p <<0.001). This suggests that the birds heard and reacted to all three stimuli equally, including stimulus 3, which only had elements above 10 kHz.

The final activity examined in the captive bird experiment was head movement before and after the stimulus (Table 11.3).

	Before	After	χ^2	Sig.
Stimulus 1	86	67	2.36	N.S.
Stimulus 2	99	78	2.49	N.S.
Stimulus 3	105	42	27.00	<0.01

Table 11.2: The total number of head movements of Brown-headed Parrots in the 10 seconds before being played a stimulus compared with the number of head movements in the 10 seconds after the stimulus.

Differences in the numbers of times that an individual moved its head before and after stimuli 1 and 2 were not significant, however, head movement was significantly reduced after stimulus 3. Again this suggests that the individuals were aware of the stimulus being played.

The results from the experiments in the wild are given as Table 11.4.

	No Response	Vocalises	Alert	χ^2	Sig.
Stimulus 1	9	61	28	76.2	<0.001
Stimulus 2	24	41	33	4.8	N.S.
Stimulus 3	14	23	54	31.8	<0.001

Table 11.4: The behavioural response of Brown-headed Parrots in the wild in the 10 seconds after being played a stimulus. No Response indicates that the individual continued with its previous activity. Vocalises indicates that the bird vocalised and alert indicates that the bird stopped its activity and remained motionless.

A significant change in behaviour occurred after replay of stimuli 1 and 3, again suggesting that individuals were aware of stimulus 3, where all the frequencies below 10 kHz had been filtered out.

Discussion

Two general conclusions emerge from these results. First both stimulus 1, which consisted of the entire call and stimulus 3, where all the frequencies below 10 kHz had been filtered out, elicited significant behavioural changes in Brown-headed Parrots. The parrots showed a significant lessening in activity in the 10 seconds after these stimuli than in the 10 seconds before they were played both in terms of the total numbers of behaviours recorded and in terms of general activity. Similarly, in the same experiment on birds in the wild the most common reaction was to stop the current activity and not commence any other positive activity.

Second, if they heard stimulus 1 by inference they must have heard stimulus 2, which only consisted of the frequency elements below 10kHz, unless the lower limit of their hearing range is 10 kHz. However, in the experiment comparing the first reaction after the stimulus with the last reaction after it, a significant change in activity for all stimuli was recorded. Clearly then the parrots distinguished all of the stimuli, yet, in all subsequent experiments the parrots showed no significant behavioural reaction to stimulus 2.

The results, therefore, indicate that Brown-headed Parrots are able to produce and react to vocalizations at an extremely wide frequency range and that some of that range includes frequencies above the accepted upper cut-off limit of non-strigiformes species of around 10 kHz.

In each experiment, the birds reacted significantly to stimulus 3. Similarly, they also reacted significantly to stimulus 1 with the exception of the experiment involving head movement. The playing of stimulus 2 elicited only a significant response when comparing the last action before the stimulus and the first action after it. Therefore, the reception of high frequency elements of the calls plays an important, possibly crucial role in parrot communication. Given that they can produce these frequencies and that they do react to them, why should their reaction be preferential?

In a discussion, Morton (1998), Naguib (1998) and Haven Wiley (1998) have argued the case for and against the "ranging hypothesis" as proposed by Morton (1982, 1986, 1998a, b). Briefly stated this hypothesis requires two crucial conditions to be satisfied. The first of these is that birds estimate distance from a calling conspecific by assessing the amount of frequency degradation in the call received. Secondly, and crucially for Morton (1998a), in order to do this, the receiver must retain the undegraded sound for comparison "with-in memory". Both Naguib (1998) and Haven Wiley (1998) have disputed that birds rely on the memorisation of the calls of individuals and suggest that through experience with other conspecifics, they build a general template of the species-specific call. It is this template, which is used to range distance.

