THE ECOLOGY OF MEYER'S PARROT (*Poicephalus meyeri*) IN THE OKAVANGO DELTA, BOTSWANA

RUTLEDGE STEPHEN BOYES

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Faculty of Science and Agriculture
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PREFACE

The data described in this thesis were collected in the Okavango Delta, Botswana, from January 2004 to January 2006, and February 2007 to July 2007. Experimental work was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Michael R. Perrin.

This thesis, submitted for the degree of Doctor of Philosophy in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

…………………………….
Rutledge S. Boyes
December 2008

I certify that the above statement is correct…

M. R. Perrin
……………………………..
Professor Michael R. Perrin
Supervisor
December, 2008

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Firstly, I would like to thank my supervisor, Professor Mike Perrin, for his support throughout the project design, fieldwork and write-up. His contribution to African parrot conservation over the last 10 years is unparalleled, and the parrot conservation community look forward to this up-coming book. Professor Steve Beissinger at the University of California, Berkeley, is thanked for allowing me to visit with him at Berkeley for most of 2006. This was an enriching experience and interacting with his students and colleagues assisted greatly in focussing my effort in processing my extensive data set. I would also like to thank Professor Colleen Downs and Mark Brown for invaluable comment on aspects of the project. Map Ives, Kai Collins and all the staff of Wilderness Safaris Botswana are thanked for their valuable support. Tony Ruemerman and Clinton Phillips are thanked their assistance in the plant and invertebrate identification. I am indebted to volunteer field assistance from Chris Boyes, Pieter Hugo, Francois Joubert and Erica Case. Kirsten Wimberger provided invaluable commentary on and support through the final drafts.

The Meyer’s Parrot Project (2004–2007) was predominantly sponsored by the Research Centre for African Parrot Conservation and British Ecological Society (Overseas Bursary). Other funding was contributed by the National Research Foundation (Doctoral scholarship), Wilderness Safaris Wildlife Trust, World Parrot Trust and Gay Langmuir Foundation (Graduate support funding). Numerous private donors made contributions through the World Parrot Trust, most notably Julie Drier.

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The love and support of my parents, Rutledge and Vikki Boyes was keystone to the completion of the Meyer’s Parrot Project.

Abstract. Meyer's Parrot *Poicephalus meyeri* is the smallest of the nine *Poicephalus* parrots, forming the *P. meyeri* superspecies complex with five congeners. Their distributional range far exceeds any other African parrot, extending throughout subtropical Africa. Meyer's Parrots had previously not been studied in the wild, and therefore, gathering high-quality empirical data on their behavioural ecology became a research and conservation priority. The primary aim of the study was to correlate environmental (e.g. rainfall, habitat availability, resource characteristics, food resource abundance and temperature) and social (e.g. inter- and intra-specific competition, predation, and human disturbance) variables with aspects of their ecology (e.g. flight activity, food item preferences, breeding activity, and group dynamics) to evaluate the degree of specialization in resource use (e.g. trophic, nesting and habitat niche metrics).

African deforestation rates are the highest in the world, resulting in twelve out of the eighteen Meyer's Parrot range states undergoing drastic loss of forest cover over the last 25 years. Most commentary on the population status of Meyer's Parrots and other *Poicephalus* parrots pre-dates this period of rapid deforestation In addition, over 75 000 wild-caught Meyer's Parrots and almost 1 million wild-caught *Poicephalus* parrots have been recorded in international trade since 1975. Empirical data from this study was used to identify ecological weaknesses (e.g. niche specialization or low breeding turnover) for evaluation within the context of deforestation in the African subtropics. Baseline data on the breeding biology and nest cavity requirements of Meyer's Parrots was also necessary to assess the viability of applying the conservative sustained-harvest model to African parrots. A unifying goal of this study was to advance our knowledge of the ecology of African parrots and other Psittaciformes by assessing the validity of current hypotheses put forward in the literature.

The Meyer's Parrot Project was initiated in January 2004 on Vundumtiki Island in the north-eastern part of the Okavango Delta, Botswana. Due to high flood waters between March and July 2004, road transects were postponed till August 2004. Transects were conducted at Vundumtiki from August 2004 to July 2005 and February 2007 to August 2007, and at Mombo from August 2005 to January 2006. During 480 road transects over 24 months, food item preferences closely tracked fruiting and flowering phenology, resulting in significant positive correlations between Levins' niche breadth, rainfall and food resource availability. Meyer's Parrot can, therefore, be considered opportunistic generalists pre-dispersal seed predator that tracks resource availability across a wide suite of potential food items, including 71 different food items from 37 tree species in 16 families. Meyer's Parrots were, however, found to be habitat specialists preferring established galleries of riverine forest and associated *Acacia*-*Combretum* marginal woodland. These strong habitat associations facilitate their wide distribution throughout the Kavango Basin, Linyanti Swamps, down the

Zambezi valley, up along the Rift Valley system in associations with the great lakes, through the Upper Nile and the Sudd, and west as far as Lake Chad through the Sahel.

Seventy-five nest cavities were measured during this study, including 28 nest cavities utilized by Meyer's Parrots within the 430ha sample area at Vundumtiki. Over 1700 hours of intensive nest observations at six nest cavities was undertaken. Meyer's Parrots formed socially monogamous pair-bonds maintained over at least four breeding seasons. Breeding pairs established breeding territories up to an estimated 160ha within which there were 1–6 nest cavities. Eggs hatched asynchronously, yet nestlings fledged synchronously with similar body size and condition. There was evidence to support the incidence of extra-pair copulations, however, mitochondrial DNA sequence data are required to confirm the incidence of extra-pair fertilizations. Meyer's Parrots had no preferences in regard to nest tree species beyond the incidence of suitable nest cavities, which are selected and further excavated to accommodate their non-random nest cavity preferences. There was a significant non-nesting Meyer's Parrot population during the breeding season, likely due to this long-lived cavity-nester delaying nesting until a suitable breeding territory becomes available.

Meyer's Parrots utilize communal roosts during summer and disperse from them according to the Foraging Dispersal Hypothesis. Due to the requirement to roost during the middle of the day to avoid heat stress, Meyer's Parrots have bimodal flight and feeding activity patterns. The highest probability of locating Meyer's Parrots is between 08h30 and 11h00 during summer when both adults are feeding on the seeds of fleshy-fruits in riverine forest communities.

Due to the paucity of data on the current distribution and population status of Meyer's Parrots and other African parrots, a continent-wide survey of all African parrots represents a conservation priority. Current deforestation rates in several Meyer's Parrot range, their specialist habitat associations, and lack of evidence to support adaptability to a changing landscape mosaic necessitate the re-classification of Meyer's Parrots as data deficient or near-threatened. Based on low breeding population due to limited breeding opportunities, the CITES Appendix II wild-caught bird trade should also be halted until the sustainability of this trade has been evaluated and the relevant information made available.

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Chapter 1:

Introduction to the Meyer's Parrot Project (2004–2007)

Abstract. Meyer's Parrot *Poicephalus meyeri* is the smallest of the nine *Poicephalus* parrots, forming the *P. meyeri* superspecies complex with five congeners. Their distributional range far exceeds any other African parrot, extending throughout subtropical Africa from the southern Sudan to South Africa. Twelve out of the eighteen Meyer's Parrot range states have undergone drastic deforestation over the last 25 years. In addition, over 75 000 wild-caught Meyer's Parrots and almost 1 million wild-caught *Poicephalus* parrots have been recorded in international trade since 1975. Meyer's Parrots and other *Poicephalus* are, therefore, likely threatened by sustained habitat loss and the wild-caught bird trade in most range states. Meyer's Parrots had previously not been studied in the wild, and therefore, gathering high-quality empirical data on their behavioural ecology for use as an ecological benchmark in future monitoring became a research and conservation priority. The primary aim of this study was to correlate environmental (e.g. rainfall, habitat availability, resource characteristics, food resource abundance and temperature) and social (e.g. inter- and intra-specific competition, predation,and human disturbance) factors with aspects of their behavioural ecology (e.g. flight activity, food item preferences, breeding activity, and group dynamics) to evaluate phenotypic plasticity and the degree of specialization in resource use (e.g. trophic, nesting and habitat niche metrics). Findings from this study were thus used to identify ecological weaknesses (e.g. niche specialization or low breeding turnover) for comparison with current threats. Baseline data on the breeding biology and nest cavity requirements of Meyer's Parrots was necessary to assess the applicability of the conservative sustained-harvest model to African parrots. A unifying goal of this study was to advance our knowledge of the ecology of African parrots and other Psittaciformes by assessing the validity of current hypotheses put forward in the literature, thus supporting effective and practical conservation prescriptions for threatened African parrot populations.

Introduction

Of the 332 recognised parrot species in the world (Forshaw 1989; Juniper and Parr 1998), very few have natural distributional ranges more extensive than Meyer's Parrot *Poicephalus meyeri*, which extend from the eastern Sahel, southern Sudan and Nile River Valley, through the Great Rift Valley and Great

Lakes system to South Africa, Namibia and Botswana (Rowan 1983; Juniper and Parr 1998; Perrin *et al.* 2002). Wilson (1989) put forward that persistence of a phyletic line through geological time is the key measure of ecological success. Ecological success is, therefore, a function of the number of species in the monophyletic group, occupation of unusual adaptive zones, extent of distributional range, and fluctuations in population size and status (Wilson 1987). As the most abundant and widespread *Poicephalus* parrot that forms the *P. meyeri* superspecies complex with five congeners, understanding the adaptive zone of Meyer's Parrot was central to identifying putative contributory factors to their apparent ecological success in comparison with other *Poicephalus* species.

Comprehensive studies have been undertaken on the feeding and breeding ecology of the Cape Parrot *P. robustus* (Wirminghaus *et al.* 2000, 2001, 2002; Symes *et al.* 2004), Rüppell's Parrot *P. rueppellii* (Selman *et al.* 2000, 2002, 2004), the Black-cheeked Lovebird *Agapornis nigrigenis* (Warburton and Perrin 2005a,b), the Brown-headed Parrot *P. cryptoxanthus* (Taylor 2002; Taylor and Perrin 2006a,b), and the Rosy-faced Lovebirds *Agapornis roseicollis* (Ndithia and Perrin 2006a,b). Preliminary studies have been conducted on the African Grey Parrot *Psittacus erithacus* (Chapman *et al.* 1993), the Red-bellied Parrot *Poicephalus rufiventris* (Massa 1995) and the Yellow-faced Parrot *P. flavifrons* (Boussekey *et al.* 2002). Due to the wide distribution and comparative ecological success of Meyer's Parrot, this study tested the hypothesis that the feeding ecology, habitat associations and breeding biology of Meyer's Parrots is significantly different to other *Poicephalus* parrots. Meyer's Parrots had previously not been studied in the wild, their conservation biology was poorly known, and no prior species-specific conservation action has been implemented for Meyer's Parrots in any of their range states (Rowan 1983; Wilkinson 1998; Perrin *et al.* 2002).

Species-specific conservation planning requires a comprehensive knowledge of their behavioural ecology and population status, thus allowing for the development of management prescriptions that accommodate all ecological requirements (Wilkinson 1998, Snyder *et al.* 2002). A species can, therefore, only be put into a threat category once sufficient ecological baseline data have been gathered, correlating current threats with ecological weaknesses to develop a strategy that will protect that species into perpetuity. African parrots are all long-lived, cavity-nesting forest specialists with a strong affinity for old-growth indigenous hardwood forest communities (Perrin *et al.* 2002). African deforestation rates are the highest in the world (UNEP 2008), resulting in twelve out of the eighteen Meyer's Parrot range states undergoing drastic loss of forest cover. Given the lack of evidence that *Poicephalus* parrots can adapt effectively to modified landscapes (e.g. agricultural or urban landscapes) in the absence of indigenous forest communities, Meyer's Parrots and other African parrots are likely undergoing net population loss and range reduction due to habitat loss. Meyer's Parrots are classified as Least Concern as per the IUCN Red List of Threatened Species (Birdlife International 2008), and therefore, are considered widespread and abundant (IUCN 2001). Global population and population trends of Meyer's Parrots and other African parrots, however, have not been quantified (Birdlife International 2008), and the majority of commentary on their population status pre-date the rapid deforestation over the last 25 years (Vincent 1944; Mackworth-Praed and Grant 1952, 1962, 1970; Irwin 1956; Traylor 1965; White 1965; Urban and Brown 1971; Fry *et al.* 1988; Lewis and Pomeroy 1989; Wirminghaus 1997; Wilkinson 1998; UNEP-WCMC CITES Trade Database 2005; UNEP 2008). Up-to-date records of the population status and ecology of all *Poicephalus* parrot populations represent a conservation priority, especially in data deficient species (e.g. Yellow-faced Parrots *P. flavifrons* and Niam-Niam Parrots *P. crassus*) and historically heavily-traded species such as Senegal Parrots *P. senegalus* (UNEP-WCMC CITES Trade Database 2005). Meyer's Parrot Project provided baseline ecological data on this analogous African parrot species towards the derivation of practical conservation prescriptions for *Poicephalus* parrots populations that are in decline.

Cape Parrots are already endangered with about 1000 remaining in the wild (Downs 2000; Perrin *et al.* 2002; Perrin 2005; Downs 2005, 2006). Surveys in Namibia, Zambia, Zimbabwe and remote areas in South Africa showed significant range reduction and population decline in areas where Rüppell's Parrots (Selman *et al.* 2004), Meyer's Parrots (Boyes 2006a), and Brown-headed Parrots (Boyes unpub. data) were previously abundant. Similarly, Black-cheeked Lovebirds have the most restricted range of any African parrot and are classified as vulnerable due to climate change and socio-economic pressures (Perrin *et al.* 2002; Warburton and Perrin 2005). In addition to habitat loss, African parrots are also threatened by the wild-caught bird trade, whereby over 3 million Africa parrots have been removed from the wild, including over 75 000 Meyer's Parrots (UNEP-WCMC CITES Trade Database 2005). Boyes (2006b; Chapter 12: Boyes and Perrin in review a) found that, according to the UNEP-WCMC trade database, the Senegal Parrot *Poicephalus senegalus* is the most traded bird on CITES Appendix II. The pressures of the wild-caught bird trade likely function to compound losses due to deforestation. Therefore, indications are that African parrots are likely under serious threat from habitat loss (Collar and Juniper 1992; Juniper and Parr 1998; Perrin *et al.* 2002), a situation that could be compounded by the wild-caught bird trade (Boyes 2006), persecution as crop pests (Rowan 1983; Juniper and Parr 1998; Boyes 2006,2008a,b) and disease (Heath *et al.* 2004). It thus became a necessity to gather baseline data on the Meyer's Parrot from a "healthy" population to support a conservation plan for African parrots. Wirminghaus (1997) reported a significant Meyer's Parrot population in the Okavango Delta, Botswana, thus prompting the Research Centre for African Parrot Conservation (University of KwaZulu-Natal) to choose this as the study population.

Systematics of the genus *Poicephalus* with special emphasis on Meyer's Parrot

There are 332 extant species in the family Psittacidae (Peters 1940; Brereton 1963; del Hoyo *et al.* 1997; Juniper and Parr 1998). Most systematists classify family Psittacidae as non-Passeriformes (Forshaw 1989; Juniper and Parr 1998). Phylogenetic analyses, however, have discovered a close relationship between passerines, parrots and falcons, thus fundamentally changing our understanding of Passeriformes and the family Psittacidae (Hacket *et al.* 2008; Pennisi 2008).

Parrots are characterised by a compact body shape and short neck (Forshaw 1989). They vary greatly in size from about 10–100cm in total length. In Africa, however, the variation is considerably less with parrots ranging from 12–35cm (Rowan 1983). Most distinctive is the short stout, strongly hooked beaks with a fleshy cere (Juniper and Parr 1998). The upper mandible is not rigid, but is articulated with the skull, thus allowing considerable vertical movement (Rowan 1983). Feet are zygodactylous, and plumage is hard, sparse and usually brightly coloured (Juniper and Parr 1998). Aftershafts are present. There are ten primaries and 12 tail feathers in all but one genus that has 14 (Rowan 1983). Members of the Psittaciformes are also recognised by various internal morphological structures (e.g. thick, fleshy tongue and specialized hyoid apparatus) (Smith 1975, Homberger 1982) and certain behavioural characteristics (Brereton 1963; Brereton and Immelmann 2008).

To accommodate the wide morphological diversity of parrots, the Psittacidae were subdivided into six sub-families (Peters 1940), the Strigopinae (Kakapo), the Nestorinae (Keas), the Loriinae (nectar-feeding lories and lorikeets), Micropsittinae (Pygmy parrots), the Kakatoeinae (Cockatoos), and Psittacinae (all the typical parrots, lovebirds, macaws, rosellas and their allies). All African parrots are part of the sub-family Psittacinae. Prior to the identification of the Cape Parrot *P. robustus* as an independent species to the Brown-necked Parrot *P. fuscicollis fuscicollis* and Grey-headed Parrot *P. fuscicollis suahelicus* (Wirminghaus *et al.* 2002; Perrin 2005), 19 continental species were recognized by White (1965) and Peters (1940) for the Ethiopian region including four genera (i.e. *Agapornis*, *Psittacus*, *Psittacula* and *Poicephalus*). Forshaw (1989) and Snyder *et al.* (2000) reported 18 predominantly allopatric parrot species for continental Africa, as *Agapornis canus* was excluded due to being on Madagascar. Therefore, this study recognizes 19 continental species in four genera with three additional species in two genera (i.e. *Agapornis* and *Coracopsis*) recognized on the associated islands. Therefore, there are five genera of African parrots, including *Agapornis*, *Psittacus, Psittacula*, *Poicephalus* and *Coracopsis*, including 22 species. In this study no comment or analysis was made for *Psittacula* and *Coracopsis* species due to disjunct distributions and unique behaviour and morphology (Forshaw 1989; Juniper and Parr 1998).

There are ten species in the genus *Poicephalus*, including the: Cape Parrot *Poicephalus robustus*, Brown-necked Parrot *P. fuscicollis*, Jardine's Parrot *P. gulielmi*, Meyer's Parrot *P. meyeri*, Senegal Parrot *P. senegalus*, Niam-Niam Parrot *P.* crassus, Red-bellied Parrot *P. rufiventris*, Brown-headed Parrot *P. cryptoxanthus*, Rüppell's Parrot *P. rueppelli*, and Yellow-faced Parrot *P. flavifrons*, (Juniper and Parr 1998; Perrin 2005). Based on morphological traits, *Poicephalus* parrots can be grouped into the *P. meyeri* and *P. robustus* superspecies complexes, thus demonstrating the close relationships within this monophyletic group. These appear as natural assemblages within the genus *Poicephalus* (Massa *et al.* 2000). *P. robustus* forms a superspecies with the Grey-headed Parrot *P. fuscicoliis suahelicus*, Brown-necked Parrot *P. fuscicollis fuscicollis* and Jardine's Parrot *P. gulielmi* (including three subspecies). *P. meyeri* forms a superspecies with the Brown-headed Parrot, Rüppell's Parrots, Senegal Parrot *P. senegalus*, Red-bellied Parrot *P. rufiventris*, and Niam-Niam Parrot *P. crassus* (White 1965; Rowan 1983; Massa *et al.* 2000). Based on distributional range (Figure 1) and morphological similarities (Figure 2), the closest congener of Meyer's Parrot is Rüppell's Parrot. Molecular evidence (Massa *et al.* 2000) and dietary similarities with Meyer's Parrot (Boussekey *et al.* 2002) indicate that the Yellow-faced Parrot *P. flavifrons* has a closer taxonomic association with the *P. meyeri* superspecies complex.

Poicephalus parrots are distributed throughout subtropical Africa, and Meyer's Parrots live in parapatry (e.g. Rüppell's Parrot) or sympatry (Red-bellied Parrot) with all other parrots in the *P. meyeri* superspecies complex, except the Senegal Parrot (Figure 1). Members of the *P. robustus* superspecies complex, however, have disjunct distributional ranges (Figure 1). The following hybrids have been reported in captivity: *P. meyeri* x *P. rueppelli*; *P. cryptoxanthus* x *P. crassus*; *P. cryptoxanthus* x *P. meyeri* (Brickell 1985). In the wild, Clancey (1977) reported that Meyer's Parrots and Brown-headed Parrots hybridize extensively in the contact zone between South Africa and Zimbabwe. Rowan (1983), however, put forward that natural colour variations in Brown-headed Parrots and Meyer's Parrots could have accounted for this apparent hybridization, thus making further investigation using mitochondrial DNA sequencing necessary to confirm or refute this.

The number of recognised subspecies for *P. meyeri* depends on the systematist, as according to Peters (1937) there are eight and according to White (1965) there are six. Based on broader acceptance in the academic community, the six subspecies put forward by White (1965) are accepted; however, the necessity for further revision is noted (Chapter 12). Meyer's Parrot *Poicephalus meyeri meyeri* was discovered in 1827 by Rüppell near Kordofan, Sudan. The skin was later described by Cretzschmar in honour of Bernhard Meyer (1767-1836) (Rowan 1983). In 1898 and 1899, Neumann described four new subspecies, including: *P. m. matschei* from Dodoma District, Malawi; *P. m. reichnowi* from Malange, Northern Angola; *P. m. transvaalensis* from the Northern Province, South Africa; and *P. m.*

damarensis from Damaraland, Namibia (Rowan 1983). Three years later, in 1901, Sharpe described the sixth subspecies, *P. m. saturatus*, from North Ankole, Uganda (Rowan 1983) (Figure 3). *P. meyeri damarensis* and *P. m. transvaalensis* are reported to overlap in the Okavango Delta, forming an intermediate (Wirminghaus 1997; Rowan 1983).

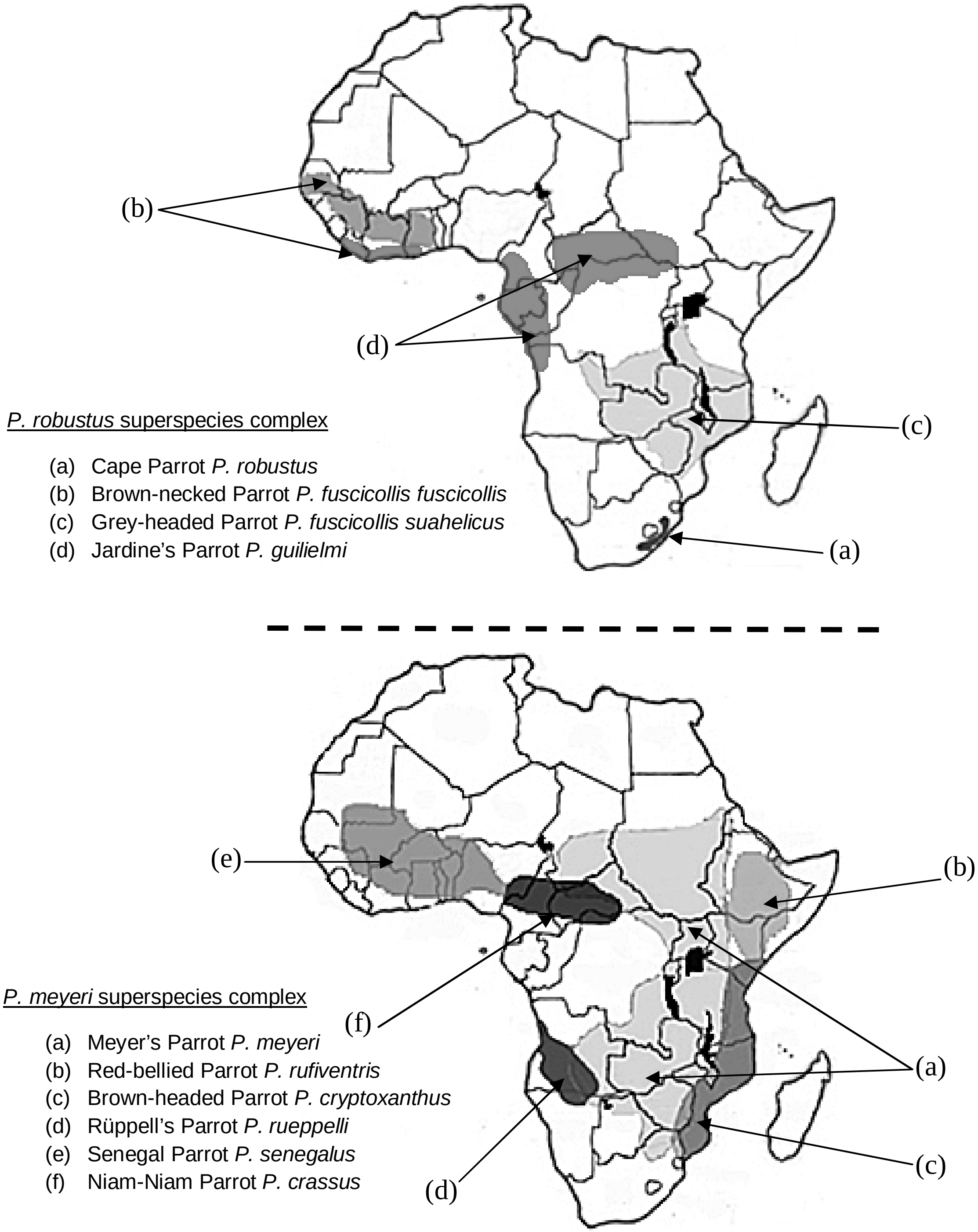


Figure 1: Distributional ranges of all *Poicephalus* parrots separated according to superspecies complex. *P. fuscicollis* kept separate due to disjunct distribution (considered one species)

Rüppell's Parrot
Poicephalus rueppelli

Damaraland, Northern Namibia

20 January 1889
C.G. Anderson

Meyer's Parrot
Poicephalus meyeri

Thamalekane River
Okavango Delta, Botswana

11 December 1962
B.P. Hall

Red-bellied Parrot
Poicephalus rufiventris

Burao, Somalia

24 January 1906
G.W. Bury

Senegal Parrot
Poicephalus senegalus versteri

Abeokuta, Nigeria

17 January 1942
W.R. Fuisch

Brown-Headed Parrot
Poicephalus cryptoxanthus

Lake Malawi, Mozambique

23 January 1932
J. Vincent

Niam-Niam Parrot
Poicephalus crassus

Bahr-el-Ghazal, Central African Republic

20 February 1936
Dr. C. Christy

Figure 2: Skins of Poicephalus parrots in *P. meyeri* superspecies complex from the Natural History Museum at Tring, U.K. (2006)

(a)

P. m. transvaalensis

1899 (Neumann): N Transvaal (South Africa)

Distributed throughout Zimbabwe, NE Mozambique, NE Botswana, and far N South Africa.

P. m. damarensis

1899 (Neumann): Damaraland (Namibia)

Restricted to S Angola, N and C Namibia, and NW Botswana.

(b)

P. m. reichnowi

898 (Neumann): Malange (N Angola)

Distributed throughout N and C Angola and adjacent regions in Democratic Republic of Congo.

P. m. matschei

1898 (Neumann): Dodoma District (Malawi)

Distributed throughout Tanzania into N Malawi, SE Kenya, SE Democratic Republic of Congo and Zambia.

(c)

P. m. meyeri
1827 (Rüppell): Kordofan (Sudan)
Distributed across the northern part of the distributional range in NE Cameroon, S Sudan, Central African Republic and W Ethiopia

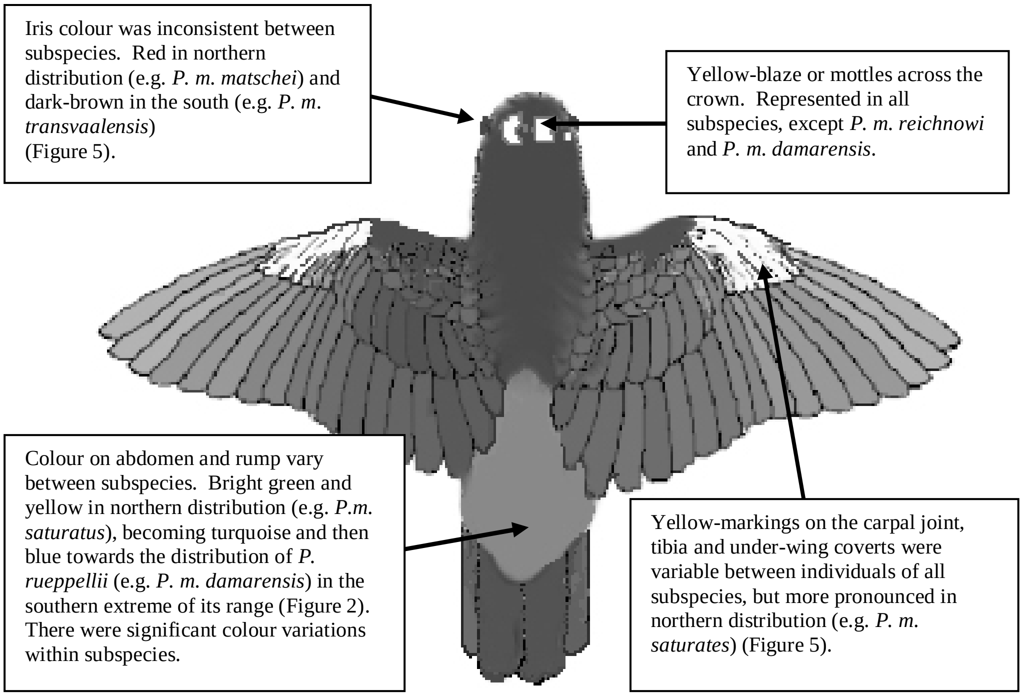
P. m. saturatus
1901 (Sharpe): North Ankole (Uganda)
Distributed throughout Uganda, W Kenya, Rwanda, Burundi, and W Tanzania.

Figure 3: Colour variation in Abdomen and rump vary between subspecies demonstrating a morphological character that is consistently different between subspecies. (a) Southern subspecies complex; (b) Central subspecies complex; and (c) Northern subspecies complex.

Description of Meyer's Parrot subspecies

Meyer's parrots are the smallest of the *Poicephalus* parrots (Rowan 1983; Juniper and Parr 1998; Wilkinson 1998). The average body mass for 12 males collected in Zimbabwe and Botswana (*P. m. transvaalensis*) was 121.1g, and for 12 females was recorded at 112.4g (Rowan 1983). A male and female taken in Angola (*P. m. damarensis*) weighed 130g and 98g respectively (Rowan 1983).

Upon examination of a collection of 124 *P. meyeri* skins at the Natural History Museum at Tring (U.K.), it became clear there were morphological characters that were inconsistent between subspecies (i.e. colouration on the rump and abdomen, and iris colour) and between individuals within subspecies (i.e. yellow-blaze on crown and wing culverts) (Figure 4; Figure 5). The only consistent characters for *P. meyeri* were the greyish-brown or ash-brown colouration on the head, back and upper breast, and the black peri-opthalmic eye ring. Colouration on the abdomen and rump varied from bright blue in *P. m. damarensis* and *P. m. transvaalensis* to turquoise and yellow-green in *P. m. saturatus* and *P. m. meyeri* (Figure 5). The incidence of blue on the abdomen and rump correlates with proximity to Ruppell's Parrots that have bright-blue colouration in these areas (Figure 2). Iris colouration varied from red (*P. meyeri* and *P. m. saturatus*) to dark-brown (*P. m. transvaalensis* and *P. m. damarensis*), with *P. m. reichnowi* and *P. m. matschei* having both iris colours represented (Figure 5).



Iris colour was inconsistent between subspecies. Red in northern distribution (e.g. *P. m. matschei*) and dark-brown in the south (e.g. *P. m. transvaalensis*) (Figure 5).

Yellow-blaze or mottles across the crown. Represented in all subspecies, except *P. m. reichnowi* and *P. m. damarensis*.

Colour on abdomen and rump vary between subspecies. Bright green and yellow in northern distribution (e.g. *P.m. saturatus*), becoming turquoise and then blue towards the distribution of *P. rueppellii* (e.g. *P. m. damarensis*) in the southern extreme of its range (Figure 2). There were significant colour variations within subspecies.

Yellow-markings on the carpal joint, tibia and under-wing coverts were variable between individuals of all subspecies, but more pronounced in northern distribution (e.g. *P. m. saturates*) (Figure 5).

Figure 4: Distinctive yellow-markings proven to be unique to every individual Meyer's Parrot

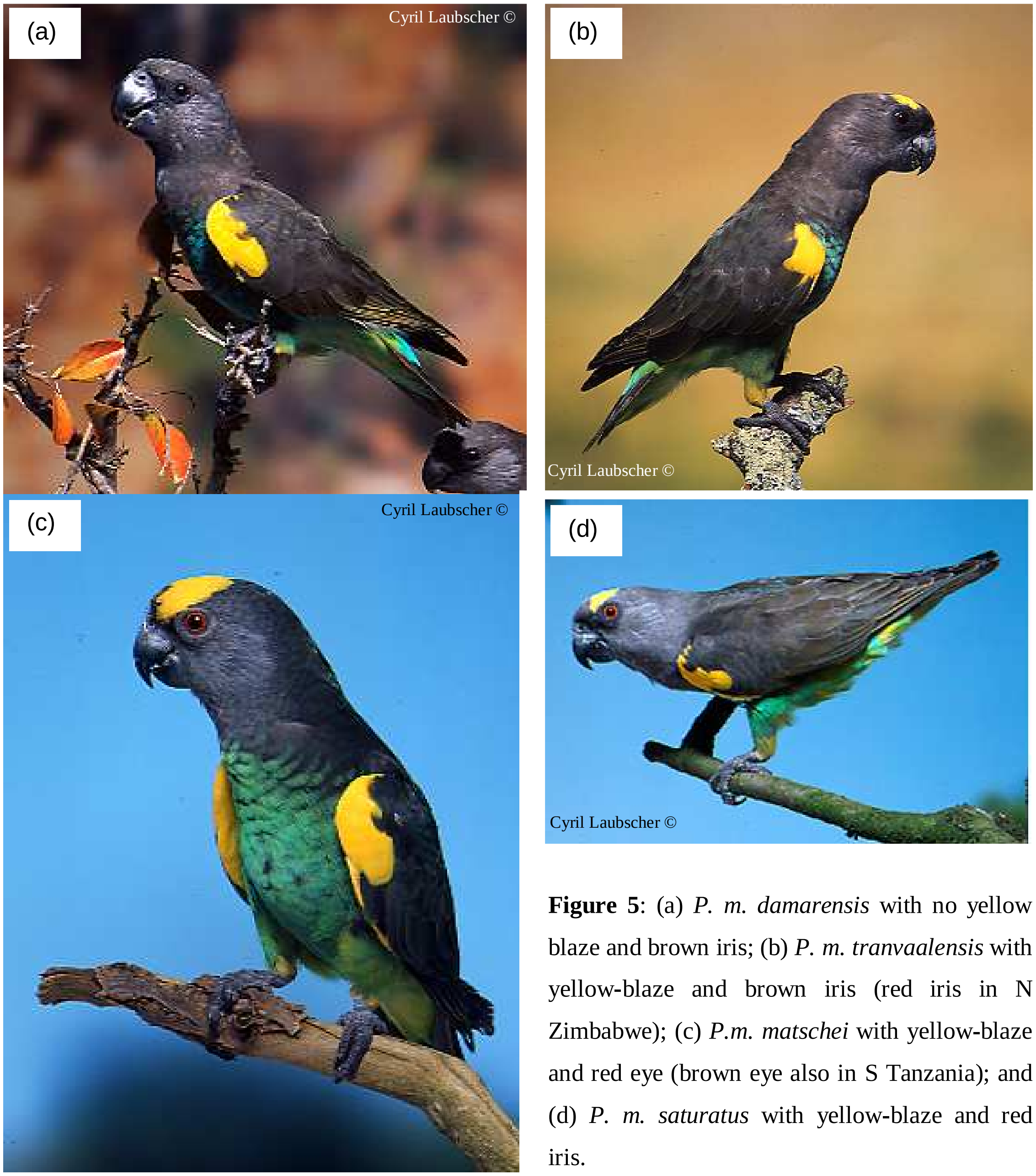


Figure 5: (a) *P. m. damarensis* with no yellow blaze and brown iris; (b) *P. m. tranvaalensis* with yellow-blaze and brown iris (red iris in N Zimbabwe); (c) *P.m. matschei* with yellow-blaze and red eye (brown eye also in S Tanzania); and (d) *P. m. saturatus* with yellow-blaze and red iris.

Meyer's Parrot subspecies can be further grouped into three subspecies "complexes" or clusters by noting the relationship between morphological traits (e.g. iris colour) and collection locations for each skin. *P. meyeri meyeri* and *P. m. saturatus* which form the North African subspecies complex, *P. m. matschei* and *P. m. reichnowi* which form the Central African subspecies complex, and *P. m. damarensis* and *P. m. transvaalensis* which form the South African subspecies complex (Chapter 12). These subspecies complexes were classified according to morphological traits as follows: (a) North African subspecies have a red iris and complete yellow-blaze on crown and carpal joint; (b) Central

African subspecies have both red and brown iris colours represented and less yellow with the yellow-blazes on the crown and carpal joints variable and often missing; and (c) South African subspecies have dark-brown iris colouration and *P. m. damarensis* have no yellow on crown, while this trait is inconsistent in *P. m. transvaalensis*. Based on the established distributional ranges of these subspecies complexes is appears that these morphological characters are consistent between subspecies due to disjunct distributions facilitated by the northern complex being distributed around the Sudd swamps (Sudan) and catchments in Uganda, the central complex centring around Lake Victoria, Lake Tanganyika and Lake Malawi, while the southern complex are distributed along the Zambezi and Chobe valleys and within the Kavango Basin (Chapter 12).

Figure 6: (a) Pied mutation of *P. m. matschei*; and (b) Blue mutation of *P. m. matschei* demonstrates how variable and inconsistent these morphological traits are.

Figure 6 illustrates what can be achieved within a few generations, most likely since the early 1990s, with the incidence of pied and blue mutations. Further analysis of morphological traits, geographical distribution and DNA sequencing of Meyer's Parrots would yield important mechanisms contributing to the speciation of *Poicephalus* parrots and other African forest specialists (e.g. "forest refugia" theory (Diamond and Hamilton 1980)). Meyer's Parrot skins at the Natural History Museum at Tring were collected between 1852 and 1964, and based on the rate of mutation in the limited gene pool in captivity, the Meyer's Parrot subspecies may have changed over the last 100 years, especially those populations isolated by climatic changes or deforestation over the last 25 years. Only new photographic and blood samples from the field will facilitate the effective delineation of Meyer's Parrot subspecies.

Individual identification

Characters that were inconsistent between individuals within a subspecies could potentially be used for individual identification (Chapter 9: Boyes and Perrin in review b). The yellow-blaze was represented in all subspecies, except *P. m. damarensis* and *P. m. reichenowi*. The specific pattern of the yellow on the crown was unique to all skins and was conspicuous enough to be used in individual identification. Similarly, the yellow-markings on the carpal joint, tibia and under-wing coverts were variable between individuals and unique to all skins (n = 124).

No sexual dimorphism is observed in the Meyer's Parrot (Rowan 1983). According to Maddock (1997), however, the female has a smaller, slender beak and a gently curved outline over the upper mandible, cere, forehead and crown, when viewed from the side. Males have a larger, broader beak and broader forehead that is flat on top (Reditt 1997). In the field, males and females are distinguishable by comparison between two individuals or according to behaviour during the breeding season (i.e. female solely responsible for incubation effort).

Meyer's Parrot Project (2004–2007)

Aims and objectives

The primary aim of this study was to gather high-quality empirical data on the feeding ecology, breeding biology and daily activity patterns of Meyer's Parrot for comparison with ecological studies on other *Poicephalus* parrots. All previous studies of *Poicephalus* parrots were restricted by low sighting frequencies due to small, localized populations consistently under threat from habitat loss (e.g. Cape Parrot (Perrin 2005)) and/or wild-caught bird trade (e.g. Rüppell's Parrot (Selman *et al.* 2000)). Due to high sighting frequencies in the Okavango Delta (Wirminghaus 1997; Chapter 7: Boyes and Perrin in review c) and a stable, healthy population (Chapter 8: Boyes and Perrin in review d), sample size was commensurate with correlation of environmental factors (e.g. food resource abundance, rainfall and habitat structure) with trophic niche breadth, breeding success and daily activity patterns. Following comprehensive literature review, the following primary objectives were laid out for the Meyer's Parrot Project, including the following:

(a) Gather baseline data on the feeding ecology of Meyer's Parrot to better understand its food item preference system (e.g. preference for unripe seeds) (Chapter 2: Boyes and Perrin in review e) and ecological function within forest ecology (e.g. pollination and seed dispersal) (Chapter 6: Boyes and Perrin in review f);

(b) Determine putative causal factors for the wide distribution and comparative ecological success of Meyer’s Parrots over other African parrot species by evaluating habitat associations in the Okavango Delta (Chapter 3: Boyes and Perrin in review g);

(c) Estimate temporal resource abundance of different fruit- and pod-bearing trees along standardized habitat transects for comparison with food item and habitat preferences (Chapter 4: Boyes and Perrin in review h);

(d) Use a modified Hurlbert’s expanded and standardized niche breadth index to calibrate the feeding activity of Meyer’s Parrots and Levins’ niche breadth index for comparison between Poicephalus parrots to evaluate associations between trophic niche breadth, body mass and distributional range (Chapter 5: Boyes and Perrin in press i);

(e) Gather baseline data on the daily activity pattern, flocking and roosting behaviour of Meyer’s Parrots in the Okavango Delta to provide prescriptions for census techniques for *Poicephalus* parrots (Chapter 7; Chapter 8); and

(f) Gather baseline data on the breeding biology of Meyer’s Parrot in the Okavango Delta to better understand pair-bonding, breeding seasonality, hatching synchrony, diet during the breeding season, territoriality and other ecological processes (e.g. parasitism of *Acacia spp.* pods by bruchid beetles) that support successful breeding (Chapter 9; Chapter 10: Boyes and Perrin in review i; Chapter 11: Boyes and Perrin in review j).

Finally, this study aimed to disseminate the results of the Meyer’s Parrot Project to as wide an audience as possible by publishing popular articles in popular magazines, giving talks, seminars and guest presentations, and publishing all findings in local and international peer-reviewed journals (Appendix I; Appendix II). The derivation of practical conservation tools for application in the conservation of *Poicephalus* parrots in the wild was also a priority.

Study populations

The Meyer’s Parrot metapopulation in the geographically-isolated Kavango Basin and associated Chobe-Zambezi Valley was chosen owing to the significant Meyer’s Parrot population reported in the Okavango Delta, Botswana (Wirminghaus 1997) and the absence of any other parrot species (Rowan 1983; Juniper and Parr 1998). This study was conducted at two primary areas: Vundumtiki Island located in the Kwedi Concession (NG22/23) in the north-eastern part of the Okavango Delta, and Mombo Camp off the northern peninsula of Chief’s Island (Figure 6).

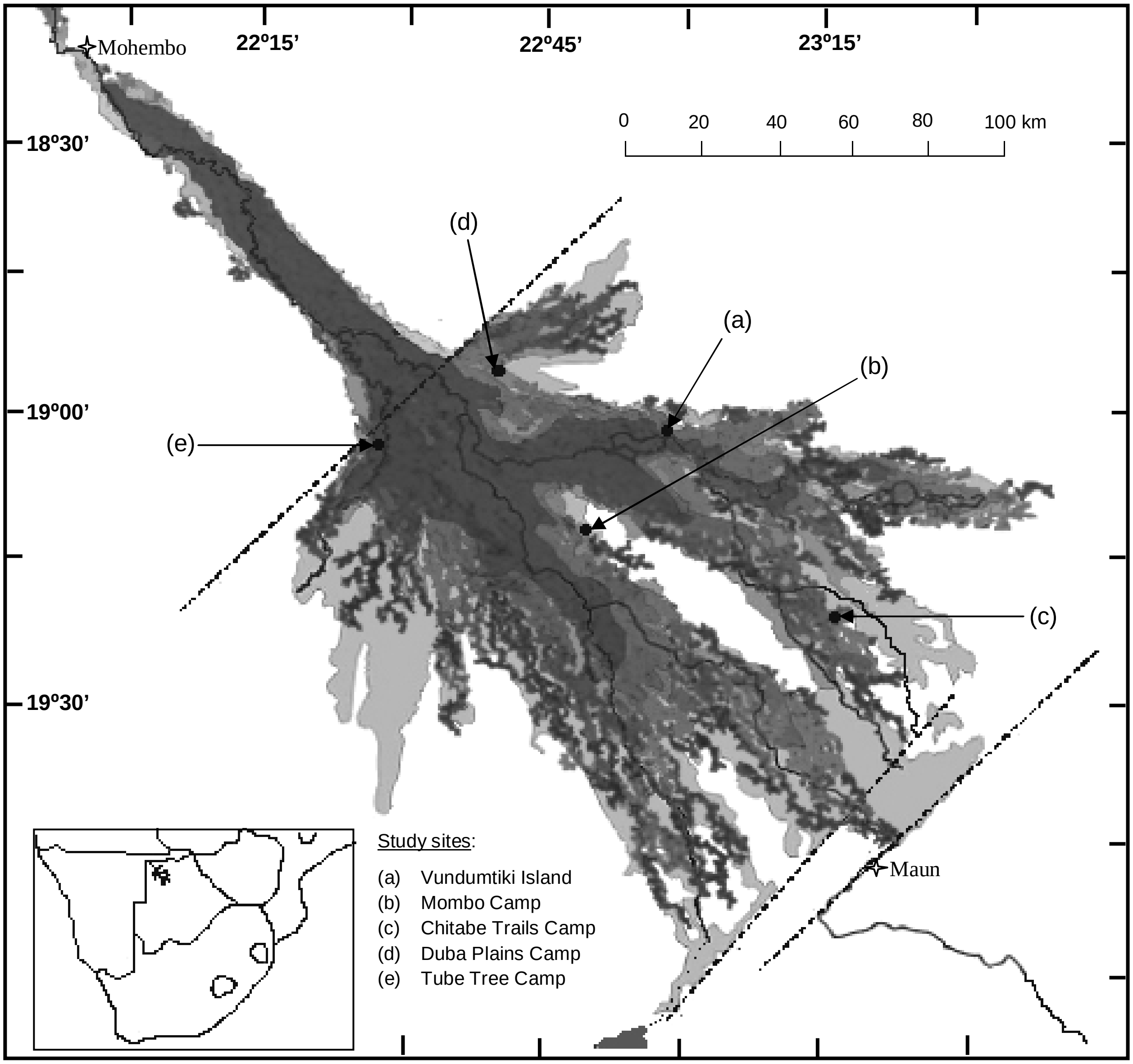


Figure 6: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

The Vundumtiki and Mombo study areas included all wetland categories (i.e. perennial swamp, seasonal swamp, seasonally-inundated grassland, intermittently-inundated grassland and rainwater seepage pans) and all dryland categories (i.e. woodland, savanna, grassland and forbland). Vundumtiki was dominated by *Acacia*-*Combretum* woodland, established galleries of riverine forest, dry Mopane woodland and *Lonchocarpus nelsii* sandveld, while Mombo was dominated by *Acacia tortilis* sandveld towards the interior of Chief's Island with riverine forest and *Acacia*-*Combretum* woodland communities dominating treelines along the floodplains. Data on feeding and breeding behaviour were also gathered from other areas in the Okavango Delta, including Chitabe Camp, Duba Plains and Tubu Tree Camp (Figure 6).

Background and functioning of the Okavango Delta

The Okavango Delta forms part of an internal drainage system known as the Kalahari Sand Basin. The Okavango River finds its catchments on the Benguela Plateau in central Angolan highlands in the form of the Cuito and Cubango sub-catchments. The river flows into a graben structure, an extension of the African Rift Valley system (Hutchins *et al* 1976), and discharges around 9km^3 of water into the resultant alluvial fan annually, augmented by another 6km^3 of rainfall per season (McCarthy & Ellery 1998). The delta system has a shallow gradient of approximately 1:3500 (MacCarthy *et al.* 1998) and a gently undulating topography with a maximum relief of 2m, thus producing a large alluvial fan of approximately 20 000km^2 of permanent swamp, floodplains, riverine forest, Acacia woodland, dry Mopane woodland, grassland, saltpans, islands, and channels (Gumbricht *et al* 2001).

This patchwork mosaic of habitat types provides for the rich diversity of plant, mammal, reptile, amphibian and bird species represented within the system. For example, there are over 134 families, 530 genera, 1256 species, and 1299 taxa of plant species represented in the Okavango Delta (Ellery *et al* 2000). In addition, there are more than 530 bird species (Hockey *et al.* 2005), 155 reptile species (Branch 1998), 150 mammal species (Skinner and Smithers 1990) and 35 amphibian species (Carruthers 2001).

Evapo-transpiration is so significant that less than 2% of the water entering the system each year (including both inflow and rainfall) leaves as surface flow and even less leaves as subsurface flow (Dincer *et al* 1981). The Okavango River transports approximately 570 000 tonnes of sediment per annum (65% dissolved chemical matter and 35% clastic, mainly sand) into the system (McCarthy and Ellery 1998; MacCarthy *et al* 2002). To this sediment inflow is added another 250 000 tonnes of aerosols that are annually deposited over the Delta (Garstang *et al* 1998). Primary water distribution within the Okavango Delta occurs via channels, which serve as an arteriole system supplying water to the permanent and seasonal swamps. The Nqoga Channel is the primary distributary channel connected directly to the Okavango River, and supplies numerous secondary and tertiary channel systems, either directly or by leakage from the primary channel. Secondary water distribution occurs mainly via overland flow through vegetated swamp (Ellery *et al* 2000). The functioning of the Okavango Delta is, therefore, based on this seasonal deposition of clastic sediment, the chemical precipitation of calcite and silica from ground water below islands, and disruptions caused by termite mounds, hippopotamus and elephant. Sedimentation functions gradually (at a rate of 5–6cm per annum) to close channels, thus facilitating channel-switching to occur, whereby water flow is diverted from one channel system to another on a 100-200 year cycle (*Ellery et al* 2003).

Channel-switching is important in that it allows water to be gradually diverted out of one channel system into another. The longer floodwaters inundate the floodplains of a specific channel system, evaptranspirational loss of groundwater increases the salinity of the groundwater beneath islands, inducing the precipitation of calcite and silica on the surface. More soluble salts, such as sodium bicarbonate, become extremely concentrated in the groundwater (McCarthy *et al.* 2003). The resulting brine is drawn to the surface by capillarity resulting in the precipitation of salts and the formation of salt crusts on the island surface (McCarthy *et al.* 2003). This saline groundwater is toxic to most plant species, and thus most areas with salt crusts are barren (Ellery *et al* 2003). Island growth is due to calcite and silica precipitation occuring predominantly around the vegetated fringes of the islands. While the islands are growing the resident plant communities are changing, tracking the changes in groundwater salinity and water level. Typically, floodwaters that have been switched into a new channel system will encounter rainfall-leeched sandy soils with dry *Colophospermum mopane*, *Lonchocarpus nelsii* (on relict sandy channel beds) or *Acacia tortillis* woodland dominating these areas. As more flow is directed into the area, these woodlands are replaced by broad-leaved evergreen forests dominated by *Diospyros mespiliformis*, *Garcinia livingstonia*, *Ficus sycamorus*, *Kigelia africana*, *Ficus thonningii*, and *Phoenix reclinata.* As salinities increase over the next few decades the palms, *Phoenix reclinata* and *Hyphaene petersiana*, begin to dominate as the centre of the island becomes more and more barren due to the precipitation of salts and the increased salinities in the groundwater. These salinities increase until the palms begin to lose condition at which point the channels should be ready to switch due to sedimentation. Upon switching these saline islands become dependent on seasonal rainfall which leeches through the island, thus lowering salinities and allowing a succession of plant communities to migrate back onto the island, thus setting up the channel-switching cycle to begin again.

The permanent swamps are permanently flooded and are dominated by extensive, sometimes homogenous, stands of tall emergent species rooted in floating peat, including *Phragmites mauritianus* reedbeds, *Cyperus papyrus* swamp and *Miscanthus junceus* swamp, which generally occur close to major distributary channels. Further away from the channels, where the water levels are consistently shallow, short emergent communities such as *Pycreus nitidus* swamp or short emergent bog communities are represented. In the deep lagoon and channels, submerged and floating-leaved species dominate, including submerged beds of *Najas horridus*, *Rotala myriophylloides*, and *Ottelia spp.*, and floating communities of *Brasenia schreberi*, *Nymphaea spp.* and *Nymphoides indica* (Ellery et al 2003).

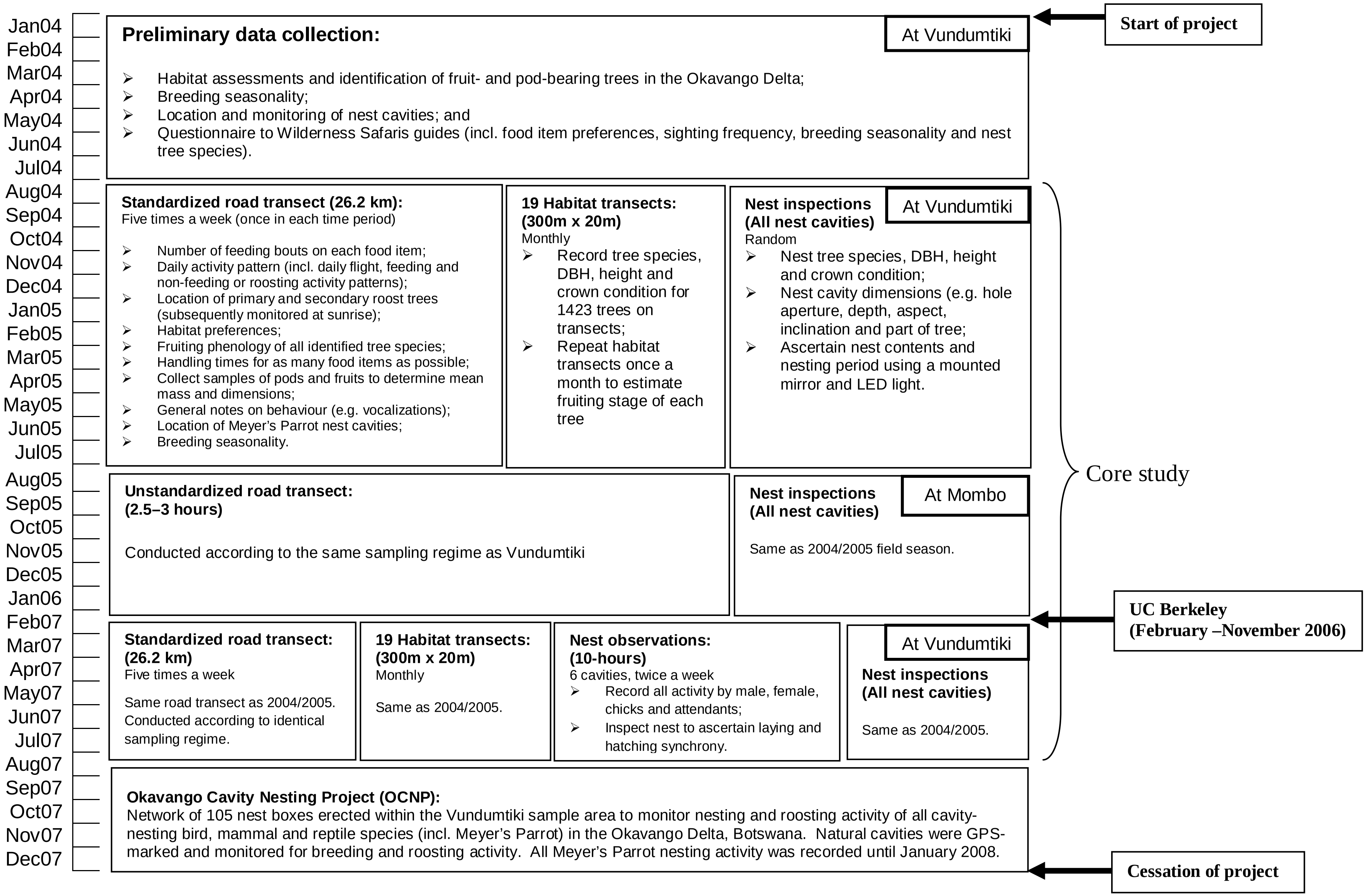
The seasonal swamps are diverse, exhibiting zonation that is dependent on the depth and duration of the flooding. Areas flooded for the longest period of time may have submerged or floating-leaved communities similar to those occurring in the permanent swamps. When the flood recedes or you move into areas with a shorter or lower flood, these species will give way to emergent communities dominated by *Cyperus articulatus*, *Schoenoplectus corymbosus* and *Oryza longistaminata*. Short grasslands of Eragrostis inamoena dominate areas flooded for the shortest period, *Panicum repens* and *Sorghastrum friesii*, followed by a zone dominated by *Imperata cylindrica* or *Cynodon dactylon* (Ellery *et al* 2000). These are the grasslands zoning back to seasonal swamps observed adjacent to islands that are not adjacent to a primary distributary channel.

Islands are typically surrounded by floodplain grassland and seasonal swamp, giving way to *Ficus verruculosa* on the periphery and *Syzigium cordatum* immediately inward. In areas that are infrequently flooded, are tall broadleaved evergreen forests or riverine forest dominated by *Diospyros mespiliformis*, *Garcinia livingstonia*, *Ficus sycamorus*, *Kigelia africana*, *Ficus thonningii*, and *Phoenix reclinata*. Further inland this community gives way laterally to deciduous woodlands dominated by species such as *Acacia nigrescens*, *Berchemia discolor*, *Combretum imberbe*, *Croton megalobotrys*, and *Lonchocarpus capassa*. *Hypaene petersiana* occurs in the saline interior of these wooded island fringes, typically surrounded by short grasslands of *Sporobolus spicatus* (which grows in these saline soils).

The mainland and sandveld areas are dominated by savanna woodland with generally homogenous *Colophospermum mopane* on the heavy textured soils and *Acacia erioloba* dominating on the sandy soils in these areas. These areas are entirely dependent on seasonal rainfall. The Meyer's Parrot is restricted to the islands, mainland and sandveld areas, feeding seasonally on *Ficus verruculosa* and *Phoenix reclinata* adjacent to the main channels.

Timing and logistical difficulties

Logistical difficulties were overcome with the support of Wilderness Safaris Botswana (Pty) Ltd., Sefofane Charters, and the staff, guides and management at Vumbura Plains in the Vundumtiki area and Mombo Camp. The support of the Botswana Department of Wildlife and National Parks and Birdlife Botswana was invaluable in getting supplies in and out of the research camp.



Preliminary data collection:

- Habitat assessments and identification of fruit- and pod-bearing trees in the Okavango Delta;
- Breeding seasonality;
- Location and monitoring of nest cavities; and
- Questionnaire to Wilderness Safaris guides (incl. food item preferences, sighting frequency, breeding seasonality and nest tree species).

Standardized road transect (26.2 km):
Five times a week (once in each time period)

- Number of feeding bouts on each food item;
- Daily activity pattern (incl. daily flight, feeding and non-feeding or roosting activity patterns);
- Location of primary and secondary roost trees (subsequently monitored at sunrise);
- Habitat preferences;
- Fruiting phenology of all identified tree species;
- Handling times for as many food items as possible;
- Collect samples of pods and fruits to determine mean mass and dimensions;
- General notes on behaviour (e.g. vocalizations);
- Location of Meyer's Parrot nest cavities;
- Breeding seasonality.

19 Habitat transects:
(300m x 20m)
Monthly

- Record tree species, DBH, height and crown condition for 1423 trees on transects;
- Repeat habitat transects once a month to estimate fruiting stage of each tree

Nest inspections
(All nest cavities)
Random

- Nest tree species, DBH, height and crown condition;
- Nest cavity dimensions (e.g. hole aperture, depth, aspect, inclination and part of tree;
- Ascertain nest contents and nesting period using a mounted mirror and LED light.

Unstandardized road transect:
(2.5–3 hours)

Conducted according to the same sampling regime as Vundumtiki

Nest inspections
(All nest cavities)

Same as 2004/2005 field season.

Standardized road transect:
(26.2 km)
Five times a week

Same road transect as 2004/2005. Conducted according to identical sampling regime.

19 Habitat transects:
(300m x 20m)
Monthly

Same as 2004/2005.

Nest observations:
(10-hours)
6 cavities, twice a week

- Record all activity by male, female, chicks and attendants;
- Inspect nest to ascertain laying and hatching synchrony.

Nest inspections
(All nest cavities)

Same as 2004/2005.

Okavango Cavity Nesting Project (OCNP):
Network of 105 nest boxes erected within the Vundumtiki sample area to monitor nesting and roosting activity of all cavity-nesting bird, mammal and reptile species (incl. Meyer's Parrot) in the Okavango Delta, Botswana. Natural cavities were GPS-marked and monitored for breeding and roosting activity. All Meyer's Parrot nesting activity was recorded until January 2008.

Figure 7: Chronology of experimental design between January 2004 and December 2007 (February 2006 – December 2006 was spent at the University of California, Berkeley).

Fieldwork was conducted between January 2004 and July 2007, with a 10-month visit to the University of California, Berkeley, between February and December 2006 to do data analysis and experimental design for the 2007 field season. Due to high floodwaters between March and July 2004, standardized data collection was postponed until August 2004, when standardized road transects were conducted five times a week in six different time period to census food item and habitat preferences, daily activity patterns, flocking and roosting behaviour, and breeding activity. Standardized road transects continued at Vundumtiki until July 2005, when the study moved to the Mombo area. Unstandardized road transects were conducted according to the same regime as Vundumtiki until January 2006. Between February and August 2007 an intensive study of the breeding biology of Meyer's Parrot was conducted, including the setting up of a dedicated research camp and a volunteer assistantship program for the 10-hour nest observations (Figure 7).

Rationale and methodology for core studies on ecology of Meyer's Parrot

The Meyer's Parrot Project investigated five aspects of the ecology of Meyer's Parrot, including the feeding ecology (Chapters 2, 4 and 5), habitat associations (Chapter 3), role in forest ecology (i.e. contribution to pollination and seed dispersal) (Chapter 6), daily activity patterns (i.e. feeding, non-feeding and flight activity) (Chapter 7), group dynamics (i.e. flocking and communal roosting behaviour) (Chapter 8), and breeding biology (Chapters 9, 10 and 11).

Very little, beyond anecdotal reports in the literature, was known about the feeding ecology of Meyer's Parrot *Poicephalus meyeri* in the wild (Perrin *et al.* 2002). This study tested the hypothesis that Meyer's Parrot is an opportunistic generalist pre-dispersal seed predator that tracks resource availability within a wide suite of food resources. Standardized road transects were conducted to ascertain the seasonal significance of different food items over 24 months and facilitate comparison between *Poicephalus* parrots to make inferences on threat status and conservation biology.

Species-habitat associations are important in conservation planning and management for identifying the potential impacts of habitat change on species survival (Brown and Stillman 1993, Marsden and Fielding 1999). To this end numerous studies have been undertaken on the habitat associations of parrots (Bryant 1994, Gilardi and Munn 1998, Marsden & Fielding 1999, Robinet *et al.* 2003, Evans *et al.* 2005). However, no research, beyond anecdotal descriptions in the literature has been done on the habitat associations of African parrots (Perrin *et al.* 2000). Habitat loss in forest communities has been identified as a primary factor threatening avian species survival (Collar *et al.* 1994). Davidar *et al.* (2001) highlighted the value of keystone forest habitat types and the requirement to identify and protect these plant communities. Deforestation rates in African countries are twice that of the rest of the world, whereby the continent loses over 4 million hectares of forest every year (UNEP 2008). Recognizing this potential threat, this study tested the impact of the loss of each forest habitat type utilized by Meyer's Parrots on their monthly dietary intake recorded over 24 months.

The role of parrots as seed dispersers and pollinators, and therefore, as agents in engineering the ecosystems they inhabit, is poorly known (Juniper & Parr 1998). Several authors have put forward that the impact of parrots on seed dispersal and recruitment of forest communities, depending on population levels, is likely significant due to high consumption of reproductive parts of plants (Jordano 1983; Terborgh *et al.* 1990; French *et al.* 1992; Galetti 1993; Renton 2001). Parrado-Rosselli and Amaya-Espinel (2006) observed that the feeding behaviour of the Purple-throated Fruitcrow *Querula purpurata* was consistent with high quantity and quality seed dispersal, whereby fruit handling techniques, effects of gut treatment on germination, and post-feeding movements support effective dispersal to viable microsites. Very few studies, however, have been conducted on the intensity of seed and flower predation by parrots (Galetti and Rodrigues 1992). This study evaluated the feeding behaviour of Meyer's Parrot for evidence of linkages between predation of seeds and flowers and forest ecology. Symes and Perrin (2003) put forward that secondary dispersal agents on the ground (e.g. rodents, ants and termites) could facilitate dispersal of viable seeds to suitable microsites for germination and establishment. This study tested the hypothesis that Meyer's Parrots play no discernible role in pollination or seed dispersal in the Okavango Delta, Botswana.

All *Poicephalus* parrots studied thus far have bimodal daily flight activity patterns, whereby flight activity peaks in the early morning and late afternoon (Skead 1964; Massa 1995; Wirminghaus *et al.* 2001; Boussekey *et al.* 2002; Symes and Perrin 2003; Taylor and Perrin 2004). Bimodality has also been reported in the daily activity patterns of Neotropical parrots (Snyder *et al.* 1987; Lindsey *et al.* 1991; Pittier and Christianson 1995; Cassagrande and Beissinger 1997; Pizo and Simão 1997; Gilardi and Munn 1998; Salinas-Melgoza and Renton 2005; Masello *et al.* 2006), Australasian parrots (Marsden 1999; Marsden and Fielding 1999; Robinet *et al.* 2003; Cameron 2005), Mexican parrots (Renton and Salinas-Melgoza 1999), and other African parrots (i.e. *Psittacus* and *Agapornis*) (Chapman et al. 1989; Warburton and Perrin 2005; Ndithia and Perrin 2006). This study, therefore, tested the hypothesis that all Poicephalus parrots have bimodal daily activity patterns.

Symes and Perrin (2003) and Taylor (2002) put forward that, due to the high protein and energy content of their food resources, feeding activity in the morning was likely sufficient to support the daily dietary requirements of Grey-headed Parrots and Brown-headed Parrots. I tested the hypothesis that Meyer's Parrots are not constrained by temporal availability of food resources in the Okavango Delta.

Most parrots are, at least, seasonally gregarious and communal roosting is common (Forshaw 1989; Chapman *et al.* 1989; Gilardi and Munn 1998; Juniper and Parr 1998). Group membership has evolutionary and behavioural significance due to its influence on inter- and intra-specific competition (Cairns and Schwager 1987), risk of predation (Walther and Gosler 2001), reproductive skew theory (Reeve *et al.* 1998), foraging efficiency and dietary intake (Cameron 2005), and social cohesion and information-sharing (Stutchbury and Morton 2001). Similar to the Cape Parrot (Skead 1964; Wirminghaus *et al.* 2001), Yellow-faced Parrot (Boussekey *et al.* 2002), Grey-headed Parrot (Symes and Perrin 2003a) and Brown-headed Parrot (Taylor & Perrin 2004), most medium- to large-sized parrots, such as the Hawk-headed Parrot *Deroptyus accipitrinus* (Strahl *et al.* 1991), Red Shining Parrot *Prosopeia tabuensis* (Rinke 1988), most macaws and amazons (Gilardi and Munn 1998), Glossy Black-Cockatoos *Calyptorhynchus lathami* (Cameron 2005), and the African Grey Parrot *Psittacus erithacus* (Chapman *et al.* 1993) typically occur in pairs or flocks of between two and four. Gilardi and Munn (1998) put forward that small parrot species (e.g. *Forpus spp.*) aggregate into larger flocks. This was corroborated by studies on the Black-cheeked Lovebird (Warburton and Perrin 2005) and Rosy-faced Lovebird (Ndithia and Perrin 2007).

Taylor and Perrin (2004) have suggested the social mechanism behind group dynamics in *Poicephalus* parrots is likely intra-specific association, whereby flocking is a function of the aggregation and dispersal of pair sub-units governed by food resource availability. Brown-headed Parrot pairs showed no special affiliation to other members of the group (except recently hatched progeny), and therefore, will join or leave the flock voluntarily (Taylor and Perrin 2004). Therefore, we tested the hypothesis that Meyer's Parrots typically occur in flocks of between two and four parrots and are organized into loose colonies associated with a central roost (Massa 1995).

Symes and Perrin (2003) put forward that Grey-headed Parrots utilize communal roost according to the Foraging Dispersal hypothesis (Chapman *et al.* 1989). This study also tested the applicability of the Information Centre hypothesis (Ward and Zahavi 1973), General Foraging hypothesis (Bradbury and Vehrencamp 1977; Chapman *et al.* 1989), and optimal foraging theory (Rakotomanana and Hino 1998; Wheelwright 1985).

Very little, beyond anecdotal reports in the literature, was known about the breeding biology of Meyer's Parrot *Poicephalus meyeri* in the wild (Perrin *et al.* 2002). This study tested the hypothesis that Meyer's Parrots are socially monogamous and breeding synchronously within an extra-pair mating system. This study evaluated putative stimuli for facultative early incubation and assessed the applicability of established hypotheses to hatching asynchrony in *Poicephalus* parrots. Hypotheses tested included: Brood Reduction hypothesis (Ricklefs 1965; Mock 1994); Energetic Constraints Hypothesis (Slagsvold 1986); Limited Breeding Opportunity Hypothesis (Beissinger and Waltman 1991; Beissinger 1996); Egg Protection Hypothesis (Bollinger *et al.* 1990; Bollinger and Gavin 2004); and Brood Parasitism Hypothesis (Lombardi *et al.* 1989; Beissinger 1996).

Due to wide distribution and comparative ecological success in comparison with other *Poicephalus* parrots this study tested the hypothesis that the nesting ecology of the Meyer's Parrot was significantly different from other *Poicephalus* parrots. This included testing the hypothesis that there is a dichotomy in *Poicephalus* parrot nesting behaviour, whereby members of the *P. meyeri* superspecies complex are nest tree generalists, while the *P. robustus* superspecies complex includes nest tree specialists.

Presentation of thesis

This thesis was presented as a collection of papers on the behavioural ecology of Meyer's Parrot in the Okavango Delta. Papers were presented in the format required of each journal; however, the tables and figures were embedded in the text. Notification of review status and journal to which the manuscript has been submitted is indicated. Repetition should be accommodated due to separate publication of findings in diverse journals. The number of cross-references between chapters has been increased in these manuscripts to better link the chapters in the thesis.

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Chapter 2:

The feeding ecology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana[1]

The diet of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana, was distinctly seasonal, comprising 71 different food items from 37 tree species in 16 families. During 480 road transects over 24 months, food item preferences closely tracked fruiting and flowering phenology, resulting in significant positive correlations between Levins' niche breadth, rainfall and food resource availability. Meyer's Parrot can, therefore, be considered opportunistic generalists that track resource availability across a wide suite of potential food items. Pre-dispersal seed predation accounted for 62% of total feeding activity, of which 37% were seeds from ripe pods and fruits. Unripe seeds were, however, preferred when seasonally available. Seeds and parasites from fruits and pods accounted for 42% and 35% of total feeding bouts respectively. Fruit pulp was predominantly consumed as byproduct of seed predation. Four arthropods, previously unknown in the diets of African parrots, were discovered during the breeding season. The most important tree species in their diet included (in order of magnitude): *K. africana*, *D. mespiliformis*, *C. imberbe*, *F. sycomorus*, *D. lycoides lycoides*, *C. hereroense* and *B. discolor*. Geophagy was reported in the questionnaire by qualified field guides operating in the study area. There was no evidence to support any local migrations.

Introduction

Very little, beyond anecdotal reports in the literature, is known about the feeding ecology of Meyer's Parrot *Poicephalus meyeri* in the wild (Perrin *et al.* 2002). Comprehensive studies, however, have been undertaken on the diets of the Cape Parrot *Poicephalus robustus* (Wirminghaus *et al.* 2002), Rüppell's Parrot *P. ruppellii* (Selman *et al.* 2002), Grey-headed Parrot *P. fuscicollis suahelicus* (Symes and Perrin 2003), Brown-headed parrot *P. cryptoxanthus* (Taylor and Perrin 2006), Black-cheeked Lovebird *Agapornis nigrigenis* (Warburton and Perrin 2005), and Rosy-faced Lovebird *A. roseicollis* (Nditkia and

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Perrin 2006). Preliminary studies of the African Grey Parrot *Psittacus erithacus* (Chapman *et al.* 1993), Red-bellied Parrot *Poicephalus rufiventris* (Massa 1995), and Yellow-faced Parrot *P. flavifrons* (Boussekey et al. 2002) have also been undertaken. Our study tested the hypothesis that, similar to Rüppell's Parrot and the Brown-headed Parrot, Meyer's Parrot is an opportunistic generalist pre-dispersal seed predator that tracks resource availability within a wide suite of food resources.

Meyer's Parrot is the smallest of the *Poicephalus* parrots and forms a superspecies with Rüppell's Parrot, Brown-headed Parrot, Senegal Parrot *P. senegalus*, Red-bellied Parrot, and Niam-Niam Parrot *P. crassus* (Rowan 1983; Juniper and Parr 1998; Massa 2000). Six subspecies are recognized with *P. meyeri damarensis* and *P. m. transvaalensis* reported to overlap in the Okavango Delta (White 1965; Rowan 1983). Meyer's Parrots have the widest distributional range of any African parrot, exceeding that of the African Parakeet *Psittacula krameri* and Red-faced Lovebird *Agapornis pullarius*. They are distributed throughout subtropical Africa with strongest associations with established riverine forest galleries (e.g. *Syzigium-Adina* woodlands or *Diospyros-Garcinia* woodlands), dry savanna woodland (e.g. *Acacia-Combretum* woodlands), Miombo woodlands (e.g. *Brachystegia* woodlands), secondary growth around cultivation, and dry Acacia scrubland with *Tamarindus* and *Adansonia* along river valleys (Snow 1978; Rowan 1983; Forshaw 1989; Juniper and Parr 1998; Chapter 3: Boyes and Perrin in review a).

The diet of Meyer's Parrot in the wild is reported to consist of fruits, nuts and seeds, including *Ficus spp.*, *Ziziphus abyssinica*, *Z. mucronata*, *Uapaca nitidula*, *Monotes glaber*, *Combretum spp.*, *Grewia spp.*, *Sclerocarya spp.*, *Pseudolachnostylis maprouneifolia*, *Afzelia quanzensis*, *Adansonia digitata*, *Melia volkensii*, *Ficus sycomorus*, and flowers of *Schotia brachypetala* (Rowan 1983; Brickell 1985; Massa 1995; Wirminghaus 1997; Juniper and Parr 1998). Raiding of citrus orchards, maize crops, and grain fields (e.g. sorghum and millet) has also been reported (Rowan 1983; Juniper and Parr 1998; Boyes 2006). Consumption of non-dietary materials (e.g. soil, bark, leaves or wood) has been observed in Rüppell's Parrots (Selman *et al.* 2002), Grey-headed Parrots (Symes and Perrin 2003), Black-cheeked Lovebirds (Warburton and Perrin 2005), Brown-headed Parrots (Taylor and Perrin 2006), and Rosy-faced Lovebirds (Ndithia and Perrin 2006; 2007). Parrots are more insectivorous than initially suspected (Forshaw 1989). Arthropods are common in the diets of Australian parrots (Rowley and Chapman 1991; Smith and Moore 1991) and incidental in Neotropical parrots (Martuscelli 1994; Renton 2001). African parrots have consistently been found to actively forage for invertebrates (Selman *et al.* 2002; Wirminghaus *et al.* 2002; Symes and Perrin 2003; Warburton and Perrin 2005; Taylor and Perrin 2006).

Phenological variations at forest community level influence food resource availability for primary consumers (e.g. parrots) which respond to scarcity in various ways, including diet-switching (Stutchbury and Morton 2001), seasonal breeding (Lack 1967), and/or changes in range use (Wirminghaus *et al.* 2001; Van Schaik *et al.* 1993). Our study monitored fruiting and flowering phenology of all trees in the diet of Meyer's Parrots for correlation with niche breadth, monthly rainfall and flood seasonality. Meyer's Parrots are reported to have some local movement to the Zimbabwean highlands likely due to wandering during the dry season (Rowan 1983). Most parrot species use local migrations and considerable foraging flight distances to ensure sufficient dietary intake (Forshaw 1989). Cape Parrots may have a foraging flight distance of over 100km per day at certain times of the year (Skead 1964; Wirminghaus *et al.* 2002). Foraging strategies such as this have high energetic costs, and therefore, it is reasonable to assume that, when possible, a species will adopt more sedentary foraging behaviour. Meyer's Parrots predominate in subtropical hardwood forests which contain a wide-variety of fruit- and pod-bearing trees suitable for consumption by *Poicephalus* parrots. Therefore, we tested the hypothesis that Meyer's Parrots are sedentary when given the opportunity by monitoring fruiting phenology of all tree species recorded in the diet of Meyer's Parrot.

The concept of keystone species has become a popular paradigm in conservation ecology (Paine 1995). Plant resources that serve disproportionately large trophic importance to specific consumers have been referred to as "pivotal species" (Howe 1977) or "keystone mutualists" (Gilbert 1980, Gautier-Hion & Michaloud 1989). Keystone plant resources are, therefore, food plant resources that produce fruit during periods of food resource scarcity (Gautier-Hion and Michaloud 1989; Levey 1990; Lambert and Marshall 1991). Our study evaluated potential keystone plant resources in the diet of Meyer's Parrots by examining four intersecting ecological attributes put forward by Peres (2000).

Methods

Study sites

The Okavango Delta was chosen as the study area because of its significant Meyer's Parrot population (Wirminghaus 1997). The study was conducted at two sites: Vundumtiki Island located in the north-eastern part of the delta, and Mombo Camp off the northern peninsula of Chief's Island. Both study sites were wilderness areas with limited human impact or disturbance to habitat or animal behaviour (Figure 1). Climatic conditions in the Okavango Delta are distinctly seasonal, comprising a wet season (November–March) and dry season (April–October). Mean annual rainfall is 450–560mm (Ellery *et al.* 2003; Wolski and Savenije 2006). During the annual flood the area covered by water expands from its annual low of 2500-4000km^2 (February–March) to its annual high of 6000–12000km^2 (August–September) (Figure 1). Arrival of the annual flood lags the rainy season and follows one or two months after the end of rainfall in the region (Gumbricht *et al.* 2001; Ellery *et al.* 2003). Rainfall was monitored daily using a rain gauge over the entire study period. The extent of the flood was monitored using flow rate data from Mohembo (Powerserve 2008) and calibrated to the study sites by recording first significant increment in water level on a measuring pole in permanent water as the start of the flood at that study site.

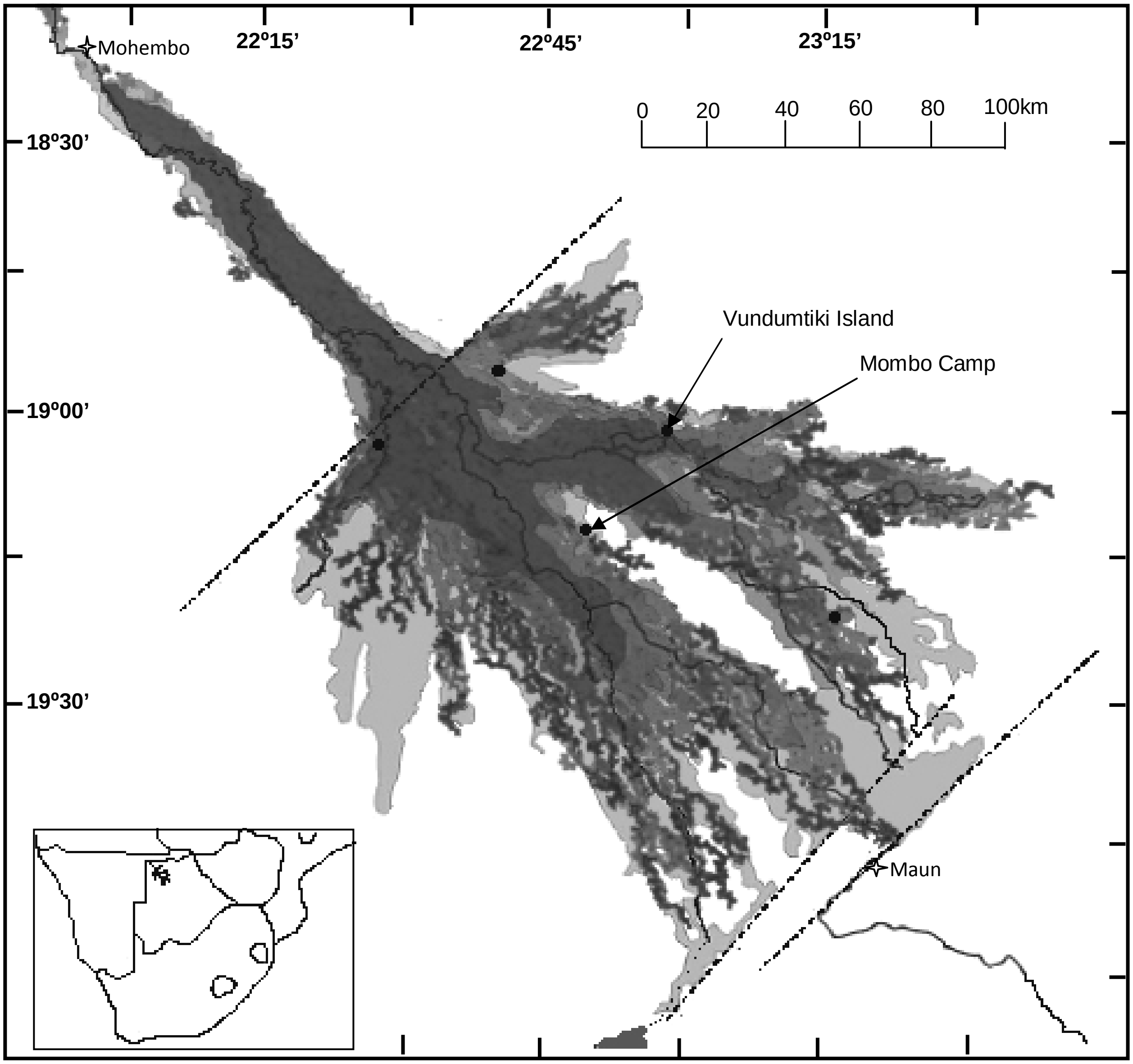


Figure 6: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

Questionnaire

Questionnaires were sent out to all Wilderness Safaris Botswana professional guides operating in the Okavango Delta. The questionnaire had a checklist of 45 potential food trees and asked the respondents to check those consumed by Meyer's Parrot in their area of operation. It also gathered information from respondents on breeding seasonality, daily sighting frequency and subjective population dynamics over the past five years.

Habitat analysis

All fruit- and pod-bearing trees potentially used by Meyer's Parrot and all representative forest habitat types at each study site were identified between July 2003 and March 2004. Fruiting phenology of all these tree species was monitored over the entire study period by recording fruiting-flowering stage once a week. Tree nomenclature followed Van Wyk and Van Wyk (1997) and Palgrave (2002). Habitat descriptions followed Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000).

Data collection

Due to high flood waters between March and July 2004, feeding data collection was postponed till August 2004. Feeding observations were conducted at Vundumtiki from August 2004 to July 2005 and February 2007 to August 2007, and at Mombo from August 2005 to January 2006. Onset and cessation of breeding activity was also monitored over this period.

At Vundumtiki: To standardize spatial distribution of Meyer's Parrot feeding observations, the total sample area was defined as the area 100m either side of the 26.2 km standardized road transect. The same observer and vehicle travelling at 15–20 km/h with an open top were used for all road transects.

At Mombo: Due to time constraints and logistical difficulties a standardized road transect was not established, however, vehicle travelling speed, observer, transect width, sampling frequency, and transect duration were standardized to the regime used at Vundumtiki. Feeding census duration in the Mombo area was limited to two and a half hours after departure from camp. This was the average time taken to complete the Vundumtiki census route.

Road transects were conducted five times a week on different days from start to finish. A systematic sampling strategy was used for the temporal distribution of feeding observations, whereby six daytime time periods were established (i.e. 06h00-08h30; 08h30-11h00; 11h00-13h30; 13h30-16h00; 16h00-18h30; and 18h30 to sunset). Road transects were conducted in all six time periods before a specific time period was sampled again.

Feeding activity and behaviour were recorded using direct observations in the field. All observations were made with a 30x Kowa spotting scope at the maximum sighting distance possible to minimize disturbance of feeding behaviour. The following data were recorded: time of day, habitat type, tree species, food item type and number of feeding bouts. A feeding bout was defined as an individual within a flock, or solitary, feeding on a specific food item at a specific sighting. A food item was defined as any plant food eaten by Meyer's Parrots described according to tree species and food item type. Food item types were classified according to the part consumed and fruiting stage, and included: ripe (r) and unripe (un) seeds from fruits or pods; flowers (f); pseudocarp and seeds of figs (p); and fruit pulp from fleshy fruits (fr). Arthropod food items were classified according to the host tree species and their family, and included: parasitic Hemiptera larvae (h); parasitic Lepidoptera caterpillars (l); and parasitic Coleopteran larvae (c). Arthropod food items were identified by inspecting all potentially-infested dietary (e.g. pods and fruits) and non-dietary (e.g. bark and leaves) food items consumed or inspected by Meyer's Parrots over the study period. Acronyms for tree species and food item types are listed in Table 1.

Data analysis

The four intersecting ecological attributes put forward by Peres (2000) were used to evaluate importance in the diet of Meyer's Parrot. These included: (a) Temporal redundancy (defined in terms of the degree to which the availability of a potential keystone plant resource synchronizes with the fruiting phenology of other potential food items); (b) Consumer specificity (defined as an inverse function of the percentage total feeding bouts over a defined period); (c) Resource reliability (defined in terms of the degree to which a potential keystone plant resource in a given area predictably provides food resources to consumers); and (d) Resource abundance (defined in terms of standing resource abundance of each tree species within the sample area (Chapter 3). Peres (2000) concluded that keystone plant resources are those plant species producing reliable, low-redundancy food resources that exhibit high consumer specificity.

Levins' niche breadth (B_i) or measure of uniformity was used to identify periods of niche specialization based on observed feeding activity (Levins 1968): $B_i = Y_i^2/\sum N_{ij}^2$, where Y_i represents total feeding bouts of all food items and N_{ij} the number of feeding bouts associate with resource state j

(Colwell and Futuyma 1971; Hurlbert 1978). Different food items were interpreted as resource states within the resource matrix. Distribution within this temporal resource matrix was measured as the total number of feeding bouts for a specific food item in a specific month. B_i is closely related to the coefficient of variation and is simply the inverse of Simpson's (1949) measure of concentration or ecological specialization (Hurlbert 1978). Therefore, it is maximized when an equal number of parrot feeding bouts are associated with each food item consumed in that specific month, thus implying generalist food item preferences and no discrimination between food items (Hurlbert 1978). Our study determined niche breadth fluctuations month-to-month to identify periods of food niche specialization.

Kolmogorov-Smirnov (K-S) and Lilliefors tests were used to test for normality. Spearman rank correlation (r_s) was used to test for correlations between Levins' niche breadth (Bi) values and floodwater flow rates, rainfall and food resource availability. Wilcoxon Matched Pair Test was used to test for significant spatial and temporal differences in food resource preferences. Chi-square ($\aleph^2$) statistic was used to evaluate the magnitude of the difference between differences in feeding activity between food items due to location, time and breeding activity. Statistical analysis followed Quinn and Keough (2002) and Zar (1984).

Results

Questionnaire

The results of 28 questionnaires confirmed the year-round presence of Meyer's Parrot throughout the Okavango Delta. All food items identified by professional guides, except *Rhus tenuinervis*, *Pterocarpus angolensis*, *Bauhenia petersiana subsp. macrocantha* and *Grewia flavescens*, were recorded in our study. Consumption of grass seeds was reported by three respondents. Consumption of *Adansonia digitata* and *Schlerocarya birrea* seed kernels was reported by 12 and 14 respondents respectively. Predation of Mopane worms *Gonimbrasia belina* was reported in three respondents, but could not be corroborated in our study or the literature. Drinking was reported throughout the year. Nectivory on *Kigelia africana* flowers was reported by several respondents. Geophagy was reported by three respondents operating in the south of the Okavango Delta (n = 1) and in the Moremi Game Reserve (n = 2). All three reports of geophagy were on floodplains in March and April, and included a maximum of four parrots. Respondents reported that population status was stable over the last five year throughout the Okavango Delta, with increasing populations reported in the Chitabe, Xigera, Tubu Tree and Duba Plains.

Rainfall and flood seasonality

Annual rainfall only exceeded the expected range in the October 2005 – March 2006 wet season when 683mm was recorded (Figure 2). The lag time for flow rate data from Mohembo was calibrated at 59 and 27 days delay for Vundumtiki and Mombo respectively (Figure 2).

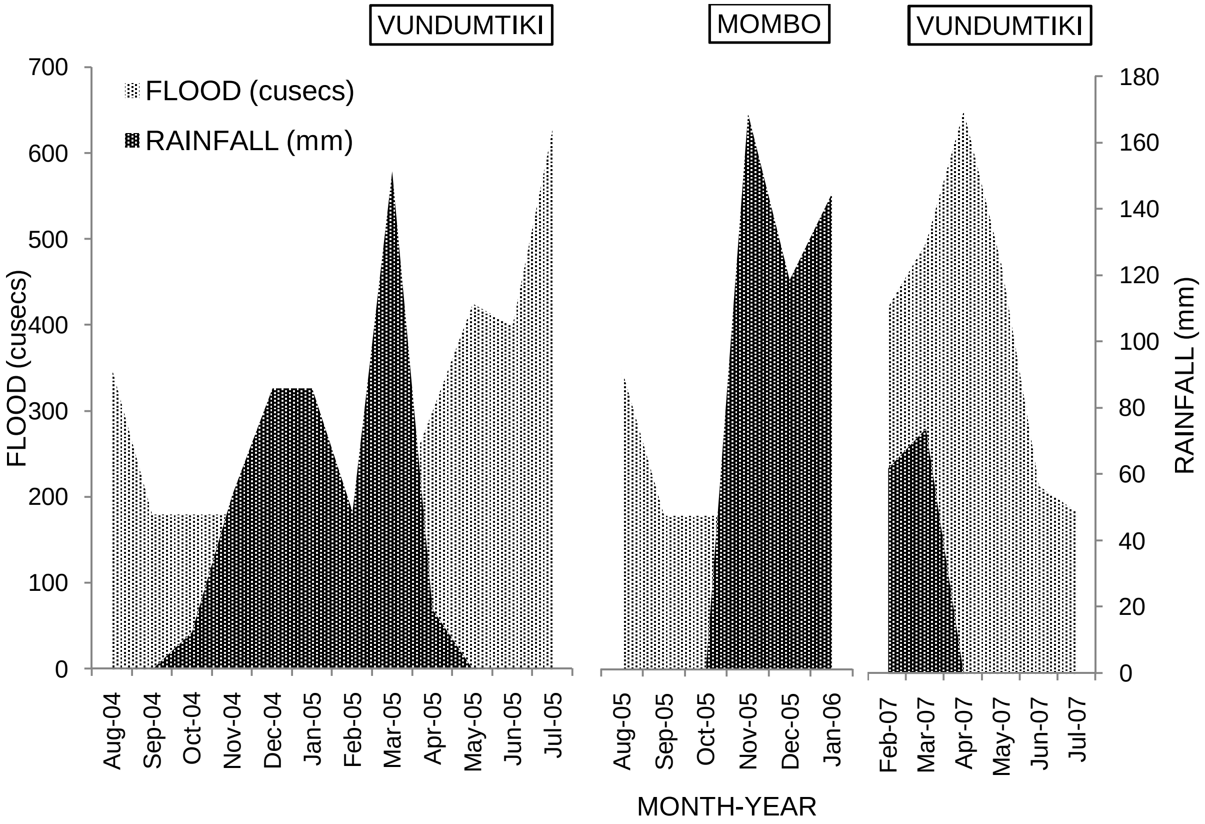


Figure 2: Flood regime (dark grey) and rainfall seasonality (light grey) at Vundumtiki and Mombo

Habitat description

Eleven primary forest habitat types representative of both study sites were identified (Table 1). *Lonchocarpus nelsii* sandveld and *Acacia erioloba* sandveld were only represented in the Vundumtiki study area, while *Acacia tortilis* sandveld, *Hyphaene petersiana* woodland and *Phoenix reclinata* thickets were only represented in the Mombo study area. *Ficus verruculosa* thickets were only represented along channels in both study areas. The study sites were representative of the Okavango Delta system, as all forest habitat types outlined by Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000) were represented at Vundumtiki and/or Mombo.

Table 1: Habitat types identified in the Vundumtiki and Mombo study areas

Habitat type/Habitat description	Habitat description
Riverine forest	Closed canopy dominated by *Diospyros mespiliformis*, *Garcinia livingstonia, Berchemia discolor, Ficus sycamorus, Croton megalobotrys* and *Kigelia africana*. Often on the edge of floodplains and lagoons.
*Acacia-Combretum*woodland	Dominated by *A. nigrescens*, *Combretum imberbe* and *C. hereroense.* Widest distribution of any forest habitat type. On silty alluvium in areas that were previously flooded.
Diospyros lycoides marginal woodland	Homogenous *D. lycoides lycoides* with C. imberbe and A. nigrescens interspersed. Often ecotone between *Acacia-Combretum* woodland and riverine forest and dry Mopane woodland.
Hyphaene petersiana woodland	Saline islands dominated by *Hyphaene petersiana* with low grass cover
Mopane woodland	Dominated by *Colophospermum mopane* with C. imberbe and *A. nigrescens*.
Lonchocarpus nelsii sandveld	Homogenous *L. nelsii* on deep sand. Old channel beds, well drained.
Acacia erioloba sandveld	Dominated by Acacia erioloba, forming the ecotone between Acacia-Combretum woodland and L. nelsii sandveld and dry Mopane woodland.
Terminalia sericea sandveld	Dominated by *T. sericea*, *T. prunoides* and *Guibourtia coleosperma.* Forest patches within the dry Mopane woodland. Represent old floodplains with a sandy substrate.
Acacia tortilis sandveld	Dominated by *A. tortilis* on silty alluvium on Chief’s Island. Situated away from the western and northern floodplains towards the interior of the island (Figure 1).
Phoenix reclinata thickets	Homogenous *P. reclinata* on floodplains and channel margins. Forest clumps on the Mombo floodplains.
Ficus verruculosa thickets	Homogenous *F. verruculosa* dominating channel margin. Forming dense thickets in the middle of lagoons. Used as heronry for multiple heron and egret species.

Food item preferences

During the 480 census transects completed over 24 months at Vundumtiki and Mombo 1975 sightings including 5048 feeding bouts were recorded. Over this period 71 food items from 37 tree species within 16 families were identified (Table 2). *Kigelia africana* (15.4%; n = 777) accounted for the highest percentage of total feeding bouts, followed by *Diospyros mespiliformis* (11.8%; n = 598), *Combretum imberbe* (8%; n = 404), *Ficus sycomorus* (7.9%; n = 400), *Diospyros lycoides lycoides* (5.9%; n = 299), *Combretum hereroense* (4.7%; n = 239), and *Berchemia discolor* (2.8%; n = 140) (Table 2). Only unripe *D. mespiliformis* seeds, *K. Africana* flowers, *F. sycomorus* figs and wasp larvae, and ripe *C. imberbe* seeds had a consumer specificity of over 40% in a given month (Table 3). Between six and sixteen food items were consumed each month with a mean of 11.13 ± 0.63 (Table 3). *Kigelia africana* was the only tree species utilized throughout the year, while *C. imberbe* and *F. sycomorus* were each consumed for more than 7 months of the year continuously. Twelve tree species, including *Grewia spp.*, *Carissa edulis*, *Lonchocarpus spp.*, *Acacia tortilis*, *Terminalia prunoides*, *Combretum mossambicense*, *Phoenix reclinata* and *Hyphaene petersiana*, were utilized for less than a month and accounted for less than 1% of the annual diet.

Seeds and parasites from fruit accounted for 42% (n = 2110) of feeding bouts, while seeds and parasites from *Leguminosae* and *Combretaceae* pods accounted for 35% (n = 1749). Seed predation accounted for 62% (n = 3140) of feeding bouts, of which 39% (n = 1975) were seeds from ripe pods and fruits. Consumption of unripe seeds was seasonal and comprised 23% (n = 1165) of foraging activity. Preference was shown for seed kernels from unripe fruits when ripe fruits and pods where available. Flowers were the third most important food item type accounting for 13% (n = 632) of feeding bouts. During September, *K. africana* flowers were the primary food item accounting for 37% and 56% of feeding bouts at Vundumtiki and Mombo respectively. Arthropod consumption, predominantly during the breeding season (February – July) accounted for 17% (n = 834) of total feeding bouts. Pseudocarp and seeds of figs represented 7% (n = 346) of foraging activity. Fruit pulp was consumed regularly as a by-product of seed predation, but was only targeted in *Syzigium guineense* and *Phoenix reclinata*, accounting for 2% (n = 95) of total feeding bouts. Grass seeds were only consumed on two occasions in March 2005 at Vundumtiki. Consumption of leaves, bark and wood was observed in fledgling Meyer's Parrots during the post-fledging period (July – December).

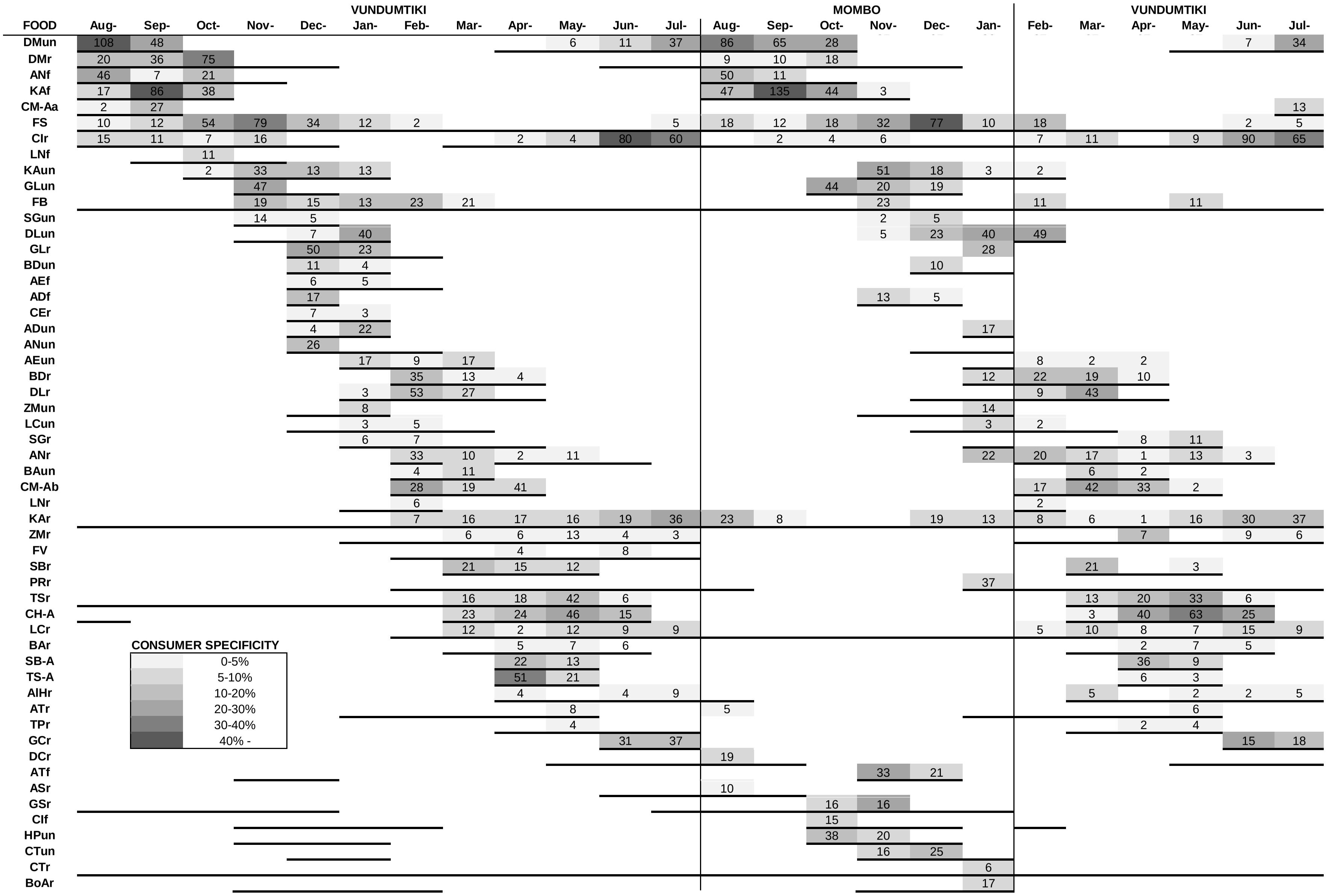
Meyer's Parrots were infrequently observed drinking in pairs at seasonal pans (n = 23) and floodplain margins (n = 11) in the early morning during the dry season (before and after the arrival of the flood).