The basis of these experiments is the double chip contact call of the species. This call develops from the double chip food begging call of the chick, which also contains high frequency elements (Chapter 8). It has also been shown that Brown-headed Parrot chicks can discriminate between parents on the basis of individual voice recognition (Chapter 7). Further, I have shown (Chapter 8) that individual adult voice differences exist in this species and suggested that these have the potential to be used as markers for individual recognition.

It has been demonstrated that differential loss of frequencies, especially high frequencies, increases with distance, 6 dB for each doubling of the distance (Richards & Wiley 1980; Wiley & Richards 1982). I suggest that Brown-headed Parrots estimate the proximity of conspecifics through the degradation of the high frequency elements of the contact calls. However, I do not suggest that this estimation is achieved through memorisation. For a gregarious species memorisation would be a highly costly, if not impossible, exercise where flock size can rise to 50 individuals at a good food source in summer (Forshaw 1989) and where the flock membership is fluid. Further, it should be remembered that many of these experiments were done on captive birds in Milan using calls from wild birds in South Africa, that the receivers had not have heard before. I propose then, that, as they already retain a template for comparison in their own contact call, the ability to memorise individual differences of other adults may not be needed for recognition.

I therefore suggest that all three stimuli are recognised by the birds. Stimulus 2, with no high frequency elements is of less significance, as they perceive the call as emanating from conspecifics some distance away. Therefore, they react less to this call and tend to continue with their original activity. Stimuli 1 and 3, which contain the high frequency elements are perceived as coming from proximal conspecifics. This results, in most cases, in the receiver stopping its current activity to be able to better follow what is happening around it.

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Chapter 12

Conclusion

The persistence in a habitat of any species depends on its ability to survive and reproduce (Morrison *et al.* 1987). Intrinsic to this ability is the individual's capacity to find, manipulate and utilise the resources it requires to complete its life cycle (Koplin 1972; Whitman 1979; Ligon *et al.* 1991). Primary, amongst these resources are food and nest site availability, and the structure and composition of the vegetation, the "niche gestalt" of James (1971).

A major emphasis throughout this study has been that widely held and published perceptions concerning the Brown-headed Parrot are not necessarily accurate and can become established through repetition. Many of these beliefs have been summarised in chapter 1 and refuted in subsequent chapters. For instance, in chapter 3, it has been shown that contrary to published accounts, the diet of the Brown-headed Parrot is extremely catholic and that unlike the Cape Parrot it is not dependent on a single species (Wirminghaus *et al.* 2002) but on a non-specific yet seasonal suite of species. In chapter 4 it is proposed that, at least for the duration of this study, switching between seasonally available prey items ensures that the parrots do not experience energy or protein constraints. This confirms that as long as a suitable suite of tree species exists, fruiting failure of any one species at any one particular time will not prevent Brown-headed Parrots from occupying an area. Indeed, the handling time of prey items indicate that the time required continually feeding to reach their basal metabolic energy and protein requirements is easily attained, in the absence of competition. These results would seem to suggest that Brown-headed Parrots are not under a pattern of density-dependent population regulation based on food supply. However, in the following chapter it is pointed out that, although the parrots are not reliant on any one tree species for nesting, long term occupancy of an area is very probably constrained by suitable nesting cavities.

A number of authors have pointed to the palpable correlation between lack of breeding opportunity and shortage of suitable nesting cavities in hole nesting birds (reviewed by Newton 1994). However, such a correlation does not address the question of why cavity nesting should evolve if nesting cavities are a constraint toward successful breeding. An apparent answer to this paradox has been suggested by comparing the ecological correlates of hole nesting birds with "nest builders".

The first of these correlates to be proposed as an explanation of nest type diversification was mortality (Cole 1954; Charlesworth 1994). This explanation predicts that where mortality is high in pre-breeding individuals this will result in a life history where longevity is sacrificed at the expense of rapid growth and increased reproductive investment. From consideration of over 100 bird species Martin (1995) has confirmed this prediction and proposed that rapid growth and increased reproductive investment are associated with species whose nests are subject to relatively high predation rates. Further comparison has shown that cavity nesting birds show significantly greater egg and chick survival and this in turn is associated with slower chick development, delayed adult reproduction and increased adult survivorship (Owens & Bennett 1995). These latter correlates will obviously affect the availability of suitable nest cavities.