Table 2: Total feeding bouts for each tree species observed at Vundumtiki and Mombo

			TOTAL FEEDING BOUTS							
			VUNDUMTIKI				**MOMBO**		**VUNDUMTIKI**	
FOOD ITEMS			**Non-breeding**		**Breeding**		**Non-breeding**		**Breeding**	
			Aug-04 - Jan-		**Feb-05 - Jul-05**		**Aug-05 - Jan-**		**Feb-07 - Jul-07**	
FAMILY/Species	**Acronym**	**Part consumed**	n	%	n	%	n	%	n	%
ANACARDIACEAE										
Sclerocarya birrea	SB	r, fr, i	-	-	83	2	-	-	69	2
APOCYNACEAE										
Carissa edulis	CE	r, un	10	<1	-	-	-	-	**	<1
ARECACEAE										
Hyphaene petersiana	HP	un	**	<1*	-	-	58	4	-	-
Phoenix reclinata	PR	r, f	**	<1*	-	-	37	3	-	-
BIGNONIACEAE										
Kigelia africana	KA	r, un, f	202	6	111	3	364	26	96	3
BOMBACEAE										
Adasonia digitata	AD	un, f	43	1	-	-	35	2	-	-
CAESALPINIACEAE										
Guibourtia coleosperma	GC	un, r	0	0	68	2	-	-	72	2
CAPPARACEAE										
Boscia albitrunca	BoA	r	-	-	-	-	17	1	-	-
Capparis tomentosa	CT	r, un	-	-	-	-	47	3	-	-
CELASTRACEAE										
Gymnosporia senegalensis	GS	r	-	-	-	-	32	2	-	-
CLUSIACEAE										
Garcinia livingstonia	GL	r, un	120	3	-	-	111	8	-	-
COMBRETACEAE										
Combretum hereroense	CH	r, i	-	-	108	3	-	-	131	4
Combretum imberbe	CI	r, f	49	1	146	4	27	2	153	4
Combretum mossambicense	CMos	r, f	**	<1	-	-	-	-	**	<1
Terminalia prunoides	TP	r, un	0	<1*	4	<1	-	-	6	<1*
Terminalia sericea	TS	r, i	0	0	154	4	-	-	81	2
EBENACEAE										
Diospyros mespiliformis	DM	r, un	287	8	54	1	216	15	41	1
Diospyros lycoides	DL	r, un	50	1	80	2	68	5	101	3
LEGUMINOSAE										
Albizia harveyi	AlH	r	-	-	17	<1	-	-	14	0
Acacia sieberiana	AS	r	-	-	-	-	10	1	-	-
Acacia erioloba	AE	r, un, f	28	1	26	<1	-	-	12	0
Acacia hebeclada	AH	r, un, f	-	-	-	-	-	-	-	-
Acacia nigrescens	AN	r, un, f	100	3	56	2	83	6	54	1
Acacia tortilis	AT	r, un, f	-	<1	8	<1	59	4	6	<1
Burkea africana	BA	r	-	-	33	<1	-	-	22	1
Colophospermum mopane	CM	r, i	29	1	88	2	-	-	107	3
Dichrostachys cinerea	DC	r, un	-	-	-	-	19	1	-	-
Lonchocarpus capassa	LC	r	3	<1	49	1	3	<1	56	2
Lonchocarpus nelsii	LN	r	11	<1	6	<1	-	-	2	0
MORACEAE										
Ficus burkei (thonningii)	FB	p, fr, i	47	1	44	<1	23	2	22	1
Ficus sycamorus	FS	p, fr, i	201	6	7	<1	167	12	25	1
Ficus verruculosa	FV	p, fr	0	<1*	12	<1	-	-	0	<1*
MYRTACEAE										
Syzigium guineense	SG	r, un, fr	25	<1*	7	<1	7	<1	19	<1*
RHAMNACEAE										
Berchemia discolor	BD	r, un, fr	15	0	52	1	22	2	51	1
Ziziphus mucronata	ZM	r, un, fr	8	0	32	<1	14	1	22	1
TILIACEAE										
Grewia bicolor	GB	r	**	<1	**	<1	**	<1	**	<1
Grewia flava	GF	r	-	-	-	-	**	<1	-	-
TOTAL FEEDING BOUTS			1228		1245		1419		1162	

*Under sampled and assumed to have higher consumption in other areas
**Observed several times when not doing transect

Table 3: Food item calendar for Vundumtiki (August 2004 – July 2005; February 2007 – July 2007) and Mombo (August 2005 – January 2006): Total number of feeding bouts per food item (number), monthly fruiting/flowering phenology (solid line) and consumer specificity (shading & key)



						VUNDUMTIKI										MOMBO						VUNDUMTIKI		
FOOD	**Aug-**	**Sep-**	**Oct-**	**Nov-**	**Dec-**	**Jan-**	**Feb-**	**Mar-**	**Apr-**	**May-**	**Jun-**	**Jul-**	**Aug-**	**Sep-**	**Oct-**	**Nov-**	**Dec-**	**Jan-**	**Feb-**	**Mar-**	**Apr-**	**May-**	**Jun-**	**Jul-**
DMun	108	48								6	11	37	86	65	28								7	34
DMr	20	36	75										9	10	18									
ANf	46	7	21										50	11										
KAf	17	86	38										47	135	44	3								
CM-Aa	2	27																						13
FS	10	12	54	79	34	12	2					5	18	12	18	32	77	10	18				2	5
CIr	15	11	7	16					2	4	80	60		2	4	6			7	11		9	90	65
LNf			11																					
KAun			2	33	13	13										51	18	3	2					
GLun				47											44	20	19							
FB				19	15	13	23	21								23			11			11		
SGun				14	5											2	5							
DLun					7	40										5	23	40	49					
GLr					50	23												28						
BDun					11	4											10							
AEf					6	5																		
ADf					17											13	5							
CEr					7	3																		
ADun					4	22												17						
ANun					26																			
AEun						17	9	17											8	2	2			
BDr							35	13	4									12	22	19	10			
DLr						3	53	27											9	43				
ZMun						8												14						
LCun						3	5											3	2					
SGr						6	7														8	11		
ANr							33	10	2	11								22	20	17	1	13	3	
BAun							4	11												6	2			
CM-Ab							28	19	41										17	42	33	2		
LNr							6												2					
KAr							7	16	17	16	19	36	23	8			19	13	8	6	1	16	30	37
ZMr								6	6	13	4	3									7		9	6
FV									4		8													
SBr								21	15	12										21		3		
PRr																		37						
TSr								16	18	42	6									13	20	33	6	
CH-A								23	24	46	15									3	40	63	25	
LCr								12	2	12	9	9							5	10	8	7	15	9
BAr									5	7	6										2	7	5	
SB-A									22	13											36	9		
TS-A									51	21											6	3		
AlHr									4		4	9								5		2	2	5
ATr										8			5									6		
TPr										4											2	4		
GCr											31	37											15	18
DCr													19											
ATf																33	21							
ASr													10											
GSr															16	16								
CIf															15									
HPun															38	20								
CTun																16	25							
CTr																		6						
BoAr																		17						

CONSUMER SPECIFICITY

0-5%
5-10%
10-20%
20-30%
30-40%
40% -

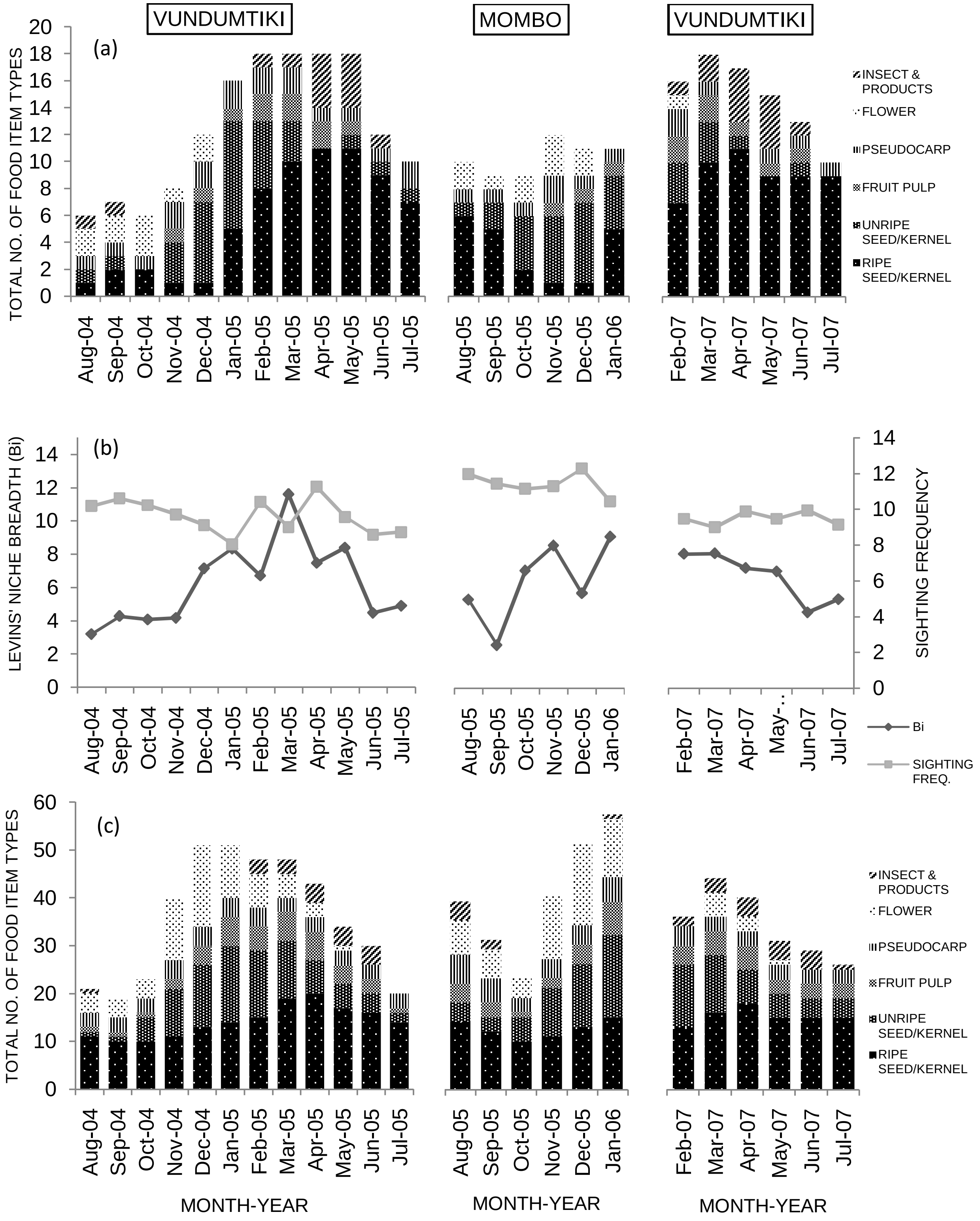


Figure 3: (a) Total number of food item types consumed at Vundumtiki and Mombo; (b) Levins' unstandardized and unexpanded niche breadth index (B_i) month-to-month and sighting frequency (feeding bouts/transect); (c) Total number of food item types available at Vundumtiki and Mombo.

Temporal and spatial variation in food item preferences

Food item preferences were distinctly seasonal, closely tracking fruiting phenology of all target food items (i.e. above 10% CS-value) (Table 3). There was a significant positive correlation between Levins’ niche breadth (B_i) and monthly rainfall ($r_s = 0.621$; $n = 24$; $p = 0.001$), monthly rainfall and total number of food items available each month ($r_s = 0.788$; $n = 24$; $p < 0.001$), and therefore, between B_i and total number of food items available each month ($r_s = 0.648$; $n = 24$; $p < 0.001$). There was, however, no significant correlation between (B*i*) and flood flow rates (adjusted for study sites) ($r_s = 0.347$; $n = 24$; $p = 0.096$) (Figure 2; Figure 3).

There was a significant difference between food item preferences at Vundumtiki and Mombo over the period August to January (Wilcoxon Matched Pair Test; $n = 54$; $T = 185.5$; $Z = 4.692$; $p < 0.001$) (Table 3). There was, however, no significant difference between food item preferences at Vundumtiki in 2005 and 2007 over the period February to July (Wilcoxon Matched Pair Test; $n = 54$; $T = 188.5$; $Z = 0.905$; $p = 0.365$) (Table 3). Chi-square ($\aleph^2$) statistic showed greatest significant difference between food item preferences during and outside the breeding season ($\aleph^2 = 6588.1$; $df = 53$; $p < 0.001$), followed by between study sites ($\aleph^2 = 2857.3$; $df = 53$; $p < 0.001$), and 2005 and 2007 at Vundumtiki ($\aleph^2 = 646.96$; $df = 53$; $p < 0.001$) (Table 3). Breeding activity was recorded between February and July each year (Chapter 9: Boyes and Perrin in review b). Sighting frequency was consistent over the entire study period (Figure 3).

Arthropod consumption

Five arthropod larvae previously unknown in the diets of African parrots were recorded during our study (Table 4). An unknown owlet moth larvae (Lepidoptera, *Noctuidae*) feeding on and incubating in *C. mopane* pods was the only specimen not identified (Figure 4). Arthropod consumption was distinctly seasonal, accounting for 20-72% of the total monthly feeding bouts during the primary breeding season (February – July) (Table 3). The only incidences of arthropod consumption outside of the breeding season were on the waxy exudate and larvae of Pssylid Beetles on *C. mopane* leaves and on fig wasps and their larvae

Figure 4: Unknown owlet moth larvae (Lepidoptera, *Noctuidae*) feeding on and incubating in *Colophospermum mopane* pods.

inside *F. sycomorus* figs (Table 4). Consumption of exudate and larvae of Pssylid Beetles accounted for 1-10% of total monthly feeding bouts between July and September, while consumption of fig wasps and larvae accounted for 25-38% of total monthly feeding bouts between October and December. All consumption of arthropods by Meyer's Parrots was deterministic, as parrots invested a significant amount of time prospecting for these food items, while ignoring any others that may be available (e.g. fruit pulp or seeds).

Table 4: Tree parasites and mutualists consumed by Meyer's Parrot at Vundumtiki and Mombo. References: 1 = Picker *et al.* (2004); 2 = Roodt (1998); 3 = Miller (1996); 4 = Compton *et al.* (1991).

TreeSpecies	Part parasitized	Arthropod	Month	Ref.
Sclerocarya birrea caffra	Fruit pulp	Red Marula caterpillar* *Mussidia nigrivenella* (Lepidotera, *Pyralidae*)	Feb-Apr	1
Combretum hereroense	Seed in pod	Bruchid Beetle larva *Caryedon spp.* * (Coleoptera, *Bruchidae*)	Mar-Jul	2
Terminalia sericea	Seed in pod	Bruchid Beetle larva *Caryedon spp.* * (Coleoptera, *Bruchidae*)	Mar-May	3
Acacia erioloba	Seed in pod	Bruchid Beetle larva *Bruchidius uberatus** (Coleoptera, *Bruchidae*)	Feb-Mar	3
Colophospermum Mopane	Petioles, leaves	Pssylid Beetle *Arytaina mopani* and exudate (Hemiptera, *Psyllidae*)	Aug-Sep	2
Colophospermum Mopane	Seed in pod	Unknown Owlet moth larva* (Lepidoptera, *Noctuidae*) (Figure 4)	Mar-May	1
Ficus sycomorus	Pseudocarp	Fig wasps and larvae *Ceratosolen arabicus* (Hymenoptera, *Agaonidae*)	Jan-Dec	4

* Important during breeding season

Discussion

Food resource availability tracking and local migrations

Food resource availability tracking by Meyer's Parrots was demonstrated by the regular pattern in the food item calendar (Table 2) and the strong correlations between rainfall seasonality, fruiting phenology and Levins' niche breadth. Even though there were no significant differences in food item preferences between years at Vundumtiki, there were significant differences in food item preferences at Mombo and

Vundumtiki, 35 kilometres apart. Spatial differences in dietary intake were likely due to differences in habitat mosaic and rainfall reported at these study sites, resulting in Meyer's Parrots tracking the availability of different food resources. This disparity in food item preferences would have been even larger had Mombo been sampled for the entire year, as predation of *A. tortilis heterocantha* flowers and seeds, *F. verruculossa* pseudocarp and seeds, unripe *H. petersiana* seeds, and *P. reclinata* fruit pulp was likely more significant over the dry season at Mombo, where *A. tortilis* sandveld, *F. verruculosa* thicket, *Hyphaene petersiana* woodland, and *Phoenix reclinata* thicket were exclusively represented in our study. These relationships demonstrate that Meyer's Parrot is an opportunistic generalist that tracks food resource availability within a restricted range of less than 35km.

No fluctuations in sighting frequency, consistent resource tracking over the study period and no period of food resource scarcity that warranted emigration in search of food demonstrated that there were no significant local migrations. Meyer's Parrots can, therefore, be considered sedentary in the Okavango Delta, probably ranging up to 4km from the primary communal roost (Chapter 8: Boyes and Perrin in review c).

Food item preferences

Meyer's Parrot is an opportunistic generalist pre-dispersal seed predator. Over 38% of feeding activity, however, was on nectar and pollen from flowers, arthropod larvae and products (e.g. exudates), pseudocarp and seeds from figs, and fruit pulp. Therefore, the diet of this generalist was more omnivorous than previously anticipated.

Fruit-bearing trees from riverine forest and *D. lycoides* marginal woodland were more important in the diet of Meyer's Parrot than pod-bearing trees from *Acacia*-*Combretum* marginal woodland, *T. sericea* sandveld, dry Mopane woodland, and *A. erioloba* sandveld. This is likely a corollary of tracking seasonal resource availability in these forest habitat types, and is expected to be different elsewhere in their distributional range. Combretaceae (e.g. *C. imberbe*) and Leguminosae (e.g. *Acacia erioloba*) pods (are nonetheless considered to be an important food resource, as these seeds are available throughout the year and no other bird species were observed to feed on them prior to dispersal. Therefore, pre-dispersal inter-specific competition for this abundant, energy and protein-rich food resource was limited. Leguminous pods are also an important food resource in most parrot communities around the world, including several *Pionus* parrots in Brazil (Galetti and Rodriquez 1992; Galetti 1993), *Amazona* and *Ara spp.* in the Amazonian forest (Gilardi and Munn 1998), and Lilac-crowned Parrots *Amazona finschi* in Central America (Renton 2001). All the *Poicephalus* parrots studied thus far, except

Cape Parrots; seasonally prefer Combretaceae and Leguminosae pods over fleshy fruits in their diet (Massa 1995; Boussekey *et al.* 2002; Selman *et al.* 2002; Wirminghaus *et al.* 2002; Symes and Perrin 2003; Taylor and Perrin 2006). This is also likely a corollary of tracking seasonal resource availability within their distributional range.

Tree species that occur sporadically in the diet of Meyer's Parrot can be separated into three groups, including those consumed opportunistically due to being hidden in the understorey (e.g. *C. edulis* and *Grewia spp.*), those consumed infrequently due to low resource abundance in the study areas (e.g. *T. prunoides* and *C. mossambicense*), and those likely under-sampled due to not sampling feeding activity at Mombo between February and July (e.g. *P. reclinata*, *H. petersiana* and *A. tortilis*). Elsewhere in their range, all of these tree species are likely more important in their diet.

Although ripe seeds were more prevalent in the diet, Meyer's Parrots showed a distinct preference for unripe fruits from *D. mespiliformis*, *K. africana* and *D. lycoides* when both food item types were available, while only consuming unripe fruit and pods from *A. erioloba*, *H. petersiana*, *C. tomentosa* and *A. digitata*. Selman et al. (2002) observed this in the Rüppell's Parrot, however, the ecological function of this is unclear. Likely reasons for this preference are avoidance of inter-specific competition (e.g. primates and large-bodied avian frugivores), preference for soft seed kernels (i.e. easier access and manipulation), and avoidance of fungal fruit rot in ripe fruits (e.g. *Diospyros spp.*).

Our study likely underestimated the importance of fruit pulp in the diet of Meyer's Parrot, as consumption was only recorded when seeds were ignored and fruit pulp was targeted (e.g. *S. guineense*). Fruit pulp is, however, a valuable resource for sugars, vitamins and minerals (Klasing 1998), and thus significance to the physiological condition of Meyer's Parrots in the wild cannot be discounted.

Consumption of non-dietary materials (e.g. soil, bark, leaves or wood) was observed during comprehensive studies of the Grey-headed Parrot (Symes & Perrin 2003), Black-cheeked Lovebird (Warburton & Perrin 2005), Brown-headed Parrot (Taylor & Perrin 2006), and Rosy-faced Lovebird (Ndithia & Perrin 2006; 2007). Consumption of bark and leaves was only observed in fledgling Meyer's Parrots during the post-fledging period (Chapter 9). This was likely a developmental stage as consumption was irregular and these fledglings were still dependent on regurgitate from attendant adults for subsistence. Selman et al. (2002) put forward that bark found in the crops of dead Rüppell's Parrot chicks may have been ingested by adults whilst foraging for boring insects. Meyer's Parrots were observed to excavate dead wood, but never to consume woody material or boring Coleopteron larvae. Selman *et al.* (2002) also suggested that leaves, high in ash and carbohydrate, and low in protein and fat, may supplement the diet of Rüppell's Parrot when the fruiting period of numerous species is ending and preferred food items are less available. The lack of consumption of leaves by adult Meyer's Parrots, therefore, indicated that they did not experience a period of food resource scarcity as severe as Rüppell's Parrot.

Geophagy has only been observed in the Black-cheeked Lovebird, African Grey Parrot *Psittacus erithacus*, Cape Parrot, and Red-faced Lovebird (Warburton and Perrin 2005). The function of intentional soil ingestion is unclear, however, the possible biochemical benefits, including acquisition of minerals and absorption of toxic plant compounds (Gilardi and Munn 1998; Selman *et al.* 2002), may also be of important for Meyer's Parrot. Several food items consumed by Meyer's Parrots are reported to be poisonous (e.g. *K. Africana* and *Lonchocarpus capassa* seeds) (Roodt 1998), and therefore, the geophagy reported in the questionnaire could have a functional purpose.

Dietary seasonality

Phenotypic changes in gut retention rate, digestive efficiency and hence feeding rate to accommodate dietary switches between seed predation, frugivory and insectivory have been demonstrated in several bird species (Levey and Karasov 1989; Levey and Martinez Del Rio 2001). There were three distinct periods of diet switching in the food item calendar of Meyer's Parrots, including the wet season diet (November–February), breeding season diet (March–June), dry season diet (July–October) and transitional diet between the dry and wet seasons (October/November).

The wet season diet began with the first rains in November when unripe seeds from *G. livingstonia* fruits became available. From December or January, the food niche breadth widens considerably as more food items become available, peaking in March at the end of the wet season. The wet season diet was dominated by ripe seeds from F. *sycomorus*, *D. lycoides lycoides*, *B. discolor, A. nigrescens* and *G. livingstonia*.

The breeding season diet was characterized by a dietary switch to a predominantly insectivorous diet in March during courtship and copulation (February–March). Arthropod consumption was linked with the breeding season of Rüppell's Parrot (Selman *et al.* 2002), but not the Brown-headed Parrot (Taylor and Perrin 2006). Our study revealed a dietary switch to arthropod consumption far more dramatic than previously recorded in *Poicephalus* parrots. Selman *et al.* (2002) put forward that arthropod consumption likely provided additional protein necessary for chick growth, egg production and supplementary metabolic water during the dry season. Provisioning males may also use insectivory to improve muscle condition prior to the breeding season by consuming Red Marula caterpillars and energy-rich *S. birrea* fruit pulp in the early breeding season (March–April). All of the arthropod larvae identified in our study during the breeding season were previously unknown in the diets of *Poicephalus* parrots. The host tree species, however, occur in the diets of Rüppell's Parrots, Brown-headed Parrots and Grey-headed Parrots during their respective breeding seasons. Therefore, the use this source of protein during the breeding season needs to be investigated in these *Poicephalus* parrots.

The dry season diet began when the parrots switched from a predominantly insectivorous diet back to plant food items during the fledging and post-fledging period. Based on B_i, there were distinct periods of niche specialization at Vundumtiki (June–November) and Mombo (August–September). This coincided with the dry season (April–October) and recession of the annual flood (July–August) during which food resource availability was lowest due low availability of fruits and flowers to supplement the predation of ripe seeds from *C. imberbe* pods, *K. africana* fruits and *G. coloesperma* pods. At Vundumtiki and Mombo this niche specialization was primarily due to the atypical fruiting of *D. mespiliformis* in the dry season and the flowering of *K. africana* and *A. nigrescens* before the first rains in November. This period of specialization was shorter at Mombo due to the added availability of ripe seeds from *Dichrostachys cinerea, Acacia sieberiana and Boscia albitrunca* and unripe seeds from *Capparis tomentosa* and *H. petersiana*. Pssilid beetles were consumed during the dry season diet, surely to supplement pod and flower predation at the end of the dry season (Selman *et al.* 2002). Black-cheeked Lovebirds consume at least two species of Psyllidae beetles, and widespread opportunistic use of psyllid nymphs by Australian parrots has also been recorded (Warburton and Perrin 2005). Consumption of Psyllidae beetles and their exudates may be an ancient practice in Psittaformes. The most significant dietary switch over this period was that to nectar and pollen predation from *K. africana*, *Adansonia digitata* and *A. nigrescens* flowers. The dry season diet ended when unripe seeds from fleshy fruit became available in November.

The transition from the dry season diet was problematic in that there is lag time between first rains and the availability of unripe fleshy fruits (e.g. *B. discolor* and *D. lycoides*) and Leguminsae pods (*A. nigrescens* and *A. erioloba*). During this transitional period, Meyer's Parrots feed on the pseudocarp, seeds and fig wasp larvae *Ceratosolen arabicus* (Hymenoptera, *Agaonidae*) from *F. sycomorus* figs. Figs were consumed infrequently and opportunistically throughout the year, however, in this period of fruit and flower scarcity they accounted for up to 38% of the diet at Vundumtiki and Mombo. Large, productive fig trees were scarce in the Vundumtiki study area (Chapter 3). This indicated that, similar to the findings of Gautier-Hion and Michaloud (1989), figs are only targeted when necessary due to resource patchiness and scarcity. Noting the year round availability of *F. sycomorus*, it could be considered an auxiliary food item used only during periods of food resource scarcity.

Dietary similarities and niche overlap with other *Poicephalus* parrots

There are distinct differences between food item preferences of *Poicephalus* parrots within the *P. meyeri* superspecies complex. Brown-headed Parrots and Rüppell's Parrots have distinct distributional ranges from the Meyer's Parrot (Rowan 1983; Juniper and Parr 1998), and thus live in allopatry or parapatry. Rüppell's Parrots share 13 tree species in their diet with Meyer's Parrot, including more of the dry and marginal woodland tree species (e.g. *A. erioloba*, *A. hebeclada* and *Grewia flava*), while Brown-headed Parrots share only ten tree species with Meyer's Parrot, including more of the riverine and hardwood forest tree species (e.g. *S. birrea*, *D. mespiliformis* and *F. sycomorus*). There are no food items in common with the Red-bellied Parrot, even though they lived in sympatry, as Meyer's Parrots tended to forage in large trees in riverine forest habitat, while Red-bellied parrots focused their foraging effort in the open savanna with scattered *A. digitata* (Massa 1995; Juniper and Parr 1998). Meyer's Parrots shared no food items with the Cape Parrot (Wirminghaus *et al*. 2002); however, they had six food trees in common with the Grey-headed Parrot (Symes and Perrin 2003) and the genera *Diospyros*, *Ficus*, *Syzigium* and *Terminalia* in common with the Yellow-faced Parrot (Boussekey *et al*. 2002). All of the other *Poicephalus* parrots are data deficient. Grey-headed Parrots live in sympatry with Meyer's Parrots (Symes and Perrin 2003), yet they preferred the unripe seeds of *Parinari curatellifolia*, *Gmelina arborea*, and *Commiphora mollis* (Symes and Perrin 2003), all of which do not occur in the diet of Meyer's Parrots.

Significantly, the ability to sufficiently open the nut-casing of *Schlerocarya birrea caffra* fruit to access the oily seed kernels demonstrated that Meyer's Parrots have a bite force comparable to that of Grey-headed Parrots which are 2.5 times larger (Symes and Perrin 2003). This supports the hypothesis that Meyer's Parrots are opportunist generalist feeders with unrestricted access to a wide range of food resources. It is unlikely that Meyer's Parrots experience significant niche overlap with any other *Poicephalus* parrots or frugivorous bird species.

Are there any keystone plant resources?

As an opportunistic generalist, the incidence of keystone plant resources was unlikely; however, the three ecological attributes put forward by Peres (2000) were nonetheless useful indicators of importance in the diet of Meyer's Parrot. *Kigelia africana* had the highest consumer specificity, followed by *D. mespiliformis*, *C. imberbe* and *Ficus sycomorus*. Of these, *D. mespiliformis* had the lowest temporal redundancy due to atypical fruiting at the end of winter. Resource reliability was high for all food resources, whereby there was a significant correlation between rainfall and food resource availability.

Our study demonstrated that the most important tree species in their diet included (in order of magnitude): *K. africana*, *D. mespiliformis*, *C. imberbe*, *F. sycomorus*, *D. lycoides lycoides*, *C. hereroense* and *B. discolor*. Although it is unlikely to be keystone to the ecological success of Meyer's Parrots in the study area, our study indicates that *K. africana* is the most important tree species in the diet of Meyer's Parrot in the Okavango Delta. The collective absence of *D. mespiliformis, K. Africana*, *C. imberbe,* and *F. sycomorus* could pose a threat to the status of Meyer's Parrots in an area. This, depending on the species composition of the different forest habitat types, introduces the possibility of "keystone habitat resources" that govern the distributional range of Meyer's Parrot (Chapter 3).

Conclusion

Results from our study represent the most comprehensive data set ever compiled on the feeding ecology of Meyer's Parrot or any other African parrot, and could be used as a benchmark for future work on the other *P. meyeri* subspecies and the three remaining data-deficient *Poicephalus* parrots in the *P. meyeri* superspecies complex. Three important points emerge from our study: (a) Meyer's Parrots are resource tracking opportunistic generalist pre-dispersal seed predators for whom seeds from fleshy-fruits are most important; (b) Meyer's Parrots are the smallest *Poicephalus* parrot with a bite force comparable to the Grey-headed Parrot which is 2.5 times larger, thus facilitating unrestricted access to a wide suite of food resources; and (c) The incidence of arthropod consumption in the diet of Meyer's Parrots is higher than any other *Poicephalus* parrot.

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Chapter 3:

Habitat associations of Meyer's Parrot (*Poicephalus meyeri*) in the Okavango Delta, Botswana[1]

ABSTRACT

Meyer's Parrots (*Poicephalus meyeri*) have the widest distributional range of any African parrot, extending throughout subtropical Africa. Here we investigated habitat associations and niche metrics to better understand this wide distribution and the maintenance of six subspecies over such a vast area. Habitat preferences at the population level over 24 months were inferred from monthly feeding activity in each identified forest habitat type at two study sites in the Okavango Delta, Botswana. Eleven forest habitat types were identified. An index of relative resource abundance or productivity for all tree species represented in each forest habitat type was calculated using results from 19 (300x20 m) forest habitat transects. Relative resource abundance was, therefore, estimated for 1439 trees from the multiple of diameter at breast height and crown condition (i.e. the proportion of the canopy capable of producing fruit). Strongest associations were with established riverine forest galleries and associated *Acacia*-*Combretum* woodlands. A modified Hurlbert's expanded and standardized niche breadth index demonstrated that Meyer's Parrots were habitat specialists between August and January, foraging in riverine forest communities almost exclusively. The predominance of riverine forest and associated dry *Acacia* grasslands, Miombo woodland (e.g. *Brachystegia* woodland), dry Mopane woodlands and *Combretum* bushlands likely facilitates their wide distribution and the establishment of six sub-species along the Kavango and Zambezi basins, Great Rift Valley system, and across the Nile Valley towards Lake Chad in the Sahel.

Keywords: Poicephalus, Okavango Delta, habitat associations, niche breadth, Africa, habitat description

MEYER'S PARROTS *POICEPHALUS MEYERI* HAVE THE WIDEST DISTRIBUTIONAL RANGE OF ANY AFRICAN PARROT, exceeding that of the African or Rose-ringed Parakeet (*Psittacula krameri*) and Red-faced Lovebird (*Agapornis pullarius*) (Snow 1978, Juniper & Parr 1998). They are distributed throughout

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[1] Formatted for *Biotropica*, The Association for Tropical Biology and Conservation: Boyes, R.S. and Perrin, M.R. (in review) Habitat associations of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana.

subtropical Africa with strongest associations with dry savanna woodland, riverine forest, secondary growth around cultivation, and dry Acacia scrubland (Snow 1978; Tarborton 1980; Forshaw 1989, Juniper and Parr 1998). Meyer's Parrot is the smallest of the *Poicephalus* parrots and forms a superspecies with Rüppell's Parrot *P. rueppellii*, Brown-headed Parrot *P. cryptoxanthus*, Senegal Parrot *P. senegalus*, Red-bellied Parrot, and Niam-Niam Parrot *P. crassus* (Rowan 1983; Juniper and Parr 1998; Massa 2000). Six subspecies are recognized with *P. meyeri damarensis* and *P. m. transvaalensis* reported to overlap in the Okavango Delta, Botswana (White 1965, Rowan 1983). Here we study the habitat associations of this analogous African parrot to better understand the potential impacts of habitat change on species survival.

Marsden (1999) cautioned that structural habitat characteristics (e.g. open and closed habitat) could introduce bias when evaluating habitat preferences of parrots, whereby flight activity surveys may overestimate the importance of disturbed habitat, while underestimating the importance of pristine forest habitat for conserving parrots. Boyes and Perrin (Chapter 7: Boyes & Perrin in review a) found that the probability of detecting a feeding parrot during road transects was over three times greater than detecting socializing or resting parrots, and over five times greater than detecting parrots in flight. Meyer's Parrots are lingual feeders (i.e. vocalize involuntarily during feeding) and most likely detected during feeding activity (Homberger 1978). Therefore, we inferred habitat preferences from total monthly feeding activity recorded in each forest habitat type on road transects. Non-feeding Meyer's Parrots (e.g. roosting and socializing) and parrots in flight were ignored in our study (Marsden & Fielding 1999).

Degree of specialization in habitat use was evaluated using a modified Hurlbert's standardized and expanded niche breadth index (B_i) (Hurlbert 1978, Renton 2001). Niche breadth is the variance in resource use by a species, and can be estimated by measuring the uniformity of the distribution of conspecifics among resource states within the resource matrix (Colwell & Futuyma 1971). Meyer's Parrot has the widest trophic niche of any *Poicephalus* parrot studied thus far (Chapter 5: Boyes & Perrin in review b). This generality in their food item preferences is facilitated by unrestricted, exclusive access to seeds from Leguminosae pods (e.g. *Acacia erioloba*) and fleshy fruits (e.g. *S. birrea*), flowers, and arthropod larvae (Chapter 2: Boyes & Perrin in review c). As opportunistic generalists, there were no food resources considered keystone to their ecological success (Chapter 2). Our study tested the hypothesis that the Meyer's Parrot is a habitat generalist, thus facilitating its wide distribution throughout subtropical Africa.

Selective removal of keystone plant resources may drastically reduce forest carrying capacity for frugivores and seed predators (Gautier-Hion & Michaloud 1989, Levey 1990, Lambert and Marshall

1991, Peres 2000, Long and Racey 2007). Boyes and Perrin (Chapter 2) put forward that the collective absence of *Diospyros mespiliformis*, *Kigelia africana*, *Combretum imberbe*, and *Ficus sycomorus* trees could pose a threat to the ecological success of Meyer’s Parrot in the Okavango Delta. Therefore, depending on species composition of different forest habitat types, there may be keystone forest habitat types that facilitate their distributional range and ecological success in comparison to other African parrots.

Species-habitat associations are important in conservation planning and management for identifying the potential impacts of habitat change on species survival (Brown & Stillman 1993, Marsden & Fielding 1999). To this end numerous studies have been undertaken on the habitat associations of parrots (Bryant 1994, Gilardi & Munn 1998, Marsden & Fielding 1999, Robinet *et al.* 2003, Evans *et al.* 2005). However, no research, beyond anecdotal descriptions in the literature has been done on the habitat associations of African parrots (Perrin *et al.* 2002). Habitat loss in forest communities has been identified as a primary factor threatening avian species survival (Collar *et al.* 1994). Davidar *et al.* (2001) highlighted the value of keystone forest habitat types and the requirement to identify and protect these plant communities. Deforestation rates in African countries are twice that of the rest of the world, whereby the continent loses over 4 million hectares of forest every year (UNEP 2008). Recognizing this potential threat, we tested the impact of the loss of each forest habitat type utilized by Meyer’s Parrots on their monthly dietary intake recorded over 24 months. We then related these findings to their current distribution to evaluate the potential threat of deforestation and habitat loss due to climate change.

METHODS

STUDY SITES.– This study was undertaken in the Okavango Delta where Meyer’s Parrot is common (Wirminghaus 1997) and there is an extensive wilderness area free from human impact or disturbance to animal behaviour. The study was conducted at two sites: Vundumtiki Island located in the north-eastern part of the delta (19°00’S, 22°59’E; 995m asl), and Mombo Camp off the northern peninsula of Chief’s Island (19°14’S, 22°46’E; 963m asl) (Figure 1). The climate in the Okavango Delta is distinctly seasonal, comprising a wet season (November–March) and dry season (April–October), with a mean annual rainfall of 450–560mm is reported in the region (Ellery *et al.* 2000, Wolski & Savenije 2006). Annual rainfall only exceeded the expected range in the October 2005–March 2006 wet season when 683mm was recorded. During the annual flood the area covered by water expands from its annual low of 2500–4000 km^2 (February–March) (dark grey) to its annual high of 6000 – 12000 km^2 (August–

September) (light grey) (Figure 1). Arrival of the annual flood lags the rainy season by one or two months after the end of the rains (Gumbricht *et al.* 2004).

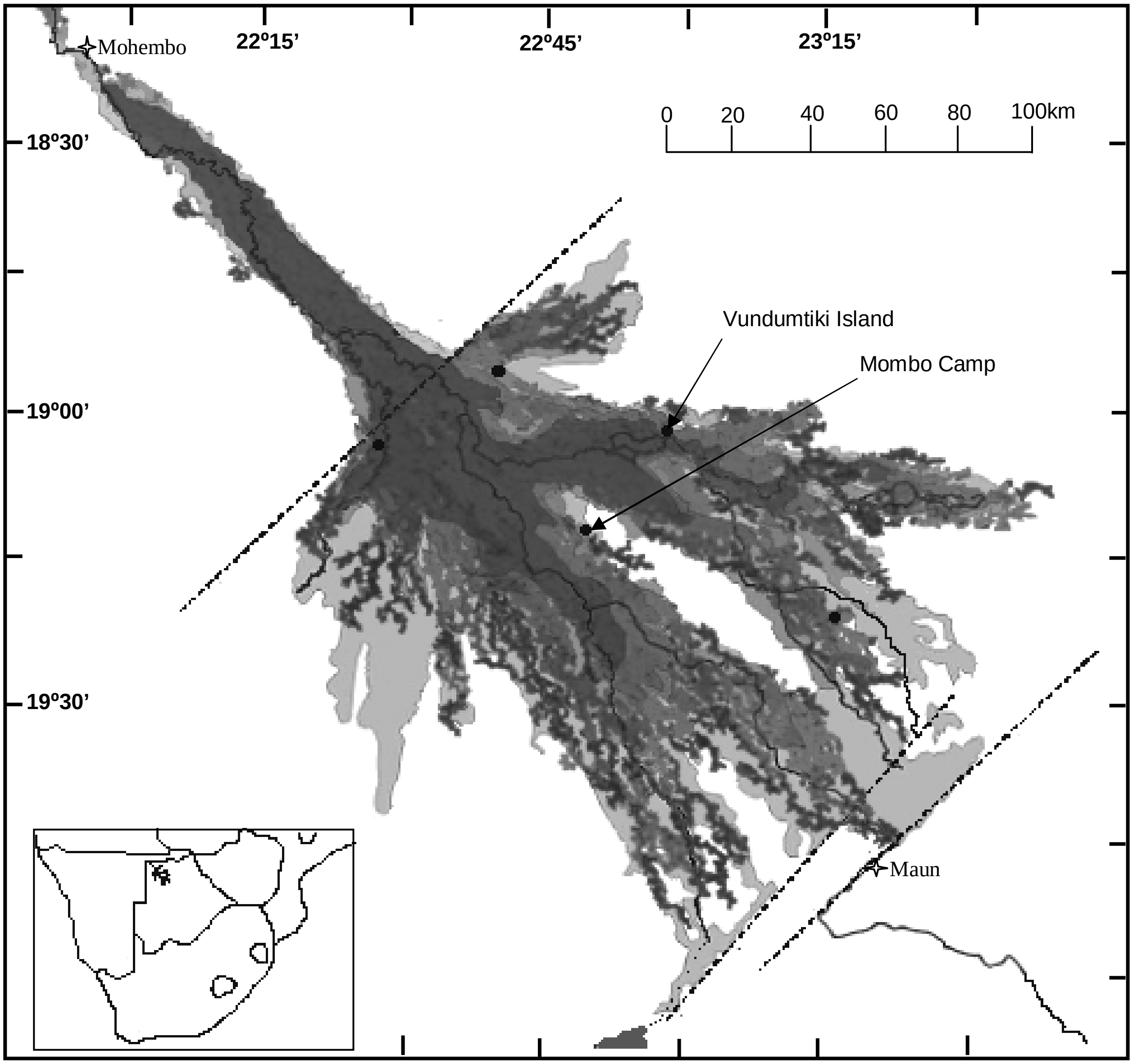

Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

HABITAT PREFERENCES.– Data collection was conducted at Vundumtiki from August 2004 to July 2005 and February 2007 to August 2007, and at Mombo from August 2005 to January 2006.

At Vundumtiki: To standardize spatial distribution of Meyer's Parrot feeding observations, the total sample area was defined as the area 100m either side of the 26.2 km standardized road transect.

The same observer and vehicle travelling at 15 – 20 km/h with an open top were used for all road transects.

At Mombo: Due to time constraints and logistical difficulties a standardized road transect was not established, however, vehicle travelling speed, observer, transect width, sampling frequency, and transect distance (i.e. 26.2 km) were standardized to the regime used at Vundumtiki.

Road transects were conducted five times a week on different days from start to finish. A systematic sampling strategy was used for the temporal distribution of feeding observations, whereby six daytime time periods were established (i.e. 06h00-08h30; 08h30-11h00; 11h00-13h30; 13h30-16h00; 16h00-18h30; and 18h30 to sunset) (Chapter 7). Road transects were conducted in all six time periods before a specific time period was sampled again.

Habitat preferences were recorded using direct observations in the field. All observations were made with a 30x Kowa spotting scope at the maximum sighting distance possible to minimize disturbance of feeding behaviour. The following data were recorded: habitat type, tree species, foraging height above ground, food item type, and number of feeding bouts. A feeding bout was defined as an individual within a flock, or solitary, feeding on a specific food item at a specific sighting. A food item was defined as any plant food eaten by Meyer's Parrots described according to tree species and food item type. Food item types were classified according to the part consumed and fruiting stage, and included: ripe (r) and unripe (un) seeds from fruits or pods; flowers (f); pseudocarp and seeds of figs (p); and fruit pulp from fleshy fruits (fr). Arthropod food items were classified according to the host tree species and their family, and included: parasitic Hemiptera larvae (h); parasitic Lepidoptera caterpillars (l); and parasitic Coleopteran larvae (c).

HABITAT ASSESSMENT.– All fruit- and pod-bearing trees potentially used by Meyer's Parrot and all representative forest habitat types at each study site were identified between July 2003 and March 2004. Fruiting phenology of all these tree species utilized by Meyer's Parrot at both study sites was also monitored by recording fruiting-flowering stage once a week on road transects. Tree nomenclature followed Van Wyk and Van Wyk (1997) and Palgrave (2002), while habitat descriptions followed Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000). Due to logistical difficulties habitat assessments were not undertaken at Mombo, and therefore, habitat niche breadth could not be estimated.

At Vundumtiki: Total habitat area of each forest habitat type within the sample area was estimated by measuring the distance along the road transect line corresponding to the different forest habitat types up to 100m either side of the road. A total of 19 (300m x 20m) habitat line transects were established within the sample area (Bullock & Solis-Magallenes 1990, Chapman *et al.* 1994, Renton 2001). Each habitat transects were mapped and transect line maintained using a Garmin Quest GPS (Garmin 2006). We used a stratified sampling design within which three resource abundance line transects were dispersed in each forest habitat type to obtain a representative sample of resource availability (Renton 2001). Due to homogeneity and high stand density of *Lonchocarpus nelsii* sandveld only one transect was done in this forest habitat type. Due to heterogeneity of *Acacia-Combretum* woodland, this forest habitat types was further stratified to include *Acacia-Combretum* woodland dominated by *Combretum imberbe*, *Combretum hereroense* and *Acacia nigrescens*. Similarly, dry Mopane woodland was stratified to include dry Mopane woodland dominated by trees under 4m in height (i.e. scrub Mopane), above 4m in height (i.e. cathedral Mopane) and with multiple-storeys. For the estimation of habitat-wide resource abundance, a habitat conversion factor (HCF) was calculated by dividing the total forest habitat area within the sample area by the total area of resource abundance line transects in each forest habitat type.

Chapman *et al.* (1992) found that diameter at breast height (DBH) predicted fruit number and biomass the best. DBH was measured for all trees over 150 mm in diameter using a large caliper (Renton 2001). We estimated the proportion of the crown that was healthy and potentially productive to overcome variance due to poor canopy condition (e.g. fire, fungal or elephant damage). Crown condition (CC) was estimated using subjective visual assessment, and scored in increments of 0.2 from 0 – 1, whereby 0 represents a snag (i.e. dead tree) and 1 represents a full healthy canopy. We recorded tree species, DBH (cm) and CC (0-1) for all trees on habitat transects. The observer was standardized for all transects and once-off subjective measurements to maximize repeatability and precision (Chapman *et al.* 1994). Therefore, we estimated the relative productivity or resource abundance of a specific tree (RA_i) using the following index: $RA_i = DBH_i{*}CC_i$. RA_i for all trees of the same species on the three resource abundance transects in each habitat type were then summed to obtain transect-wide relative resource abundance for each tree species within each forest habitat type ($TW\text{-}RA_i$). $TW\text{-}RA_i$ was then multiplied by the HCF to obtain an index of habitat-wide relative resource abundance for each tree species ($HW\text{-}RA_i$). Total relative resource abundance of a specific tree species (RRA_i) was estimated by summing all the $HW\text{-}RA_i$ values. Therefore, we estimated total relative resource abundance for each tree species using the following equation:

$$\mathrm{RRA_i} = \sum_{j=1}^{7} \left\{ \sum_{k=1}^{\infty} (\mathrm{DBH_k} \times \mathrm{CC_k}) \times \mathrm{HCF_j} \right\}$$

Where: i represents each food item; j represents each habitat type; and k represents each tree on the habitat transects.

HABITAT NICHE METRICS.– A modified Hurlbert’s standardized and expanded niche breadth index (β_i) was used to estimate habitat niche fluctuations within the resource matrix (Hurlbert 1978, Renton 2001). Therefore, the following equation was used to calculate habitat niche breadth:

$$\beta_{\mathrm{i}} = \left[\frac{1}{\sum_{\mathrm{j}}\left(10000 \times \frac{\mathrm{N}_{ij}}{\sum_i d_j k \times \mathrm{N}_{ij}}\right)}\right]\left[\frac{1}{9999}\right]$$

A resource matrix is a table formed by using different competing species as rows and resource states as columns. Resource states are subdivisions within a heterogeneous habitat considered individually (e.g. food item types) or grouped on the basis of similarity (e.g. habitat types) (Hurlbert 1978). We evaluated monthly niche breadth fluctuations, and therefore, the resource matrix was modified to include different months as rows and different forest habitat types as resource states. Distribution within this species-specific “temporal resource matrix” was measured as the number of feeding bouts in a specific forest habitat type in a specific month. Habitat-wide relative resource abundance (HW-RA_{i}) should provide adequate information on the ecological distinctness of resource states (Colwell & Futuyma 1971), thus allowing for the expansion (k = 10 000) of the temporal resource matrix. For β_i, a value close to 0 indicates habitat specialization, and a value tending to 1 indicates broader habitat preferences (Hurlbert 1978).

POTENTIAL KEYSTONE HABITAT TYPES.– Forest habitat types that, when removed from the temporal resource matrix, had the most significant impact on monthly dietary intake of Meyer’s Parrots at Vundumtiki. To determine the potential loss in productivity or resource abundance for a specific tree species due to the removal of a specific forest habitat type, we calculated the proportion of $\mathrm{RRA}_{\mathrm{i}}$ represented within each forest habitat type separately. We then multiplied the total number of feeding bouts observed on a specific food item in a specific month by this proportion to obtain the number of feeding bouts lost due to the removal of that specific forest habitat type. The output of this stimulation was the total percentage loss to observed dietary intake due to the systematic removal of each forest habitat type.

The significance of putative keystone forest habitat types to the diet of the Meyer’s Parrot was established using four intersecting ecological attributes put forward by Peres (2000). These included: (a) Temporal redundancy (defined in terms of the degree to which food resource availability of a potential keystone forest habitat type synchronizes with other forest habitat types); (b) Consumer specificity (CS_i) (defined as an inverse function of the percentage total feeding bouts over a defined period); (c) Resource reliability (defined in terms of the repeatability of fruiting phenology in potential keystone forest habitat types); and (d) Resource abundance (defined in terms of the relative resource abundance of a potential keystone forest habitat types).

DATA ANALYSES.– Mann-Whitney U-test was used to test for significant differences in habitat preferences over time and between study sites. Spearman's rank correlations were used to test for a significant correlation between food resource availability of different forest habitat types. Statistical analysis followed Quinn and Keough (2002) and Zar (1984).

RESULTS

RESOURCE ASSESSMENT.– The study sites were representative of the Okavango Delta system, as all habitat types outlined by Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000) were represented at Vundumtiki and/or Mombo (Table 1). Habitat mosaics at Vundumtiki and Mombo were significantly different. Mombo was dominated by riverine forest and *Acacia*-*Combretum* tree-lines between *Phoenix reclinata* thickets on the floodplains, *Hyphaene petersiana* woodlands on the saline islands, and dry, nutrient-deficient *Acacia tortilis* sandveld away from the water. Vundumtiki was dominated by large stands of *Acacia*-*Combretum* woodland with established riverine forest galleries on the islands and either *Lonchocarpus nelsii* sandveld, *Terminalia sericea* sandveld or dry Mopane woodland away from the water. Mombo and Vundumtiki were approximately 35 kilometres apart.

At Vundumtiki, there were significant differences in forest habitat structure, whereby riverine forest and *Acacia*-*Combretum* woodland had the highest number of tree species, canopy height, and mean DBH (Table 1). Total sample area at Vundumtiki was 524ha, of which 384ha was forest habitat and 141ha was floodplains, seasonal pans, and seasonally-flooded grassland.

Fruiting phenology was distinctly seasonal, whereby food resources were mostly available in riverine forest during summer (October to March) and in *Acacia*-*Combretum* woodland during winter (March to September) (Figure 2). *Acacia*-*Combretum* woodland had the highest $HW\text{-}RA_i$ value and accounted for over 42% of total relative resource abundance in the sample area, followed by riverine forest (23%), *L. nelsii* sandveld (14%) and dry Mopane woodland (13%) (Figure 3; Table 2).

TABLE 1. *Habitat types identified at Vundumtiki and Mombo. Described according to Ellery and Ellery (1997), Roodt (1998) and Ellery et al. (2000). (Acronyms are listed for reference in other tables)*

LOCATION/Habitat type		*Description*	Stand density (stems/ha)	No. of tree species	n	Mean tree height (m ± SD)	Mean DBH (cm ± SD)
VUNDUMTIKI							
Acacia erioloba sandveld	AES	Dominated by *Acacia erioloba*.	98	7	95	6 ± 3.1	39 ± 24.1
Lonchocarpus nelsii sandveld	LNS	Homogenous *L. nelsii* on deep sand.	161	3	158	5 ± 1.2	40 ± 19.5
Mopane woodland	MW	Dominated by *Colophospermum mopane* with *C. imberbe* and *A. nigrescens*.	106	10	190	17 ± 9.1	60 ± 21.3
BOTH STUDY SITES							
Riverine forest	RF	Closed canopy dominated by *Diospyros mespiliformis*, *Garcinia livingstonia, Berchemia discolor*, *Ficus sycomorus* and *Kigelia africana*.	128	13	231	20 ± 9.1	60 ± 21.3
Acacia-Combretum woodland	ACW	Dominated by *A. nigrescens*, *Combretum imberbe* and *C. hereroense.*	102	14	183	14 ± 9.0	58 ± 51.0
Diospyros lycoides woodland	DLW	Dominated by *D. lycoides lycoides thickets*.	207	9	373	4 ± 1.8	27 ± 9.3
Terminalia sericea sandveld	TSS	Dominated by *T. sericea*, *T. prunoides* and *Guibourtia coleosperma.*	116	8	209	6 ± 4.5	37 ± 14.2
MOMBO							
Hyphaene petersiana woodland	HPW	Saline islands dominated by *Hyphaene petersiana.*	-	-	-	-	-
Acacia tortilis sandveld	ATS	Dominated by *A. tortilis* on silty alluvium on Chief's Island.	-	-	-	-	-
Phoenix reclinata thickets	PRT	Homogenous *P. reclinata* on floodplains and channel margins.	-	-	-	-	-
ALONG CHANNELS							
Ficus verruculosa thickets	FVT	Homogenous *F. verruculosa* dominating channel margin.	-	-	-	-	-

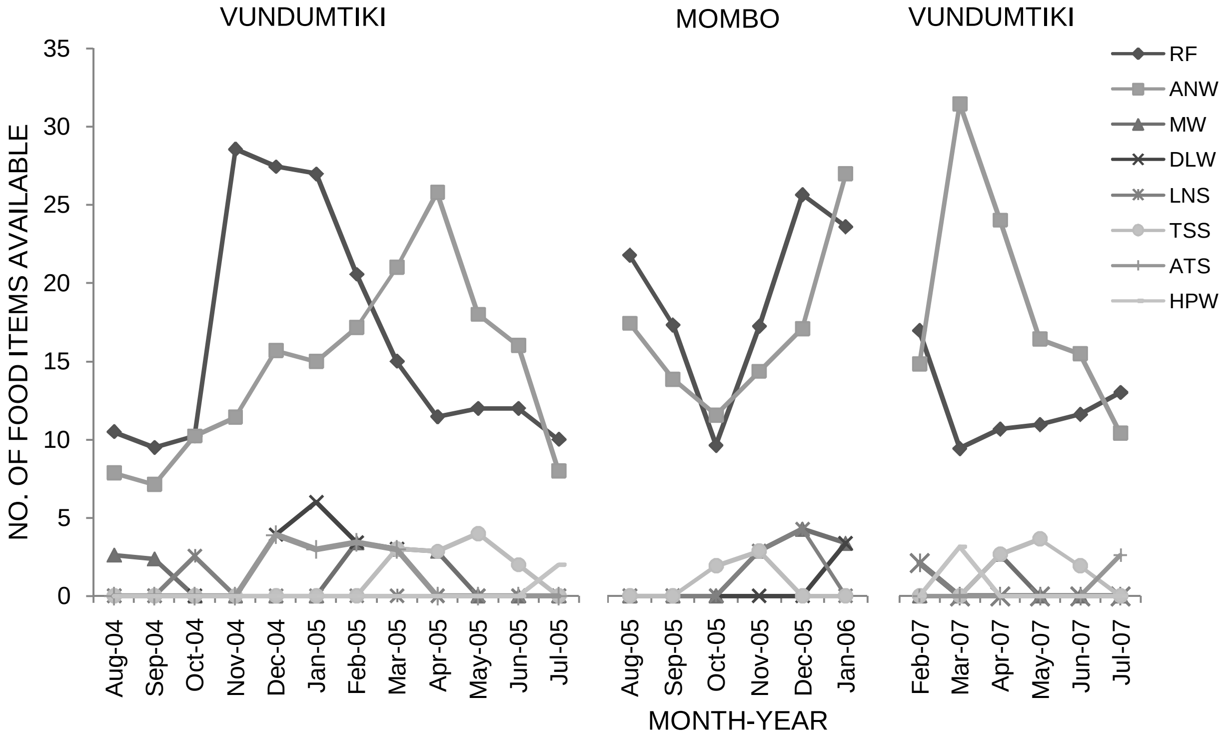

FIGURE 2. *Total number of food item available to Meyer's Parrots in each forest habitat type over 24 months at Vundumtiki and Mombo. Acronyms in Table 1.*

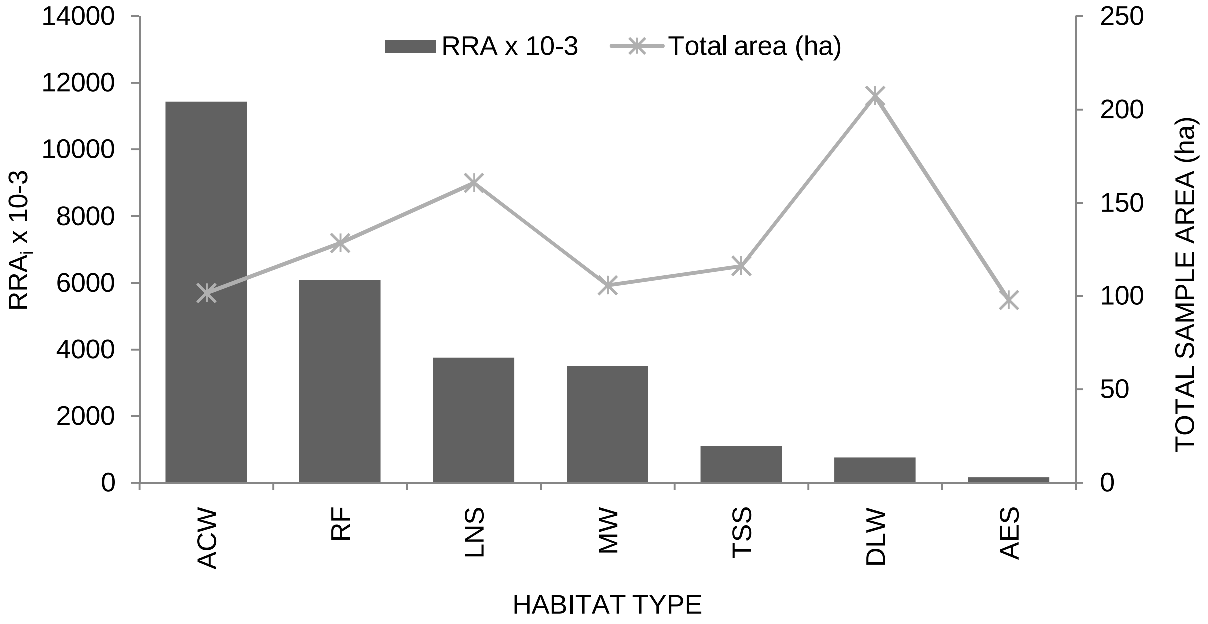

FIGURE 3. *Total resource abundance (*RRA$_i$ x 10^{-3}*) and total forest habitat area within sample area (ha) in the Vundumtiki study area. Acronyms in Table 1.*

TABLE 2. *Total relative resource abundance (RRA_i) and food item types for each tree species in each forest habitat type at Vundumtiki. Acronyms in Table 1. Food item types: r = ripe seed; un = unripe seed; fr = fruit pulp; p = pseudocarp and seeds of figs; and I = arthropod larvae or products (e.g. exudates).*

		Habitat Types						
FAMILY/Species	Food item type	RF	ACW	DLW	MW	TSS	LNS	AES
ANACARDIACEAE								
Sclerocarya birrea	r, fr, i	51	49					
APOCYNACEAE								
Carissa edulis	r, un	100						
BIGNONIACEAE								
Kigelia africana	r, un, f	100						
BOMBACEAE								
Adasonia digitata	un, f		100					
CAESALPINIACEAE								
Guibourtia coleosperma	un, r					100		
CLUSIACEAE								
Garcinia livingstonia	r, un	96				4		
COMBRETACEAE								
Combretum hereroense	r, i	12	82	5	1			
Combretum imberbe	r, f		74	9	15	3		
Combretum mossambicense	r, f	63	37					
Terminalia sericea	r, i					92		8
EBENACEAE								
Diospyros mespiliformis	r, un	96	4					
Diospyros lycoides	r, un			89	2	9		
EUPHORBIACEAE								
Croton megalobotrys	-	50	48			2		
LEGUMINOSAE								
Acacia erioloba	r, un, f				1		3	96
Acacia hebeclada	r, un, f		100					
Acacia nigrescens	r, un, f	5	92	1	1			1
Acacia tortilis	r, un, f				100			
Burkea africana	r				6	94		1
Colophospermum mopane	r, i		1	1	93	3		2
Lonchocarpus capassa	r	1	76	2	21			
Lonchocarpus nelsii	r			10	1		79	10
MORACEAE								
Ficus burkei (thonningii)	p, fr, i	53	47					
Ficus sycamorus	p, fr, i	100						
RHAMNACEAE								
Berchemia discolor	r, un, fr	96		4				
Ziziphus mucronata	r, un, fr		100					

TABLE 3. *No. of feeding bouts per month in each forest habitat type at Vundumtiki and Mombo (numbers). Consumer specificity (CSi) values are the proportion of the total number of feeding bouts consumed in a specific habitat type in a specific month (key and shading).*

	VUNDUMTIKI											
Forest habitat	Aug-04	Sep-04	Oct-04	Nov-04	Dec-04	Jan-05	Feb-05	Mar-05	Apr-05	May-05	Jun-05	Jul-05
Riverine forest	163	174	167	186	128	74	83	87	74	60	36	81
Acacia-Combretum woodland	49	23	27	5	52	29	29	18	14	81	104	69
Dry Mopane woodland	2	27		4			27	39	41	4		
D. lycoides woodland	4	3	3	11	9	47	50	25			4	9
L. nelsii sadnveld			11				12	10	5	7	22	25
T. sericea sandveld				2				16	69	63	21	12
P. reclinata thicket									10			
A. erioloba sandveld					6	22	11	17				
F. verruculosa thicket									4		6	

	MOMBO						**VUNDUMTIKI**					
Habitat	Aug-05	Sep-05	Oct-05	Nov-05	Dec-05	Jan-06	Feb-07	Mar-07	Apr-07	May-07	Jun-07	Jul-07
Riverine forest	195	207	201	126	148	68	82	46	52	50	48	82
Acacia-Combretum woodland	51	9	15	38	30	52	30	49	19	35	132	74
Dry Mopane woodland							18	45	75	69		13
D. lycoides woodland	2	27		23	23	46	38	37	0	2	2	5
L. nelsii sadnveld							4	6	4	7	20	18
T. sericea sandveld								13	26	36	7	
P. reclinata thicket						37						
A. erioloba sandveld							8	2	2			
F. verruculosa thicket												
A. tortilis sandveld	19			33	21	17						
H. petersiana woodland			9	20								

Monthly consumer specificity index (CS*i*) values

0–0.1	0.1– 0.25	0.25–0.5	0.5–0.75	0.75–1

HABITAT PREFERENCES.– Habitat preferences were distinctly seasonal at Mombo and Vundumtiki, whereby 72–89% of feeding bouts were observed in riverine forest between August and November at Vundumtiki and Mombo, after which activity extended into *Acacia-Combretum* marginal woodland, *Terminalia sericea* sandveld and dry Mopane woodland (Table 3). Consumer specificity was highest in riverine forest and *Acacia-Combretum* woodland (Table 3). There was no significant difference between recorded habitat preferences between Vundumtiki and Mombo over the period August to January (Mann-Whitney U-test: U = 59.0, Z = -0.098, p = 0.922). There was also no significant difference between habitat preferences at Vundumtiki in 2005 and 2007 (Mann-Whitney U-test: U = 56.0, Z = 0.295, p = 0.768).

Over 70% (n = 3571) of all feeding bouts was over 20 m above the ground in the high canopy. Only 8% (n = 422) of all feeding activity was between 10-20 m above the ground. Feeding activity below 10 m was only observed between December and July, accounting for 21% (n = 1055) of total feeding bouts (Figure 4).

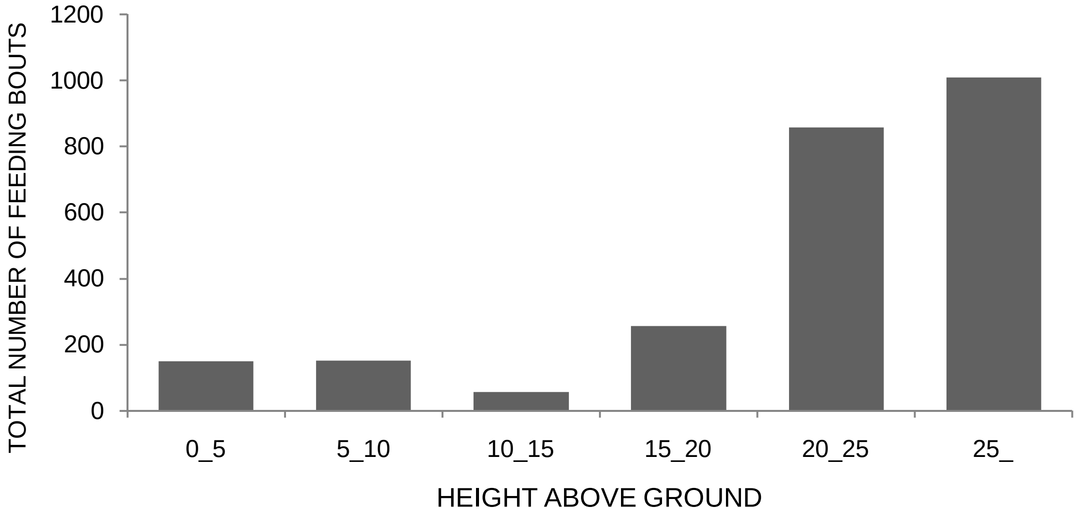

FIGURE 4. *Total number of feeding bouts observed in the different foraging heights classes at Vundumtiki and Mombo over 24 months*

HABITAT NICHE METRICS.– There were two distinct periods of habitat niche metrics, whereby there was a period of niche specialization between August and December (i.e. β_i remained below 0.5) followed by a period of more general habitat use between February and July during the primary breeding season (Figure 5).

The results of the simulated removal of all forested habitat types at Vundumtiki are presented in Table 4.

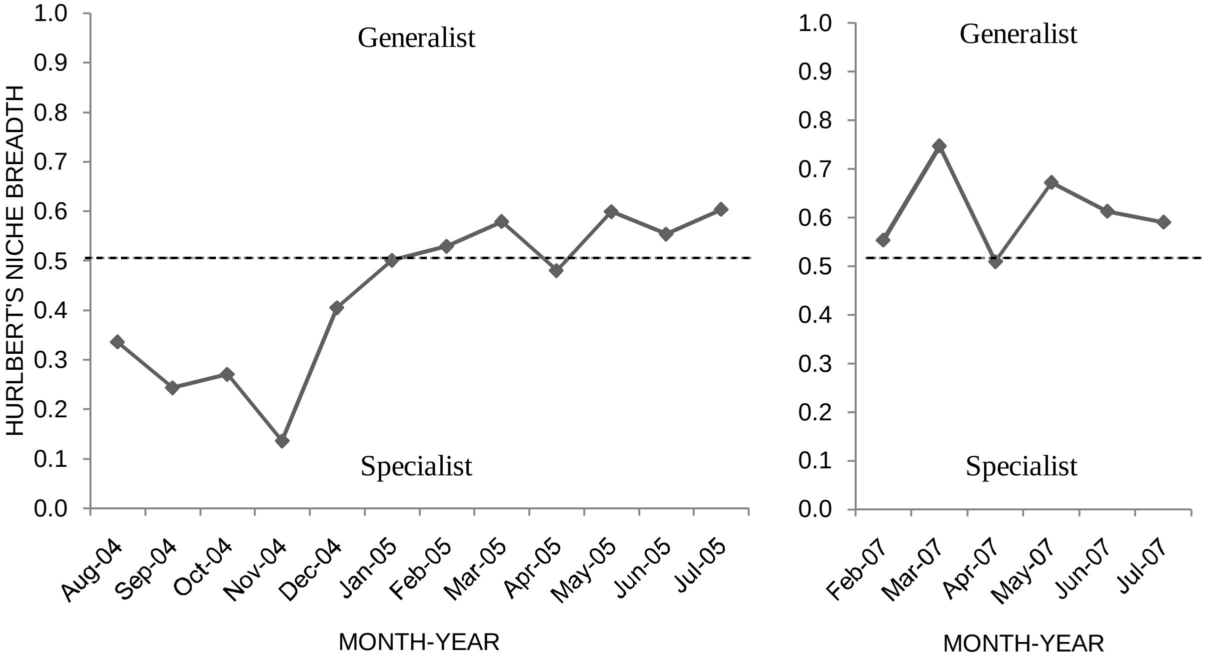

FIGURE 5. *Modified Hurlbert's standardized and expanded niche breadth index for habitat preferences at Vundumtiki. Where: 0 = perfect specialist utilizing one food resource; and 1 = perfect generalist with no pre-determined food item preferences (i.e. utilizes all food resources according to their abundance).*

TABLE 4. *Percentage dietary intake lost due to removal of habitat type from resource matrix at Vundumtiki.*

Forest habitat Type	Aug-04	Sep-04	Oct-04	Nov-04	Dec-04	Jan-05	Feb-05	Mar-05	Apr-05	May-05	Jun-05	Jul-05
Riverine forest	70	80	80	84	64	35	36	24	24	16	25	46
Acacia-Combretum woodland	27	8	13	16	28	27	30	33	22	40	42	28
Diospyros lycoides woodland	2	0	1	0	4	25	12	13	1	1	4	2
Dry Mopane woodland	2	12	0	0	0	0	13	10	18	10	7	5
Terminalia sericea sandveld	0	0	0	0	1	1	2	12	32	30	22	19
Lonchocarpus nelsii sandveld	0	0	4	0	0	0	2	0	0	0	0	0
Acacia erioloba sandveld	0	0	0	0	3	12	4	8	3	2	0	0

Forest habitat Type	Feb-07	Mar-07	Apr-07	May-07	Jun-07	Jul-07
Riverine forest	33	23	16	25	20	41
Acacia-Combretum woodland	19	22	41	47	41	35
Diospyros lycoides woodland	32	22	1	2	3	3
Dry Mopane woodland	10	22	23	6	6	12
Terminalia sericea sandveld	0	10	16	20	30	10
Lonchocarpus nelsii sandveld	1	0	0	0	0	0
Acacia erioloba sandveld	4	1	2	1	0	0

DISCUSSION

HABITAT ASSOCIATIONS.– Our study demonstrated strong associations at the population level between Meyer's Parrots and established riverine forest galleries and *Acacia*-*Combretum* woodlands (especially those dominated by Combretaceae trees). All *P. meyeri* subspecies studied thus far prefer broad-leaved, fleshy fruit-bearing riverine forest communities during summer, followed by a preference for associated pod-bearing dry savanna woodland communities (e.g. Combretaceae and Leguminsae trees) during winter (Tarboton 1980; Rowan 1983; Forshaw 1989; Wirminghaus 1997; Juniper & Parr 1998; Wilkinson 1998). Tarboton (1980) noted that *P. meyeri transvaalensis* preferred broad-leafed woodlands dominated by *Burkea africana*, *Ochna pulchra* and *Terminalia sericea* over microphyllous woodlands dominated by *Acacia* spp in the Limpopo Province, South Africa. Rowan (1983) and Wirminghaus (1997) reported that *P. meyeri damarensis* preferred either riverine forest communities along watercourses and/or associated dry woodland habitats. Elsewhere in their range: *P. meyeri meyeri* prefers riparian communities associated with *Tamarindus* and *Adansonia* along river valleys; *P. meyeri reichnowi* prefers dry *Terminalia laxiflora* and *Isoberlinia doka* woodlands; *P. meyeri matschiei* prefers riverine forest (e.g. *Syzigium-Adina* woodlands) and Miombo woodland (e.g. *Brachystegia* woodland); and *P. meyeri saturatus* prefer *Combretum* bushlands and *Acacia* grassland (Juniper & Parr 1998; Wilkinson 1998). Therefore, preference for riverine forest and associated dry subtropical hardwood woodlands (e.g. dry Acacia savanna and Miombo woodlands) are central to their biogeography (see *Implications for biogeography*).

Meyer's Parrots also demonstrated a distinct preference for multi-storey habitat structure (i.e. riverine forest, dry Mopane woodland and *Acacia*-*Combretum* woodland), thus foraging almost exclusively in the high canopy above 20m, only venturing below 5–10 m to feed on *D. lycoides lycoides* fruits between December and February. This preference could be as a result of anti-predatory behaviour, avoidance of inter-specific competition (e.g. Chacma baboon *Papio ursinus*) and/or visual assessment of food resource availability in the high canopy from the air (Chapter 4). All habitat associations noted by other authors can be explained by this preference for tall trees and high canopy. This relationship, however, is considered primarily due to the interrelationship of food item preferences, roosting behaviour (Chapter 8: Boyes & Perrin in review e), and social considerations (e.g. avoidance of predation risk and inter-specific competition).

Monthly habitat preferences were likely a function of food resource tracking by an opportunistic generalist feeder (Chapter 4), whereby Meyer's Parrots make optimal use of a wide variety of preferred food resources that seasonally become available in the different forest habitat types. Therefore, there was an innate bias in our study for habitat associations that support feeding requirements. Seasonal preference for riverine forest could, therefore, be exaggerated by the atypical fruiting of *Diospyros mespiliformis* at the end of winter and high availability of *Kigelia africana* flowers in September, which displace feeding activity from Combretaceae and Leguminosae pods in associated *Acacia-Combretum* woodland and *T. sericea sandveld* communities to riverine forest (Chapter 2). As a function of food resource tracking, habitat preferences were likely dependent on relative food resource abundance and resultant probability of encountering or locating that food resource within the habitat mosaic (Chapter 4). *Acacia-Combretum* woodland, however, had relative food resource abundance twice that of riverine forest and occupied an area of over three times that of riverine forest, thus indicating the functioning of food item and habitat preference systems beyond a generalist foraging model that targets the most abundant food resources. Potential factors contributing to the demonstrated preferences likely include bi-coloured fruit displays in the high canopy (Chapter 4), multi-storey habitat structure, and breeding seasonality (Chapter 9).

The habitat mosaics, rainfall and flood regime were significantly different at Vundumtiki and Mombo, whereby these study sites only shared four out of eleven forest habitat types, rainfall recorded at Mombo was almost double that at Vundumtiki, and flood seasonality was a month earlier and significantly higher at Mombo (Chapter 2). *Acacia tortilis* at Mombo replaces *Colophospermum mopane* and *Lonchocarpus nelsii* at Vundumtiki, and there were nine food items consumed exclusively at Vundumtiki and seven at Mombo (Chapter 2). Sighting frequency and mean group size were also significantly higher at Mombo (Chapter 7; Chapter 8). Therefore, we expected habitat preferences to be significantly different. There were, however, no significant differences in habitat preferences at Vundumtiki and Mombo or between 2005 and 2007, demonstrating that Meyer's Parrots have a high tenacity for riverine forest and *Acacia-Combretum* marginal woodland. This supports the assumptions of behavioural coherence within a species, whereby preferences of individuals within a species are consistent across context (Schuck-Paim & Kacelnik 2002). Meyer's Parrots are also dependent on riverine forest, *Acacia-Combretum* woodland and dry Mopane woodland for nest cavities within the habitat mosaic (Chapter 10: Boyes and Perrin in review f). Our study, therefore, indicates that Meyer's Parrot habitat associations are the product of a pre-defined habitat preference system governed by food item preferences, nesting requirements and visual cues from the air. Habitat associations recorded during our study likely extend to Meyer's Parrots in other parts of the Okavango Delta, and possibly to other *P. m. damarensis* and *P. m. transvaalensis* populations.

KEYSTONE HABITAT RESOURCES.– According to the modified Hurlberts' expanded and standardized niche breadth index, Meyer's Parrots were habitat specialists between August and

December, after which preferences became more general due to increased foraging effort in *T. sericea* sandveld and dry Mopane woodland during the breeding season while prospecting for arthropod larvae incubating inside Combreatceae and Leguminosae pods (Chapter 9: Boyes & Perrin in review g). Riverine forest was the only habitat type with CS_i values consistently above 0.5 and seasonally over 0.75, thus indicating specialist habitat preferences. Consumer specificity alone is not an indicator of a keystone habitat type, as high resource redundancy, and low resource reliability and abundance could undermine this relationship, especially in the case of a food resource generalist such as Meyer's Parrot. Resource abundance was demonstrated to be significantly higher in riverine forest and *Acacia-Combretum* woodland, and due to no significant difference in habitat preferences between 2005 and 2007 the impact of resource reliability was insignificant. To evaluate resource redundancy we assessed the feasibility of Meyer's Parrot subsisting exclusively on food resources in less significant forest habitat types (e.g. *T. sericea* sandveld) than riverine forest and *Acacia-Combretum* woodland. The majority of the relative resource abundance of *Diospyros lycoides lycoides*, *L. nelsii*, *Acacia tortilis*, *Acacia erioloba*, *Burkea africana*, *Terminalia sericea* and *Guibourtia coleopserma* was distributed outside of riverine forest and *Acacia-Combretum* woodland communities. However, only *D. lycoides* and *T. sericea* accounted for more than 5% of total feeding activity and had resource abundance comparable to other important food resources (e.g. *K. africana*). Both of these food resources, however, were only available for three months of the year, while all major food resources (e.g. *C. imberbe*, *K. africana* and *D. mespiliformis*) were found within riverine forest and *Acacia-Combretum* woodland. There appear to be no forest habitat types, other than riverine forest and *Acacia-Combretum* woodland that can sustain the significant Meyer's Parrots population in the Okavango Delta. The simulated removal of riverine forest and *Acacia-Combretum* woodland from the habitat mosaic resulted in an 88 – 100% reduction in recorded dietary intake between August and December, and a 47–74% reduction for the rest of the year (Table 4). In the Okavango Delta, it is likely these forest habitat types are pivotal in the ecological success of Meyer's Parrots, however, whether or not either of these habitat types is keystone to the persistence of Meyer's Parrots in a specific area requires further study in an area that has been disturbed by conversion of land to agriculture or deforestation.

The period August to November when Meyer's Parrots are riverine forest specialists is the driest part of the year, thus making dry savanna woodlands less productive, while riverine forest communities along channels and floodplains remained productive due to floodwater and high groundwater. Meyer's Parrots maintain this specialist habitat association until January when Leguminosae and Combretaceae seeds become available and Meyer's Parrots undergo a dietary switch to facultative insectivory prior to the breeding season (Chapter 2; Chapter 9). Therefore, it is feasible that Meyer's Parrots specialize in riverine forest communities during periods of resource scarcity in associated dry savanna woodlands, and thus riverine forest communities could be considered more important than *Acacia-Combretum* woodlands.

Boyes and Perrin (Chapter 9) found that over 70% of nest cavities utilized by Meyer's Parrots and all of nest cavities that achieved fledging were located in *Acacia-Combretum* marginal woodland and riverine forest. All primary roost sites were also located in these two habitat types (Chapter 8). Therefore, riverine forest and *Acacia-Combretum* woodland are also important to the breeding effort, thus reinforcing the supposition that Meyer's Parrots should be considered to be habitat specialists, dependent, in the Okavango Delta, on these two habitat types. Understanding the distribution of river systems and associated tropical dry forest (e.g. *Combretum* bushland and *Acacia* shrubland) in subtropical Africa is thus central to the biogeography of the Meyer's Parrot and associated *Poicephalus* parrots.

IMPLICATIONS FOR BIOGEOGRAPHY.– Speciation of these three *Poicephalus* parrots and other forest specialists (e.g. woodpeckers) can be explained by the hypothesis of forest refugia (Diamond & Hamilton 1980; Crowe & Crowe 1982). It is likely that during climatic vicissitudes Meyer's Parrots remained in river valleys, Brown-headed Parrots in coastal forest refugia, and Rüppell's Parrots in a forest refuge in southern Angola identified by Crowe and Crowe (1982).

As dietary generalists, with a considerable bite force (Chapter 2) and a demonstrated ability to switch to a predominantly insectivorous diet, the Meyer's Parrot may be able to adjust to drastic changes in habitat composition for a short period of time. It is more likely, however, that such drastic changes would result in seasonal migrations in search of suitable habitat and departure from the area within a few seasons. This was observed in the Northern Province, South Africa, due to deforestation, persecution as a crop pest and conversion of land to agriculture (Rowan 1983).

The distributional ranges of Meyer's Parrots, Brown-headed Parrots and Rüppell's Parrots all correspond with the recognized distribution of savanna and tropical dry forest IUCN/SSC first-level habitat types in Africa (Magin & Chape 2004). Rüppell's Parrot has 13 tree species represented in its diet that correspond with the Meyer's parrot, including more of the dry and marginal woodland tree species (e.g. *A. erioloba*, *A. hebeclada* and *Grewia flava*) (Selman 2002). Whereas, the Brown-headed Parrot had ten tree species in common with the Meyer's Parrot, including more of the riverine and hardwood forest tree species (e.g. *S. birrea*, *D. mespiliformis* and *F. sycomorus*). This is reflected in the distributional ranges of these species, where Brown-headed Parrots are restricted to the moist coastal and lowveld regions (Rowan 1983; Taylor 2002) and Rüppell's Parrots are distributed in the dry woodland and thornveld of northern Namibia and south-western Angola (Juniper & Parr 1998; Selman *et al.* 2002). The preference of Meyer's Parrots for riverine forest and *Acacia*-*Combretum* woodland is supported by their distribution in the Okavango Delta, Linyanti Swamps, throughout the Kavango Basin, down the Zambezi valley, up along the Rift Valley system in associations with the great lakes, through the Upper Nile and the Sudd, and west as far as Lake Chad through the Sahel. Any range reduction up until recently has been the result of deforestation (e.g. Zambia) or higher aridity (e.g. Lake Chad) (Chapter 12: Boyes and Perrin in review h). Riverine forest communities along river systems within this habitat mosaic likely functions as natural "conservation corridors" facilitating gene flow and wandering during periods of resource scarcity. It is, therefore, likely this affinity for riverine forest habitat has facilitated the wide distribution of Meyer's Parrots in comparison with other *Poicephalus* parrots. In addition, it is also likely that Meyer's Parrot metapopulation, represented by the six subspecies are centered around watercourses, as can be seen in the distribution of *P. m. meyeri* and *P. m. saturatus* around the Sudd swamps (Sudan) and catchments in Uganda, *P. m. matschei* and *P. m. reichnowi* around Lake Victoria, Lake Tanganyika and Lake Malawi, and *P. m. damarensis* and *P. m. transvaalensis* along the Zambezi and Chobe valleys and within the Kavango Basin (Chapter 12).

IMPLICATIONS FOR CONSERVATION BIOLOGY.– Deforestation rates in African countries are twice that of the rest of the world, whereby the continent loses over 4 million hectares of forest cover every year (UNEP 2008). Logging, land conversion to agriculture and settlement, wildfires, cutting of firewood and charcoal, and civil unrest are the primary causes of African deforestation (Kelatwang and Garzuglia 2006). All of these are primarily driven by population growth, poverty and climate change (UNEP 2008). As a result twelve out of the eighteen Meyer's Parrot range states have undergone drastic loss of forest cover (UNEP 2008). Meyer's Parrots are cavity-nesting, forest habitat specialists in the Okavango Delta, and are likely dependent on similar old growth riverine forest and dry savanna or subtropical hardwood forest (e.g. *Brachystegia* woodland, Mopane woodland and *Acacia*-*Combretum* woodland) throughout their range. Due to their reliance on these forest communities for food resources, roosting sites and nest cavities, Meyer's Parrot are unlikely to persist in an area where these forest habitat types have been degraded. The affiliation between Meyer's Parrots and riverine forest communities is likely strong enough for us to infer population decline and range reduction due loss of these pivotal forest communities from the habitat mosaic.

Elephant damage, fires set by hunters and fisherman, and increased water consumption upstream due to agricultural developments in Angola and Namibia are the primary threats to forest communities in the Okavango Delta. Mosugelo *et al.* (2002) found that due to African Elephant

Loxodonta africana damage coverage of *Acacia-Combretum* woodland, riverine forest and dry Mopane woodland communities in the Chobe National Park decreased from 60% to 30% between 1962 and 1998, while shrubland vegetation increased from 5% to 33% over the same period. Riverine forest characterized by *D. mespiliformis* was found to gradually retreat from the riverfront (Mosugelo *et al.*, 2002), whereby what was a continuous area along the Chobe River in 1962 was only represented by fragments in 1998. Herremans (1995) put forward that even dramatic vegetation changes in which elephants were involved are not necessarily irreparable ecological conditions, but rather part of a long-term vegetation oscillation between woodland and grassland, thus supporting species diversity on an extended time scale. Current range conditions for elephants have restricted their movements and eliminated opportunity for emigration, resulting in local population densities detrimental to the concurrent phase of vegetation. The continued increase of elephant populations in northern Botswana at between 3–7% annually resulted in a population of over 123 000 in 2003 (Chase & Griffin 2003). Findings from this study indicate that continued elephant damage to riverine forest and *Acacia-Combretum* marginal woodland communities will likely have an effect on roosting behaviour (Chapter 8), local movements (Chapter 2; Chapter 7), breeding biology (Chapter 9), and feeding behaviour (Chapter 2) of Meyer's Parrots. Meyer's Parrots are likely to benefit from elephant disturbance at "natural" or even moderately-elevated levels due to the resultant increase in nest cavity availability, however, as soon as forest gaps begin to evolve and forest structure begins to change, then Meyer's Parrots are expected to be detrimentally affected by this disturbance. At present levels, Meyer's Parrots are likely being adversely affected by elephant disturbance in Chobe, but likely are benefiting from this disturbance in the Okavango Delta (Chapter 10).

FURTHER RESEARCH.– Further research is required on the habitat associations of other Poicephalus parrots to better understand their distributional ranges and vulnerability to habitat loss. In addition, the ability of Meyer's Parrots to persist in a recently disturbed habitat mosaic needs to be evaluated in order to calibrate threats due to deforestation and forest management policies (e.g. sustainable removal of large hardwoods from subtropical forests may have an impact Meyer's Parrot populations)

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Chapter 4:

Temporal food resource abundance tracking by Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana[1]

Meyer's Parrots *Poicephalus meyeri* were found to track temporal food resource abundance of all significant food resources in their diet. Feeding activity on food resources available throughout the year (e.g. ripe *Kigelia africana* fruit) or not visible from the air (e.g. unripe *Diospryos lycoides lycoides* fruit), however, did not correlate significantly with temporal food resource abundance fluctuations. We monitored feeding activity 100m either side of a 26.2 km standardized road transect over 18 months in the Okavango Delta, Botswana. An index of relative resource abundance (RRA_i) was derived from the diameter at breast height and visual assessment of fruit or flower production. We estimated relative resource abundance using 19 (300 x 20 m) line transects stratified according to seven forest habitat types. Using diameter at breast height and a subjective fruit productivity index, RRAi was estimated once a month to measure temporal resource abundance fluctuations for correlation with total monthly feeding activity on specific food resources. Tracking resource abundance of food items visible from the air at landscape scale indicates that minimization of foraging flight distance to maximize net gain per unit foraging time is an important consideration in optimal foraging theory. Aerial habitat assessment, prior knowledge of food resources distribution and lingual feeding (i.e. constant vocalizations during feeding) likely facilitate habitat-wide food resource abundance tracking over time.

Little is known about the relationship between African parrots and food resources (Perrin *et al.* 2002), however, it may be predicted that seed predators such as parrots track food resource availability to exploit temporal and spatial fluctuations in fruit, pod and flower production (Gautier-Hion & Michaloud 1989; Galetti 1993, Renton 2001, Robinet *et al.* 2003). Based on dietary studies of African parrots in the wild there is clear evidence that all four continental genera track resource availability within specialist or

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[1] Formatted for *Ibis* – International Journal of Avian Science, British Ornithologists' Union, Edward Grey Institute, Department of Zoology, University of Oxford: Boyes, R.S. and Perrin, M.R. (in press). Food resource abundance tracking by Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. *Ibis*.

generalist food item preference systems (Wirminghaus *et al.* 2001, Selman *et al.* 2002, Symes & Perrin 2003; Warburton & Perrin 2005; Taylor & Perrin 2006; Nditkia & Perrin 2007; Chapter 2: Boyes & Perrin in review a).

Presence of African Grey Parrots *Psittacus erithacus* in Kanyawara, western Uganda, corresponded closely with the fruiting period of *Pseudospondias microcarpa* (Chapman *et al.* 1993). Similarly, Grey-headed Parrots *Poicephalus fuscicollis suahelicus* were attracted to areas with a high abundance of *Parinari curatellifolia*, thus seeming to track availability of this preferred food item (Symes & Perrin 2003). Cape Parrots *Poicephalus robustus* are specialist feeders that consume different food items at different times of the year, suggesting that they track changes in food availability (Koen 1992; Wirminghaus *et al.* 2001). Ruppell's Parrots *Poicephalus rueppellii*, Brown-headed Parrots *Poicephalus cryptoxanthus* and Meyer's Parrots *Poicephalus meyeri*, however, have distinctly seasonal diets that function within a generalist food item preference system (Selman *et al.* 2002, Taylor & Perrin 2006; Chapter 2), and therefore, likely to track seasonal availability within a wide range of food items. Our study tested the hypothesis that Meyer's Parrots are resource abundance tracking pre-dispersal seed predators that make dietary choices according to the probability of encountering edible seeds of a particular food species within a generalist food item preference system.

Meyer's Parrots *Poicephalus meyeri* have the widest distributional range of any African parrot, exceeding that of the Rose-ringed Parakeet *Psittacula krameri* and Red-faced Lovebird *Agapornis pullarius* (Snow 1978, Juniper & Parr 1998). They also have the widest trophic niche of any *Poicephalus* parrot studied thus far (Chapter 5: Boyes & Perrin in review b). This opportunistic generalist food item preference system is facilitated by unrestricted, exclusive access to seeds from woody pods (e.g. Leguminosae and Combretaceae pods) and fleshy fruits (e.g. *Schlerocarya birrea*), flowers, and arthropod larvae (Chapter 2). As opportunistic generalists, there were no food resources considered keystone to their ecological success (Chapter 2). The most important tree species in their diet included (in order of magnitude): *Kigelia africana*, *Diospyros mespiliformis*, *Combretum imberbe*, *Ficus sycomorus*, *Diospyros lycoides lycoides*, *Combretum hereroense* and *Berchemia discolor* (Chapter 2).

Optimal foraging theory predicts that foragers should prefer prey that yields higher net energy gain per unit foraging time (Rakotomanana & Hino 1998, Sih & Christensen 2001). Therefore, food item preferences are presumably dependent on behaviour, morphology and nutritional requirements, in relation to fruiting and flowering phenology, distribution and temporal availability, and fruit characteristics such as size, hardness, taste, colour and nutritional value (Wheelwright 1985). For a particular species at a specific point in time and space, food item preferences should thus be governed by resource abundance and fruit characteristics.

Most studies of the food item preferences of frugivores and seed predators focus on fruit characteristics, including taste (Sorensen 1983), nutritional value (Johnson *et al.* 1985), colour (Willson *et al.* 1990), seed clutch size (Hegde *et al.* 1991), hardness (Dumont 1999), and fruit size (Mello *et al.* 2005). Our study inferred the influence of structural fruit characteristics (e.g. hardness, size and seed clutch size) from the mean rate of protein and energy acquisition during feeding based on handling time and nutritional value of a specific food resource. Our study tested the hypothesis that, due to unrestricted access to most food resources (Chapter 2) and the high costs of flight (Chapter 7: Boyes & Perrin in review c), structural fruit characteristics (e.g. hardness and difficulty to open) are insignificant in the food item preference system of Meyer's Parrot. The importance of bi-coloured displays as beacons was, however, investigated further.

Fruits with bi-coloured displays (i.e. the fruit or part of the fruit is one colour (e.g. red or yellow) and the adjacent structure (e.g. leaf or peduncle) is a contrasting colour (e.g. green)) are typically eaten by birds (Wheelwright & Janson 1985; Willson & Whelan 1990; Wenny 2003; Whitney 2005). Birds have very high visual acuity and well-developed colour vision (Arruda *et al.* 2008) and probably use colour to locate fruit (Wheelwright & Janson 1985) and measure fruit quality (Greg-Smith 1986; Wenny 2003). The contrast hypothesis predicts that frugivores select fruit colours according to the degree to which they contrast with their background (Arruda *et al.* 2008). For example, red fruit has a higher removal rate when displayed against background foliage (Burns & Dalen 2002; Schmidt *et al.* 2004). Our study classified fruit colours according to a fruit colour wheel derived from the Crystal Real Color Wheel developed by Jusko (2008). Here we evaluated the importance of bi-coloured fruit displays in the location of food resources by Meyer's Parrots.

Most studies of tropical fruiting phenology report seasonality, especially in forests with distinct wet and dry seasons (Bullock & Solis-Magallanes 1990, Chapman *et al.* 1992, Chapman *et al.* 1994, Murali & Sukumar 1994, Renton 2001, Wirminghaus *et al.* 2001, Komonen *et al.* 2004). All plants compete for effective dispersal of their seeds, and thus some fruit-bearing plants compete for predation by birds, while most pod-bearing plants typically avoid avian predation and focus on other forms of dispersal (e.g. wind-blown and epizoochory) (Snow 1965). This often produces staggered fruiting seasons that provide a year-round food resource to frugivores and seed predators, together with effective dispersal for the widest range of plant species (Stutchbury & Morton 2001; Wirminghaus *et al.* 2001). We estimated food resource abundance fluctuations at landscape level for correlation with observed feeding activity of Meyer's Parrots at population level. Our study, therefore, tested the hypothesis that Meyer's Parrots track food resource abundance of each significant tree species in their diet.

METHODS

Study area

The Okavango Delta was chosen as the study site because of its significant Meyer's Parrot population (Wirminghaus 1997). The study was conducted at Vundumtiki Island located on the junction of the Maunachira and Kiankiandavu channels in the north-eastern part of the alluvial fan (19°00'S, 22°59'E; 995m asl) (Figure 1).

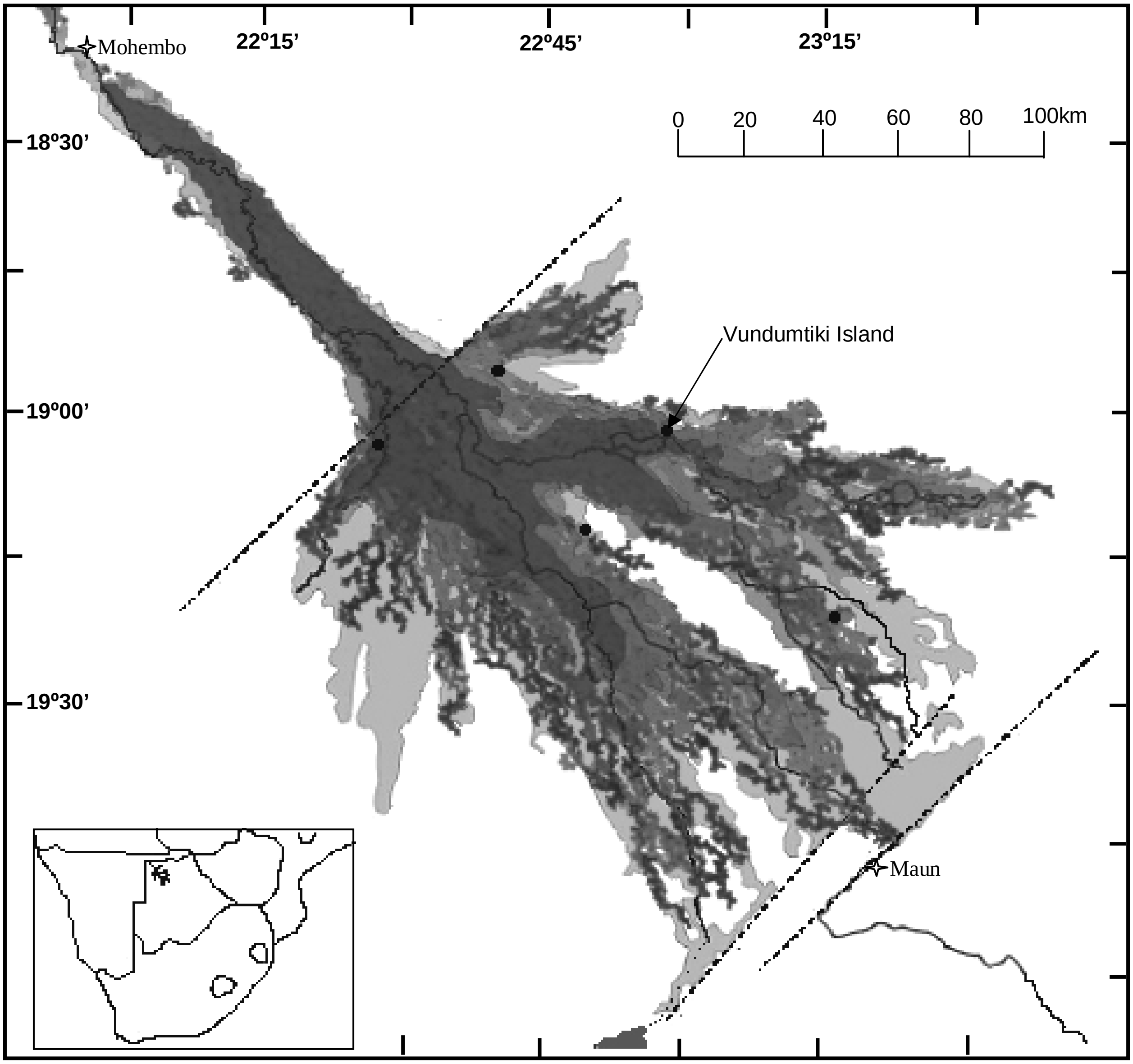

Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

Seven primary habitat types were identified for the Vundumtiki study area (Chapter 3: Boyes & Perrin in review a), including: Riverine forest (dominated by *Diospyros mespiliformis*, *Garcinia livingstonia*, *Berchemia discolor*, *Ficus sycamorus* and *Kigelia africana*); *Acacia nigrescens*-*Combretum* marginal woodland (dominated by *A. nigrescens*, *Combretum imberbe* and *C. hereroense*); Mopane woodland (dominated by *Colophospermum mopane*); *Diospyros lycoides* marginal woodland (almost homogenous *Diospyros lycoides*); *Lonchocarpus nelsii* sandveld (almost homogenous *Lonchocarpus nelsii*); *Acacia erioloba* sandveld (dominated by *Acacia erioloba*); and *Terminalia sericea* sandveld (dominated by *T. sericea*, *T. prunoides* and *L. nelsii*). Habitat descriptions followed Ellery and Ellery (1997), Roodt (1998) and Ellery *et al*. (2000).

Climatic conditions

Climatic conditions in the Okavango Delta are distinctly seasonal, comprising a wet season (November-March) and dry season (April–October). Mean annual rainfall is 450–560mm (Ellery *et al.* 2003; Wolski and Savenije 2006). During the annual flood the area covered by water expands from its annual low of 2500–4000km^2 in February-March to its annual high of 6000–12000km^2 in August–September. Arrival of the annual flood lags the rainy season and follows one or two months after the end of rainfall in the region (Gumbricht *et al.* 2001; Ellery *et al*. 2003).

Rainfall was monitored daily using a rain gauge at the study site over the entire study period. The extent and timing of the annual flood was monitored using flow rate data from Mohembo and calibrated to the study sites by recording first significant increment in water level on a measuring pole in permanent water as the start of the flood at that study site.

Fruit characteristics

Fruit size and colour were recorded for all food items in the diet of Meyer's Parrot during feeding observations using a sample of 20 fruits, pods or flower species. Fruit colour was classified according to a fruit colour wheel adapted from the Crystal Real Color Wheel developed by Jusko (2008). The colour spectrum from green to magenta was included in the analysis, whereby green was given a value of 0 and magenta a value of 180 (Figure 2). White, blue, purple and magenta were given the value of 180 due to being the most contrasting to green. This system, therefore, measured the degree to which a fruit contrasts with green and the significance of the bi-colour display. Each of the food items were matched to its corresponding colour on the fruit colour wheel and scored accordingly. These colour scores were then multiplied by the total feeding bouts over 12 months for each food item to determine the mean colour score from the relative frequency of colour preferences by Meyer's Parrots at the population level.

The impact of fruit size and hardness on the ability of Meyer's Parrots to procure was protein and energy were inferred from mean protein and energy acquisition rates based on mean fruit consumption rate and nutritional value of as many food items as possible. Fruit consumption rates were estimated from direct observations in the field (Chapter 6: Boyes & Perrin in review d; Chapter 7). Nutritional analyses of the different food items were done by Selman *et al.* (2002), Taylor (2002), Symes and Perrin (2003), and Ndithia and Perrin (2006) using standardized methods (Helrich 1990). Dry weight was obtained from samples (n = 20) of seeds taken from the study site.

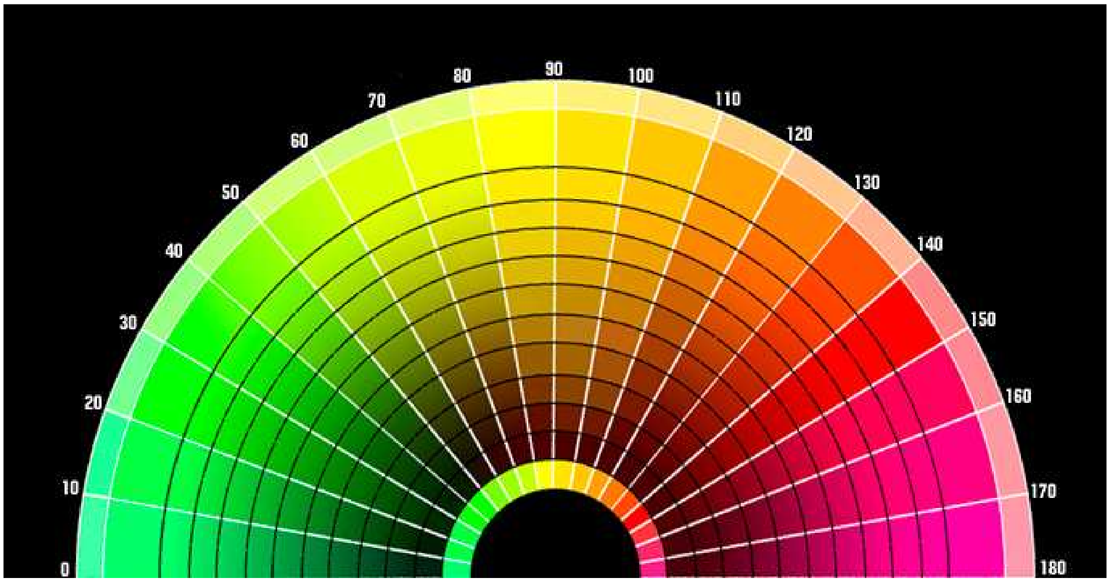

Figure 2. Fruit colour wheel using Crystal Real Color Wheel developed by Jusko (2008)

Food item preferences

Feeding observations were conducted from August 2004 to July 2005 and February 2007 to August 2007. To standardize spatial distribution of Meyer's Parrot feeding observations, the total sample area was defined as the area 100m either side of the 26.2 km standardized road transect. The same observer and vehicle travelling at 15–20 km/h with an open top were used for all road transects. Road transects were conducted five times a week on different days from start to finish. A systematic sampling strategy was used for the temporal distribution of feeding observations, whereby six daytime time periods were established (i.e. 06h00-08h30; 08h30-11h00; 11h00-13h30; 13h30-16h00; 16h00-18h30; and 18h30 to sunset) (Chapter 7). Road transects were conducted in all six time periods before a specific time period was sampled again.

Feeding activity was recorded using direct observations in the field. The following data were recorded: height above ground, tree species, food item type and number of feeding bouts. A feeding bout was defined as an individual within a flock, or solitary, feeding on a specific food item at a specific sighting. A food item was defined as any plant food eaten by Meyer's Parrots described according to tree species and food item type. Food item types were classified according to the part consumed and fruiting stage, and included: ripe (r) and unripe (un) seeds from fruits or pods; flowers (f); pseudocarp and seeds of figs (p); and fruit pulp from fleshy fruits (fr). Arthropod food items were classified according to the host tree species and their family, and included: parasitic Hemiptera larvae (h); parasitic Lepidoptera caterpillars (l); and parasitic Coleopteran larvae (c). Arthropod food items were identified by inspecting all potentially-infested dietary (e.g. pods and fruits) and non-dietary (e.g. bark and leaves) food items consumed or inspected by Meyer's Parrots over the study period. Tree nomenclature followed Van Wyk and Van Wyk (1997) and Palgrave (2002). Acronyms and food items are listed in Table 1.

Resource assessment

Total habitat area of each forest habitat type within the sample area was estimated by measuring the distance along the standardized road transect line corresponding to the different forest habitat types up to 100m either side of the road. Nineteen (300m x 20m) resource abundance line transects were established within the sample area. We used a stratified sampling design within which three resource abundance line transects were dispersed in each forest habitat type to obtain a representative sample of resource availability (Chapter 3: Boyes & Perrin in review e). Due to homogeneity and high stand density of *Lonchocarpus nelsii* sandveld only one transect was done in this forest habitat type. For the estimation of habitat-wide resource abundance, a habitat conversion factor (HCF) was calculated by dividing the total forest habitat area within the sample area by the total area of resource abundance line transects in each forest habitat type.