Tree felling, especially of older trees, severely limits the number of cavities available in any one area. This factor coupled with the physical requirements of the cavity in terms of depth, opening radius and orientation signifies a degree of habitat specificity for Brown-headed Parrots, which is not apparent when considering their diet alone. Such ecological rarity (Rabinowitz *et al.* 1986) is further compounded when the ecological correlates are considered.

Slower chick development results in longer nest occupancy, thus precluding potential nesters, that have not claimed a site or at least forcing them to attempt to breed 1/ in sites, which are of marginal value or 2/ at times when the ecological conditions are marginal. Delayed adult reproduction and increased adult survivorship will combine to render established pairs more adept at selecting suitable sites at the correct time, further limiting the quantity of available cavities.

The ecological correlates, combined with threats from live trapping and habitat degradation, fragmentation and alteration has probably resulted in a general decline in both numbers and distribution for Brown-headed Parrots (Juniper & Parr 1998). This is the same situation that has arisen with the Cape Parrot (*Poicephalus robustus*) (Wirminghaus *et al.* 1999, 2000). However, unlike the Cape Parrot the fate of the Brown-headed Parrot is largely unknown and its status is described as common in field guides (Forshaw 1989; Maclean 1993; Sinclair *et al.* 1993).

Woodward & Woodward (1897) recorded Brown-headed Parrots on the White Umfolozi in Zululand, an area where they certainly do not occur now. More recently, a number of professional ornithologists have reported areas where Brown-headed Parrots were common but have not been seen for many years; KwaZuluNatal (outside protected areas) (Johnston pers. comm.), Venda (Fenn pers. comm.). It would seem then that the remaining Brown-headed Parrots in South Africa are concentrated in protected areas demonstrating that the species is under active threat.

As a first step towards the conservation of the species, I would advocate that a serious attempt is made to calculate the status of the species within southern Africa. Probably, this would need to involve interested parties across the eastern side of South Africa in much the same way as the Cape Parrot Birding days involves volunteers to count Parrots across its range. Alternatively, the status of the species in particular areas could be assessed using call individuality (Baptista & Gaunt 1997; Riede 1998; Peake & McGregor 1999).

The second section of this study considers the vocalizations of Brown-headed Parrots, particularly focusing on parent-offspring recognition, individual differences and the ability to hear frequencies above the normally accepted avian auditory threshold.

Circumstantial and experimental evidence in previous studies of parent-offspring recognition have implicated learning and no evidence has been accumulated suggesting that recognition is innate. All recognition is based on previous experience (Falls 1982). Therefore the question arises, if chicks recognise their parents, when does this develop and do chicks recognise one or both parents. Further, if the pair bond is stable over time and the chicks recognise both parents, selective pressure could exist for both parents to have similar voice signatures, thereby reducing the learning curve of the chicks. This has been found in a study of Spectacled Parrotlets (*Forpus conspicillatus*) where a graded similarity in contact calls exists, with long term pair bonded individuals having the most similar calls (Wanker & Fischer 2001). The same study demonstrated similarities in contact calls between flock members and Wright (1996) found similarities at a regional level in the Yellow-naped Amazon (*Amazona auropalliala*).

Chapter 11 offers behavioural evidence showing unusual hearing abilities in Brown-headed Parrots. Although they make no comment, Wanker & Fischer (2001) report frequencies in the contact calls of Spectacled Parrotlets of 11633 Hz. This is above the avian auditory threshold.