Each of the 19 resource abundance line transects were mapped and each transect line maintained using a Garmin Quest GPS (Garmin 2006). Chapman *et al.* (1992) found that diameter at breast height (DBH) predicted fruit number and biomass the best for several methods evaluated. DBH was measured for all trees over 100 mm in diameter using a large caliper and was used as a correlate of fruit crop abundance (Renton 2001). We marked with spray paint and hazard tape, numbered and recorded DBH and tree species once-off for all trees on the resource abundance line transects. To obtain a temporal scale of relative resource abundance, we visually assessed fruit production of each of these trees using a crown score (CS_i) in the first two weeks of each month between August 2004 and July 2005, and February 2007 and July 2007. CS_i was scored in increments of 0.2 between 0 and 1, whereby 0 represented no fruit or flower production and 1 represented the full canopy producing fruit or flowers. Ripe and unripe fruits could be present on the same tree. The observer was standardized for all transects and once-off subjective measurements to maximize repeatability and precision (Chapman *et al.* 1994, Casagrande & Beisssinger 1997).

We estimated the relative resource abundance of a specific tree (RRA_i) in a specific month using the following equation: $RRA_i = DBH_i*CS_i$. RRA_i for all trees of the same species on all three resource abundance transects in each habitat type were then summed to obtain transect-wide relative resource abundance for each tree species within each forest habitat type ($TW\text{-}RRA_i$). $TW\text{-}RRA_i$ was then multiplied by the HCF to obtain an index of habitat-wide relative resource abundance for each tree species ($HW\text{-}RA_i$). Total relative resource abundance of a specific tree species (RRA_i) in a specific month was estimated by summing all the $HW\text{-}RA_i$ values. Therefore, we estimated total relative resource abundance for each tree species using the following equation:

$$\mathrm{RRA_i} = \sum_{j=1}^{7}\left\{\sum_{k=1}^{\infty}(\mathrm{DBH_k} \times \mathrm{CC_k}) \times \mathrm{HCF_j}\right\}$$

Where: i represents each food item; j represents each habitat type; and k represents each tree on the habitat transects.

We estimated standing relative abundance for a specific tree species ($S\text{-}RRA_i$) in the same way, except that CS_i was excluded from the equation used to estimate RRA_i. S-RRAi was a corollary of the potential productivity of a specific tree species in the study area.

Infestation rates of the different tree species were estimated weekly (n = 500) over the entire study period (Chapter 9: Boyes & Perrin in review f). These infestation levels were then multiplied by the RRAi for these tree species to obtain an estimate of relative resource abundance of each of the insect food items.

Food niche metrics

Degree of specialization in feeding activity on different food resources was evaluated by using Hurlbert’s standardized and expanded niche breadth index (β_i) (Hurlbert 1978, Renton 2001):

$$\beta_{\mathrm{i}} = \left[\frac{1}{\sum_{\mathrm{j}}\left(10000 \times \frac{\mathrm{N}_{ij}}{\sum_i d_j k \times \mathrm{N}_{ij}}\right)}\right]\left[\frac{1}{9999}\right]$$

Where: N_{ij} represents the number of feeding bouts associate with resource state j, and $d_j k$ is the proportion of the total resource abundance represented by resource state j expanded to k = 10 000. Niche breadth is the variance in resource use by a species, and can be estimated by measuring the uniformity of the distribution of conspecifics among resource states within the resource matrix (Colwell & Futuyma 1971). Our study determined niche breadth fluctuations month-to-month over the study period, and thus the resource matrix was modified to include different months as rows and different food items as resource states. Distribution within this “temporal habitat matrix” was measured as the total number of feeding bouts in a habitat type in a specific month along the standardized census route. Total relative resource abundance (T-RRA_i) should provide adequate information on the ecological distinctness of resource states (Colwell & Futuyma 1971). T-RRA_i was thus used in the weighted expansion of the resource matrix (k = 10000), thus accounting for error caused by nonlinearity and ecological inequality of spacing among resource states (Colwell & Futuyma 1971), allowing for the expansion (k = 10 000) of the temporal resource matrix. For β_i, a value close to 0 indicated food resource specialization, and a value tending to 1 indicated broader food resource preferences (Hurlbert 1978).

Data analyses

Spearman rank correlation (r_s) was used to evaluate the relationship between temporal food resource abundance and observed feeding activity and monthly rainfall. Wilcoxon Matched Pair Test was used to look for significant difference in temporal resource abundance over the study period. Statistical analysis followed Quinn & Keough (2002) and STATISTICA 7.1 (Statsoft 2006).

RESULTS

Fruit characteristics

There was no correlation between mean protein consumption rate and feeding activity (n = 16; $r_s = -0.306$, $t(n-2) = -1.20$, $p = 0.249$) or mean energy consumption rate and feeding activity on specific food items (n = 11; $r_s = -0.174$, $t(n-2) = -0.53$, $p = 0.610$).

Fruit characteristics are listed in Appendix I. Green fruits accounted for 29% (n = 597) of the feeding bouts recorded between August 2004 and July 2005, followed by yellow (22%; n = 459), red (18%; n = 385), brown (15%; n = 320), purple (11%; n = 235), orange (3%; n = 73) and white (1%; n= 17). The mean fruit colour score was 95.45 (Figure 2; Appendix I).

Environmental and resource relationships

Rainfall and flood seasonality was significantly different between the 2004-2005 and 2006-2007 field seasons (Figure 3). Arrival of the flood coincided with the dry season and was calibrated at 59 days lag time after entrance of water at Mohembo (Figure 3). There was a significant positive correlation between monthly rainfall and cumulative resource abundance for all tree species ($n = 18$, $r_s = 0.474$, $t(n-2) = 2.15$, $p = 0.047$), whereby food resource availability was significantly higher during the wet season (Figure 3). Conversely, there was a significant negative correlation between mean monthly flow rate of floodwater and cumulative resource abundance for all tree species ($n = 18$, $r_s = -0.650$, $t(n-2) = -3.418$, $p = 0.004$) (Figure 3). The influence of flood seasonality on temporal resource abundance was insignificant beyond correlating with the cessation of rainfall and a period of relative food resource scarcity.

Temporal resource abundance of different food item types was distinctly seasonal (Figure 4). Without the Bonferonni procedure for multiple testing, there was a significant positive correlation between Meyer's Parrot feeding activity and all flowers in their diet (Table 1).

Resource abundance of different food item types was significantly lower in 2007 compared with 2005 (Wilcoxon Matched Pairs Test: $n = 36$; $T = 6.0$; $Z = 4.984$; $p < 0.001$) (Figure 4). Monthly resource abundance was significantly different for all food item types (Kruskal-Wallis test: $H (5, n = 108) = 38.93$, $p < 0.001$). There were significant positive correlations between monthly food resource abundance and monthly rainfall for ripe seeds from *Berchemia discolor*, *Garcinia livingstonia* and *Combretum imberbe*, and unripe seeds from *Diospyros mespiliformis* and *Lonchocarpus capassa.* There were significant positive correlations between monthly food resource abundance and total feeding bouts over 12 months for ripe seeds from *Diospyros lycoides lycoides*, *B. discolor*, *Schlerocarya birrea caffra*, and *Terminalia sericea*, unripe seeds from *D. mespiliformis*, *Kigelia africana*, *B. discolor*, *Acacia erioloba* and *Adansonia digitata*, figs from Ficus sycomorus, and flowers from *K. africana* and *Acacia nigrescens* (Table 1; Table 2).

Meyer's Parrots tracked the temporal resource abundance of flowers and arthropod larvae closer than any other food resource (Figure 5). The relative resource abundance of pods within their diet was largely ignored even though these were important food resources in the diet (Figure 5).

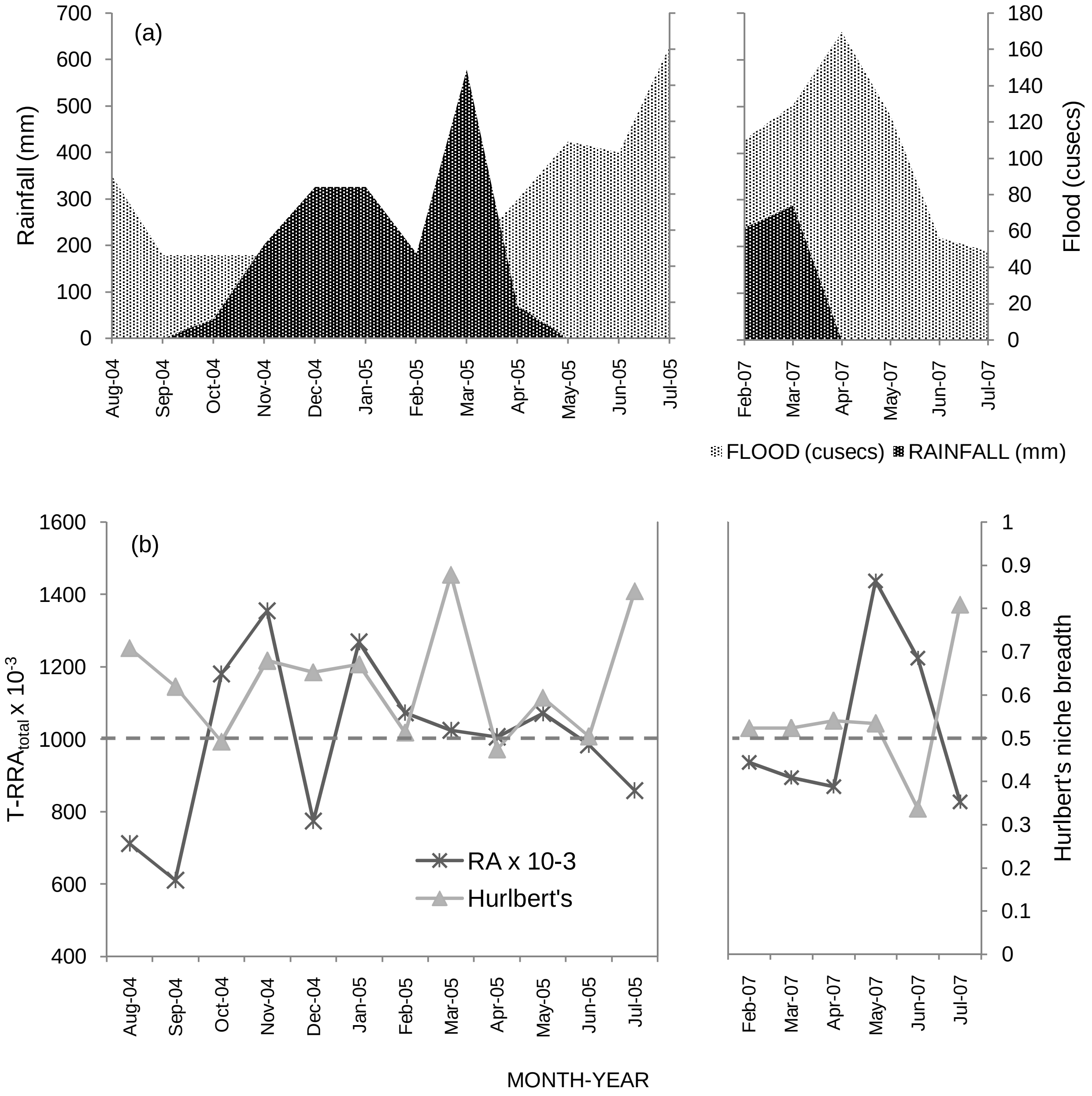

Figure 3: (a) Rainfall and flood seasonality at over the entire study period; (b) Hurlbert's expanded and standardized niche breadth (β_i) and T-RRA$_i$ of all food resources in sample area. For β_i, 0 = specialist; 1 = generalist.

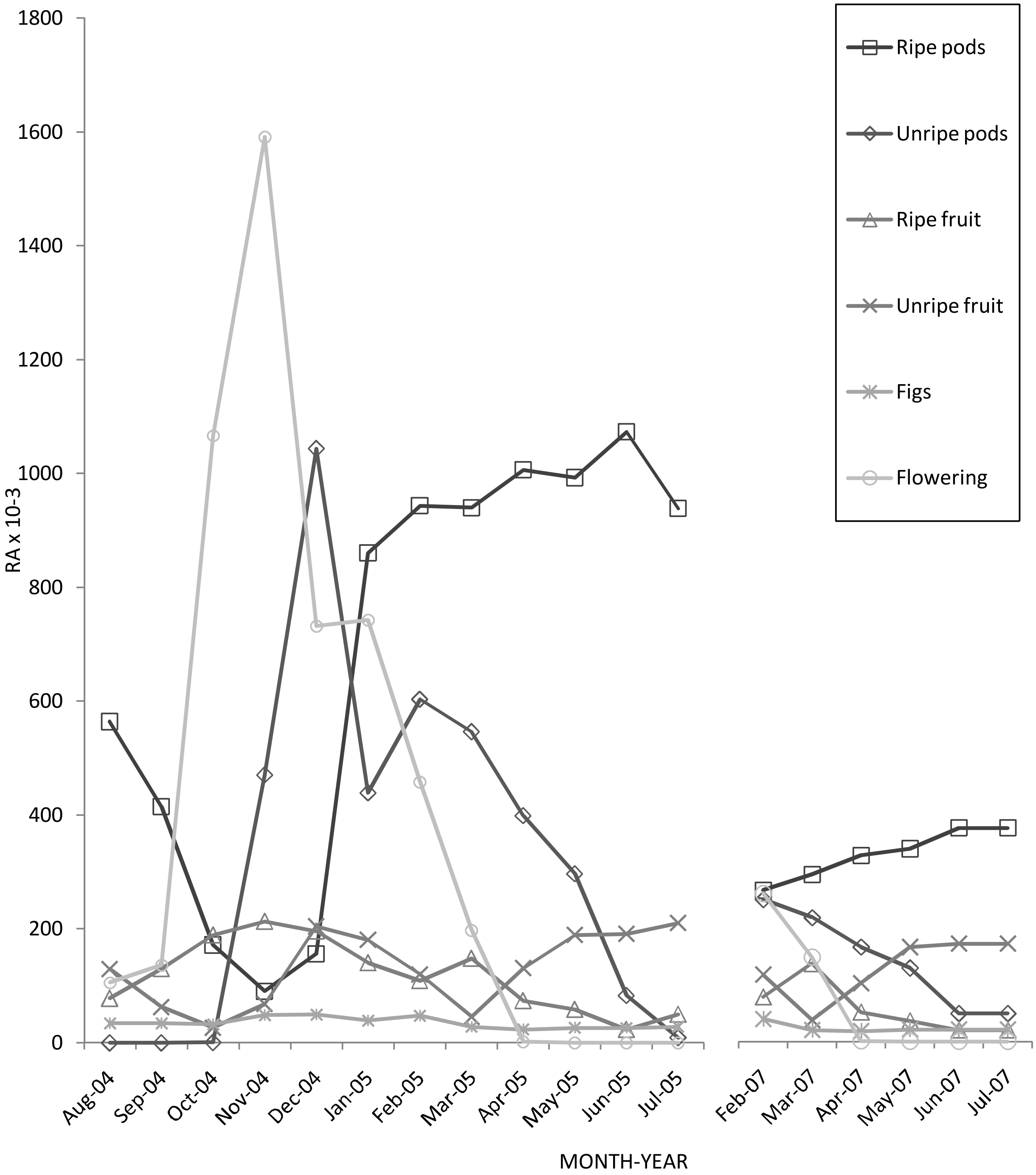

Figure 4: Total monthly relative resource abundance (T-RRA$_i$) of all plant food item types consumed by Meyer's Parrot at Vundumtiki

Table 1. Spearman's Rank correlations for total monthly relative resource abundance (RRA_i) and monthly rainfall, total feeding bouts and flood flow rate for all food item over 18 months (Significant at $p < 0.0012$ due to Bonferonni procedure for multiple testing). * indicates significance.

FAMILY	Species	Food item	r_s	t(N-2)	p-level
Ripe seeds from fleshy fruits					
BIGNONIACEAE	*Kigelia africana*	KAr	0.451	2.02	0.061
EBENACEAE	*Diospyros lycoides*	DLr	0.717	4.12	0.001*
EBENACEAE	*Diospyros mespiliformis*	DMr	0.514	2.4	0.001*
RHAMNACEAE	*Berchemia discolor*	BDr	0.749	4.53	<0.001*
CLUSIACEAE	*Garcinia livingstonia*	GLr	0.596	2.97	0.009
ANACARDIACEAE	*Sclerocarya birrea*	SBr	0.639	3.32	0.001*
MYRTACEAE	*Ziziphus mucronata*	ZMr	0.48	3.42	0.0432
APOCYNACEAE	*Carissa edulis*	CEr	0.998	67.88	<0.001*
Ripe seeds from woody pods					
COMBRETACEAE	*Combretum imberbe*	CIr	0.593	2.95	0.009
COMBRETACEAE	*Terminalia sericea*	TSr	0.809	5.51	<0.001*
LEGUMINOSAE	*Acacia nigrescens*	ANr	0.466	2.11	0.051
CAESALPINIACEAE	*Guibourtia coleosperma*	GCr	0.582	2.87	0.011
LEGUMINOSAE	*Lonchocarpus capassa*	LCr	0.439	1.96	0.068
LEGUMINOSAE	*Burkea africana*	BAr	0.397	1.73	0.103
LEGUMINOSAE	*Albizia harveyi*	AlHr	0.507	2.35	0.032
LEGUMINOSAE	*Acacia tortilis*	ATr	0.582	2.87	0.011
LEGUMINOSAE	*Lonchocarpus nelsii*	LNr	0.285	1.19	0.251
Unripe seeds from fleshy fruits					
EBENACEAE	*Diospyros mespiliformis*	DMun	0.681	3.72	0.001*
EBENACEAE	*Diospyros lycoides*	DLun	0.197	0.8	0.433
BIGNONIACEAE	*Kigelia Africana*	KAun	0.924	9.66	<0.001*
CLUSIACEAE	*Garcinia livingstonia*	GLun	0.54	2.56	0.021
RHAMNACEAE	*Berchemia discolor*	BDun	0.841	6.21	<0.001*
MYRTACEAE	*Ziziphus mucronata*	ZMun	0.52	2.44	0.027
Unripe seeds from woody pods					
LEGUMINOSAE	*Acacia erioloba*	AEun	0.806	5.44	<0.001*
BOMBACEAE	*Adasonia digitata*	ADun	0.841	6.21	<0.001*
LEGUMINOSAE	*Acacia nigrescens*	ANun	0.481	2.2	0.043
LEGUMINOSAE	*Burkea Africana*	BAun	0.407	1.83	0.083
LEGUMINOSAE	*Lonchocarpus capassa*	LCun	0.541	2.58	0.020
Fruit pulp only					
MYRTACEAE	*Syzigium guineense*	SGfr	-0.061	-0.25	0.809
Seeds and pseudocarp from Moraceae					
MORACEAE	*Ficus sycamorus*	FS	0.795	5.24	<0.001*
MORACEAE	*Ficus burkei (thonningii)*	FB	0.345	1.47	0.161
Nectar and pollen from flowers					
BIGNONIACEAE	*Kigelia Africana*	KAf	0.884	7.57	<0.001*
LEGUMINOSAE	*Acacia nigrescens*	ANf	0.8	5.34	<0.001*
BOMBACEAE	*Adasonia digitata*	ADf	0.642	3.35	0.001*
LEGUMINOSAE	*Acacia erioloba*	AEf	0.574	2.81	0.013
LEGUMINOSAE	*Lonchocarpus nelsii*	LNf	0.54	2.56	0.021
Insect larvae and products (e.g. exudate)					
COMBRETACEAE	*Combretum hereroense*	CHc	0.858	6.69	<0.001*
LEGUMINOSAE	*Colophospermum mopane*	CMl	0.655	3.46	0.001*
COMBRETACEAE	*Terminalia sericea*	TSc	0.996	45.21	<0.001*
EBENACEAE	*Sclerocarya birrea*	SBl	0.541	2.57	0.020
LEGUMINOSAE	*Colophospermum mopane*	CMh	0.985	23.09	<0.001*

Table 2. Total relative resource abundance (T-RRA$_i$ x 10^{-3}) (numbers) and % total monthly feeding bouts (shading & key) for all food resources represented in the diet of Meyer’s Parrot

FOOD ITEM	AUG04	SEP04	OCT04	NOV04	DEC04	JAN05	FEB05	MAR05	APR05	MAY05	JUN05	JUL05	FEB07	MAR07	APR07	MAY07	JUN07	JUL07
DMun	129	63	12	1					121	189	191	210			97	165	171	171
DMr	71	124	186	209	158	67	19	4				35	12	4				1
ANf	73	94	132	100														
KAf	24	24	15	3														
CM-Aa	2	1																2
FS	8	8	10	16	15	16	15	5	4	4	8	10	19	5	4	4	8	8
Clr	122	116	55	32	27	21	14	6	49	89	173	182	5	2	16	28	54	54
LNf			646	653	2													
KAun			6	22	23	18	2						2					
GLun				15	24	10												
FB	16	16	12	21	19	11	14	17	14	14	12	12	5	9	8	8	7	7
SGun			1	2	2	2	2	1				1	2	1	2			
DLun			9	17	120	118	102	30					105	29				
GLr					29	45	23	5	4				23	5	4			
BDun				2	6	3												
AEf			12	12	22	11	10						6					
ADf				49	25													
ADun					25	49	12											
ANun				72	121	129												
AEun					2	18	16	11					9	6	1	1		
BDr				1	1	6	5	3	2				5	3	2			
DLr						4	20	84	15	2	1		13	97	14	1		
ZMun					10	10												
LCun				73	79	85	68	47	5				20	14	1	1		
SGr						1	6	10	7	5			6	4	2			
ANr	48	30	9	1	6	7	139	126	90	81	81	74	43	38	29	27	27	27
BAun						13	13	6					10	4	1			27
CM-Ab							28	29	8	16				19	3	7	14	
LNr	150	84	44	24	22	577	427	356	352	350	268	182	87	75	71	74	59	14
KAr	7	7	3	3	6	14	26	25	25	23	15	15	26	25	25	23	15	15
ZMr							10	10	7	5				6	10	10	7	5
FV							3	3	2	2	1			3	3	2	2	1
SBr							7	8	12	22	6			2	6	10	3	3
PRr						5	5	6	5	3	2			1	2	6	1	
TSr						1	35	66	68	58	34	19	33	63	64	55	32	3
CH-A								77	72	44	42			25	23	14	13	
LCr	46	37	19	7	8	9	40	71	78	82	82	70	13	22	24	25	25	32
BAr									8	13	13	9	7		6	10	10	13
SB-A							6	6	10	19	5			2	5	9	3	25
TS-A									22	19	11				21	18	11	11
AlHr									1	1	1	1	1	1		1	1	3
ATr	1							5	9	7	5	2			4	4	4	11
TPr									7	5	9	7			5	9	7	5
DCr	8									7	5	2				7	5	2
GCr								5	5	6	11	11		5	5	6	10	
ATf				2	9													

% TOTAL FEEDING BOUTS

░	0 – 5%
▒	5 – 10%
▒	10 – 20%
▓	20 – 30%
▓	30 – 40%
█	40% ➔

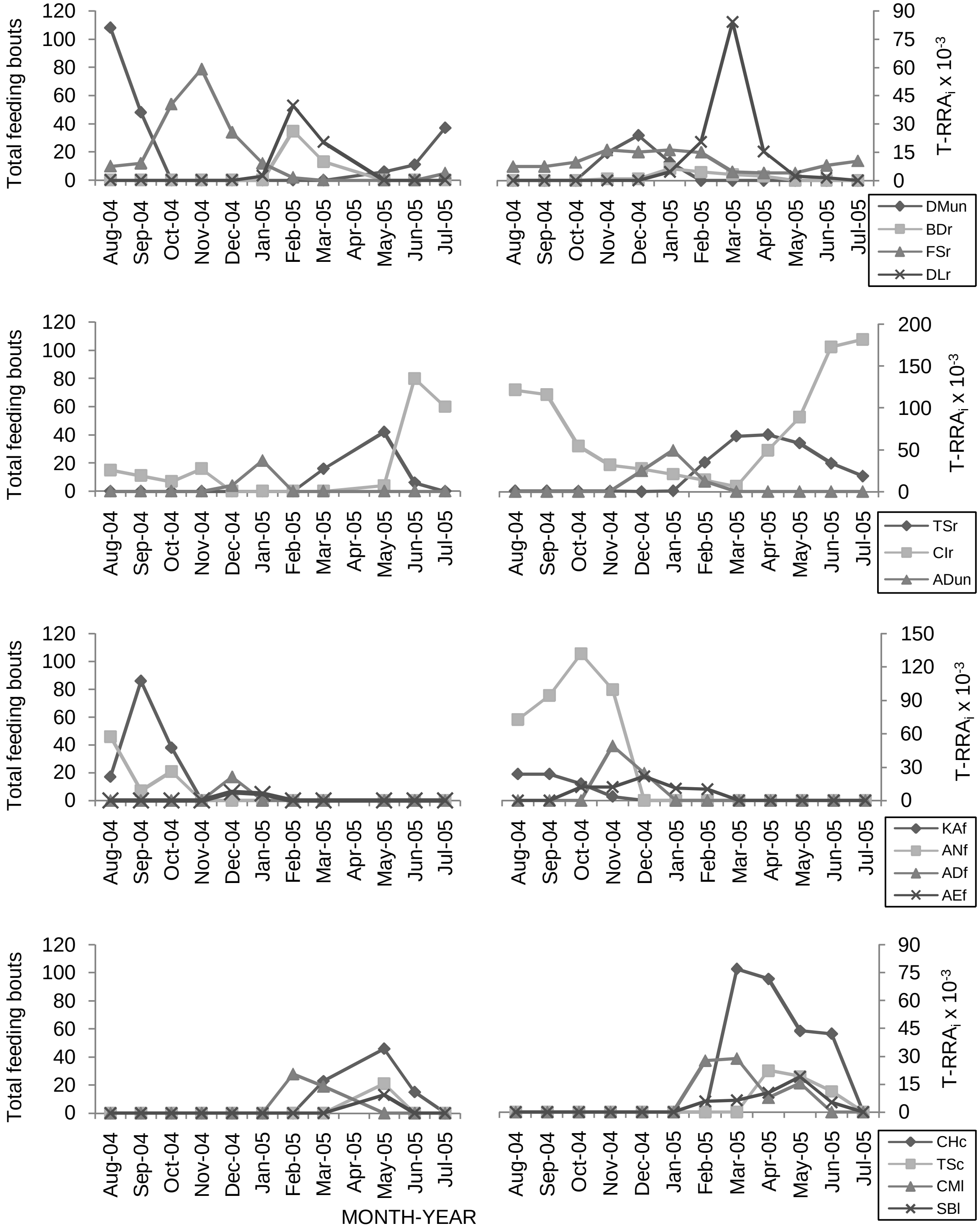

Figure 5. Total number of feeding bouts and relative resource abundance (RRA_i) of: (a) Seeds from ripe and unripe fleshyfruit and figs; (b) Ripe and unripe seeds from woody pods; (c) Pollen and nectar of flowers; and (d) Insect larvae feeding on pods and fruits.

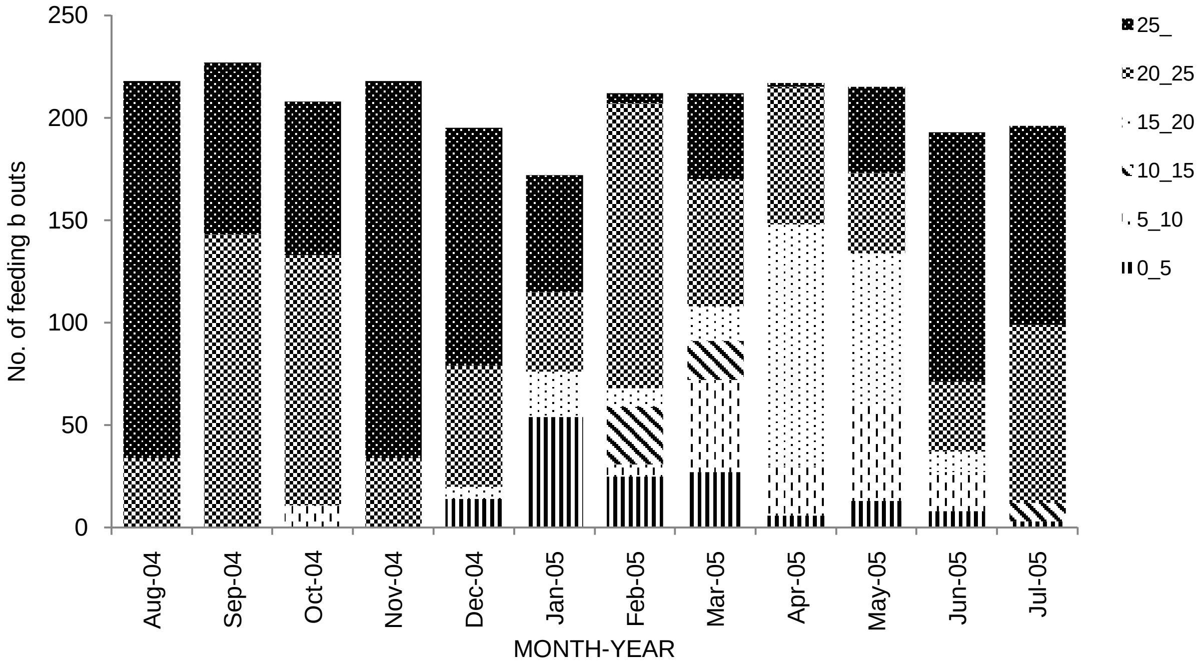

Figure 6. Total number of feeding bouts observed in each tree canopy height class.

Over 70% of all feeding bouts were over 20 m above the ground in the high canopy. Only 8% of all feeding activity was between 10–20 m above the ground. Feeding activity below 10 m was only observed between December and July, accounting for 21% of total feeding bouts (Figure 6).

DISCUSSION

Food item preference system

According to a modified Hurlbert's expanded and standardized niche breadth index, Meyer's Parrots are food resource generalists, as β_i was consistently above 0.5 throughout the study period. There was a brief period of niche specialization in June 2007 during the nestling period when both adults are provisioning young with a specialized diet of *C. imberbe* pulp and arthropod larvae from a broader variety of habitat types and food resources (Chapter 2; Chapter 9). Meyer's Parrot feeding activity on different food resources was not significantly different between 2005 and 2007 in the Okavango Delta (Chapter 2), and therefore, even though Meyer's Parrots utilize a wide variety of food resources, they do so with regularity, and thus have a food item preference system according to which they make food resource decisions. Here we attempt to evaluate putative mechanisms that likely function within this decision-making system.

In the Okavango Delta, Meyer's Parrots were demonstrated to track temporal food resource abundance of all significant food resources in their diet over 18 months, especially flowers and ripe fleshy-fruits. At the population level, Meyer's Parrots tracked the relative resource availability of 19 food items in their diet, 9 of which were fleshy fruits with bi-coloured fruit displays (Table 1; Appendix A). Four of the seven pods tracked by Meyer's Parrot contained arthropod larvae likely keystone to the breeding effort in the area (Chapter 2; Chapter10: Boyes & Perrin in review g). The remaining food items were flowers with white or coloured inflorescences in bi-coloured displays with the green leaves (Appendix A). Feeding activity on food resources available throughout the year (e.g. ripe *Kigelia africana* fruit and *F. sycomorus* figs) or not visible from the air (e.g. unripe *Diospryos lycoides lycoides* fruit), however, did not correlate significantly with temporal food resource abundance fluctuations. Failure to correlate rate of nutritional intake (i.e. protein and energy acquisition rates) with observed feeding activity was likely due to inadequate sample size for the nutritional and consumption rate analyses or that energetic costs of flight, prospecting and inter-specific competition outweighs the benefits from feeding on the most nutritious food resources. Significantly, this also shows that Meyer's Parrots do not make food resource decisions according to their ability to open and process the seeds inside a fruit or pod.

Boyes & Perrin (Chapter 7) showed that protein and energy acquisition rates were significantly different for different food resources, thus indicating that Meyer's Parrots could derive significant benefit from feeding on specific food resources. Making foraging decisions according to relative resource abundance at the landscape level benefits Meyer's Parrots by minimizing energy expenditure by foraging for the food resource with the highest probability of being located from the air. Aerial surveillance and lingual feeding (i.e. constant vocalizations during feeding activity) likely interact to ensure that the majority of the population can locate preferential foraging sites at low energy expenditure. This likely enables Meyer's Parrots to persist throughout the African subtropics where there are distinct wet and dry seasons, and therefore, periods when seed predators experience a food resource bottleneck. This hypothesis is supported by the assumptions of optimal foraging theory (Rakotomanana & Hino 1998, Sih & Christensen 2001). Boyes and Perrin (Chapter 8: Boyes & Perrin in review h) demonstrate that Meyer's Parrots are central place foragers departing from the communal roost according to the Foraging Dispersal (FD) Hypothesis (Caccamise & Morrison 1986; Symes & Perrin 2003b). The minimization of foraging flight distance by foraging for the most abundant food resource at landscape level fits into the model of a central place forager within the FD hypothesis. The only anomaly in the data set is the correlation between feeding activity on *Carissa edulis*, which usually forms part of the under-storey in riverine forest, and temporal resource abundance. This tree does, however, have a significant bi-coloured display with a fruit colour score (FCS) of 135. Therefore, we identified three potential mechanism that interact to facilitate food resource abundance tracking at the landscape level, including: (a) Aerial assessment of bi-coloured displays that are visible from the air in the high canopy (e.g. riverine forest) or low open habitat (e.g. *D. lycoides* marginal woodland); (b) Minimization of energy expenditure due to high costs of flight by minimizing foraging flight distance from a central point (e.g. communal roost or nest cavity) within the predictions of optimal foraging theory (Caccamise and Morrison 1986); (c) Opportunistic sampling of food resources at the population level and lingual feeding behaviour facilitate resource abundance tracking at population and landscape level; and (d) Prior knowledge of resource availability based on unknown stimuli (e.g. photoperiod (Sharp 2006) or rainfall (Lloyd 1999)).

Aerial assessment of conspicuous fruit displays

We found that the majority of the foraging activity was in the high canopy, thus indicating that Meyer's Parrots likely make their food resource decisions from the air and then descended to feed. The only significant feeding activity below 5m was between December and March when Meyer's Parrots were feeding on *D. lycoides lycoides* fruits. *Diospyros lycoides* marginal woodland comprises homogenous stands of *D. lycoides lycoides* at very high stand density in forest gaps and on channel margins. Therefore, ripe *D. lycoides* fruits are easily visible from the air and thus seasonally targeted as a food resource and resource abundance tracked effectively by Meyer's Parrots at landscape level. The same, however, is not true for unripe *Diospyros lycoides* fruits, which are a significant food resource, but feeding activity did not correlate with temporal food resource abundance. Unripe *Diospyros lycoides* fruits are green, and thus difficult to locate from the air. Under-storey tree species often not visible from the air such as *Ziziphus mucronata*, *Carissa edulis* and *Grewia spp*. only occurred in the diet of Meyer's Parrots sporadically (Chapter 2), thus supporting the hypothesis that Meyer's Parrots track resource abundance through aerial assessment from a central point (i.e. communal roost). The preference for bi-coloured fruit displays, which accounted for 55% of all feeding bouts, indicate preference for fruits and pods that are more easily visible from a distance. This moderate preference for bi-colour displays is characteristic of field experiments (Arruda *et al*. 2008). All food resources that were tracked by Meyer's Parrots had conspicuous pods or fruits (e.g. *A. digitata* and *K. africana*) or bi-coloured fruit displays (e.g. *D. lycoides lycoides*, *B. discolor*, *S. birrea caffra*, and *T. sericea*, and *D. mespiliformis*). In addition, five out of the seven most important food resources in the diet of Meyer's Parrots in the Okavango Delta had bi-colour displays. The mean fruit colour score was 95.45 indicated that yellow was the "mean" or dominant fruit colour in the diet of Meyer's Parrot, thus demonstrating an overall preference for fruit and flower colours that contrast with green (Appendix I).

Minimization of energy expenditure due to high costs of flight

Within the predictions of optimal foraging theory (Caccamise & Morrison 1986) it appears that Meyer’s Parrots make food resource decisions that maximize the probability of encountering the food resource. Boyes and Perrin (Chapter 7) found that the ability of Meyer’s Parrot to procure protein and energy from any food resource in their diet was unlikely to restrict their daily activity pattern and daily nutritional requirements could easily be achieved, as long as they manage to locate the food resources, energy expenditure is minimized, and no external factors inhibit feeding (e.g. increased vigilance due to predation risk or disturbance).

Differences in flight costs are associated with different foraging models (Carlson & Moreno 1992). Aerial feeders that habitually forage on the wing during large parts of the day employ low-cost flight at metabolic rates ranging from 2.9 to 5.7 BMR (Flint and Nagy 1984), whereas the short flights employed by some non-aerial foragers can cost as much as 23 BMR (Tather & Bryant 1986). Meyer’s Parrots are non-aerial foragers and have very short wings that allow them to maneuver in dense tree canopies when foraging, and thus are expected to maintain a very high metabolic rate during flight. Minimization of foraging flight distance by feeding on locally common or abundant food resource at a specific point in time should, therefore, be an important consideration for Meyer’s Parrots. Then there is the old adage: “The quickest way is the way you know”, whereby Meyer’s Parrots could feasibly maintain a prior knowledge of the location and timing of fruiting within the habitat mosaic.

Prior knowledge of resource availability

The ability to navigate is demonstrated in birds by their ability to forage over wide areas and then successfully return to a characteristically inconspicuous nest site. In addition, Boyes & Perrin (Chapter 8) found that Meyer’s Parrots are central place foragers (Lair *et al.* 1994) that likely utilize activity centres (e.g. trees near communal roosting sites) to facilitate dispersal in search of food resources according to the Foraging Dispersal hypothesis (Caccamise & Morrison 1986). This indicates that Meyer’s Parrots likely have an independent, pre-determined knowledge of the location of food resources and avoid the assistance of conspecifics. Specific fruits and pods remain available for extended periods of time and phenology was relatively synchronous at the landscape level, and therefore, once a food resource has been identified as suitable the parrots could feasibly use prior knowledge of the local area to find other trees of that species. Food resources within riverine forest and dry *Acacia*-*Combretum*/*Brachstegia*/*Adansonia* woodland communities preferred by Meyer’s Parrots throughout their range (Snow 1978; Tarboton 1980; Forshaw 1989, Juniper & Parr 1998; Chapter 3); however, are dispersed within a patchwork mosaic of different tree species, and thus difficult to locate. Therefore, lingual feeding and vocalizations are likely important in food resource abundance tracking at landscape level.

Opportunistic investigation by a lingual feeder

Meyer's Parrots are lingual feeders, and thus vocalize constantly during feeding activity based on the quality of the food resource (Chapter 2). Boyes and Perrin (Chapter 8) found that Meyer's Parrots disperse from activity centres in the early morning to forage, but gradually aggregate during the morning to form smaller secondary roosts. Lingual feeding likely facilitates this aggregation, as feeding flock size was recorded to increase as time passed during the morning (Chapter 8). Therefore, Meyer's Parrots could feasibly disperse randomly from a central point and then make decisions on dietary intake based on the vocalizations of other parrots in the area or their own investigation for and discovery of suitable food resources. Meyer's Parrots are reported to be crop pests in Zambia and South Africa (Rowan 1983; Boyes 2006). Grain and millet crops represent a super-abundant, localized food resource and attract large flocks of up to 40 Meyer's Parrots during harvest season (Chapter 8). Flocks this size would necessitate the aggregation of Meyer's Parrots from a large area, thus indicating that Meyer's Parrots either had prior knowledge of this food resource or have the ability to communicate food resource availability over large distances. More research is required on the distance at which Meyer's Parrots and other parrots can hear each other vocalizing, and thus potentially benefit from lingual feeding.

Conclusion

Meyer's Parrots track the temporal resource abundance of targeted food resources, but more work is required on specific stimuli within their generalist food item preference system (Chapter 2). Food resource tracking by Meyer's Parrots is likely due to the inter-relationship of Meyer's Parrots surveying for bi-coloured fruit displays from the air, listening for contact calls of feeding parrots, and as far as possible attempt to energy-efficiently navigate through their local environment. Significantly, Meyer's Parrots likely use fruit colour as an indicator to track, rather than select (Willson *et al.* 1990), specific food items.

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Chapter 5:

Short Note

Generalists, specialists and opportunists: Niche metrics of *Poicephalus* parrots in southern Africa[1]

Introduction

Little is known about the relationship between African parrots and food resources (Perrin *et al.* 2002), however, it may be predicted that seed predators such as parrots track food resources closely in order to exploit temporal and spatial abundances in seed production (Skeate 1987; Gautier-Hion and Michaloud 1989; Galetti and Rodriquez 1992; Renton 2001). In the African subtropics, where *Poicephalus* parrots predominate, interactions between plant and animal species play a key role in the evolution of their behavioural ecology and biogeography (Wirminghaus *et al.* 2001). Based on dietary studies of African parrots there is clear evidence that all three continental genera track resource availability within specialist or generalist food item preference systems (Chapman *et al.* 1993; Wirminghaus *et al.* 2001; Selman *et al.* 2002, Symes and Perrin 2003; Taylor and Perrin 2006; Chapter 2: Boyes and Perrin in review a; Chapter 4: Boyes and Perrin in review b).

The superspecies *P. meyeri* and *P. robustus* appear as natural assemblages within the genus *Poicephalus* (Massa *et al.* 2000). *P. robustus* forms a superspecies with the Grey-headed Parrot, Brown-necked Parrot *P. fuscicollis fuscicollis* and Jardine's Parrot *P. gulielmi*. *P. meyeri* forms a superspecies with Rüppell's Parrots and Brown-headed Parrot in southern Africa, and with three extralimitals, including the Senegal Parrot *P. senegalus*, Red-bellied Parrot *P. rufiventris*, and Niam-Niam Parrot *P. crassus* (White 1965; Rowan 1983; Massa *et al.* 2000). Differences in foraging behaviour and separation of trophic niches are important in taxonomic status and distributional range of *Poicephalus* parrots (Perrin 2005). Comprehensive studies undertaken on the feeding ecology of

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Poicephalus parrots in southern Africa classified Cape Parrots *Poicephalus robustus* and Grey-headed Parrots *P. fuscicollis suahelicus* as specialist feeders (Wirminghaus *et al*. 2002; Symes and Perrin 2003; Perrin 2005), Rüppell's Parrots *P. ruppelli* as generalist feeders (Selman *et al*. 2002), and Meyer's Parrots *P. meyeri* and Brown-headed Parrots *P. cryptoxanthus* as opportunistic generalist feeders (Chapter 2; Taylor and Perrin 2006) (Table 1). Therefore, there is a dichotomy in the food item preferences of Poicephalus according to superspecies complex.

Table 1: Location, timing and classifications from studies on the feeding ecology of *Poicephalus* parrots in southern Africa

Species	Study period	Location	Feeding classification	Ref:
Cape Parrot	1993-1996	Hlabeni and Ingelki Forests, KwaZulu-Natal (South Africa)	Specialist	1
Ruppell's Parrot	1996-1997	Waterberg Plateau Park (Namibia)	Generalist	2
Brown-headed Parrot	1996-1999	Kruger National Park (South Africa) and Ponta Malongane (Mozambique)	Opportunistic generalist	3
Grey-headed Parrot	1999	Levubu District (South Africa)	Specialist	4
Meyer's Parrot	2003-2007	Okavango Delta (Botswana)	Opportunistic generalist	5

Reference: 1 = Wirminghaus *et al.* (2002); 2 = Selman *et al.* (2002); 3 = Taylor and Perrin (2006); 4 = Symes and Perrin (2003); 5 = Chapter 2.

Niche metrics have been used by several authors to evaluate dietary specialization and degree of niche overlap in birds (Rusterholtz 1981; Brandl *et al.* 1994; Brandle and Brandl 2001; Renton 2001; Martinez 2003). Niche breadth is the variance in resource use by a species, and can be estimated by measuring the uniformity of the distribution of conspecifics among resource states within the resource matrix (Colwell and Futuyma 1971). We determined to calibrate the degree of dietary specialization of Meyer's Parrots in the Okavango Delta, Botswana, over 12 months using the a modified Hurlbert's expanded and standardized niche breadth index (Colwell and Futuyma 1971; Hurlbert 1978), for comparison using Levins' niche breadth (Levins 1968), with the food item calendars of the other *Poicephalus* parrots in southern Africa.

Based on the ecological specialization hypothesis, species with the widest niche breadth should be more widespread and locally abundant than specialized species (Gaston and Lawton 1990; Pomeroy and Ssekabiira 1990). Brandle and Brandl (2001) demonstrated a significant positive correlation between habitat niche breadth and distributional range of non-passerine afro-tropical birds in Tsavo East National Park, Kenya. Our study, therefore, compared the niche metrics of *Poicephalus* parrots in southern Africa with their distributional ranges to test the hypothesis that Meyer's Parrots have the widest distribution of any *Poicephalus* parrot due to their comparatively wide niche breadth. In addition, we attempted to correlate body size with distributional range and food niche breadth of *Poicephalus* parrots in southern Africa.

Methods

Food item preferences of Meyer's Parrots in the Okavango Delta are presented in Boyes and Perrin (Chapter 2). Temporal resource abundance at landscape scale for all food items in the diet of Meyer's Parrot in the Okavango Delta are presented in Boyes and Perrin (Chapter 4). Seasonal food item preferences of all other *Poicephalus* parrots in southern Africa are detailed in studies by Wirminghaus *et al.* (2002), Symes and Perrin (2003), Taylor and Perrin (2006) and Selman *et al.* (2002) (Table 1). For purposes of standardization between studies all food items accounting for less than 10% of the overall recorded feeding activity in a given month were dropped from the food item calendar (Taylor and Perrin 2006).

A resource matrix is a table formed by using different competing species as rows and resource states as columns. Resource states are subdivisions within a heterogeneous habitat considered individually (e.g. food item types) or grouped on the basis of similarity (e.g. habitat types) (Hurlbert 1978). We determined to evaluate niche breadth fluctuations month-to-month, and therefore, the resource matrix was modified to include different months as rows and different food items as resource states within the resource matrix. Distribution within this species-specific "temporal resource matrix" was measured as the number of feeding bouts for a specific food item in a specific month. A feeding bout was defined as an individual within a flock, or solitary, feeding on a specific food item. Use of a temporal resource matrix allows for comparison of niche breadth between allopatric species over time.

Niche breadth of all *Poicephalus* parrots was calculated using the Levin's niche breadth (γ_i):

$$\gamma_i = \frac{X_i^2}{\sum_j \mathrm{N}_{ij}}$$

Where X_i represents total feeding bouts of all food items and N_{ij} the number of feeding bouts associate with resource state j (Levins 1968; Colwell and Futuyma 1971; Hurlbert 1978). B*i* is maximized when an equal number of individuals of species *i* are associated with each available resource state, thus implying that species *i* does not discriminate among the resource states (Hurlbert 1978).

Levins' niche breadth is not standardized, and thus is only useful as a measure of relative specialization in food resource utilization. In addition, this measure does not account for error caused by nonlinearity and ecological inequality of spacing among resource states (Colwell and Futuyma 1971). These problems were overcome by weighting resource states according to their distinctness from other resource states in the resource matrix. Relative resource abundance among resource states provides adequate information on the ecological distinctness (Colwell and Futuyma 1971). The following equation was used to calculate the modified Hurlbert's standardized and expanded niche breadth index (βi):

$$\beta_{\mathrm{i}} = \left[\frac{1}{\sum_{\mathrm{j}}\left(10000 \times \frac{\mathrm{N}_{ij}}{\sum_{i} d_j k \times \mathrm{N}_{ij}}\right)}\right]\left[\frac{1}{9999}\right]$$

Where: N_{ij} represents the number of feeding bouts associate with resource state j, and $d_j k$ is the proportion of the total resource abundance represented by resource state j expanded to k = 10 000. For β_i, a value close to 0 indicated food resource specialization, and a value tending to 1 indicated broader food resource preferences (Colwell and Futuyma 1971; Hurlbert 1978; Renton 2001).

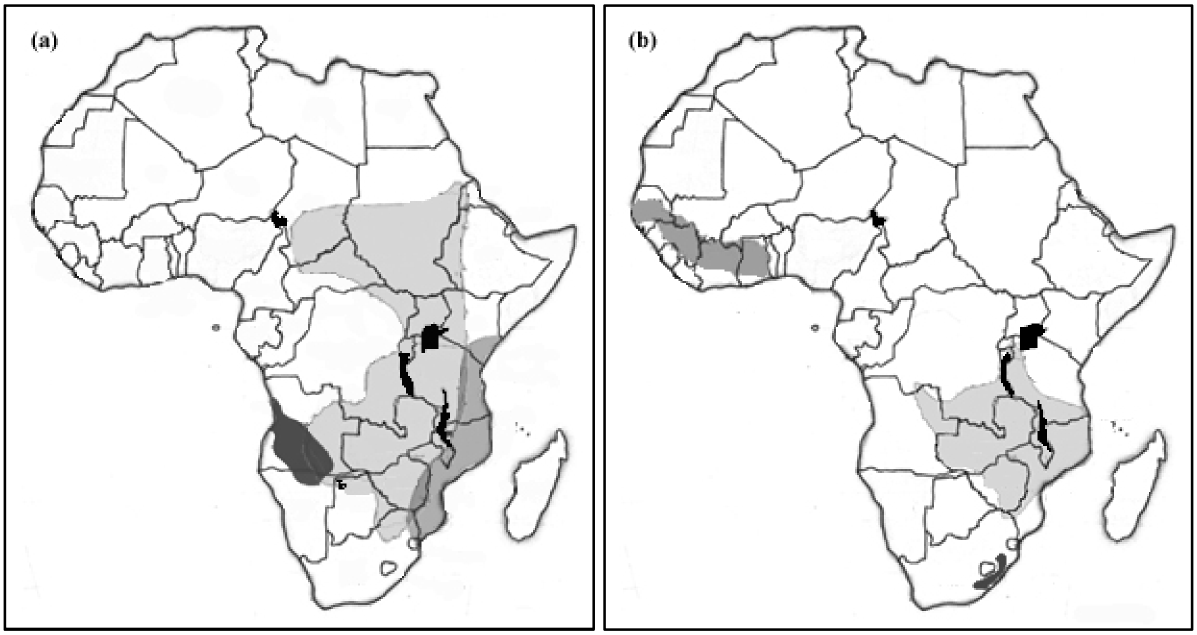

Figure 1: Distributional ranges of southern African *Poicephalus* parrots. (a) *P. meyeri* superspecies: *P. meyeri* (light grey), *P. rueppellii* (dark grey) and *P. cryptoxanthus* (medium grey); (b) *P. robustus*

superspecies complex: *P. robustus*) (dark Grey), *P. fuscicollis suahelicus* (light grey) and *P. fuscicollis* (medium grey)

Distributional ranges for all *Poicephalus* parrots evaluated in our study were derived from species accounts in Rowan (1983), Juniper and Parr (1998) and Wirminghaus (1997) (Figure 1). For the analysis, the grid quadrat system used by Crowe and Crowe (1982) to extract atlas data (grids without numbers were numbered accordingly) was used to estimate percentage coverage of the African continent by each species. Body size was inferred from the median body mass reported by Rowan (1983).

Kolmogorov-Smirnov (K-S) and Lilliefors tests were used to test for normality. T-test for independent samples were used to test for significant differences between niche breadth fluctuations over 12 months for Poicephalus parrots in southern Africa. Spearman rank correlations (r_s) were used to check for correlations between Levins' niche breadth, extent of distributional range, and body size. Statistical analysis followed Quinn and Keough (2002) and Zar (1984).

Results and discussion

According to the modified Hurlbert's standardized and expanded niche breadth index, Meyer's Parrots can be classified as generalist feeders for the entire year (Figure 2). Having calibrated the food item preference system of the Meyer's Parrot we then ran the inter-specific comparison using Levins' niche breadth. Over 12 months, Meyer's Parrots had a significantly wider niche breadth than Rüppell's Parrots (df = 22; t-value = 2.53; p = 0.02); Brown-headed Parrots (df = 22; t-value = 4.86; $p < 0.001$), Grey-headed Parrots (df = 22; t-value = 5.50; $p < 0.001$) and Cape Parrots (df = 22; t-value = 5.72; $p < 0.001$) (Figure 3). There were, however, no significant differences between the niche breadth fluctuations of Cape Parrots and Grey-headed Parrots (df = 22; t-value = -0.479; p = 0.636), and Grey-headed Parrots and Brown-headed Parrots (df = 22; t-value = 1.927; p = 0.067) (Figure 3). In addition, there was a significant difference between niche breadths of Brown-headed Parrots and Rüppell's Parrotss (df = 22; t-value = 2.986; p = 0.006) and Cape Parrots (df = 22; t-value = 2.650; p = 0.014) (Figure 3). Our analysis, therefore, confirmed the food item preference system classifications put forward for *Poicephalus* parrots studied thus far, except Brown-headed Parrots which appears to have more specialist food item preferences than previously put forward by Taylor and Perrin (2006).

Results from our study support the hypothesis that Meyer's Parrots have the widest distribution of any *Poicephalus* parrot studied thus far due to their comparatively wide trophic niche breadth. Our study, however, undermined the assumptions of the ecological specialization hypothesis supported by

Brandle and Brandl (2001), Gaston and Lawton (1990) and Pomeroy and Ssekabiira (1990), as Levins' niche breadth for all five *Poicephalus* parrots had no significant correlation to the extent of their distributional ranges ($r_s = 0.60$, t(N-2) = 1.29, p = 0.285) (Table 2). This relationship between niche breadth and distributional range of *Poicephalus* parrots could have been undermined by the low statistical power of this analysis, the restricted distribution and wide niche breadth of Rüppell's Parrots and/or variance introduced by the impact of rapid changes in extent and spatial distribution of African forest habitat types over the last 100 years (e.g. deforestation or climate change). The restricted distribution and wide niche breadth of Rüppell's Parrots is likely due to range isolation by the Kalahari Sand Basin and trophic response to seasonal aridity and resultant food resource scarcity in their natural habitat.

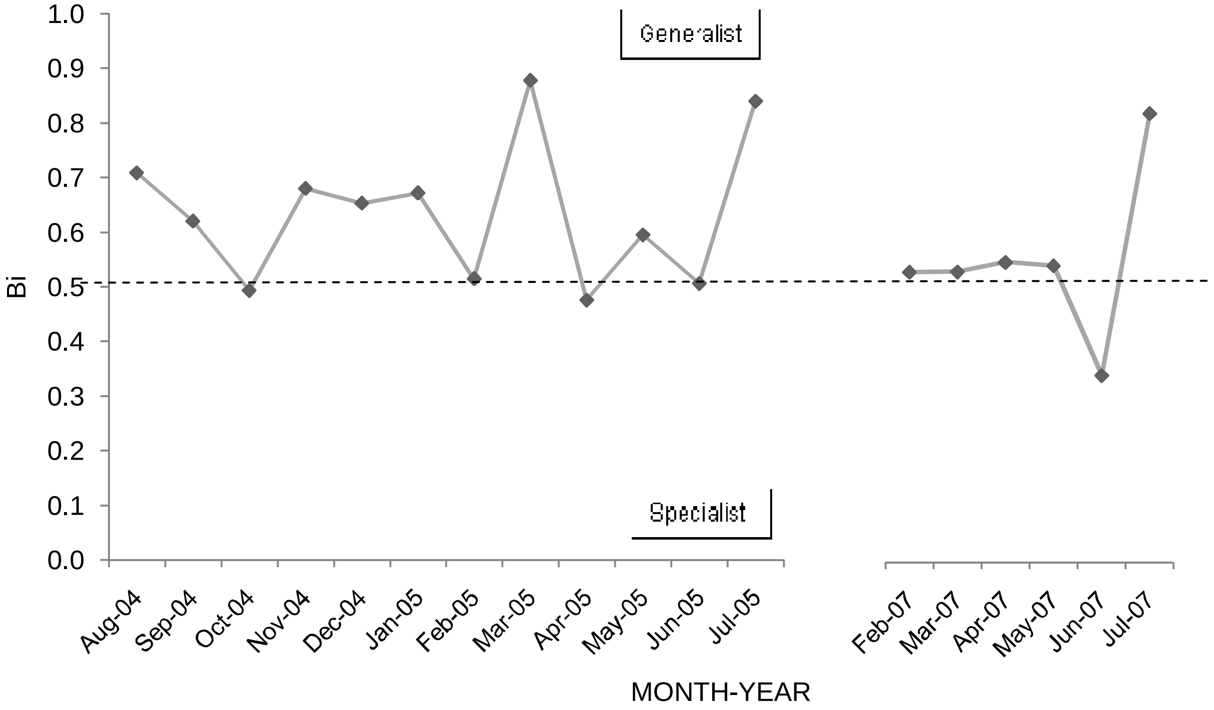

Figure 2: Modified Hurlbert's standardized and expanded niche breadth (Bi) for Meyer's Parrot at Vundumtiki (0 = specialist utilizing only one food resource; 1 = generalist utilizing all available food resource proportionally according to their relative resource abundance.

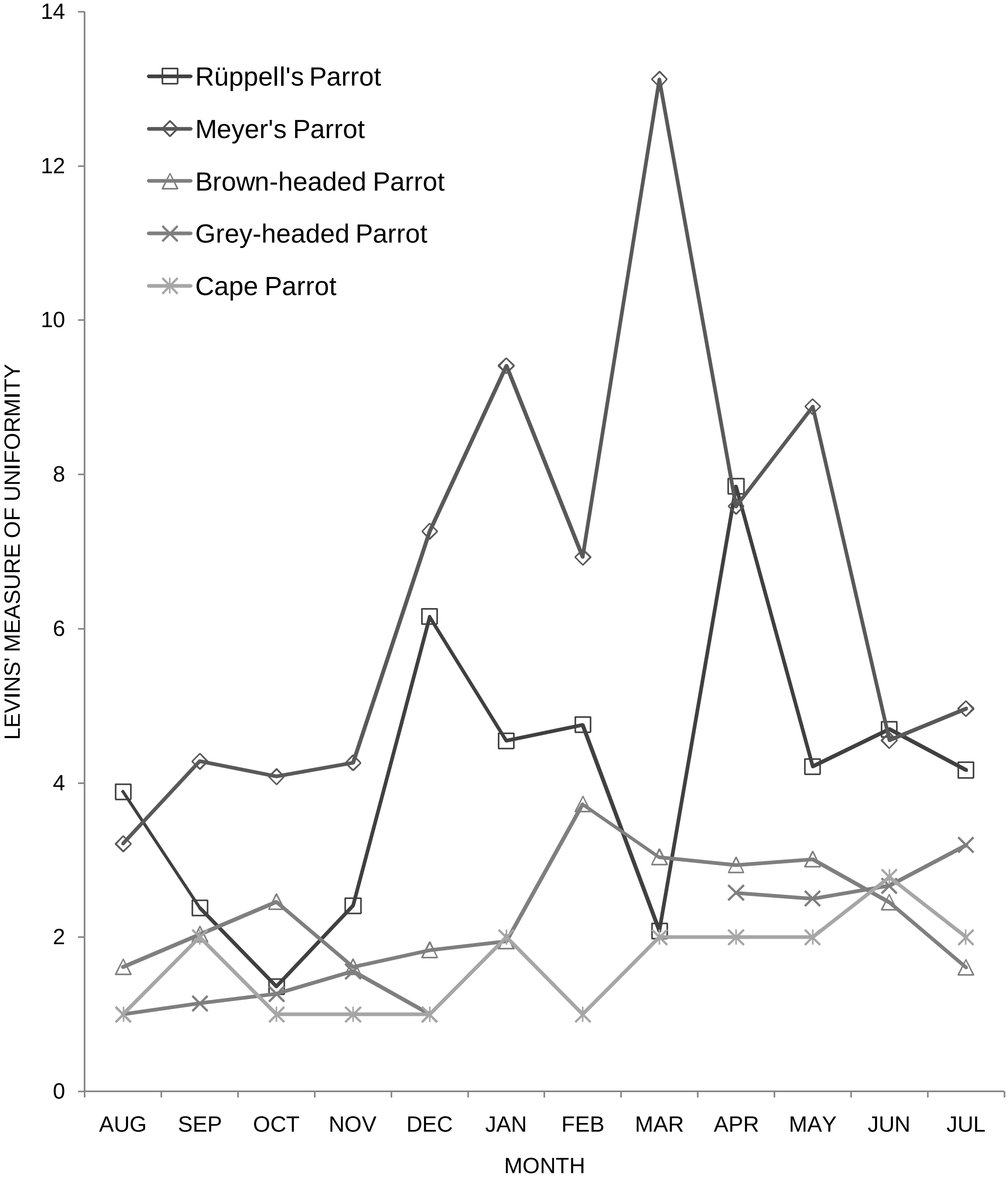

Figure 3: Modified Levins' measure of uniformity applied to all *Poicephalus* parrots in southern Africa

Table 2: Comparison of food item preference systems for all *Poicephalus* parrots

Poicephalus parrot	Levins' measure of uniformity (B_i)	No. of food items (n)	Feeding system	Extent of distributional range (%)	Body size (g)	Threat category (rank)
Meyer's Parrot	20.5	37	Generalist	34	118	LC(5)
Ruppell's Parrot	9.1	37	⇩	4	125	LC(2)
Brown-headed Parrot	6.5	16 - 17	Opportunist	8	145	LC(4)
Grey-headed Parrot	3.7	6 - 11	⇩	11	323	LC(3)
Cape Parrot	1	7	Specialist	0.5	295	CR(1)

Interestingly, there was a significant negative correlation between Levins' niche breadth and median body mass of *Poicephalus* parrots ($r_s = 0.90$, $t(N-2) = -3.57$, $p = 0.037$) (Table 2). Therefore, for *Poicephalus* parrots, this study indicates that degree of dietary specialization is inversely correlated with body mass, whereby the narrower the trophic niche, the larger the body size. There was no significant correlation between distributional range and body size ($r_s = -0.30$, $t(N-2) = -0.545$, $p = 0.624$) (Table 2). From this, it follows that the common ancestor of the *P. robustus* superspecies complex evolved to be larger by focusing on fewer, highly nutritious, super-abundant food resources (e.g. *Podocarpus* fruits). *Podocarpus falcatus*, for example, has an extended fruiting period and high fruit yield rich in fat and energy (Wirminghaus et al. 2002; Perrin 2005). Massa et al. (2000) showed that Jardine's Parrot separated from the ancestral Cape Parrot before the Grey-headed Parrot and Brown-necked Parrot. Solms (1999) found that Grey-headed Parrots and Brown-necked Parrots are more closely related to each other than the Cape Parrot. Jardine's Parrot is considerably smaller than the Cape Parrot; however, the subspecies *P. g. massaicus* also feed on *Podocarpus* fruits and flowers (Juniper and Parr 1998). During the Quaternary palaeoclimatic changes, glacial periods were arid and interglacials were humid (Diamond and Hamilton 1980). During the last dry period, there was fragmentation of forest and savanna habitats into forest refugia (Crowe and Crowe 1982), likely confining relict populations of the ancestral *P. robustus* to the *Podocarpus* Afromontane forests of southeastern South Africa (Perrin 2005). The results of our study indicate that the ancestor of *P. robustus* likely increased in body size due to dietary specialization during this period of isolation in the *Podocarpus* Afromontane forests. This ancestor did not have to track resource availability or accommodate seasonal fluctuations in resource abundance like other *Poicephalus* parrots, thus allowing them to sustainably achieve greater size. Then in subsequent vegetation shifts between 9 500 – 12 500 BP that advanced forest communities ancestors of Grey-headed Parrots and Brown-necked Parrots were allowed to extend their range into their present distributions (Perrin 2005), maintaining the large size due to inter-specific competition in the African subtropics. Conversely, Meyer's Parrots are the smallest of the *Poicephalus* parrots with the widest niche breadth and distributional range. They are approximately 2.5 times smaller than Cape Parrots, and therefore, likely have considerably lower absolute protein and energy requirements, allowing them to proliferate in the dry savanna woodland and *Acacia* scrubland predominant in central and eastern sub-Saharan Africa. Their generalist feeding system supports this relationship, making them more robust to macroclimatic and historical factors noted as possible restrictions by Brandle and Brandl (2001).

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Chapter 6:

Do Meyer's Parrots *Poicephalus meyeri* benefit pollination and seed dispersal of trees in the Okavango Delta, Botswana?[1]

Abstract

Parrots have been considered potential agents of pollination and seed dispersal, but there are few detailed studies of their behaviour when feeding on flowers and fruits or its consequences for forest ecology. We investigated the interactions between Meyer's Parrots and trees in the Okavango Delta, Botswana. Meyer's Parrots were not implicated in endo- or epizoochory, however, they dropped uneaten fruit pulp and seeds to the ground during feeding bouts, thus providing ripe, undamaged seeds to secondary seed dispersers. This link with forest recruitment was weak, as all tree species utilized by Meyer's Parrots either had more significant primary dispersal agents or were primarily wind-dispersed. In most cases, the negative effect of seed predation outweighed any positive effects in terms of dispersal. Only *Sclerocarya birrea caffra* recorded marginal net dispersal benefit from utilization by Meyer's Parrots. Utilization of flowers of *Kigelia africana* and *Adansonia digitata* by parrots likely had a significant negative impact on pollination. Feeding on *Acacia nigrescens* flowers, however, was potentially advantageous to their pollination. We conclude that *Poicephalus* parrots are net consumers of ripe, undamaged seeds and flowers, thus having an overall negative impact on forest recruitment in subtropical Africa.

Key words. Okavango Delta; seed dispersal; pollination; Poicephalus; parrot, seed rain.

Introduction

Numerous studies have documented the ecological role of birds and mammals, as pollinators and dispersal agents, in forest ecology (Howe 1986; Fleming & Sosa 1994; Clark *et al.* 2001; Ingle 2004; Vander Wall *et al.* 2005; Parrado-Rosselli & Amaya-Espinel 2006). Very few studies, however, have been conducted on the intensity of seed and flower predation by parrots and the resultant impact on

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forest recruitment (Galetti & Rodrigues 1992; Juniper & Parr 1998). Parrots form an important component of most canopy bird communities (Terborgh *et al.* 1990; Gilardi & Munn 1998), and therefore, depending on population levels, likely have a significant impact on pollination and seed dispersal due to high consumption of the reproductive apparatus of plants (Jordano 1983; French *et al.* 1992; Galetti 1993; Renton 2001). Comprehensive studies of the feeding ecology of the Cape Parrot *Poicephalus robustus* (Wirminghaus *et al.* 2002), Rüppell's Parrot *P. rueppellii* (Selman *et al.* 2002), Grey-headed Parrots *P. fuscicollis suahelicus* (Symes & Perrin 2003), Brown-headed Parrot *P. cryptoxanthus* (Taylor & Perrin 2006) and Meyer's Parrot *P. meyeri* (Chapter 2: Boyes & Perrin in review a) all concluded that *Poicephalus* parrots are major pre-dispersal seed predators in the wild. In addition, nectivory has been reported in all *Poicephalus* parrots studied thus far (Oatley & Skead 1972; Fynn 1991; Selman *et al.* 2002; Wirminghaus *et al.* 2002; Symes & Perrin 2003; Taylor & Perrin 2006; Chapter 2). Our study evaluated the feeding behaviour of Meyer's Parrot for evidence of linkages with forest ecology.

Meyer's Parrot is the smallest of the *Poicephalus* parrots (≈118g) and forms a superspecies with Rüppell's Parrot *P. rueppelli* and Brown-headed Parrot *P. cryptoxanthus* in southern Africa (Rowan 1983; Massa *et al.* 2000). They have the widest distributional range of any African parrot, extending throughout subtropical Africa from north-eastern South Africa to the southern Sudan (Snow 1978; Forshaw 1989; Juniper & Parr 1998). Meyer's Parrots are opportunistic generalists with a distinctly seasonal diet that tracks fruiting phenology (Chapter 2; Chapter 4: Boyes & Perrin in review b; Chapter 5: Boyes & Perrin in review c). Flower predation and arthropod consumption both form an important part of their diet (Chapter 2). They have short, strong bills observed to open the hard nut-casing of *Sclerocarya birrea caffra* fruits and *Acacia erioloba* pods, and thus have apparatus for unrestricted destructive seed and flower predation (Chapter 2).

Evidence implicating African parrots in seed dispersal is very limited. The only instance of endozoochory (i.e. seed dispersal through defecation) was recorded in Lesser Vasa Parrots *Coracopsis nigra* in Madagascar, which dispersed *Commmiphora guillaumini* seeds in their faeces (Bohning-Gaese *et al.* 1999; Vander Wall & Longland 2004). African Grey Parrots *Pssitacus erithacus* (Chapman *et al.* 1993) and Black-cheeked Lovebirds *Agapornis nigrigenis* (Warburton & Perrin 2005) both fly with food items, and thus could be implicated in epizoochory (i.e. seed dispersal through transportation on body surface). As put forward by Galetti and Rodrigues (1992) in regard to parrots in Brazil, Symes & Perrin (2003) recognized that secondary dispersal agents on the ground (e.g. rodents, ants and termites) could facilitate dispersal of ripe, undamaged seeds to suitable microhabitats for germination and establishment. Secondary seed dispersal has been demonstrated to be important in the reproductive cycle of several plants (Chambers & MacMahon 1994; Bohning-Gaese *et al.* 1999; Vander Wall & Longland 2004; Vander Wall *et al.* 2005; Garcia-Castano *et al.* 2006). Therefore, depending on the presence of secondary dispersers and dispersal rates of ripe, undamaged seeds to the ground during seed predation, *Poicephalus* parrots could play a role in seed dispersal of certain tree species.

Australian and Neotropical parrots have been reported as the main pollinators for certain plants species (Christensen 1971; Hopper & Burbridge 1979; Hopper 1979; Cannon 1984; Cotton 2001; Brereton *et al.* 2004). There is, however, no evidence implicating *Poicephalus* parrots in pollination. Meyer’s Parrots have the highest incidence of flower predation in their diet of any *Poicephalus* parrot studied thus far, whereby flower predation accounted for 13% of total feeding activity over 24 months (Chapter 2). Our study investigated net benefit of Meyer’s Parrot flower predation and linkages between flower structure and the potential for pollination by *Poicephalus* parrots.

We tested the hypothesis that Meyer’s Parrots have a negative net impact on pollination and seed dispersal of targeted tree species through destructive flower utilization and pre-dispersal seed predation.

Materials and methods

Study area

The Okavango Delta was chosen as the study area because of its significant Meyer’s Parrot population (Wirminghaus 1997). The study was conducted in the Kwedi Concession (NG22) on Vundumtiki Island located in the north-eastern part of the Okavango Delta (Figure 1). The study site was remote and there was limited disturbance to habitat and animal behaviour.

Data collection

Feeding activity data collection was conducted from August 2004 to July 2005. To standardize spatial distribution of Meyer’s Parrot feeding observations, the total sample area was defined as the area 100m either side of the 26.2 km standardized road transect. Road transects were conducted five times a week on separate days from start to finish. The same observer and vehicle travelling at 15–20 km/h with an open top were used for all road transects.

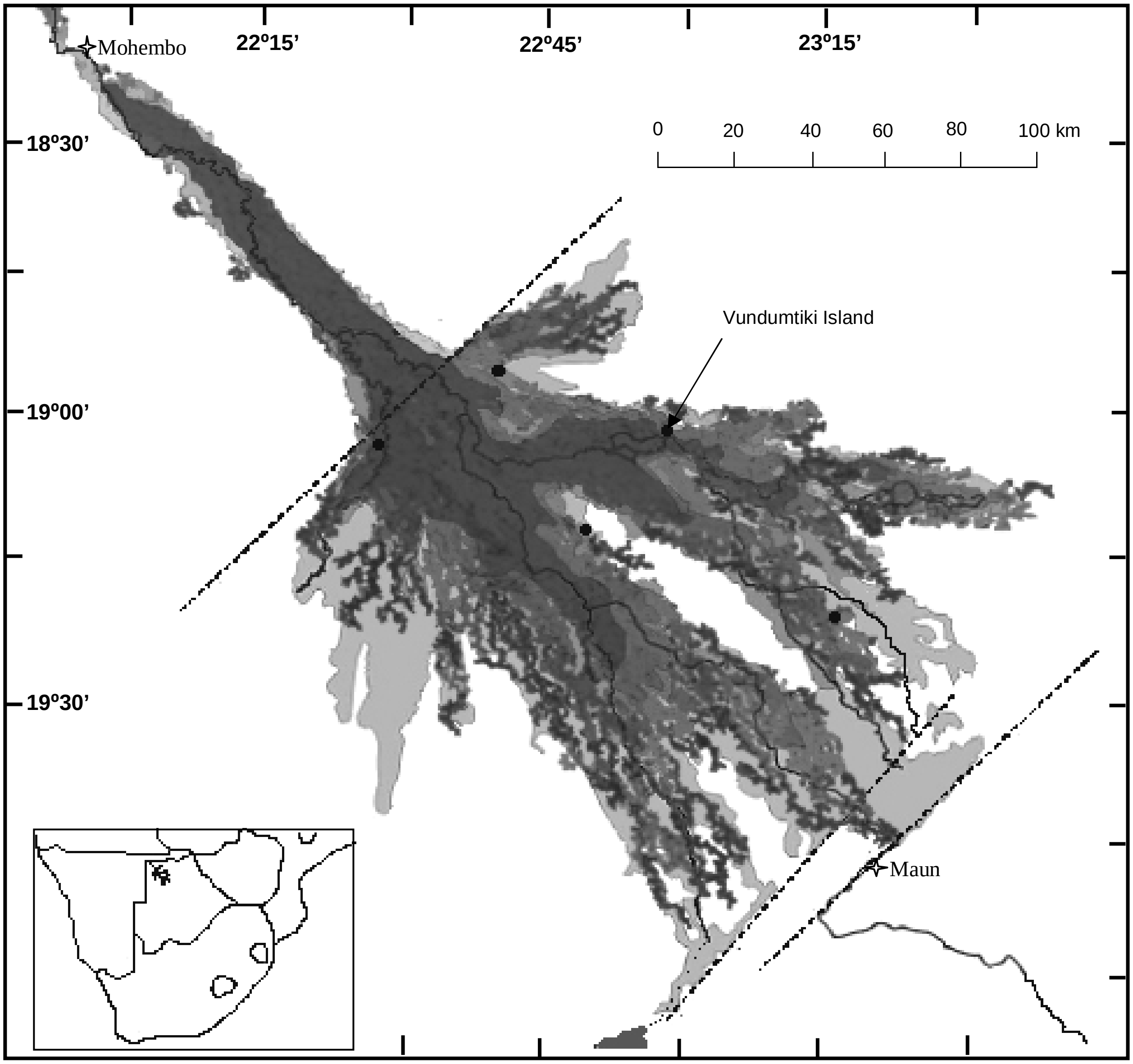

Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

A systematic sampling strategy was used for the temporal distribution of feeding observations, whereby six daytime time periods were established (i.e. 06h00-08h30; 08h30-11h00; 11h00-13h30; 13h30-16h00; 16h00-18h30; and 18h30 to sunset) (Chapter 7: Boyes & Perrin in review d). Road transects were conducted in all six time periods before a specific time period was sampled again.

Meyer's Parrots are lingual feeders (i.e. vocalize constantly during feeding) (Homberger 1989), and thus were detected by following their vocalizations. At each sighting the following data were recorded: tree species, food item type, habitat type, number of feeding bouts, and presence of frugivores or potential secondary seed dispersers. A feeding bout was a feeding event defined as an individual within a flock, or solitary, feeding on a specific food item. A food item was any plant food eaten by Meyer's Parrots described according to tree species and food item type. Food item types were classified according to the part consumed and fruiting stage, and included: ripe (r) and unripe (un) seeds from fruits or pods; flowers (f); pseudocarp and seeds of figs (p); and fruit pulp from fleshy fruits (fr). Arthropod food items were classified according to the host tree species and their family, and included: parasitic Hemiptera larvae (h); parasitic Lepidoptera caterpillars (l); and parasitic Coleopteran larvae (c). Acronyms for tree species and food item types are listed in Table 1. Tree nomenclature followed Van Wyk and Van Wyk (1997) and Palgrave (2002). The basic unit was a seed in a fruit or pod. During observations, the number of seeds dispersed and destroyed over the longest period possible within the observation period was estimated.

In addition to number of feeding bouts, seed dispersal and destruction rates were estimated opportunistically when visibility was optimal. Observation period was limited to 20 minutes due to time constraints in completing the road transect. All observations were made with a 30x spotting scope at the maximum sighting distance possible (≈20–40m) in order to minimize disturbance of feeding behaviour. The same observer was used for all observations.

For fruits and pods with one seed kernel, dispersal rates for different species were estimated by dividing the total number of seeds dispersed to the ground by the sample period. Only ripe seeds undamaged during feeding and subsequent dispersal from the canopy were counted during observation period. This was confirmed through subsequent inspection on the ground. Destruction rates were estimated by dividing the total number of unripe and ripe seeds damaged during seed predation by the sample period.

Counting the number of seeds dispersed and destroyed in fruits and pods with multiple seeds was more problematic. To solve this we estimated the mean proportion of the whole fruit or pod dispersed to the ground or destroyed during seed predation over the observation period. Therefore, the total number of seeds dispersed to the ground was estimated by multiplying the total number of fruits or pods dispersed to the ground by the estimated mean proportion of each fruit or pod destroyed (EMP_s) and the mean number of seeds in each fruit or pod ($n = 50$). EMP_s was scored subjectively in increments of 0.2 between 0–1, whereby 0 indicates that all seeds in the pod or fruit were destroyed and 1 indicates that all seeds were dispersed to the ground. This was determined either through observation in the canopy or inspection of pods and fruits dispersed to the ground. Similarly, the total number of seeds destroyed during seed predation was estimated by multiplying total number of fruits or pods predated upon by one minus EMP_s and the mean number of seeds in each fruit or pod. Seed dispersal and destruction rates were estimated by dividing the estimated total number of seeds dispersed or damaged by the sample period. Where possible (e.g. with large pods and good visibility) the proportion of each fruit or pod dispersed or destroyed was estimated, summed and then divided by the sample period to get the dispersal and destruction rates.

Pollination and flower destruction rates were also estimated opportunistically when visibility was optimal. Pollination rates were estimated by counting the incidence of non-destructive contact with the reproductive apparatus of flowers during the sample period. Flower destruction rates were estimated by dividing the number of flowers destroyed by the sample period. Destructive flower predation was confirmed through visual inspection following the observation period. For composite flowers (e.g. Leguminosae and Combretaceae), the proportion of each flower remaining undamaged was recorded and pollination assumed after confirmation of pollen on the head and beak of the foraging parrot. Therefore, to determine the pollination rate these proportions were summed and divided by the sample period. Conversely, flower destruction rates for composite flowers recorded the proportion of each flower consumed or dispersed to the ground during flower predation over the sample period.

Resource assessment

A total of 19 (300x20m) habitat line transects were established within the sample area (Bullock & Solis-Magallenes 1990, Chapman *et al.* 1994, Renton 2001). Each habitat transects were mapped and transect line maintained using a Garmin Quest GPS (Garmin 2006). We used a stratified sampling design within which three resource abundance line transects were dispersed in each forest habitat type to obtain a representative sample of resource availability (Renton 2001). Due to homogeneity and high stand density of *Lonchocarpus nelsii* sandveld only one transect was done in this forest habitat type. Due to heterogeneity of *Acacia-Combretum* woodland, this forest habitat type was further stratified to include *Acacia-Combretum* woodland dominated by *Combretum imberbe*, *Combretum hereroense* and *Acacia nigrescens*. Similarly, dry Mopane woodland was stratified to include dry Mopane woodland dominated by trees under 4m in height (i.e. scrub Mopane), above 4m in height (i.e. cathedral Mopane) and with multiple-storeys. For the estimation of habitat-wide resource abundance, a habitat conversion factor (HCF) was calculated by dividing the total forest habitat area within the sample area by the total area of resource abundance line transects in each forest habitat type.

Chapman *et al.* (1992) found that diameter at breast height (DBH) predicted fruit number and biomass the best. DBH was measured for all trees over 150 mm in diameter using a large caliper (Renton 2001). We estimated the proportion of the crown that was healthy and potentially productive to overcome variance due to poor canopy condition (e.g. fire, fungal or elephant damage). Crown condition (CC) was estimated using subjective visual assessment, and scored in increments of 0.2 from 0 – 1, whereby 0 represents a snag (i.e. dead tree) and 1 represents a full healthy canopy. Boyes and Perrin (Chapter 4: Boyes and Perrin in review b). We recorded tree species, DBH (cm) and CC (0-1) for all trees on habitat transects. The observer was standardized for all transects and once-off subjective measurements to maximize repeatability and precision (Chapman *et al.* 1994). Therefore, we estimated the relative productivity or resource abundance of a specific tree (RA_i) using the following index: $RA_i = DBH_i{*}CC_i$. RA_i for all trees of the same species on the three resource abundance transects in each habitat type were then summed to obtain transect-wide relative resource abundance for each tree species within each forest habitat type ($TW\text{-}RA_i$). $TW\text{-}RA_i$ was then multiplied by the HCF to obtain an index of habitat-wide relative resource abundance for each tree species ($HW\text{-}RA_i$). Total relative resource abundance of a specific tree species (RRA_i) was estimated by summing all the $HW\text{-}RA_i$ values. Therefore, we estimated total relative resource abundance for each tree species using the following equation:

$$\mathrm{RRA_i} = \sum_{j=1}^{7}\left\{\sum_{k=1}^{\infty}(\mathrm{DBH_k} \times \mathrm{CC_k}) \times \mathrm{HCF_j}\right\}$$

Where: i represents each food item; j represents each habitat type; and k represents each tree on the habitat transects.

Data analysis

Data could not be normalized. Kruskal-Wallis test was used to analyze differences in dispersal and destruction rates among different food items and food item types. Mann-Whitney U-test was used to test for significant differences between independent variables (e.g. consumption and wastage rates for pods and fleshy fruits). Statistical analysis followed Quinn and Keough (2002) and Zar (1984).

Relative impact of Meyer's Parrots on seed dispersal was evaluated using the Dispersal Value Index (DVI). DVI was determined by dividing the difference between the minimum projected total number of seeds destroyed and dispersed over 12 months by the relative resource abundance index for each tree species separately. The minimum projected total number of seeds destroyed over a 12 month period (X) was determined by multiplying the estimated number of seeds destroyed in 20 minutes by the total number of feeding bouts. Minimum feeding bout duration was taken to be 20 minutes, as this was the observation period used during data collection. Similarly, the projected number of seeds dispersed over a 12 month period (Y) was determined by multiplying the estimated number of seeds dispersed in

20 minutes by the total number of feeding bouts. We then used the relative resource abundance to generate an index to evaluate the relative impact or value of seed predation for each tree species. Therefore, DVI for each tree species was determined using the following equation: $DVI_i = (Y_i - X_i)/RRA_i$.

Relative impact of Meyer's Parrots on pollination of different tree species in the sample area was evaluated using the Pollination Value Index (PVI). PVI was determined by dividing the difference between the estimated total number of flowers destroyed (M) and pollinated (N) over 12 months by the RRA_i of that specific tree species. Therefore, PVI for each tree species was determined using the following equation: $PVI_i = (N_i - M_i)/RRA_i$.

DVI and PVI were used to evaluate the net benefit of seed and flower predation by Meyer's Parrots relative to resource abundance, whereby a positive value indicates a positive contribution to pollination or seed dispersal and the higher the positive or negative value the more significant the relative contribution of Meyer's Parrots.

Results

Feeding activity

A total of 241 road transects were completed, including 992 feeding sightings and 2473 feeding bouts. The diet of Meyer's Parrot observed in this study was distinctly seasonal, comprising 47 food items from 26 tree species in 12 families. Seed predation accounted for 62% of total feeding bouts, of which 42% were ripe seeds. Fig and insect predation were the next most frequent accounting for 13% each. Flower predation accounted for 10% of total feeding activity observed over 12 months, and was distinctly seasonal (August–October). Fruit pulp was consumed regularly as a by-product of seed predation, but was never exclusively targeted. The tree species most utilized by Meyer's Parrot was *Diospyros mespiliformis*, followed by *Kigelia africana*, *Combretum imberbe* and *Ficus sycomorus* (Table 1).

Relative resource abundance

Nineteen (300x20m) resource abundance transects included 1439 trees. The tree species with the highest relative resource abundance in the sample area was *D. mespiliformis*, followed by *Lonchocarpus nelsii*, *Colophospermum mopane* and *C. imberbe* (Table 1). Seven forest habitat types were identified along the road transect. Over 72% (= 380 ha) of the sample area was forest habitat (Table 2).

Table 1 Acronyms of food items recorded in the diet of Meyer’s Parrots, total feeding bouts for each food item, relative resource abundance (RRA_i). (Where: un = unripe seed; r = ripe seed; f = flower; *l* = parasitic Lepidoptera larvae; *h* = Hemiptera and exudate; and *c* = parasitic Coleoptera larvae).

FAMILY	Scientific binomial	Acronym	RRA*i* x 10^{-3}	Food item	Total feeding bouts
ANACARDIACEAE	*Sclerocarya birrea caffra*	SB	535	SBun	15
				SBr	48
				SB*l*	35
APOCYNACEAE	*Carissa edulis*	CE	12	CEr	10
BIGNONIACEAE	*Kigelia africana*	KA	410	KAf	141
				KAun	61
				KAr	111
BOMBACEAE	*Adasonia digitata*	AD	831	ADf	17
				ADun	26
CAESALPINIACEAE	*Guibourtia coleosperma*	GC	227	GCr	68
CLUSIACEAE	*Garcinia livingstonia*	GL	744	GLun	47
				GLr	73
COMBRETACEAE	*Combretum hereroense*	CH	1612	CHc	108
	Combretum imberbe	CI	2902	CIf	22
				Cir	195
	Terminalia prunoides	TP	-	TPr	4
	Terminalia sericea	TS	502	TSr	82
				TSc	72
EBENACEAE	*Diospyros mespiliformis*	DM	4794	DMun	210
				DMr	131
	D. lycoides lycoides	DL	526	DLun	47
				DLr	83
LEGUMINOSAE	*Albizia harveyi*	AlH	-	AlHr	17
	Acacia erioloba	AE	101	AEf	11
				AEun	43
				AEr	18
	Acacia nigrescens	AN	3114	ANf	74
				ANun	26
				ANr	56
	Acacia tortilis heterocantha	AT	49	ATf	12
				ATr	8
	Burkea africana	BA	141	BAun	15
				BAr	18
	Colophospermum mopane	CM	3591	CM*l*	88
				CMh	29
	Lonchocarpus capassa	LC	1188	LCun	8
				LCr	44
	Lonchocarpus nelsii	LN	3877	LNf	11
				LNr	6
MORACEAE	*Ficus burkei thonningii*	FB	697	FBr	91
	Ficus sycamorus	FS	237	FSr	211
	Ficus verruculosa	FV	-	FVr	12
MYRTACEAE	*Syzigium guineense*	SG	-	SGun	19
RHAMNACEAE	*Berchemia discolor*	BD	56	BDun	15
				BDr	52
	Ziziphus mucronata	ZM	38	ZMun	8
				ZMr	32

Table 2 Forest habitat descriptions, habitat sample area and habitat conversion factor (HCF).

Habitat type/Habitat description	Habitat description	Habitat sample area (ha)	Habitat Conversion Factor (HCF)
Riverine forest	Closed canopy dominated by *Diospyros mespiliformis*, *Garcinia livingstonia, Berchemia discolor, Ficus sycamorus* and *Kigelia africana*.	37.04	20.6
Acacia-Combretum marginal woodland	Dominated by *A. nigrescens*, *Combretum imberbe* and *C. hereroense.*	136.943	76.1
Diospyros lycoides marginal woodland	Homogenous *D. lycoides lycoides*.	36.805	20.4
Mopane woodland	Dominated by *Colophospermum mopane* with *C. imberbe* and *A. nigrescens*.	34.425	19.1
Lonchocarpus nelsii sandveld	Homogenous *L. nelsii* on deep sand.	78.463	130.8
Acacia erioloba sandveld	Dominated by *Acacia erioloba*, forming the ecotone between *Acacia-Combretum* marginal woodland and *L. nelsii* sandveld.	16.785	9.3
Terminalia sericea sandveld	Dominated by *T. sericea*, *T. prunoides* and *Guibourtia coleosperma.*	39.449	21.9

Role in seed dispersal

Dispersal rates to the ground of ripe, undamaged seeds were significantly higher for Leguminosae and Combretaceae pods than fleshy fruits (Mann-Whitney U-test: $U = 41.5$, $Z = -2.01$, $p = 0.045$) (Table 3). There was no significant difference in dispersal rate from the canopy when feeding on pods and fruits containing a single seed and multiple seeds (Mann-Whitney U-test: $U = 57.5$, $Z = 1.07$, $p = 0.286$) (Table 3).

The tree species with the highest projected minimum number of ripe, undamaged seeds dispersed to the ground by Meyer’s Parrots included (in order of magnitude): *Ficus sycomorus*, *D. mespiliformis*, *Diospyros lycoides lycoides*, *Berchemia discolor* and *Schlerocarya birrea caffra* (Table 4). Only *S. birrea caffra* benefitted marginally from seed predation by Meyer’s Parrot (Table 4). Based on the DVI, impact of seed predation (in order of magnitude) was most severe for *B. discolor*, *Terminalia sericea*, *Garcinia livingstonia*, *F. sycomorus* and *D. lycoides lycoides* (Table 4).

Potential secondary seed dispersal agents were recorded for all food items consumed by Meyer’s Parrots during this study, included: Impala *Aepyceros melampus*, Greater Kudu *Tragelaphus strepsiceros*, Chacma baboon *Papio ursinus*, African Elephant *Loxodonta africana* and Tree Squirrel *Paraxerus cepapi* during the day, and Porcupine *Hystrix africaeaustralis* and African Civet *Civettictus civetta* at night. Ants and termites, as well as Single-striped Mouse *Lemmiscomys rosalia* and Red Veld Rat *Aethomys chrysophilus*, were also observed foraging in the leaf litter below trees utilized by Meyer’s Parrots.

Role in pollination

Pollination rates were significantly different when feeding on different flowers (Kruskal-Wallis, $F_{3,40} = 29.79$, $p < 0.001$), and were significantly higher when feeding on composite flowers (e.g. racemes) than large pendulous flowers (Table 5). According to PVI, only *Acacia nigrescens* benefitted from flower predation by Meyer’s Parrots and the likely impact of flower predation on pollination (in order of magnitude) was most severe for *K. africana*, *A. digitata*, *C. imberbe* and *Acacia erioloba* (Table 6).

Table 3 Destruction rates, dispersal rates and mean dimensions for 25 food items from 15 tree species (Where: S = seed). Acronyms for food items on Table 1.

		Destruction rate (S/min)			Dispersal rate (S/min)			(HxW)
Food item	n	Mean	±	SE	Mean	±	SE	(mm)
Unripe seeds from fruits with multiple seed kernels								
DMun	21	0.99	±	0.12				21x18
DLun	11	1.67	±	0.28				11x19
KAun	3	1.07	±	0.03				30x80
Unripe seeds from fruits with one seed kernels								
SBun	8	0.38	±	0.04				45x28
GLun	9	4.64	±	1.05				12x13
BDun	4	3.14	±	0.36				17x8
Ripe seeds from fruits with multiple seed kernels								
DMr	18	1.67	±	0.23	0.80	±	0.10	24x22
DLr	21	3.28	±	0.28	1.57	±	0.15	13x20
KAr	17	0.17	±	0.03		±		750x150
Ripe seeds from fruits with one seed kernels								
SBr	4	0.76	±	0.15	0.60	±	0.14	50x30
GLr	12	3.21	±	0.31	0.69	±	0.11	15x12
BDr	7	2.96	±	0.31	0.74	±	0.16	19x10
Ripe seeds and pseudocarp from Moraceae								
FS	20	0.23	±	0.03	0.59	±	0.09	30x26
Unripe seeds from Leguminosae pods (multiple seeds)								
AEun	4	0.91	±	0.16				125x65
ANun	16	1.31	±	0.19				100x15
ADun	5	0.16	±	0.02				110x32
Ripe seeds from Leguminosae pods (multiple seeds)								
AEr	5	0.44	±	0.05	0.36	±	0.04	120X50
ANr	16	1.31	±	0.19	0.86	±	0.14	140x15
Ripe seeds from Combretaceae pods								
CIr	27	3.92	±	0.34	0.90	±	0.15	15x15
TSr	16	3.66	±	0.39	1.78	±	0.27	30x22
GCr	6	2.53	±	0.37	1.43	±	0.29	32x15
Insect larvae feeding on fleshy mesocarp of fruit								
SB-L	10		±		0.45	±	0.06	-
Insect larvae incubating in woody pod								
CH-H	19	4.10	±	0.38	1.40	±	0.20	-
TS-H	11	6.39	±	0.85	2.53	±	0.42	-
CM-L	13	16.32	±	2.43	7.20	±	1.23	-

Table 4 Estimated net dispersal of ripe, undamaged seeds to the ground (corrected for consumption and destruction) for 15 tree species over 12 months, and Dispersal Value Index (DVI) (Where: S = seed). Box indicates net dispersal benefit due to seed predation. Acronyms for food items on Table 1.

			Destroyed		Dispersed			
Food item	Total Feeding bouts	RRA_i x 10^{-3}	S/20min	S/12 mnths	S/20min	S/12 mnths	Net Dispersal	Dispersal Index (DVI)
African Ebony *Diopsyros mespiliformis*								
DMun	210		28.4	5971.7	-	-		
DMr	131	4793.6	37.2	4875.5	17.3	2266.8	-8580.4	-1.8
Sausage Tree *Kigelia africana*								
KAun	61		21.3	1301.3	-	-		
KAr	116	410.0	3.4	395.8	-	-	-1697.1	-4.1
Bird Plum *Berchemia discolor*								
BDun	15		62.7	940.7	-	-		
BDr	62	55.5	59.1	3664.3	14.8	918.6	-3686.4	-66.4
Red Star Apple *Diospyros lycoides lycoides*								
DLun	47		33.4	1568.3	-	-		
DLr	55	525.5	65.5	3604.0	31.4	1728.2	-3444.0	-6.6
Marula *Sclerocarya birrea caffra*								
SBun	15		7.7	114.9	-	-		
SBr	48		15.1	726.0	12.0	576.0		
SB*l*	35	535.0	-	-	9.0	315.0	50.1	$\boxed{0.09}$
African Mangostene *Garcinia livingstonia*								
GLun	47		92.8	4359.6	-	-		
GLr	73	744.2	64.3	4693.8	13.8	1006.9	-8046.4	-10.8
Sycomore Fig *Ficus sycomorus*								
FS	211	237.5	32.9	6947.4	22.0	4640.3	-2307.1	-9.7
Camelthorn *Acacia erioloba*								
AEun	43		22.3	959.6	-	-		
AEr	18	101.4	8.7	156.6	7.2	130.1	-986.1	-9.7
Knobthorn *Acacia nigrescens*								
ANun	26		26.2	680.2	-	-		
ANr	61	3114.4	26.2	1595.9	17.1	1043.4	-1232.8	-0.4
Leadwood *Combretum imberbe*								
CIr	195	2902.3	78.4	15285.3	18.0	3515.8	-11769.4	-4.1
Large False Mopane *Guibourtia coleosperma*								
GCr	68	226.9	50.6	3441.1	28.6	1946.0	-1495.1	-6.6
Silver Clusterleaf *Terminalia sericea*								
TSr	82		73.3	6007.7	35.6	2917.1		
TSc	72	501.9	127.8	9203.7	50.7	3649.5	-11562.0	-23
Russet Bushwillow *Combretum hereroense*								
CHc	108	1612.1	82.0	8850.7	27.9	3015.6	-5835.1	-3.6
Mopane *Colophospermum mopane*								
CM*l*	88	3590.7	326.5	28729.7	144.0	12675.7	-16054.0	-4.5
Baobab *Adansonia digitata*								
ADun	26	830.8	3.2	83.2	-	-	-83.2	-0.1
TOTAL				114157		40345		

Table 5 Estimated destruction and pollination rate for five flower species consumed by Meyer's Parrots. Acronyms for food items on Table 1.

		Destruction rate (FL/min)			Pollination rate (FL/min)			(HxW)
Food item	n	Mean	±	SE	Mean	±	SE	(mm)
KAf	22	1.29	±	0.14	0.00	±	0.00	160x175 (cup-shaped)
ADf	5	0.73	±	0.15	0	±	0	100x120 (pendulous)
ANf	10	1.38	±	0.21	1.81	±	0.32	90 (raceme)
AEf	3	0.67	±	0.14	0.56	±	0.14	15X15 (balls)
CIf	7	2.445	±	0.45	0.775	±	0.26	55x15 (axillary spikes)

Table 6 Pollination Value Index for five flower species consumed by Meyer's Parrots (FL = flower). Acronyms for food items on Table 1.

			Destroyed		Potentially pollinated		
Food item	RRA$_i$ x 10^{-3}	Total Feeding bouts	FL/20 min	FL/12 months	FL/20 min	FL/12 months	Pollination Index (PVI)
KAf	410.0	141	26	3650	-	-	-8.9
ADf	830.8	17	15	249	-	-	-0.3
ANf	3114.4	74	28	2047	36.17	2677	0.2
AEf	101.4	11	13	148	11.29	124	-0.2
CIf	2902	22	49	1076	15.5	341	-0.3

When feeding on *K. africana* and *A. digitata* flowers the base of the corolla was opened to drain the nectar, destroying the ovaries and often causing the corolla to fall to the ground. In addition, by October when most of the flowers had been pollinated, Meyer's Parrots removed any remaining petals, drained the nectar and removed the seeds forming in the ovaries. Even bare ovaries developing into fruit were targeted until they became too hard to open quickly in January. There was no evidence of pollen on head or beak during feeding on *K. africana* and *A. digitata* flowers.

Predation of Leguminosae and Combretaceae flowers (e.g. *A. nigrescens*, *A. erioloba*, *Acacia tortilis*, *Combretum imberbe* and *L. nelsii*) was also destructive, whereby the florets were removed and manipulated by the tongue to remove nectar and pollen, however, not all florets were destroyed (Table 6). Pollen was noted on the head and beak of parrots feeding on all Leguminosae and Combretaceae flowers.

Discussion

Net benefit to seed dispersal

There were no instances in which the Meyer's Parrot played any role in endo- or epi-zoochory, and therefore, played no direct role in seed dispersal beyond the very low probability that seeds they accidentally dispersed from the canopy are consumed and dispersed by potential secondary dispersal agents to microhabitats suitable for germination and establishment. These probabilities are almost impossible to compute and very few studies have examined the importance of secondary seed dispersal due to difficulties in monitoring this multistep process (Vander Wall *et al.* 2005).

The observation of potential secondary seed dispersal agents for all food items established this weak link between Meyer's Parrot feeding activity and forest ecology, whereby a specific tree species would experience net benefit from Meyer's Parrot feeding activity if more seeds were dispersed from the canopy than were destroyed or consumed. In the literature, baboons are confirmed as dispersal agents for *D. mespiliformis* (Lieberman *et al.* 1979), Impala and Greater Kudu for *Acacia* spp. seeds (Miller 1996), and African elephants for *S. birrea caffra, D. mespiliformis, T. sericea, A. erioloba, A. nigrescens, A. tortilis, Guibourtia coleosperma, B. discolor* and *F. sycomorus* (Dudley 2000), thus corroborating this link and the applicability of PVI_i and DVI_i.

Under the assumption of the incidence of effective secondary seed dispersal, only *S. birrea caffra* benefitted marginally from Meyer's Parrot feeding activity. This was due to Meyer's Parrots seeking Red Marula caterpillars (*Mussidia nigrivenella* (Lepidotera, *Pyralidae*)) under the skin of the fruits (Chapter 2; Chapter 9: Boyes and Perrin in review e), thus dispersing significant numbers of undamaged seeds to the ground. *Schlerocarya birrea caffra* likely exhibits elephant-dependent seed dispersal mutualism (Dudley 2000) and Meyer's Parrots could supplement the number of fruits dispersed to the ground by elephants. Predation of unripe *S. birrea caffra* seed kernels by Meyer's Parrots functioned to reduce the net benefit from this non-destructive dispersal of fruit from the canopy. Due to low RRA_i and high destruction rates, feeding activity on *B. discolor* fruit may be significant enough to influence its spatial distribution and abundance. The absence of Meyer's Parrots would likely have a positive influence on the recruitment of this species by increasing the probability those dispersal agents, implicated in endo-zoochory (e.g. Vervet monkeys *Cercopithecus pygerythrus* and Grey Lourie *Corythaixoides concolor*), consume the fruits. All other fleshy fruits most severely affected by Meyer's Parrot seed predation had small seeds (i.e. less than 6mm in diameter), and thus are likely dispersed by diurnal avian frugivores (e.g. starlings *Lamprotornis spp.*) and Peter's Epauletted Fruit Bats *Epomophorus gambianus crypturus*. Any reduction in seed load by Meyer's Parrots would be in direct competition with these plant-targeted dispersal agents, and thus have a negative effect on dispersal and probability of recruitment of that tree. Overall, Meyer's Parrots were estimated to consume or destroy almost three times more seeds than they dispersed to the ground, and thus their function as significant pre-dispersal seed predators far outweighed any primary seed dispersal to the ground. Meyer's Parrots likely have a negative impact on recruitment of fruit-bearing trees in the Okavango Delta.

Consumption of Combretaceae and Leguminosae pods is common to all parrots in the *P. meyeri* superspecies complex studied thus far (Massa 1995; Selman *et al.* 2002, Taylor & Perrin 2006) and the Yellow-faced Parrot (Boussekey *et al.* 2002). Combretaceae pods (e.g. *C. imberbe*) are dependent on wind-dispersal, and therefore, primary dispersal of ripe, undamaged seeds from the canopy by Meyer's Parrots was unnecessary. The high destruction rate of Combretaceae seeds may also be insignificant due to the extremely high seed load on these trees. Leguminous pods are an important food resource in most parrot communities around the world, including *Amazona* and *Ara spp.* in the Amazonian forest (Gilardi & Munn 1998), Lilac-crowned Parrots *Amazona finschi* on the Pacific coast of Central America (Renton 2001), and Scaly-headed Parrots *Pionus maximiliani* in a semi-deciduous forest in south-eastern Brazil (Galetti 1993). No Leguminosae tree species experienced net benefit to seed dispersal from Meyer's Parrot seed predation. *Acacia erioloba* and *A. tortillis* are indehiscent, and Meyer's Parrots facilitated the premature opening of these pods, but were shown to destroy more seeds than they potentially dispersed to the ground. Dehiscent pods in the diet of Meyer's Parrots, including *A. nigrescens*, *A. hebeclada* and *Albizia harveyi*, facilitated their own dispersal, and therefore, any seed predation was counter-productive.

Net benefit to pollination

Meyer's Parrots play a predominantly counter-productive role in pollination, whereby all flower predation was destructive and pollination of Leguminosae and Combretaceae florets was subject to part of the inflorescence remaining. Pollen on the head and beak during predation of Leguminosae and Combretaceae florets established the link with pollination. They were, therefore, found to play a minor role in the pollination of several Leguminosae and Combretaceae flowers that seasonally occur in their diet, including: *A. nigrescens*, *A. erioloba*, and *A. tortilis*. Other tree species in the diet of Meyer's Parrot that could potentially benefit include *A. hebeclada*, *C. imberbe*, *L. nelsii*, and *C. hereroense* (Chapter 2). Flower destruction rates, however, far outweighed the number of flowers potentially pollinated during feeding activity, except in the case of *A. nigrescens* which was the most important Leguminosae flower in their diet.