As has been pointed out the vast majority of studies of avian vocalisations have been carried out on passerines, yet songbirds are not necessarily typical of the class Aves (Bretagnolle 1996). Vocal cultural transmission, whilst well developed in the oscines is unknown in the sub-oscines and has only been reported in the parrots and hummingbirds (Kroodsma 1982; Baptista 1996). Frequently, passerine vocalisations are interpreted in terms of individual fitness and as an important criteria in mate choice (Searcy & Andersson 1986; Lambrechts & Dhondt 1986, 1987), yet studies have shown that the female may base her decision on the quality of a male's territory (Radesater *et al* 1987; Arvidsson & Neergaard 1991).

Parrot vocalisations offer an interesting comparison with the oscines. Vocal cultural transmission probably evolved separately in three orders; the Passeriformes (Kroodsma 1982), the Psittaciformes (Gramza 1970; Rowley & Chapman 1986) and the Apodiformes (Wiley 1971; Baptista & Schuchmann 1990). The vocal repertoire of parrots is extremely complex and they show an innate capability for intra- and interspecific vocal imitation. Further this ability is retained throughout their lives. Although, studies have been carried out on the perception, production and development of parrot calls, the question of why this ability evolved remains (Todt 1975; Dooling *et al* 1987; Pepperberg 1990).

It was pointed out in chapter 1 of this study that the Brown-headed Parrot has often been placed in a superspecies with Meyer's Parrot, (*Poicephalus meyeri*) and Ruppell's Parrot (*P. ruppelli*) (White 1965). The general ecology of the three species seem to be similar, yet vocalisation differences are powerful isolating mechanisms (Martens 1996). Therefore comparative vocalization studies of these species may well provide evidence of the mechanization of speciation.

The object of this study has been the Brown-headed Parrot and as far as has been possible, I have endeavored to test hypotheses relevant to avian life histories and ecology, although much of the study has by necessity been descriptive. Like all studies, many of the answers concerning the species' ecology and vocalizations have produced more questions. My hope, therefore, is that this study promotes others to seek more understanding about this fascinating little bird.

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Appendix 1

Bird	1	2	3	4	5	6	7	8	9	10	11	12
1		15	159	159	173	184	176	189	192	184	141	140
2	*130*		162	164	182	173	187	188	187	181	136	137
3	*60*	*55*		22	160	163	177	180	199	197	136	131
4	*64*	*58*	*132*		156	163	181	182	203	197	144	139
5	*46*	*43*	*57*	*63*		23	155	164	185	177	136	135
6	*51*	*48*	*56*	*70*	*124*		156	167	192	182	137	134
7	*65*	*51*	*69*	*71*	*78*	*78*		21	190	192	169	148
8	*59*	*56*	*63*	*66*	*69*	*68*	*161*		181	183	164	141
9	*40*	*39*	*36*	*38*	*41*	*38*	*59*	*59*		24	131	116
10	*38*	*36*	*31*	*35*	*39*	*37*	*52*	*52*	*114*		119	116
11	*4*	*3*	*6*	*6*	*4*	*4*	*8*	*6*	*5*	*5*		45
12	*25*	*24*	*29*	*29*	*25*	*26*	*39*	*38*	*33*	*27*	*7*	
13	*25*	*24*	*24*	*24*	*21*	*22*	*36*	*35*	*29*	*23*	*7*	*45*
14	*17*	*15*	*16*	*18*	*17*	*16*	*23*	*25*	*20*	*17*	*0*	*24*
15	*33*	*31*	*22*	*26*	*21*	*23*	*42*	*44*	*41*	*39*	*4*	*23*
16	*14*	*12*	*8*	*11*	*8*	*6*	*17*	*18*	*14*	*13*	*1*	*15*
17	*15*	*13*	*8*	*11*	*9*	*7*	*19*	*18*	*15*	*14*	*3*	*16*
18	*16*	*15*	*7*	*10*	*19*	*20*	*25*	*22*	*10*	*9*	*2*	*6*
19	*16*	*15*	*8*	*12*	*18*	*19*	*26*	*24*	*11*	*10*	*2*	*5*
20	*10*	*10*	*13*	*14*	*17*	*17*	*26*	*25*	*18*	*18*	*2*	*9*
21	*9*	*9*	*15*	*16*	*18*	*17*	*26*	*25*	*18*	*18*	*3*	*10*
22	*11*	*11*	*11*	*12*	*3*	*3*	*17*	*20*	*8*	*6*	*4*	*12*
23	*42*	*41*	*34*	*34*	*36*	*38*	*51*	*51*	*45*	*37*	*0*	*21*
24	*38*	*39*	*32*	*32*	*34*	*37*	*46*	*47*	*44*	*37*	*0*	*22*

Table 1.1; Punda Maria. Values for *n* for number of times birds were located together, in italics below the line. Number of times one of the two birds were located without the other above the line.

	13	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
1	139	137	181	134	134	154	155	190	192	138	198	198
2	136	136	180	133	133	151	152	185	187	133	195	191
3	140	138	202	145	147	171	170	183	179	137	213	209
4	148	142	202	147	149	173	170	189	185	143	221	217
5	142	132	200	141	141	143	146	171	169	149	205	201
6	141	135	197	146	146	142	145	172	172	150	202	196
7	153	161	199	164	162	172	171	194	194	162	216	218
8	146	148	186	153	155	169	166	187	187	147	207	207
9	123	123	157	126	126	158	157	166	166	136	184	178
10	123	117	149	116	116	148	147	154	154	128	188	180
11	44	40	108	29	27	51	52	75	73	21	153	143
12	9	33	111	42	42	84	87	102	100	46	150	140
13		38	112	43	39	81	84	103	101	45	151	141
14	*21*		112	17	21	63	62	97	97	37	143	137
15	*22*	*13*		105	107	137	136	149	151	113	183	175
16	*14*	*18*	*12*		4	54	53	84	84	34	140	132
17	*17*	*17*	*12*	*21*		52	51	86	86	36	144	136
18	*7*	*7*	*8*	*7*	*9*		9	96	96	58	154	148
19	*6*	*8*	*9*	*8*	*10*	*42*		95	97	55	153	149
20	*8*	*2*	*14*	*4*	*4*	*10*	*11*		4	78	170	164
21	*9*	*2*	*13*	*4*	*4*	*10*	*10*	*68*		76	170	162
22	*12*	*7*	*7*	*4*	*4*	*4*	*6*	*6*	*7*		132	128
23	*20*	*15*	*33*	*12*	*11*	*17*	*18*	*21*	*21*	*15*		22
24	*21*	*14*	*33*	*12*	*11*	*16*	*16*	*20*	*21*	*13*	*127*	

Table 1.1; ***Cont.***

Bird	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1		57	187	163	189	167	145	197	210	163	181	167
2	*289*		243	217	210	191	219	167	157	253	214	235
3	*134*	*113*		52	167	184	259	234	219	239	210	172
4	*96*	*125*	*279*		259	218	239	184	205	176	193	203
5	*89*	*83*	*53*	*91*		203	229	194	186	180	226	248
6	*78*	*54*	*44*	*51*	*62*		230	229	145	193	107	222
7	*56*	*47*	*58*	*104*	*90*	*43*		67	213	226	230	195
8	*81*	*89*	*49*	*56*	*85*	*59*	*213*		214	207	172	200
9	*121*	*92*	*61*	*72*	*71*	*83*	*40*	*60*		39	211	169
10	*105*	*138*	*37*	*69*	*84*	*75*	*57*	*49*	*203*		191	218
11	*61*	*118*	*49*	*91*	*83*	*40*	*83*	*80*	*48*	*59*		225
12	*89*	*78*	*60*	*49*	*101*	*57*	*78*	*35*	*59*	*40*	*40*	
13	*121*	*64*	*57*	*76*	*70*	*59*	*59*	*47*	*60*	*56*	*59*	*197*
14	*73*	*72*	*41*	*67*	*68*	*73*	*70*	*101*	*51*	*73*	*43*	*50*
15	*79*	*81*	*48*	*83*	*93*	*87*	*56*	*89*	*101*	*69*	*81*	*47*
16	*200*	*93*	*42*	*74*	*107*	*80*	*93*	*121*	*92*	*79*	*99*	*79*
17	*115*	*83*	*69*	*78*	*72*	*97*	*81*	*104*	*89*	*91*	*51*	*83*
18	*82*	*91*	*82*	*49*	*79*	*56*	*76*	*51*	*62*	*104*	*60*	*67*
19	*71*	*79*	*69*	*59*	*87*	*104*	*100*	*72*	*94*	*48*	*34*	*80*
20	*79*	*87*	*82*	*72*	*46*	*50*	*69*	*88*	*62*	*55*	*97*	*61*