Far more important in the diet of Meyer's Parrot were *K. africana* and *A. digitata* flowers, which have large pendulous flowers (up to 15cm in diameter) likely adapted for pollination by specialist pollinators such as Peters' Epauletted Fruit Bat (Taylor 2000). Peters' Epauletted Fruit Bats still remove the corolla of the *K. africana* and *A. digitata* flowers when extracting nectar, but using their long snout and tongue suited to nectar extraction, they do not damage the reproductive apparatus of the flowers (Taylor 2000; Boyes *pers obs.*). Due to high flower predation, no contact with reproductive apparatus, high predation of seeds forming in the ovaries, and low RRA_i, the relative impact of Meyer's Parrots on the pollination of *K. africana* flowers was almost 30 times greater than on *A. digitata* flowers.

Meyer's Parrots, like most parrots, are characteristically very powerful, destructive foragers, and thus flower adaptations for specialist pollinators have proven to be counter-productive. *Eucalyptus* flowers pollinated by Purple-crowned Lorikeets *Glossopsitta porphyrocephala* (Hopper & Burbridge 1979) have an open inflorescence similar to Leguminosae and Combretaceae florets. Similarly, *Erythrina fusca* flowers pollinated by two Neotropical parrot species (Cotton 2001) have relatively open flowers offering access to pollen and nectar. *Erythrina fusca* flowers were, however, destroyed by five other Neotropical parrots species, demonstrating that composite flowers with open florets are optimal for pollinations by parrots. Any restrictions to access will encourage parrots to destroy the reproductive apparatus of the flower to gain access to pollen and nectar.

Overall, Meyer's Parrots play a counter-productive role in pollination and based on lack of adaptations for nectivory (e.g. longer tongues) in other *Poicephalus*, the same is likely true for them too.

Implications

Two important points emerge from this study. First, feeding activity by Meyer's Parrots is likely counter-productive to pollination, seed dispersal and forest recruitment in subtropical Africa, whereby only *Schlerocarya birrea caffra* benefited marginally from seed predation, and only tree species with composite flowers (e.g. *Acacia nigrescens*) likely benefitted marginally from flower predation. Second, Meyer's Parrots are powerful destructive foragers with no mutualistic relationship with any plant species and are able to bypass specialist plant adaptations for pollination (e.g. large pendulous flowers) and seed dispersal (e.g. hard indehiscent pods and seed kernels). More work is required on the role of other large frugivores in primary dispersal from the forest canopy to fully appreciate the significance of seed predation by Meyer's Parrots on forest recruitment in the Okavango Delta.

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Chapter 7:

Daily activity pattern of Meyer's Parrot (*Poicephalus meyeri*) in the Okavango Delta, Botswana[1]

Abstract. Most parrots from Africa, Australasia and the Neotropics have bimodal daily activity patterns due to physiological restrictions (e.g. limited crop size and digestive requirements) and climatic constraints (e.g. seasonal temperature fluctuations). We monitored the daily flight, feeding and non-feeding activity patterns of Meyer's Parrots (*Poicephalus meyeri*) over 24 months at two study sites for correlation with climatic conditions (e.g. ambient temperature) to extend this generalization. Nutritional value of food resources was compared to consumption rates to determine the time required to achieve basal daily protein and energy requirements. Daily feeding activity patterns were strongly correlated with seasonal ambient temperature fluctuations, demonstrating avoidance of high and low temperatures. Feeding activity between 08h30 and 11h00 was likely obligate, while feeding between 16h00 and 18h30 was seasonally required to achieve daily protein requirements. Daily protein and energy requirements, mean consumption rates for available food resources, digestive requirements in the middle of the day, and fixed crop size likely facilitated the observed bimodality in the daily feeding activity pattern. The bimodal daily flight activity pattern was a function of communal roosting. Breeding activity had no significant impact on the feeding activity pattern at population level. All *Poicephalus* parrots likely have bimodal activity patterns due to their daily protein and digestive requirements. Most parrots are likely constrained in their daily activity patterns by similar physiological and climatic factors. Surveying feeding Meyer's Parrots between 08h30 and 11h00 in representative habitat types would yield a useful index of relative abundance between different locations and over time.

Introduction

Understanding the daily activity pattern of parrots is important in estimating population size and dynamics (Cassagrande and Beissinger 1997). To maximize repeatability and precision and detection probability of parrots requires an understanding of breeding seasonality (i.e. females in nest cavities during breeding season), mobility of individuals (i.e. enumerating individuals twice due to high

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[1] Formatted for *Emu* – Austral Ornithology, Royal Australasian Ornithologists' Union: Boyes and Perrin (in review) Daily activity pattern of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana.

mobility), and animal behaviour (e.g. counting during the middle of the day when parrots are hidden in canopy) (Collinson 1985; Cassagrande and Beissinger 1997; Marsden 1999). Aided by their bright colours and conspicuous contact calls, most studies infer daily activity patterns of parrots indirectly from survey data on their flight activity, (Marsden 1999; Salinas-Melgoza and Renton 2005). Survey data on flight activity patterns of parrots have three important sources of bias, including bias towards sighting large flocks departing and returning to communal roosts (Gilardi and Munn 1998), bias towards above-canopy flight characteristics of large flocks (Marsden 1999), and varying detectability of individuals at certain times of the day (Salinas-Melgoza and Renton 2005). Marsden (1999) cautioned that structural habitat characteristics could also introduce bias, whereby flight activity surveys may overestimate the importance of disturbed habitat. Here we evaluated daily flight, feeding and non-feeding (e.g. socializing or roosting) activity patterns to ascertain time period and daily activity best suited to estimating Meyer's Parrot *Poicephalus meyeri* population dynamics between locations.

African deforestation rates are the highest in the world, and all *Poicephalus* parrot metapopulations are likely near-threatened by habitat loss and the compounding influence of the wild-caught-bird trade (Chapter 12: Boyes and Perrin in review a). Range reduction has been recorded in all *Poicephalus* parrots studied and surveyed in southern Africa (Boyes 2006a,b; Chapter 12). Most records of the population status of other Poicephalus parrots pre-date the chronic loss of forest cover in over 20 range states (Chapter 12). Therefore, it is a conservation priority to derive census techniques with high repeatability and highest probability of encountering Poicephalus parrots and other African parrots.

Meyer's Parrots are the smallest of the *Poicephalus* parrots and have the widest distributional range of any African parrot, extending throughout subtropical Africa from north-eastern South Africa to the southern Sudan (Snow 1978; Forshaw 1989; Juniper & Parr 1998). There are six *P. meyeri* subspecies, of which *P. m. damarensis* and *P. m. transvaalensis* are reported to overlap in the Okavango Delta. They form a superspecies with six of the nine *Poicephalus* species (Snow 1978; Rowan 1983). Meyer's Parrots are generalist pre-dispersal seed predators that track food resource availability within a wide suite of potential food item, including ripe and unripe seeds, figs, arthropod larvae, fruit pulp, and flowers (Chapter 2: Boyes and Perrin in review b). Their breeding season is predominantly during the winter dry season between February and July (Chapter 9: Boyes and Perrin in review c).

All *Poicephalus* parrots studied thus far have bimodal daily flight activity patterns, whereby flight activity peaks in the early morning and late afternoon (Skead 1964; Massa 1995; Wirminghaus *et al.* 2001; Boussekey *et al.* 2002; Symes and Perrin 2003; Taylor and Perrin 2004). Bimodality has also been reported in the daily activity patterns of Neotropical parrots (Snyder *et al.* 1987; Lindsey *et al.*

1991; Pittier and Christianson 1995; Cassagrande and Beissinger 1997; Pizo *et al.* 1997; Gilardi and Munn 1998; Salinas-Melgoza and Renton 2005; Masello *et al.* 2006), Australasian parrots (Marsden 1999; Marsden and Fielding 1999; Robinet *et al.* 2003; Cameron 2005), Mexican parrots (Renton and Salinas-Melgoza 1999), and other African parrots (i.e. *Psittacus* and *Agapornis*) (Chapman et al. 1989; Warburton and Perrin 2005; Nditkia and Perrin 2006). Avoidance of heat stress in the middle of the day and breeding activity, have been put forward as physiological factors contributing to this bimodal activity pattern (Gilardi and Munn 1998; Cameron 2005; Salinas-Melgoza and Renton 2005). Cameron (2005) found that Glossy Black Cockatoos (*Calyptorhynchus lathami*) responded to high temperatures exceeding 30ºC by ceasing feeding and moving to shade. A digestive passage rate for avian seed predators estimated at between 40–100 minutes (Klasing 1998) likely necessitates secondary roosting during the middle of the day (Salinas-Melgoza and Renton 2005). Dietary protein and energy requirements in relation to consumption rates for available food resource and fixed crop size are physiological constraints that may significantly influence the daily activity pattern (Klasing 1998; Symes and Perrin 2003). Due to the high protein and energy content of their food resources bimodality is likely unnecessary for *Poicephalus* parrots (Symes and Perrin 2003; Taylor 2002). The primary objective of our study was to evaluate the influence of physiological constraints on the daily feeding activity patterns of Meyer's Parrots to better understand this behaviour in the sub-family Psittacinae (Peters 1940).

Rainfall seasonality and food resource availability have been put forward as environmental factors that significantly impact daily activity patterns (Cameron 2005; Salinas-Melgoza and Renton 2005). In the African subtropics, where *Poicephalus* parrots predominate, there are distinct seasons with substantial fluctuations in temperature, rainfall and food resource availability (Gautier-Hion & Michaloud 1989; Wirminghaus *et al.* 2001). Based on dietary studies of African parrots there is clear evidence that all three continental genera track resource availability (Chapman *et al.* 1993; Wirminghaus *et al.* 2001; Selman *et al.* 2002, Symes and Perrin 2003; Taylor and Perrin 2006; Chapter 2). The secondary objective of our study was to evaluate the influence of environmental factors on the daily feeding activity patterns of Meyer's Parrots.

Methods

Study population

Our study population was the significant Meyer's Parrot population in the Okavango Delta, Botswana (Wirminghaus 1997). The study was conducted at two sites: Vundumtiki Island located in the north-eastern part of the delta, and Mombo Camp off the northern peninsula of Chief's Island (Figure 1). Both study sites were wilderness areas with limited human impact or disturbance to habitat or animal behaviour. All representative forest habitat types were identified at Vundumtiki and Mombo between July 2003 and August 2004 when formal data collection commenced.

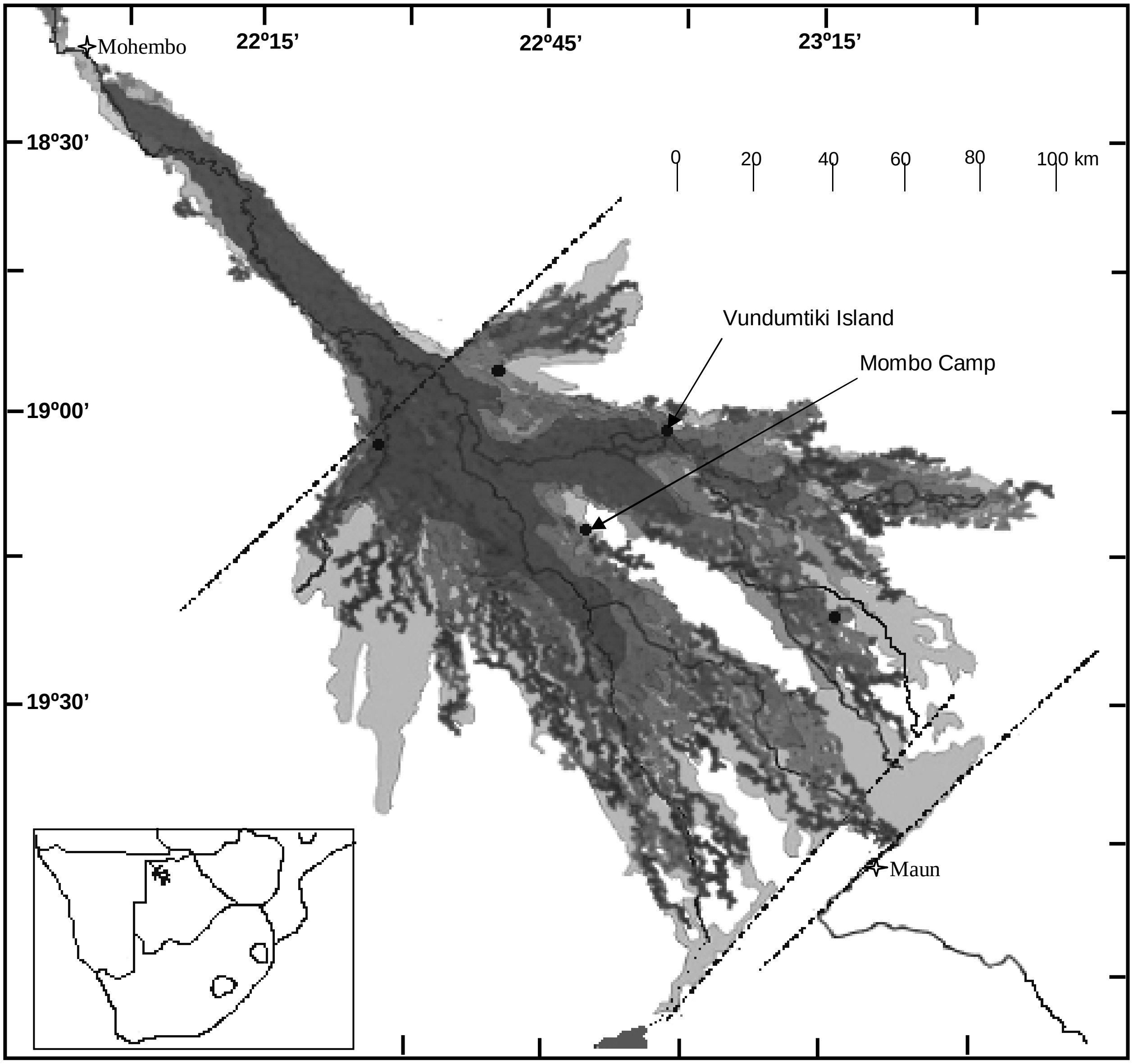


Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

Climatic conditions

Climatic conditions in the Okavango Delta are distinctly seasonal, comprising a wet season (November–March) and dry season (April–October). Mean annual rainfall is 450-560mm (Ellery *et al.* 2003; Wolski and Savenije 2006). During the annual flood the area covered by water expands from its annual low of 2500–4000km^2 (February–March) to its annual high of 6000–12000km^2 (August–September) (Figure 1). Arrival of the annual flood lags the rainy season and follows one or two months after the end of rainfall in the region (Gumbricht *et al.* 2001; Ellery *et al.* 2003).

Rainfall was monitored daily using a rain gauge over the entire study period. The extent of the flood was monitored using flow rate data from Mohembo, at the entrance of the panhandle (Figure 1), and calibrated to the study sites by recording first significant increment in water level on a measuring pole in permanent water as the start of the flood at that study site. Daily minimum and maximum temperatures were recorded in the shade at Vundumtiki and Mombo using a capillary thermometer.

DALLAS Thermochron data loggers (Fairbridge Technologies 2006) were used to measure daily ambient temperature fluctuations. Mean ± SE plots for daily ambient temperatures were generated for different time intervals (e.g. 30min, 40min and 50min) over three months to identify an interval that best represent daily temperature fluctuations.

Sampling design

Data collection was conducted at Vundumtiki from August 2004 to July 2005 and February 2007 to August 2007, and at Mombo from August 2005 to January 2006. Onset and cessation of breeding activity was also monitored over this period.

At Vundumtiki: To standardize spatial distribution of Meyer’s Parrot feeding observations, the total sample area was defined as the area 100m either side of the 26.2 km standardized road transect. The same observer and vehicle travelling at 15–20 km/h with an open top were used for all road transects.

At Mombo: Due to time constraints and logistical difficulties a standardized road transect was not established, however, vehicle travelling speed, observer, transect width, sampling frequency, and transect duration were standardized to the regime used at Vundumtiki. Feeding census duration in the Mombo area was limited to two and a half hours after departure from camp. This was the average time taken to complete the Vundumtiki census route.

Road transects were conducted five times a week on different days from start to finish. A systematic sampling strategy was used for the temporal distribution of feeding observations, whereby six daytime temperature time periods were established (refer to *Climatic conditions*). Road transects were conducted in all six time periods before a specific time period was sampled again. The road transects conducted in both study sites were representative of the Okavango Delta system, as all forest habitat types outlined by Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000) were represented at Vundumtiki and/or Mombo.

Feeding activity pattern

Feeding activity pattern was monitored by direct observations in the field. Meyer's Parrots are lingual feeders (i.e. vocalize constantly during feeding), and thus were detected by following their vocalizations. The following data were recorded at each sighting: time of day, location, habitat type, tree species, food item type, and number of feeding bouts. A feeding bout was defined as an individual within a flock, or solitary, feeding on a specific food item. Food item types were described according to the tree species and classified according to the part consumed and fruiting stage, and included: ripe (r) and unripe (un) seeds from fruits or pods; flowers (f); pseudocarp and seeds of figs (p); and fruit pulp from fleshy fruits (fr). Arthropod food items were classified according to the host tree species and their family, and included: parasitic Hemiptera larvae (h); parasitic Lepidoptera caterpillars (l); and parasitic Coleopteran larvae (c). Arthropod food items were identified by inspecting all potentially-infested dietary (e.g. pods and fruits) and non-dietary (e.g. bark and leaves) food items consumed or inspected by Meyer's Parrots over the study period. Tree nomenclature followed Van Wyk and Van Wyk (1997) and Palgrave (2002).

Flight and non-feeding activity pattern

Flight activity and non-feeding activity, including roosting behaviour and socializing, was monitored during road transects. The following data were recorded: time of day, location, habitat type, flock size and signs of heat stress (e.g. panting and drooping wings).

Fruit consumption rates

Fruit consumption rates were estimated on road transects. Observation time was limited to 20 minutes due to time constraints in completing the road transect. Boyes and Perrin (Chapter 2) found that

Meyer's Parrots consumed fruit pulp predominantly as a byproduct of seed predation (i.e. consuming fruit pulp while extracting the seed kernel). Therefore, consumption rates were estimated for both seeds and fruit pulp. All observations were made with a 30x spotting scope when visibility was optimal. The same observer was used for all observations.

Mean consumption rate (C) was calculated for each sighting by dividing the multiple of the total number of food units consumed (n) by the sample period (t). One food unit was either all the seeds in a fruit or pod or all the fruit pulp. The sample period was the longest period possible within the 20 minute observation period. Parrots frequently waste food material during feeding activity (Symes and Perrin 2003). Therefore, at each sighting we estimated the mean proportion of seeds (EMP_s) and fruit pulp (EMP_{fr}) consumed in increments of 0.1 between 0 - 1, whereby consuming one food unit meant feeding on all the seeds inside a pod or fruit or all the fruit pulp. From this, we could estimate mean consumption rate for seeds and fruit pulp at each sighting using the following equation: $C_j = (n_j \times [EMP_s \text{ or } EMP_{fr}])/t_j$, where n_j is the number of fruit consumed in observation period j. Where possible the proportion of each seed consumed was estimated through observation during feeding or subsequent inspection on the ground, and the number of seeds consumed adjusted. For analysis, fruit handling times were then taken as the inverse of the fruit consumption rate.

Daily dietary requirements

Daily metabolizable energy requirements (E) of a free-living adult parrots from body weight (BW) was determined using the following equation: $E_i = 959 * kgBW_i^{0.73}$ (Koutsos *et al.* 2001). Koutsos *et al.* (2001) derived equations from estimates of basal metabolic rate and activity costs (Buttemer et al. 1986; McNab 1988; Williams *et al.* 1991). Median body mass for male Meyer's Parrots (=121.2g) reported by Rowan (1983) was used in our study. Therefore, the daily energy requirement of a free-living Meyer's Parrot is 205.48 kJ day^{-1}.

Daily protein requirements (P) for maintenance of an adult male Meyer's Parrot from BW was determined using the following equation: $P_i = 3489 * kgBW^{0.58}$ (Klasing 1998). Therefore, the daily protein requirement of a free-living Meyer's Parrot is 1024.2 mg day^{-1}.

Nutritional analyses of the different food items were done by Selman *et al.* (2002), Taylor (2002), Symes and Perrin (2003), and Ndithia and Perrin (2006) using standardized methods (Helrich 1990). Dry weight was obtained from samples (n = 20) of seeds taken from the study site.

Data analyses

Kolmogorov-Smirnov (K-S) and Lilliefors tests were used to test for normality. Spearman rank correlations (r_s) were used to test for relationships between total number of feeding bouts in each time period and mean temperature, rainfall, flood level, and total number of food item available each month. Mann-Whitney U-tests were used to look for significant differences in daily feeding activity between Vundumtiki and Mombo, and between the breeding and non-breeding season. The Bonferroni procedure was used to adjust significance levels to control Type 1 error rates in multiple testing situations. Kruskal-Wallis ANOVA was used to test for significant difference between monthly feeding activity in the six time periods. Statistical analysis followed Quinn and Keough (2002) and STATISTICA 7.1 (Statsoft (USA) 2006). Mean consumption rates were related to nutritional value and estimates of daily protein and energy requirements to calculate estimated time required per day for free-living Meyer's Parrots to achieve these dietary requirements. Probability of encountering Meyer's Parrots in flight, feeding and engaged in non-feeding activities (e.g. roosting) at the population level was estimated as the proportion of the total observations along the standardized road transect over 24 months and between different time periods.

Results

Time periods

We established six distinct periods of daytime temperature for analysis of daily activity patterns, including 06h00-08h30 (a); 08h30-11h00 (b); 11h00-13h30 (c); 13h30-16h00 (d); 16h00-18h30 (e); and 18h30 to sunset (f) (Figure 2).

Daily activity pattern

Over the 24-month study period, 480 road transects were completed, during which a total of 5047 parrots were observed feeding, 1568 were observed roosting or socializing, and only 984 were observed in flight (Figure 3). Sighting frequency was significantly higher at Mombo (μ = 12.14) than Vundumtiki (μ = 10.02) (U = 5.0; Z = -3.27; p-level = 0.001). Sighting frequency was also significantly higher during the non-breeding season (μ = 11.23) than breeding season (μ = 9.88) (U = 28.0; Z = 2.54; p-level = 0.011) (Figure 3).

Due to lack of relief in the landscape and below canopy flight behaviour, Meyer's Parrots were only observed in flight when crossing the road transects or when flying over open floodplains or grasslands. Flight activity was bimodal and peaked in the early morning (33%; n = 323) and late afternoon (39%; n = 375) prior to and after feeding activity (Figure 3).

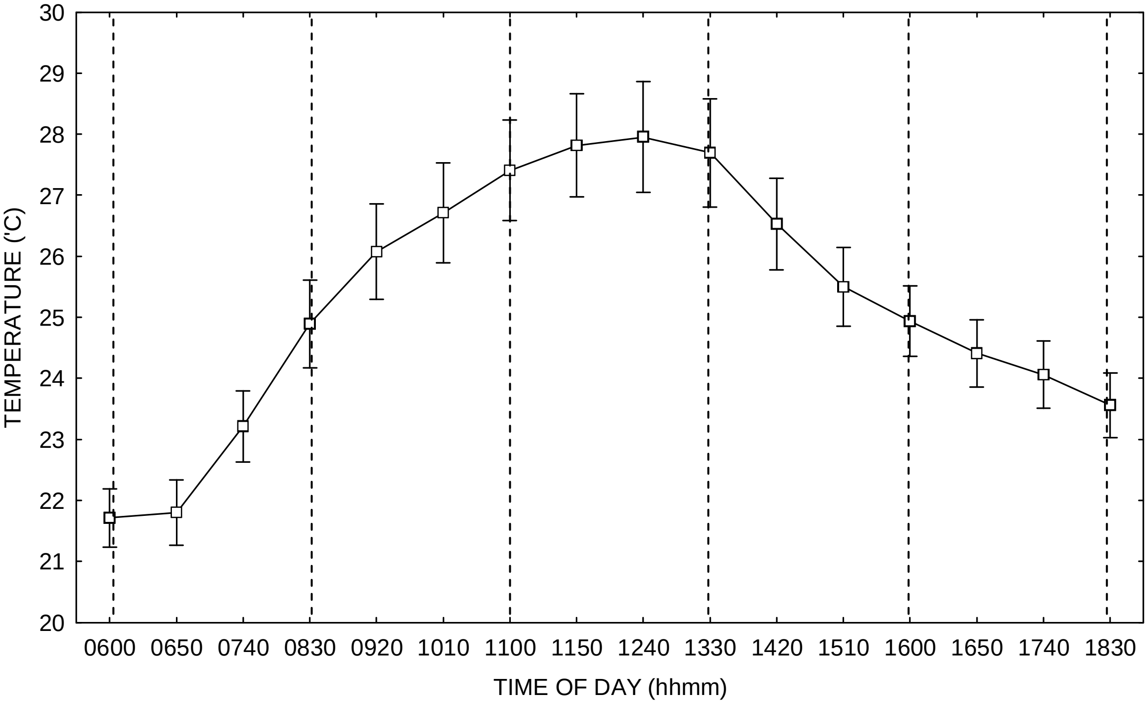


Figure 2: Mean ± SE daytime ambient temperature fluctuations recorded using temperature data loggers to illustrate temperature fluctuations within different time periods between March and June 2007.

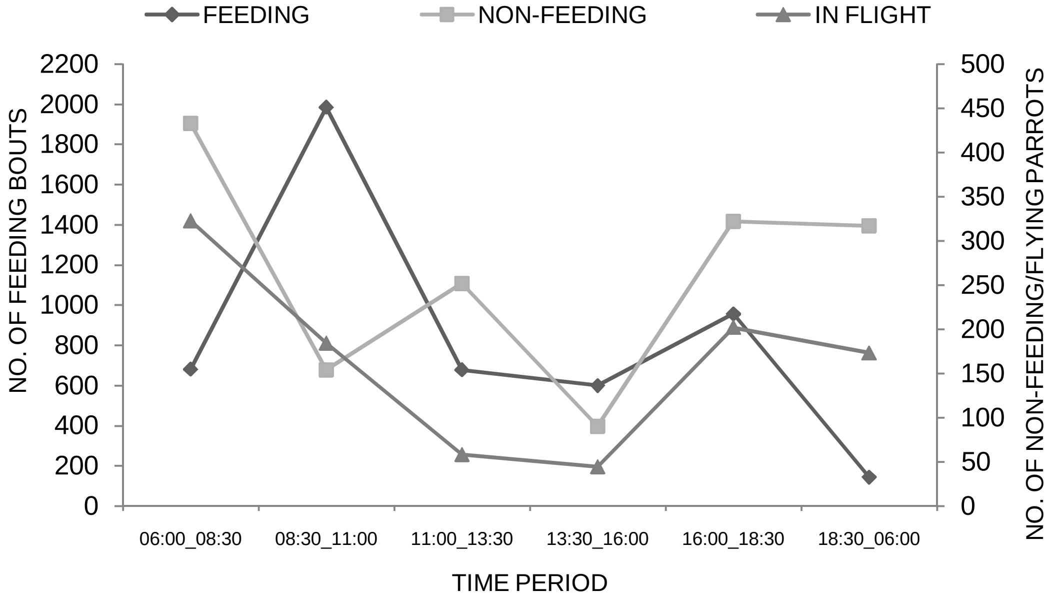


Figure 3: Total number of feeding, non-feeding and flying parrots sighted in each time period over the entire study period

Non-feeding activity was trimodal (Figure 3) and focussed on primary and secondary roosting behaviour in conjunction with socializing at morning and afternoon activity centres. Activity centres were typically *Combretum imberbe* or *Acacia nigrescens* snags (i.e. dead trees) in an east-oriented forest gap with good sunlight. Activities during socializing, included preening, allo-preening and frequent and synchronous vocalizations. Over 41% (n = 639) of non-feeding activity was observed between 16h00 and sunset when Meyer's Parrots were preparing for roosting (Figure 3). After socializing at morning activity centres, Meyer's Parrots dispersed in pairs in different directions. During feeding they gradually aggregate due to vocalizations and information-sharing, resulting in small flocks gathering at secondary roosts during the middle of the day. Non-feeding activity during the middle of the day was hard to monitor due to cryptic way in which Meyer's Parrots utilize secondary roost sites.

Over 39% (n = 1992) of feeding activity was observed between 08h30 and 11h00, with a second peak comprising 19% (n = 956) of total feeding bouts between 16h00 and 18h30 (Figure 3). There was a significant difference between monthly feeding activity in the six time periods (Kruskal-Wallis ANOVA: H (5, N= 144) =87.711; $p < 0.001$) (Figure 3).

Environmental factors

Eleven primary forest habitat types representative of both study sites were identified, including: Riverine forest; *Acacia-Combretum* marginal woodland; *Diospyros lycoides* marginal woodland; *Hyphaene petersiana* woodland; *Lonchocarpus nelsii* sandveld; *Acacia erioloba* sandveld; *Terminalia sericea* sandveld; *Acacia tortilis* sandveld; *Phoenix reclinata* thickets; and *Ficus verruculosa* thickets. *Lonchocarpus nelsii* sandveld and *Acacia erioloba* sandveld were only represented in the Vundumtiki study area, while *Acacia tortilis* sandveld, *Hyphaene petersiana* woodland and *Phoenix reclinata* thickets were only represented in the Mombo study area. *Ficus verruculosa* thickets were only represented along channels in both study areas. Although not proven with empirical data, the habitat mosaics at Vundumtiki and Mombo were significantly different. The study sites were representative of the Okavango Delta system, as all forest habitat types outlined by Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000) were represented at Vundumtiki and/or Mombo However, the only significant difference between feeding activity patterns at Mombo and Vundumtiki were recorded between 08h30 and 11h00.

There was a significant difference in feeding activity between 08h30 and 11h00 at Vundumtiki and Mombo over the same period (Table 1). Breeding activity had no significant influence on feeding activity at any time of day; however, if Bonferonni is ignored, the results indicate that Meyer's Parrots had to feed more between 13h30 and 16h00 during the breeding season. There was no clear correlation between the feeding activity pattern and monthly rainfall and flow rate of the flood (i.e. degree of inundation) (Table 2; Figure 4). There was, however, a significant negative correlation between monthly rainfall and feeding activity between 11h00 and 16h00 (Table 2).

Table 1: Mann-Whitney U-test results comparing daily feeding activity between Vundumtiki and Mombo, and between the breeding and non-breeding season (Significant at $p < 0.0083$ due to Bonferonni procedure for multiple testing)

	VUNDUNTIKI vs MOMBO			BREEDING vs NON-BREEDING		
Time period	U	Z	p-level	U	Z	p-level
06h00-08h30	23	2.07	0.039	30	2.34	0.019
08h30-11h00	7	-3.13	0.002	69.5	-0.03	0.977
11h00-13h30	47.5	-0.43	0.665	44.5	-1.49	0.135
13h30-16h00	49.5	0.30	0.764	32	-2.23	0.026
16h00-18h30	51	-0.20	0.841	57.5	0.73	0.464
18h30-Sunset	47	-0.47	0.641	41	1.70	0.089

Table 2: Spearman Rank Correlations (r_s) correlating monthly rainfall (mm), flood flow rate (cusecs) and number of food item available that specific month with total number of feeding bouts in each time period month-to-month (Significant at $p < 0.0083$ due to Bonferonni procedure for multiple testing)

		RAINFALL			FLOOD			FOOD ITEM AVAILABILITY		
	n	r_s	t(n-2)	p-level	r_s	t(n-2)	p-level	r_s	t(n-2)	p-level
06:00_08:30	24	0.376	1.903	0.070	-0.050	-0.235	0.816	0.238	1.148	0.263
08:30_11:00	24	-0.080	-0.379	0.709	-0.182	-0.870	0.394	-0.162	-0.770	0.449
11:00_13:30	24	-0.607	-3.581	0.002	0.272	1.324	0.199	-0.564	-3.204	0.004
13:30_16:00	24	-0.697	-4.556	<0.001	0.481	2.577	0.017	-0.483	-2.590	0.017
16:00_18:30	24	0.468	2.486	0.021	0.143	0.676	0.506	0.623	3.738	0.001
18:30_06:00	24	0.311	1.532	0.140	-0.296	-1.456	0.160	0.100	0.473	0.641

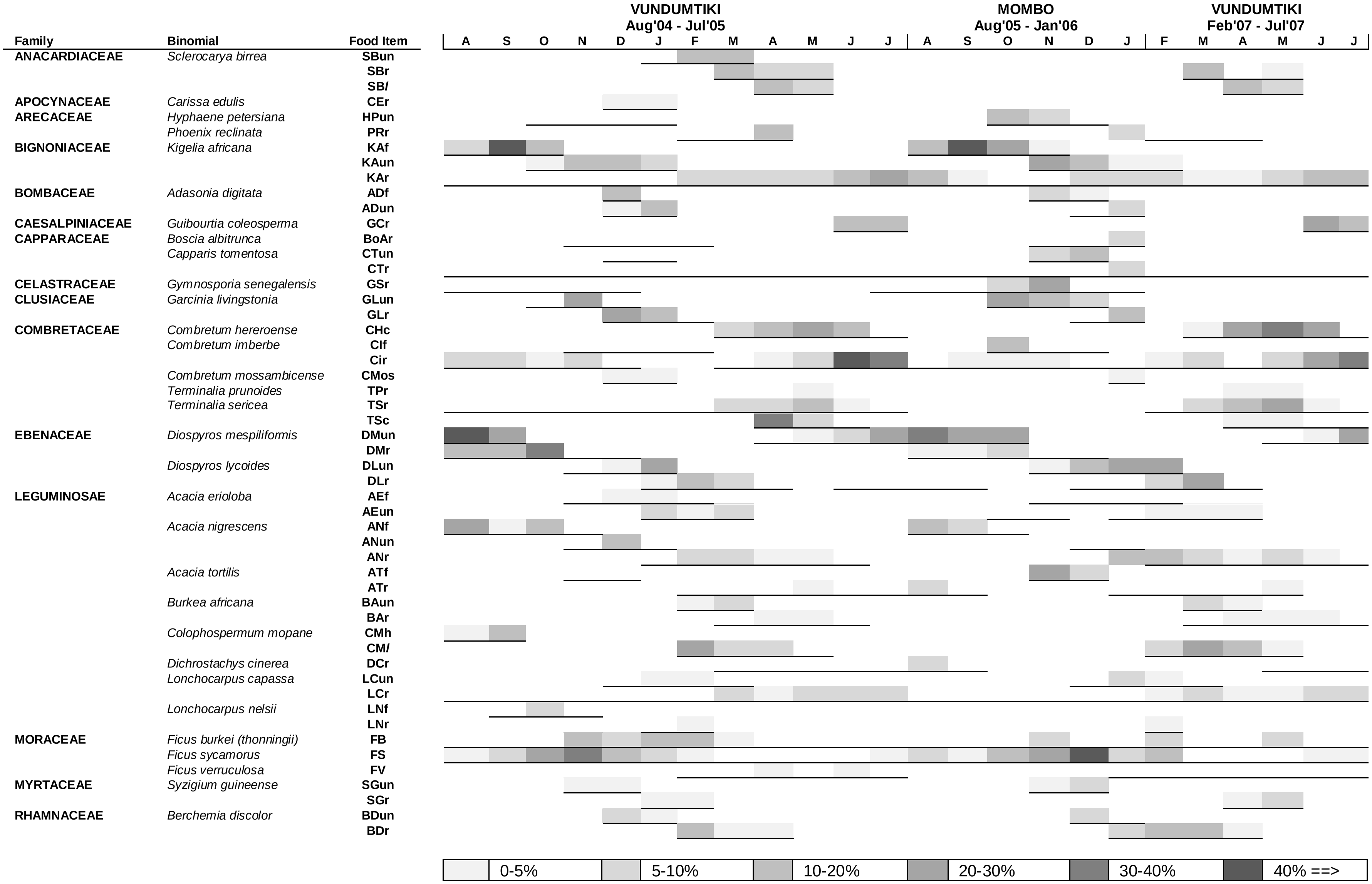
There was a significant negative correlation between monthly food item availability and feeding activity between 11h00 and 13h30, and a significant positive correlation between availability and feeding activity between 16h00 and 18h30 (Table 2). As can be seen in the regular pattern between years, the feeding activity pattern of Meyer's Parrots was distinctly seasonal (Table 3), including 71 food items from 37 tree species in 16 families (Chapter 2). *Grewia spp.*, *Albizia harveyi*, *Acacia hebeclada* and *A. sieberiana* were omitted from the feeding activity pattern due to low frequency in their diet. *Acacia tortilis* seeds and flowers, unripe *Hyphaene petersiana* nuts, *Phoenix reclinata* fruits, and *Dichrostachys cinerea* seeds and flowers were likely under-sampled, as these tree species were rare at Vundumtiki and abundant at Mombo, where their fruiting and flowering period (February to July) was not sampled.

Feeding activity between 11h00 and 16h00 had a significant negative correlation with ambient temperatures over the entire study period (Table 4), whereby as temperatures increase feeding activity decreases (Figure 4). Over this period feeding activity all but stopped when maximum temperatures rose to between 36°C and 40°C (Figure 4). There were, however, no signs of heat stress in Meyer's Parrots roosting during the middle of the day. There were no significant correlations between feeding activity between 08h30 and 11h00 and ambient temperature (Table 4). Feeding activity between 18h30 and sunset was positively correlated with temperature (Table 4), which was positively correlated with day length ($r_s = 0.837$; $n = 24$; $t(n-2) = 4.82$; $p < 0.001$). Similarly, feeding activity between 06h00 and 08h30 was positive correlated with mean ambient temperature (Table 4). There was no correlation between feeding activity in the early morning and day length ($r_s = 0.557$; $n = 24$; $t(n-2) = 2.12$; $p < 0.0594$).

Physiological factors

Our study demonstrated that feeding on any food resource it takes Meyer's Parrots 10–90 minutes to achieve field metabolic energy requirements, and 5–43 minutes to achieve basal metabolic protein requirements (Table 5).

Table 3: Food item calendar for Vundumtiki and Mombo: % Total feeding bouts observed in specific month (shading & key) and monthly fruiting/flowering phenology (solid line). Food item acronyms: First two letters of scientific binomial and code for food item type, where: un = unripe seed, r = ripe seed, f = flower, h = Hemipteron larvae, l = lepidopteron larvae, c = coleopteron larvae.



Family	Binomial	Food Item
ANACARDIACEAE	*Sclerocarya birrea*	SBun
		SBr
		SB*l*
APOCYNACEAE	*Carissa edulis*	CEr
ARECACEAE	*Hyphaene petersiana*	HPun
	Phoenix reclinata	PRr
BIGNONIACEAE	*Kigelia africana*	KAf
		KAun
		KAr
BOMBACEAE	*Adasonia digitata*	ADf
		ADun
CAESALPINIACEAE	*Guibourtia coleosperma*	GCr
CAPPARACEAE	*Boscia albitrunca*	BoAr
	Capparis tomentosa	CTun
		CTr
CELASTRACEAE	*Gymnosporia senegalensis*	GSr
CLUSIACEAE	*Garcinia livingstonia*	GLun
		GLr
COMBRETACEAE	*Combretum hereroense*	CHc
	Combretum imberbe	CIf
		CIr
	Combretum mossambicense	CMos
	Terminalia prunoides	TPr
	Terminalia sericea	TSr
		TSc
EBENACEAE	*Diospyros mespiliformis*	DMun
		DMr
	Diospyros lycoides	DLun
		DLr
LEGUMINOSAE	*Acacia erioloba*	AEf
		AEun
	Acacia nigrescens	ANf
		ANun
		ANr
	Acacia tortilis	ATf
		ATr
	Burkea africana	BAun
		BAr
	Colophospermum mopane	CMh
		CM*l*
	Dichrostachys cinerea	DCr
	Lonchocarpus capassa	LCun
		LCr
	Lonchocarpus nelsii	LNf
		LNr
MORACEAE	*Ficus burkei (thonningii)*	FB
	Ficus sycamorus	FS
	Ficus verruculosa	FV
MYRTACEAE	*Syzigium guineense*	SGun
		SGr
RHAMNACEAE	*Berchemia discolor*	BDun
		BDr

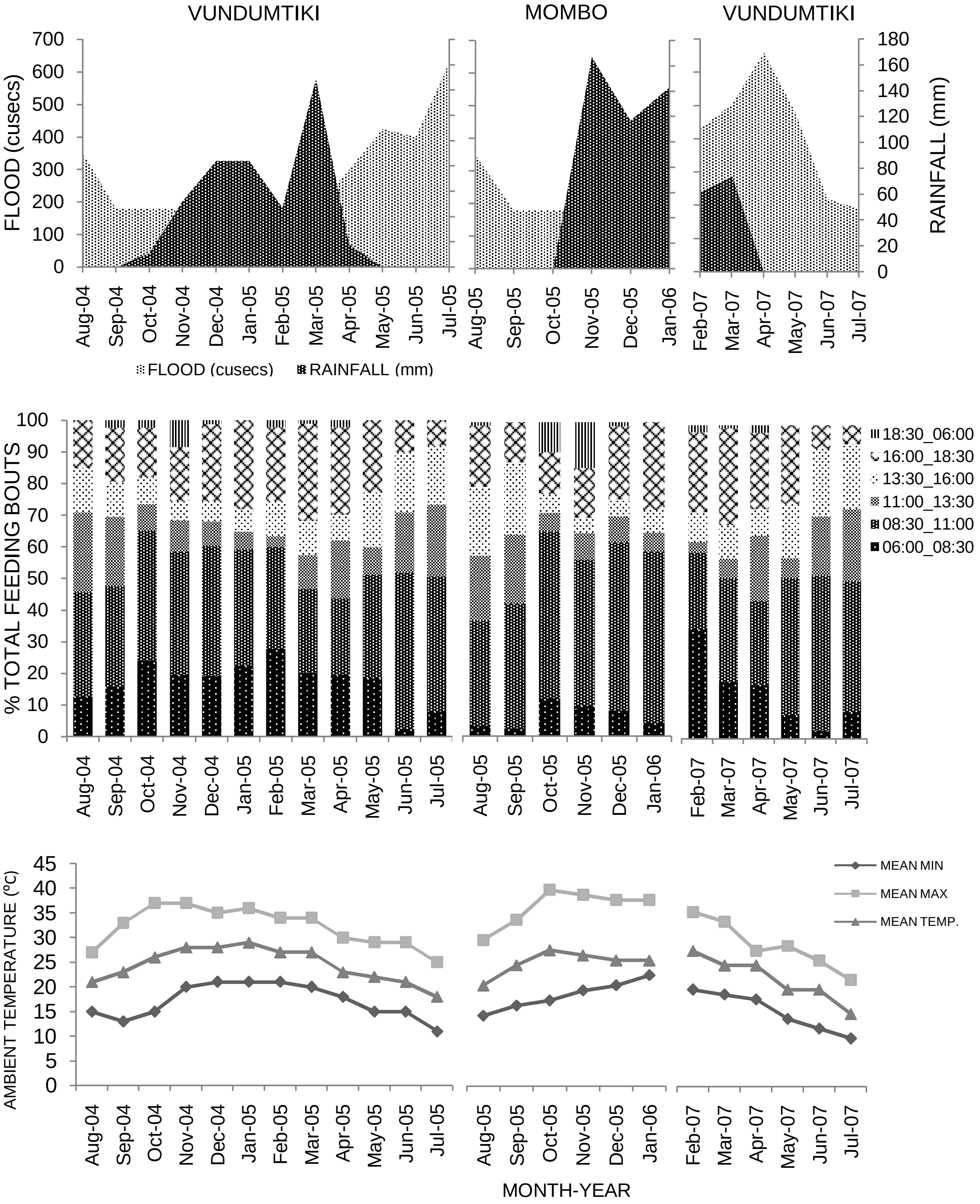


Figure 4: (a) Rainfall and flood seasonality; (b) Percentage total feeding bouts in each time period; (c) Mean daily ambient temperatures at Vundumtiki and Mombo over 24 months.

Table 4: Spearman Rank Correlations (r_s) correlating mean monthly maximum, median and minimum temperatures (°C) with total number of feeding bouts in each time period month-to-month (Significant at $p < 0.0083$ due to Bonferonni procedure for multiple testing – significant correlations highlighted).

		MAXIMUM TEMPERATURE			MEAN TEMPERATURE			MINIMUM TEMPERATURE		
	n	r_s	t(n-2)	p-level	r_s	t(n-2)	p-level	r_s	t(n-2)	p-level
06:00_08:30	24	0.318	1.573	0.130	0.606	3.570	0.002	0.425	2.201	0.039
08:30_11:00	24	0.185	0.882	0.388	-0.217	-1.045	0.308	-0.206	-0.985	0.335
11:00_13:30	24	-0.703	-4.635	<0.001	-0.685	-4.412	<0.001	-0.717	-4.823	<0.001
13:30_16:00	24	-0.791	-6.062	<0.001	-0.726	-4.949	<0.001	-0.691	-4.482	<0.001
16:00_18:30	24	0.230	1.108	0.280	0.408	2.098	0.048	0.546	3.054	0.006
18:30_06:00	24	0.592	3.449	0.002	0.562	3.183	0.004	0.315	1.554	0.134

Table 5: Number of food items and handling time required to fulfill minimum protein and energy requirements from different food items (Sources: (1) Taylor (2002); (2) Selman *et al.* (2002);(3) Banjo *et al.* (2007); and (4) Symes and Perrin (2003)) – Acronyms in Table 1.

Food item (FI)	Energy (KJ/g)	Protein (%)	Source	DM (g)	Energy (n)	Protein (n)	Fruit handling time (Seconds)	Energy (min)	Protein (min)
Seeds from Combretaceae pods									
TPr	25.267	42.54	2	0.07	116	34	31.84	61.65	18.25
TSr	25.267	42.54	*	0.06	136	40	31.84	71.92	21.29
CIr	19.817	20.81	2	0.05	207	98	26.51	91.62	43.49
Seeds from Leguminosae pods									
AEun	18.00	45.62	2	0.48	24	5	74.13	29.38	5.78
ANr	18.00	45.62	*	0.28	41	8	132.47	90.01	17.70
Ripe seeds from fruits									
DMr	28.616	26.00	4	0.79	9	5	68.96	10.45	5.73
DLr	28.616	26.00	*	0.32	22	12	35.19	13.16	7.22
ZMr	-	44.80	2	0.15	-	15	37.07	-	9.42
SBr	31.184	31.53	4	6.2	1	1	768.00	13.60	6.71
Fruit pulp only									
DMfr	15.49	1.28	1	3.2	4	25	271.54	18.76	113.17
SBfr	16.44	1.77	1	8.4	1	7	626.57	15.54	71.94
Ripe seeds and pseudocarp from Moraceae									
FS	17.055	8.10	2	2.8	4	5	265.27	19.02	19.97
Parasitic insect larvae									
CH-H	-	28.42	3	0.12	-	30	53.57	-	26.82
CM-L	-	28.42	3	0.12	-	30	48.60	-	24.33
TS-H	-	28.42	3	0.15	-	24	41.14	-	16.47
SB-L	-	28.42	3	0.51	-	7	222.06	-	26.15

*Extrapolated from congener

Discussion

Physiological factors contributing to bimodality in daily activity pattern

Symes and Perrin (2003) put forward that, due to the high protein and energy content of their food resources, feeding activity in the morning was likely sufficient to support the daily dietary requirements of Grey-headed Parrots (*Poicephalus fuscicollis suahelicus*). Similarly, Taylor (2002) found that Brown-headed Parrots (*P. cryptoxanthus*) could sustain their field metabolic rate by feeding for 30 minutes on any food resource. It is, therefore, unlikely that these pre-dispersal seed predators require a bimodal feeding activity pattern. Similar to juvenile Lilac-crowned Parrots (*Amazona finschi*) (Salinas-Melgoza and Renton 2005), these parrots probably remained inactive during the middle of the day to facilitate digestion.

The only physiological factor contributing to bimodality that was assessed directly in our study was the ability of Meyer's Parrots to procure protein and energy from their environment (i.e. fruit consumption rates relative to nutritional value for specific food items). Caution must be used in interpreting the ecological significance of fruit consumption rate and dietary requirements data sets due to the following sources of error: fruit and pod samples were taken from different geographical areas; no data for crucial food items (e.g. *K. africana* and flowers); and small sample size for many of the food item samples. Regardless, this analysis provides a valuable insight into physiological factors that constrain daily feeding activity patterns of Meyer's Parrots. In addition to potential sources of error in the nutritional analyses, there are numerous considerations that need to be accommodated before we can make inferences about the daily energy and protein requirements of Meyer's Parrots. The allometric equations used by Klasing (1998) to calculate daily protein requirements fails to accommodate the high cost of flight (Carlson and Moreno 1991), and therefore protein requirements are likely significantly higher. Differences in flight costs are associated with different foraging models (Carlson and Moreno 1992). Aerial feeders that habitually forage on the wing during large parts of the day employ low-cost flight at metabolic rates ranging from 2.9 to 5.7 basal metabolic rate (BMR) (Flint and Nagy 1984), whereas the short flights employed by some non-aerial foragers can cost as much as 23 BMR (Tather and Bryant 1986). Meyer's Parrots are non-aerial foragers and have very short wings that allow them to maneuver in dense tree canopies when foraging, and thus are expected to maintain a very high metabolic rate during flight and foraging effort. If, for instance, the BMR was conservatively multiplied by ten to accommodate free-living, feeding activity in the mid-morning would be insufficient to satisfy daily protein requirements. Foraging time to achieve daily protein requirements would go up to between 134 and 370 minutes for Combretateae seeds, 40 and 105 minutes for Leguminosae seeds, 50 to 80 minutes for seeds from fleshy fruits, and approximately 170 minutes for the pseudocarp and seeds from figs. Already, this conservative conversion demonstrates that feeding activity in the morning alone is insufficient to achieve daily protein requirements. Therefore, daily protein requirements were likely important in the bimodal feeding activity pattern, as following digestive passage in secondary roost during the middle of the day, Meyer’s Parrots probably have to fill their crops before returning to the primary roost. Mean consumption rates accommodated both the amount of each seed eaten and movement between fruits, and therefore, the above estimates represent total time required in the focal tree. In contrast, equations developed by Koutsos *et al.* (2001) to estimate daily metabolizable energy requirements accommodated field metabolic rates and the inherent costs of free-living. Therefore, our results show that acquiring the necessary metabolizable energy is likely not restricting at any time of year, except when feeding on Leguminosae and Combretaceae pods during winter.

Dietary protein deficiency is considered a major obstacle in the evolution of highly specialized nectarivorous and frugivorous birds (Pryor 2003). Although, only a facultative frugivores, dietary protein was also expected to be limiting for *Poicephalus* parrots. Pryor (2003) found that Pesquet's Parrots (*Psittrichas fulgidus*) had lower endogenous protein losses and reduced crude protein requirements than nectarivorous Red Lories (*Eos bornea*) and granivorous budgerigars (*Melopsittacus spp.)*. Based on nitrogen balance analyses, diets containing 10mg/g DM, 32mg/g dry mass (DM), and 82mg/g DM crude protein, would meet the minimal protein requirements for maintenance for Red Lories, Pesquet's Parrots, and budgerigars, respectively. Therefore, the protein requirements of Meyer’s Parrots may be considerably lower. More research is required into the dietary requirements and field metabolic rates of *Poicephalus* parrots in the wild to better understand their daily feeding activity pattern and the significance of different food resources. Understanding these relationships will be important in determining the optimal foraging requirements of Meyer’s Parrots within altered landscapes in the future. For example, there may be a stand density below which tree and food resources are too sparsely distributed to support the protein and energetic requirements of Meyer’s Parrots, thus causing population decline. These are the ways in which we could measure threat in the future.