Table 1.2; Pretoriuskop. Values for *n* for number of times birds were located together, in italics below the line. Number of times one of the two birds were located without the other above the line.

	13	**14**	**15**	**16**	**17**	**18**	**19**	**20**
1	195	176	192	219	305	271	312	342
2	251	236	242	261	213	241	223	177
3	148	112	100	204	233	210	222	209
4	187	146	231	200	197	148	136	149
5	180	209	238	240	182	167	142	185
6	245	262	232	227	169	197	213	224
7	210	167	221	236	170	192	226	182
8	175	166	217	228	178	209	163	188
9	204	171	232	219	197	162	233	209
10	201	175	193	226	241	207	227	174
11	204	182	190	231	189	206	179	209
12	42	217	209	193	226	217	224	183
13		214	157	176	180	162	219	217
14	*48*		40	180	216	209	158	196
15	*50*	*196*		213	230	229	191	184
16	*63*	*47*	*84*		45	203	218	178
17	*71*	*39*	*59*	*207*		224	173	180
18	*84*	*51*	*67*	*39*	*43*		50	212
19	*91*	*70*	*82*	*67*	*59*	*196*		205
20	*101*	*83*	*73*	*52*	*70*	*43*	*59*	

Table 1.2; ***Cont.***

Bird	1	2	3	4	5	6	7	8	9	10	11	12
1		12	200	217	220	238	239	203	223	226	194	205
2	152		204	221	224	240	239	201	229	232	196	203
3	34	33		167	170	194	197	165	187	186	164	149
4	28	27	30		9	207	206	158	184	185	159	162
5	27	26	29	112		206	205	159	185	186	158	161
6	22	22	21	17	18		13	157	221	220	160	161
7	21	22	19	17	18	118		158	222	221	157	160
8	12	14	8	14	14	19	18		166	167	117	118
9	29	27	24	28	28	14	13	14		3	155	164
10	27	25	24	27	27	14	13	13	122		158	163
11	15	15	7	12	13	16	17	10	18	16		113
12	4	6	9	5	6	10	10	4	8	8	5	
13	8	8	5	8	8	5	5	6	5	5	8	4
14	16	15	5	10	9	10	10	0	8	8	3	0
15	12	11	11	12	12	14	14	2	4	13	8	2
16	10	9	9	8	8	13	14	1	7	7	2	1
17	19	18	9	16	15	13	13	2	9	8	4	1

Table 1.3; Ponta Malongane. Values for *n* for number of times birds were located together, in italics below the line. Number of times one of the two birds were located without the other above the line.

	13	**14**	**15**	**16**	**17**
1	187	149	163	156	153
2	189	153	167	160	157
3	147	125	119	112	127
4	146	120	122	119	118
5	147	123	123	120	121
6	161	129	127	118	133
7	160	128	126	115	132
8	104	94	96	87	100
9	160	132	126	129	140
10	159	131	127	128	141
11	97	85	81	82	93
12	94	80	82	73	88
13		66	72	57	72
14	2		42	31	34
15	2	6		39	50
16	4	6	5		37
17	4	12	7	8	

Table 1.3; ***Cont.***