Sensitivity to environmental factors

There was a distinct relationship between feeding activity and ambient temperatures at Vundumtiki and Mombo (Figure 4). Our results indicate that Meyer’s Parrots were more tolerant of high and low temperatures between 08h30 and 11h00 and 16h00 and 18h30, indicating that feeding at these times was likely obligate due to daily dietary requirements, thus introducing behavioural variance not predicted by temperature fluctuations. Feeding during early morning, middle of the day, and late afternoon, however, was significantly influenced by ambient temperature fluctuations, indicating that they would opportunistically feed at these times when temperatures were optimal, but were never forced to feed at these times due to physiological constraints (e.g. long food processing times). Meyer's Parrots, similar to the Glossy Black Cockatoo (Cameron 2005), avoided temperatures above 35ºC and below 15ºC. Unlike Glossy Black Cockatoo (Cameron 2005), Meyer's Parrots did not show signs of heat stress (e.g. panting), indicating that maximum temperatures never reached critical levels.

Meyer's Parrots were observed to forage throughout the day; however, due to their relative inactivity at secondary roosts in the middle of the day (Chapter 8: Boyes and Perrin in review d), their daily feeding activity pattern was bimodal. Afternoon feeding activity was often insignificant, especially during summer, demonstrating that *Poicephalus* parrots, like juvenile Lilac-crowned Parrots (Salinas-Melgoza and Renton 2005) and Glossy Black Cockatoos (Cameron 2005), will minimize energy expenditure and heat stress, when possible, by resting in the shade.

The influence of monthly rainfall was insignificant beyond its relationship with food resource availability (Chapter 2; Chapter 4: Boyes and Perrin in review e). Low food resource availability seemed to encourage foraging after 11h00, while high food resource availability encouraged feeding activity in the late afternoon. Furthermore, significant differences in feeding activity between 08h30 and 11h00 at Mombo and Vundumtiki over the same period demonstrate the influence of significant differences in habitat mosaic and monthly rainfall. It is feasible, however, based on sighting frequency, that the Meyer's Parrot population at Mombo was greater than Vundumtiki, and that the significant difference in feeding activity between 08h30 and 11h00 was due to more parrots feeding at this time.

Daily flight activity: avoidance of heat stress?

Although infrequently observed in flight, similar to the Red-bellied Parrot (Massa 1995), Cape Parrot (Wirminghaus *et al.* 2002), Yellow-faced Parrot (Boussekey *et al.* 2002), Grey-headed Parrot (Symes and Perrin 2003) and Brown-headed Parrot (Taylor and Perrin 2006), Meyer's Parrot had a bimodal daily flight activity pattern. Bimodal flight activity patterns are, therefore, likely common to all *Poicephalus* parrots. Most parrot species use local migrations and considerable foraging flight distances to ensure sufficient dietary intake (Forshaw 1989). Cape Parrots (*Poicephalus robustus*), for example, may have foraging flight distances of over 100km per day at certain times of the year (Skead 1964; Wirminghaus *et al.* 2002). With short wings and large heads, *Poicephalus* parrots like most parrots are not suited to long distance flight, and thus the costs of flight are likely very high (Carlson and Moreno 1992). Therefore, bimodal flight activity is likely due to avoiding higher temperatures and winds (e.g. thermals) during the middle of the day that could feasibly increase flight costs. Meyer’s Parrots were observed to fly over 2–3 km across open floodplains, and therefore, the energetic costs of flight are likely an important consideration in their behavioural ecology. There was no evidence to support local migrations in the Okavango Delta (Chapter 2; Chapter 8), indicating that Meyer’s Parrots prefer more sedentary foraging behaviour. Therefore, our findings support the hypothesis that Meyer’s Parrots are sedentary, avoid wide-ranging foraging forays, and minimize energy expenditure during foraging forays by undertaking these trips in the early morning and late afternoon.

Possible census technique

Meyer’s Parrots have green under-parts, are arboreal and very skittish. Therefore, to ensure the highest probability of detection without flushing them, thus risking subsequent double-counting, line transects should be conducted when Meyer’s Parrots are stationary and vocalizing most frequently. Meyer’s Parrots are lingual feeders, and thus the probability of detecting a feeding parrot was over three times greater than detecting socializing or resting parrots, and over 5 times greater than detecting parrots in flight. In addition, the probability of observing a Meyer’s Parrot feeding between 08h30 and 11h00 was between two and three times higher than at any other time of day. Therefore, population estimates should be derived from survey counts of feeding Meyer’s Parrots between 08h30 and 11h00. Feeding activity between 08h30 and 11h00 was not significantly influenced by seasonal temperature fluctuations, rainfall, flood regime, food resource availability or change in location, and therefore, will likely provide a useful index of relative abundance between different sites and over time. Future work on one of the other *P. meyeri* subspecies is required to test the utilization of these prescriptions on a different study population.

Conclusion

Although, difficult to be proven statistically, it is unlikely that feeding activity in the morning is sufficient for *Poicephalus* parrots as put forward by Taylor and Perrin (2006) and Symes and Perrin (2003). Susceptibility to heat stress, fixed crop size, mean consumption rate and time required for digestion passage are physiological constraints, and thus, based on the hypothesis that *Poicephalus* parrots are a natural assemblage, a bimodal daily feeding activity pattern is likely common to all nine congeners. *Poicephalus* parrots are distributed in the African subtropics, and thus experience similar climatic conditions to the parrots of the Neotropics and Australasia. All of these parrots feed on seeds, figs and flowers, and therefore, likely have similar digestive and energetic requirements to *Poicephalus* parrots, resulting in their congruent daily activity patterns.

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Chapter 8:

Flocking dynamics and roosting behaviour of the Meyer's Parrot, *Poicephalus meyeri*, in the Okavango Delta, Botswana[1]

Group dynamics and communal roosting of Meyer's Parrots (*Poicephalus meyeri*) is a function of social monogamy, food item preferences relative to resource abundance, anti-predatory behaviour and breeding activity. Aggregation during feeding was likely facilitated by lingual feeding, whereby Meyer's Parrots seemed to vocalize involuntarily while actively foraging. Meyer's Parrots are sedentary in the Okavango Delta, as there was no temporal variation in feeding flock size or sighting frequency at the two study sites. Foraging flights from roosts and activity centres were used to disperse into homogenous habitat in pairs, thus supporting the Foraging Dispersion hypothesis and General Foraging theory. Meyer's Parrots utilized both primary and secondary roost sites. Breeding seasonality had a significant impact on their feeding flock size and roosting behaviour.

Keywords: *Meyer's Parrot, Okavango Delta, communal roost, flocking dynamics*

INTRODUCTION

Most parrots are, at least, seasonally gregarious and communal roosting is common (Forshaw 1989; Chapman *et al.* 1989; Juniper & Parr 1998; Gilardi & Munn 1998). Group membership has evolutionary and behavioural significance due to its influence on inter- and intra-specific competition (Cairns & Schwager 1987), risk of predation (Walther & Gosler 2001), reproductive skew theory (Reeve *et al.* 1998), foraging efficiency and dietary intake (Cameron 2005), and social cohesion and information-sharing (Stutchbury and Morton 2001). Similar to the Cape Parrot *Poicephalus robustus* (Skead 1964; Wirminghaus *et al.* 2001), Yellow-faced Parrot *P. flavifrons* (Boussekey *et al.* 2002), Grey-headed Parrot

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[1] Formatted for *African Zoology* – Zoological Society of Southern Africa: Boyes and Perrin (in press). Flocking dynamics and roosting behaviour of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. *African Zoology*.

P. fuscicollis suahelicus (Symes & Perrin 2003a) and Brown-headed Parrot *P. cryptoxanthus* (Taylor & Perrin 2004), most medium- to large-sized parrots, such as the Hawk-headed Parrot *Deroptyus accipitrinus* (Strahl *et al.* 1991), Red Shining Parrot *Prosopeia tabuensis* (Rinke 1988), most macaws and amazons (Gilardi & Munn 1998), Glossy Black-Cockatoos *Calyptorhynchus lathami* (Cameron 2005), and the African Grey Parrot (*Psittacus erithacus*) (Chapman *et al.* 1993) typically occur in pairs or flocks of between two and four. Gilardi & Munn (1998) put forward that small parrot species (e.g. *Forpus spp.*) aggregate into larger flocks. This was corroborated by studies on the Black-cheeked Lovebird *Agapornis nigrigenis* (Warburton & Perrin 2005) and Rosy-faced Lovebird *A. roseicollis* (Ndithia & Perrin 2007).

Taylor & Perrin (2004) have suggested the social mechanism behind group dynamics in *Poicephalus* parrots is likely intra-specific association, whereby flocking is a function of the aggregation and dispersal of pair sub-units governed by food resource availability. Brown-headed Parrot pairs showed no special affiliation to other members of the group (except recently hatched progeny), and therefore, will join or leave the flock voluntarily (Taylor & Perrin 2004). Therefore, *Poicephalus* parrots typically forage in pairs or flocks of up to four parrots (Chapman *et al.* 1989; Wirminghaus *et al.* 2001; Symes & Perrin 2003; Taylor & Perrin 2004; Warburton & Perrin 2005; Ndithia and Perrin 2007). Comprehensive studies have been undertaken on the flocking dynamics of the African Grey Parrot (Chapman *et al.* 1989), Red-bellied Parrot (*Poicephalus rufiventris*) (Massa 1995), Cape Parrot (*P. robustus*) (Skead 1964; Wirminghaus *et al.* 2001), Grey-headed Parrot (*P. fuscicollis suahelicus*) (Symes & Perrin 2003a), Brown-headed parrot (*P. cryptoxanthus*) (Taylor & Perrin 2004), Black-cheeked Lovebird (*Agapornis nigrigenis*) (Warburton & Perrin 2005), and Rosy-faced Lovebird (*A. roseicollis*) (Ndithia & Perrin 2007). Here we determined to gather baseline data on flocking dynamics and roosting behaviour of Meyer's Parrot *Poicephalus meyeri*.

Meyer's Parrot is the smallest of the *Poicephalus* parrots and forms a superspecies with the Rüppell's Parrot *P. rueppelli* and the Brown-headed Parrot in southern Africa (Rowan 1983; Massa 2000). Meyer's Parrots have the widest distributional range of any African parrot, exceeding that of the Rose-ringed Parakeet *Psittacula krameri* and Red-faced Lovebird *Agapornis pullarius.* Meyer's Parrot is an opportunistic generalist feeders with a distinctly seasonal diet, comprising 71 food items from 16 families including 37 tree species (Chapter 2: Boyes & Perrin in review a). Seed predation accounted for 62% of feeding bouts, of which 37% were seeds from ripe pods and fruits. Meyer's Parrots breed predominantly between March and July (Chapter 9: Boyes & Perrin in review b); however, there are sporadic breeding attempts between October and January. Our study determined to compare the flocking dynamics and roosting behaviour of Meyer's Parrot *Poicephalus meyeri* with work done on other *Poicephalus* parrots to test the hypothesis that this behaviour is common to all nine congeners.

Single-species flocking is the voluntary aggregation of conspecifics, usually in pairs or family groups, in order to benefit from group membership. This becomes dysfunctional when the abundance and spatial distribution of food resource cannot support large flocks (e.g. food resources sparsely distributed). Similarly, as time spent travelling between communal food resources increases there is a point at which energy expenditure in foraging flight distance exceeds energy intake from the environment, thus making small flock size advantageous on sparse resources (Caccamise & Morrison 1986; Chapman *et al.* 1989). Meyer's Parrots appear to be lingual feeders, whereby they vocalize involuntarily during feeding activity (Chapter 2), and therefore, aggregation of conspecifics likely occurs during feeding activity.

Most ecological studies that consider determinants of diurnal flock size suggest that the density and distribution of food resources restrict group size by influencing the number of individuals that can efficiently and sustainably forage together, thus adhering to the General Foraging (GF) theory (Bradbury & Vehrencamp 1977; Chapman *et al.* 1989). Optimal diet theory predicts that foragers of immobile prey (e.g. seeds) should prefer prey that yield more energy per unit foraging time (Sih & Christensen 2001). Similarly, optimal foraging theory predicts that Meyer's Parrots should prefer activities (e.g. flocking) that optimize foraging efficiency, thus maximizing energy intake per unit foraging time (Rakotomanana & Hino 1998; Wheelwright 1985). Feeding flock size should, therefore, be largest when resources are abundant and uniformly distributed (Bradbury & Vehrencamp 1977). Flocking, however, also functions to reduce predation risk by improving detection of predators and diluting risk of capture, and therefore, birds are expected to aggregate on food resources when these resources are abundant or the cost of sharing food resources is less than the anti-predatory benefits of larger feeding flock sizes (Todd & Cowie 1990; Krams 1996; Walther & Gosler 2001). Our study determined to evaluate probable determinants of flocking dynamics and roosting behaviour of Meyer's Parrot.

Similar to aggregation during feeding, communal roosting behaviour is also a function of a classical fission-fusion model, whereby individuals of a species aggregate through vocalizations or at a predetermined location before long periods of inactivity (e.g. sunset). This excludes the resting places of a single coherent group (e.g. troop of Chacma Baboons *Papio ursinus* (Ward & Zahavi 1973). Apart from primary communal roosts, which accommodate the entire roosting population, there may be secondary communal roosts utilized in the middle of the day in order to avoid heat stress and allow time for digestion before afternoon foraging (Ward & Zahavi 1973). Our study evaluated the existence and utilization of both primary and secondary communal roosts.

The Information Centre hypothesis suggests that birds congregate in large communal roosts to facilitate the exchange of information regarding the location of food resources (Ward & Zahavi 1973). The Foraging Dispersion hypothesis, however, suggests that successive groups leaving the roost avoid the flight path of preceding groups, thus facilitating dispersion into unknown habitat (Chapman *et al.* 1989). Therefore, the Information Centre hypothesis predicts aggregation during periods of resource scarcity, while the Foraging Dispersion hypothesis only predicts aggregation during periods of food resource scarcity. The primary function of communal roosting in *Poicephalus* parrots is unknown, however, benefits likely include information-sharing on food resources near the roost, dilution of predation risk, increased predator detection, allo-preening and socializing, and formation of pair bonds (Taylor & Perrin 2004). Our study evaluated the roosting behaviour and flocking dynamics of Meyer's Parrots within the context of the Information Centre and Foraging Dispersion hypotheses in order to more fully understand the function and utilization of primary communal roosts.

Most parrot species use local migrations and considerable foraging flight distances to ensure sufficient dietary intake (Forshaw 1989). Aggregation of large flocks during feeding and local migrations has been recorded in the Cape Parrot (Skead 1964; Wirminghaus *et al.* 2001), Brown-headed Parrot (Taylor & Perrin 2004), Black-cheeked Lovebird (Warburton & Perrin 2005) and Rosy-faced Lovebird (Ndithia & Perrin 2006). Cape Parrots may have a foraging flight distance of over 100km per day at certain times of the year (Skead 1964; Wirminghaus *et al.* 2002). Foraging strategies such as this have high energetic costs, and therefore, it is reasonable to assume that, when possible, a species will adopt more sedentary foraging behaviour. Meyer's Parrots are reported to have some local movement to Zimbabwean highlands during the summer, likely due to wandering during the dry season (Rowan 1983). Sighting frequency and seasonal flock size fluctuations were evaluated for evidence of a local migration.

The influence of climatic conditions (e.g. monthly rainfall, daily ambient temperature and flood regime), inter-specific competition, breeding activity, food item availability, and differences in habitat mosaic on feeding flock size is poorly represented in the literature. Warburton & Perrin (2005), however, reported a smaller feeding flock size for arboreal than ground foraging activity. This study monitored feeding, roosting and socializing flock size to facilitate comparison with environmental variables, niche breadth, food item preferences and breeding activity.

MATERIALS & METHODS

Study sites

The Okavango Delta was chosen as the study site because of its significant Meyer's Parrot population (Wirminghaus 1997). The study was conducted at two sites: Vundumtiki Island located at the junction of the Maunachira and Kiankiandavu channels in the north-eastern part of the delta, and Mombo Camp off the northern peninsula of Chief's Island (Figure 1). Both study sites were wilderness areas with no human impact or disturbance to habitat or animal behaviour.

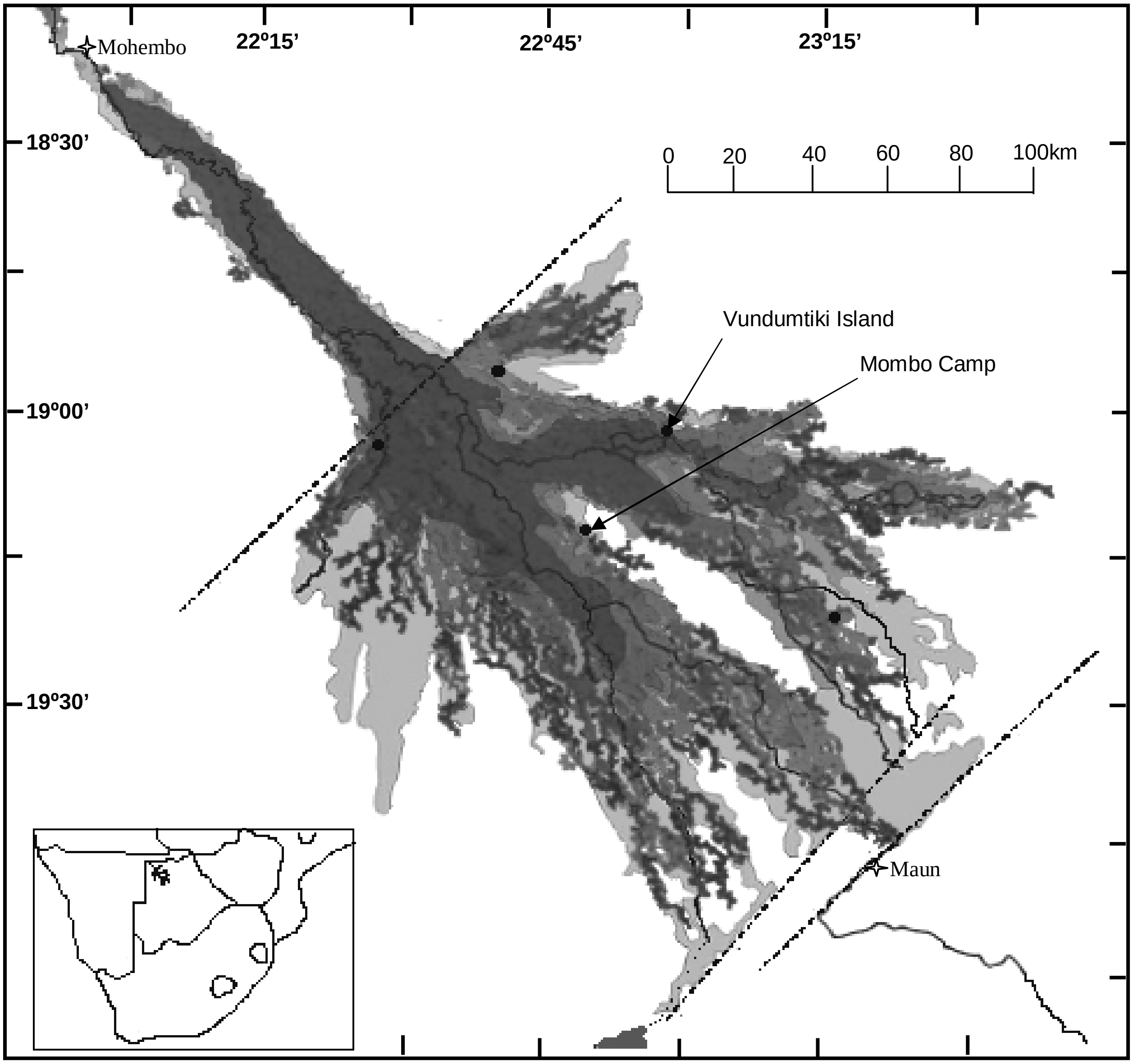

Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

The climatic conditions in the Okavango Delta are distinctly seasonal, comprising a wet season (November-March) and dry season (April-October). Mean annual rainfall is 450–560mm (Wolski and Savenije 2006; Ellery *et al.* 2000). During the annual flood the area covered by water expands from its annual low of 2500–4000km^2 in February-March to its annual high of 6000–12000km^2 in August-September. Arrival of the annual flood lags the rainy season and follows one or two months after the end of rainfall in the region (Gumbricht *et al.* 2004).

Rainfall was monitored daily using a rain gauge (udometer) over the entire study period. The flood cycle was monitored using flow rate data from Mohembo (PowerServe 2007) and calibrated to the study sites by recording first significant increment in water level on a measuring pole in permanent water as the start of the flood.

Timing

Flocking dynamics and roosting behaviour were recorded at Vundumtiki between August 2004 and July 2005, and February 2007 and August 2007, and at Mombo between August 2005 and January 2006.

Flocking dynamics

All other studies on flocking dynamics of African parrots have inferred feeding activity from analyses of parrots in flight. Marsden (1999), however, cautioned against the use of these data due error brought about by differences in habitat structure (e.g. open and closed habitat). Our study separated flock size analyses into the following groups: flock size in flight, feeding flock size, non-feeding flock size and roosting flock size.

At Vundumtiki: A standardized, 26.2 km, road transect was established along the existing road network to standardize spatial distribution of feeding flock observations. Transect width was 100m either side of the road (≈maximum distance at which parrots could be detected). The same vehicle and observer were used on each transect and the travelling speed was 15 - 20km/h. All observations were made within the transect width from the vehicle or on foot. Meyer's Parrots were located by listening for vocalizations and then following these until the parrot was found.

At Mombo: Due to time constraints and logistical difficulties at Mombo, a standardized road transect was not established, however, vehicle travelling speed, observer, transect width, sampling frequency, and transect duration were standardized to the regime used at Vundumtiki. Therefore, feeding census duration was limited to two and a half hours after departure from camp.

To ensure systematic sampling of flocking and roosting behaviour, six daytime time periods were established, including: 06h00-08h30; 08h30-11h00; 11h00-13h30; 13h30-16h00; 16h00-18h30; and 18h30 to sunset (Chapter 7). Road transects were conducted in all six time periods before a specific time period was sampled again.

All observations were made using a 30x spotting scope at the maximum sighting distance possible to minimize disturbance of behaviour. The following data were recorded: time of day, flock size, and presence/absence of competing species. Meyer's Parrots are arboreal feeders with green under-parts and are skittish, making observation in the tree canopy difficult.

Non-feeding flocks between 06h00 and 08h30 and between 18h30 and sunset were considered to be parrots at activity centres prior to primary communal roosting. Non-feeding flocks during the middle of the day were recorded as parrots at secondary roosts. Both of these sightings were infrequent in comparison with feeding flock size observations.

Primary and secondary communal roosting behaviour

Primary roosting behaviour was monitored outside of census transects by following Meyer's Parrots while aggregating in the afternoon or stopping due to loud and synchronous vocalizations at roost trees and adjacent activity centres. Activity centres were usually dead *Combretum imberbe* or *Acacia nigrescens* on which parrots were observed to aggregate in the early morning and late afternoon to vocalize, preen and allo-preen. When possible the type of communal roost, height above the ground (HAG), and crown condition of the host tree were recorded to evaluate roosting preferences. Crown condition was scored in increments of 0.1 from 0 - 1, whereby 0 represents a snag (i.e. dead tree) and 1 represents a full healthy canopy. Locations were GPS-marked, and then subsequently monitored in the early morning and late afternoon, when possible. The following observations were dictated into a Sony MD-Walkman MZ-NH700: flock size, preening and allo-preening, whether pair sub-units socialized with other parrots, posturing, and frequency of vocalizations.

Data analyses

The Kolmogorov-Smirnov (K-S) test was used to test for normality in the data set. T-tests for independent samples were used to test for temporal and spatial differences in feeding flock size. The Spearman rank correlation (r_s) was used to test for associations between feeding activity and ambient temperatures. The Mann-Whitney U-test was used to look for significant differences in daily feeding activity between Vundumtiki and Mombo. The Wilcoxon Matched Pairs Test was to test for significant difference between overall number of feeding bouts during each time period over the entire study period. The Bonferroni procedure was used to adjust significance levels to control Type 1 error rates in multiple testing situations. Kruskal-Wallis ANOVA by Ranks was used to test for significant difference between feeding flock size in the feeding activity time periods. Statistical analysis followed Quinn & Keough (2002) and Statsoft-STATISTICA 7.1 (2006).

RESULTS

Climatic conditions

Annual rainfall only exceeded the expected range in the November 2005 – March 2006 wet season when 683mm were recorded (Figure 2). Lag time for the flow rate data from Mohembo was calibrated at a 59 and 27 days lag for Vundumtiki and Mombo respectively (Figure 2).

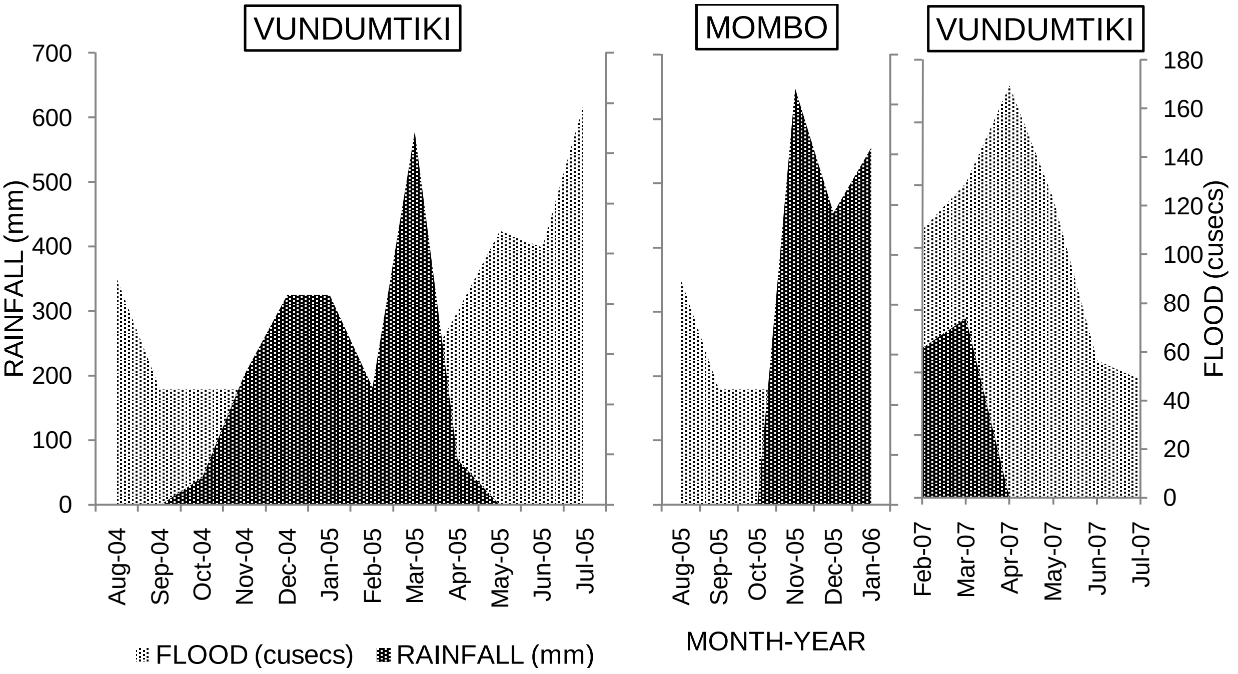

Figure 2: Flood regime (dark grey) and rainfall seasonality (light grey) at Vundumtiki and Mombo

Feeding flock size fluctuations

Feeding flock size with the highest frequency was two, followed by three and then one (Figure 3). There were significant differences between feeding flock sizes in the breeding and non-breeding season, and between the two study sites (Table 1; Figure 4). There were, however, no significant differences between feeding flock size in the wet and dry season, and between the 2005 and 2007 breeding seasons (Table 1; Figure 4). On 127 occasions Meyer's Parrots were observed to arrive at the feeding site, thus increasing the feeding flock size. Lingual feeding was observed at all feeding sightings. All feeding flocks were located in a single tree or in adjacent canopies, maintaining a close proximity to conspecifics. Disturbance by the observer or otherwise, resulted in all parrots flushing from the tree and dispersing in groups of two to four in different directions.

Daily flock size fluctuations were not significantly different in each of the six time periods (ANOVA: F (5, 985) = 1.4329, p = 0.20977) (Figure 5). There was no significant correlation between mean monthly feeding flock size and Hurlbert's niche breadth index for Meyer's Parrot feeding activity over the study period (rs = -0.007; t(n-2) = -0.029; p-level = 0.98).

Table 1: Influence of rainfall seasonality, breeding season, location and time on feeding flock size

GROUP 1 vs GROUP 2	GROUP 1		GROUP 2					
Rainfall seasonality and breeding comparison	Mean ± SE	n	Mean ± SE	n	t-value	df	p	F-ratio
WET vs DRY SEASON	2.51 ± 0.043	818	2.58 ± 0.041	1160	-1.00	1976	0.316	1.312
BREEDING vs NON-BREEDING SEASON	2.36 ± 0.051	521	2.76 ± 0.040	1653	-5.83	2172	**< 0.001**	1.444
Spatial and temporal comparison								
VUNDUNTIKI vs MOMBO (August - January)	2.58 ± 0.056	475	3.01 ± 0.071	471	-4.72	944	**< .0001**	1.595
2005 vs 2007 (Vundumtiki)	2.25 ± 0.052	517	2.40 ± 0.053	515	-2.03	1030	0.042	1.039

(Bonferonni procedure: Significant at $p < 0.0125$)

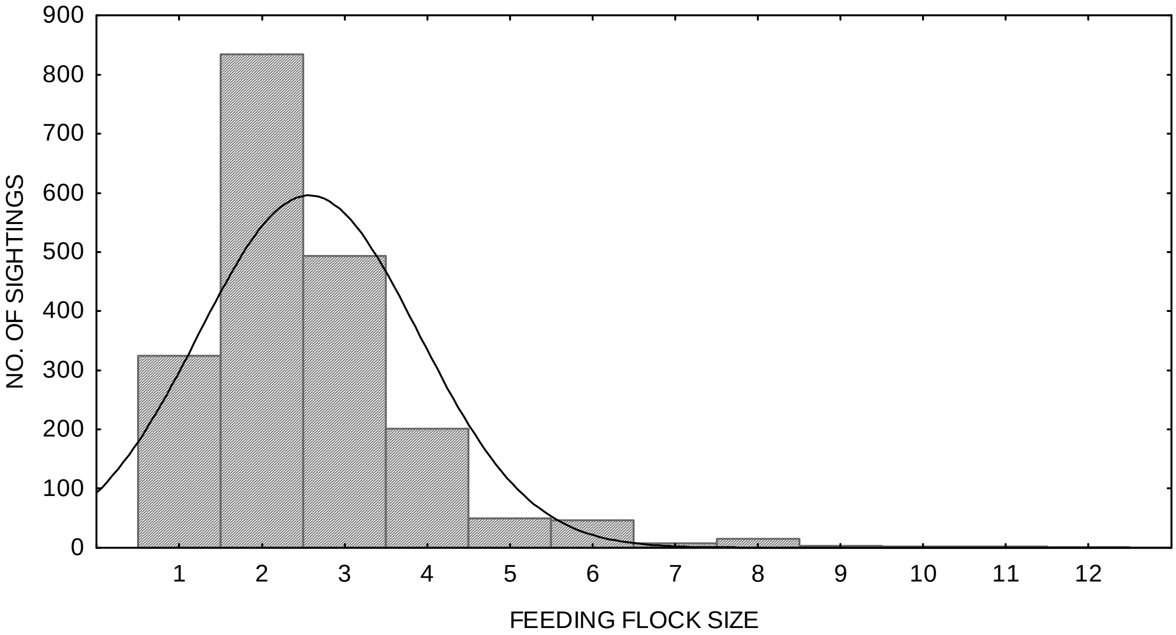

Figure 3: Frequency of Meyer's Parrot feeding flock sizes at Vundumtiki and Mombo over the entire study period

Non-feeding flock size fluctuations

Mean non-feeding flock size was significantly different in each of time periods (Kruskal-Wallis ANOVA: H (4, N= 287) =32.014; p < 0.001) (Figure 6). However, mean non-feeding flock size was not significantly different month-to-month over the entire study period (Kruskal-Wallis ANOVA: H (23, N= 287) = 33.156; p = 0.0783). Analysis of the daily non-feeding flock size fluctuations over the entire study period shows evidence for both primary and secondary roosting behaviour (Figure 6). The most frequently used secondary roost trees were *Kigelia africana* (n = 84) and *C. imberbe* (n = 46). The primary activities at socializing activity centres were preening and allo-preening, sunning, and frequent and synchronous vocalizations. Allo-preening was observed within pair sub-units or family units, whereby observations of more than three birds preening each other were very infrequent. The most frequently used socializing trees were dead *A. nigrescens* (n = 57) and damaged *Colophospermum mopane* (n = 49). The most frequent non-feeding flock size was four (Figure 7).

Parrots in flight

There was a peak in daily flight activity between 08h30 and 11h00, and 16h00 and sunset (Figure 8). Mean flock size over the entire study period for parrots in flight was 2.06 (n = 467; SE = 0.038), whereby Meyer's Parrots were most frequently observed flying long distances in pairs (64.7%; n = 306), followed by individuals and in threes (Figure 9). Observations of parrots in long distance flights were infrequent due to lack of vantage points. In winter, the frequency of parrots observed in flight was considerably lower. There was no significant difference between flock size in flight at Mombo and Vundumtiki (Kruskal-Wallis ANOVA: H(1, N= 358) = 0.217; p = 0.641).

Roosting and socializing activities

Three types of primary roost site were recorded during this study, including open cavities in the tree trunk (e.g. crooks or crevices), open branches under closed canopy, and large roosting cavities (Table 2). The mean height of trees used for roosting was 28.7m, and the mean diameter at breast height was over 140cm. The mean roosting flock size was 7.74 (n = 31; SE = 0.55) (Table 2). All of the roost tree species occur in riverine forest, *Acacia-Combretum* marginal woodland and Mopane woodland habitat (Figure 10). All roosting activity in *Hyphaene petersiana* was recorded in the Mombo study area. Huddling in the crook near the trunk in the closed canopy accounted for 65% (n = 20) of roost sites, with utilization of natural cavities and branches in the canopy accounting for 23% (n = 7) and 13% (n = 4) of roost sites respectively.

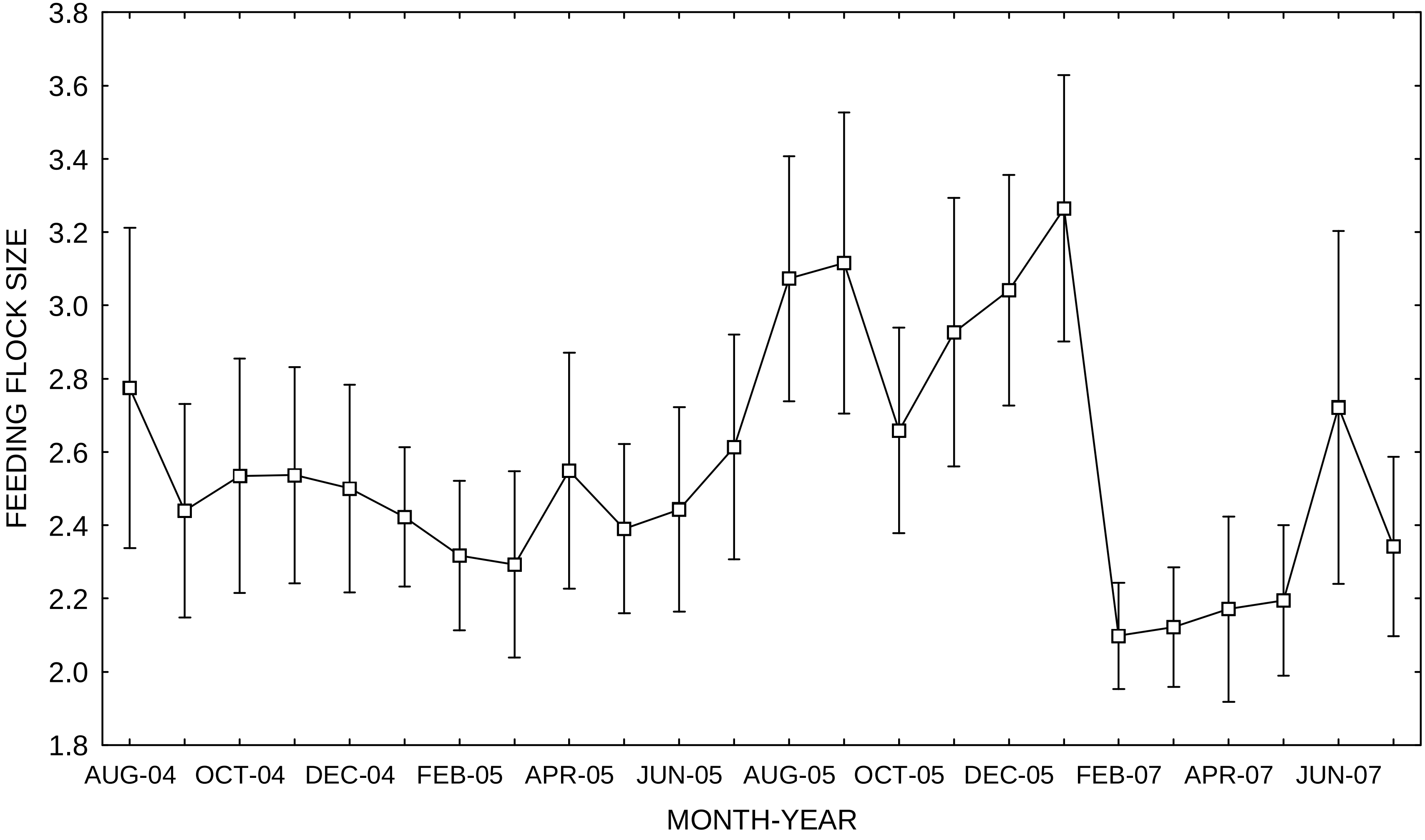

Figure 4: Spatial and temporal variation in feeding flock size at Vundumtiki (August 2004 – July 2005; February 2007 – July 2007) and Mombo (August 2005 – January 2006) (Vertical bars denote 0.95 confidence intervals). Primary breeding season is between February and July (Chapter 9). (n = 1975)

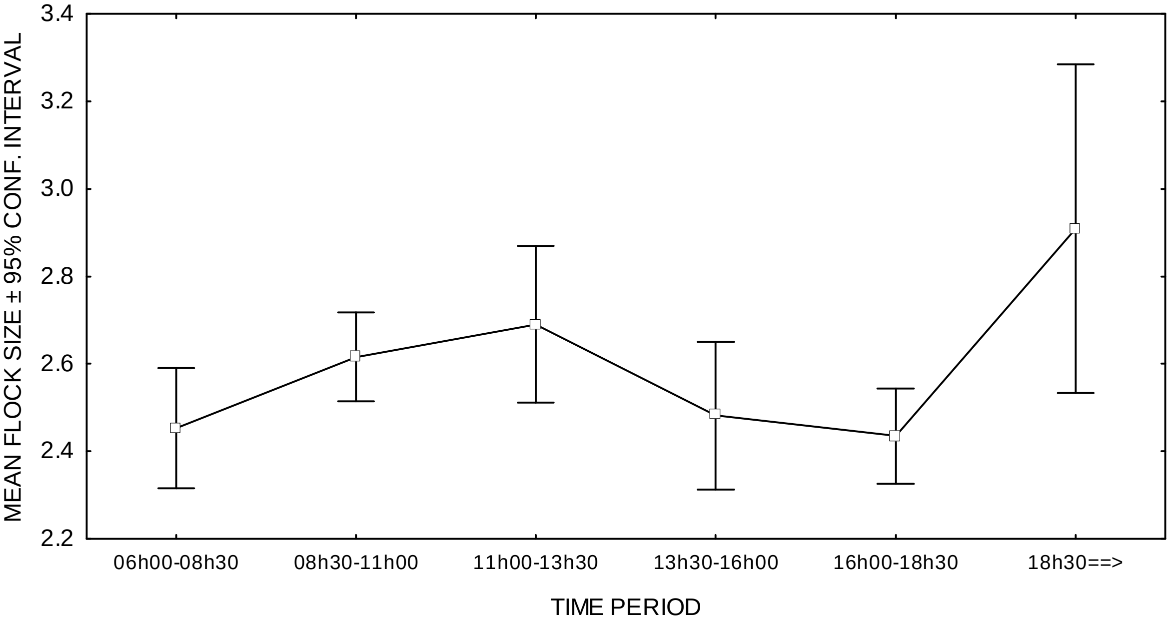

Figure 5: Daily feeding flock size fluctuations at Vundumtiki and Mombo (n = 1979) (Vertical bars denote 0.95 confidence intervals)

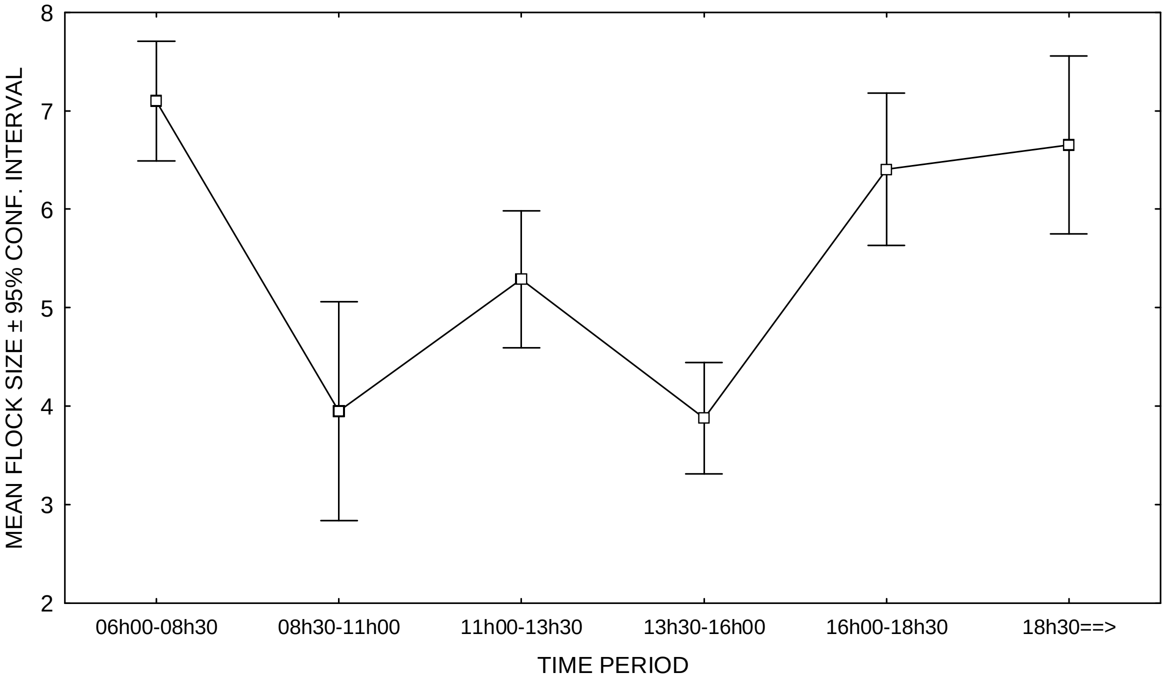

Figure 6: Daily non-feeding flock size fluctuations at Vundumtiki and Mombo (n = 259) (Vertical bars denote 0.95 confidence intervals)

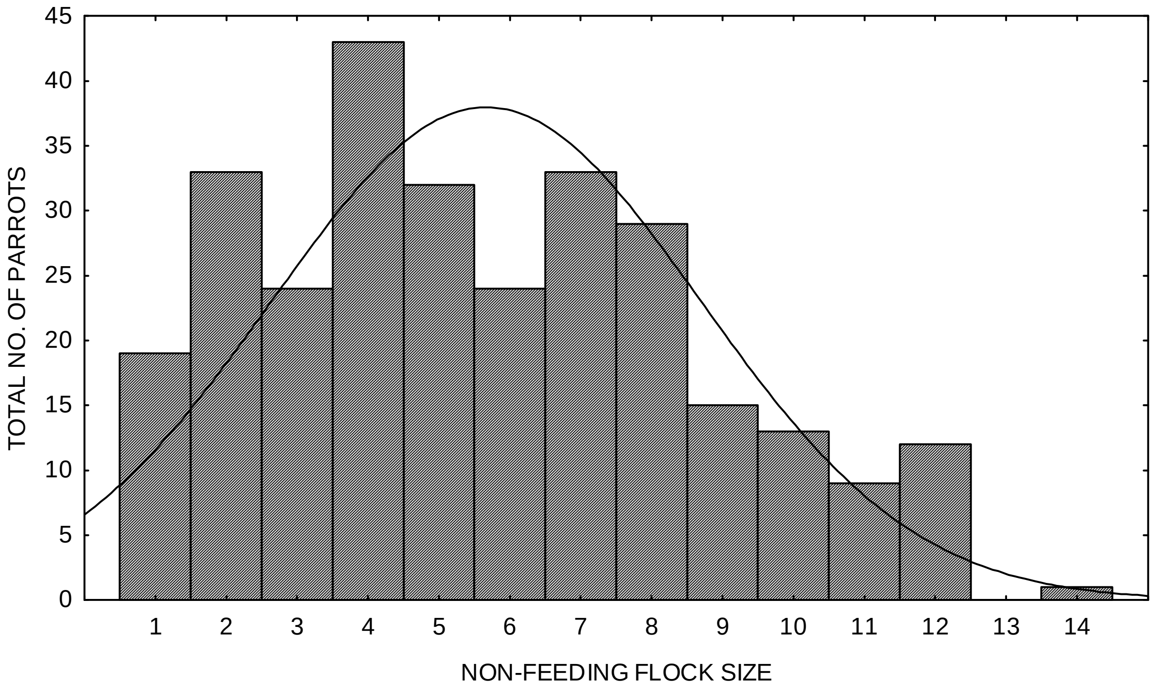

Figure 7: Frequency of Meyer's Parrot non-feeding flock sizes at Vundumtiki and Mombo over the study period

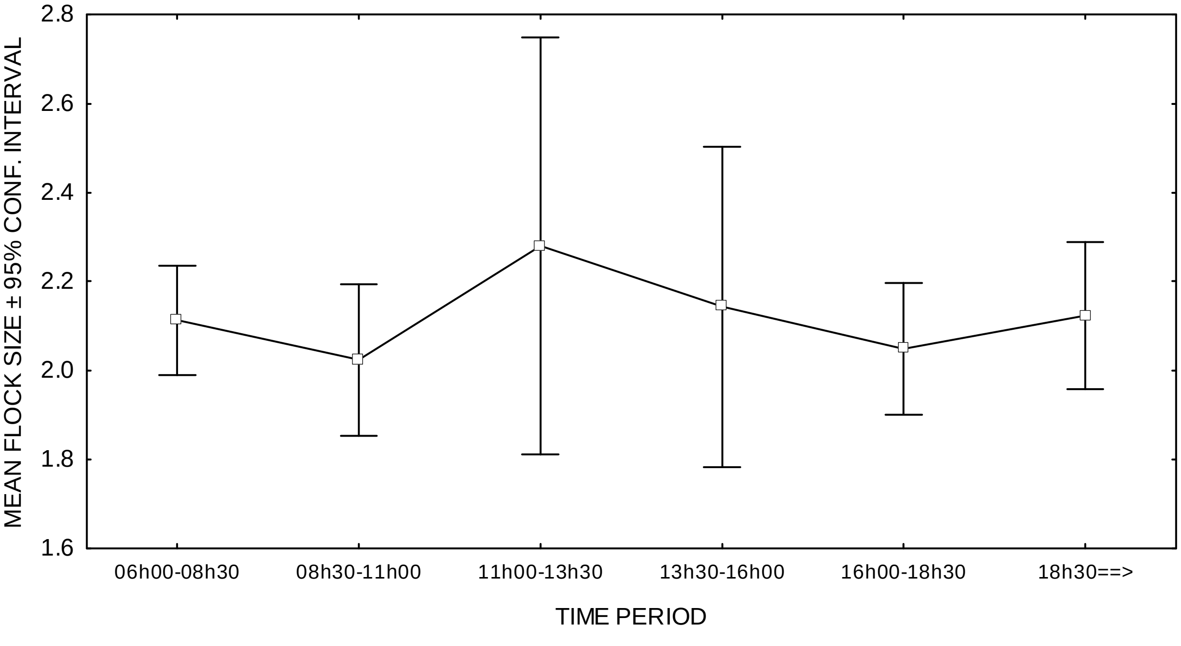

Figure 8: Mean flock size in each time period for Meyer's Parrots in flight at Vundumtiki and Mombo (Vertical bars denote 0.95 confidence intervals)

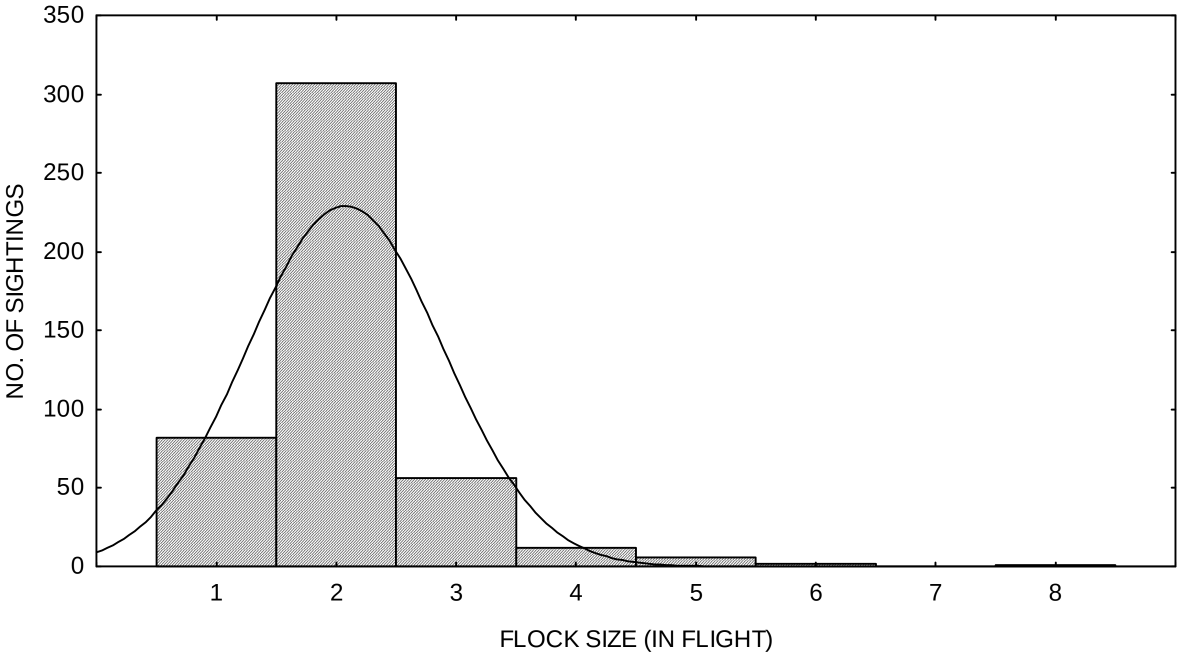

Figure 9: Total number of sightings of flock sizes of Meyer's Parrots in flight over the entire study period

Table 2: Primary roost site characteristics of the Meyer's Parrot recorded during this study

	n	FLOCK SIZE (Mean ± SE)	HEIGHT ABOVE GROUND (Mean ± SE)	CROWN CONDITION (Mean ± SE)
WET SEASON (Nov - Apr)				
Crook or crevice in tree trunk	20	7.95 ± 0.727	29.35 ± 1.253	4.75 ± 0.123
Open branch under canopy	4	8.25 ± 1.493	33.5 ± 1.848	4.76 ± 0.25
DRY SEASON (May - Oct)				
Roosting cavity	7	6 ± 1.155	25.14 ± 2.492	1.71 ± 0.286

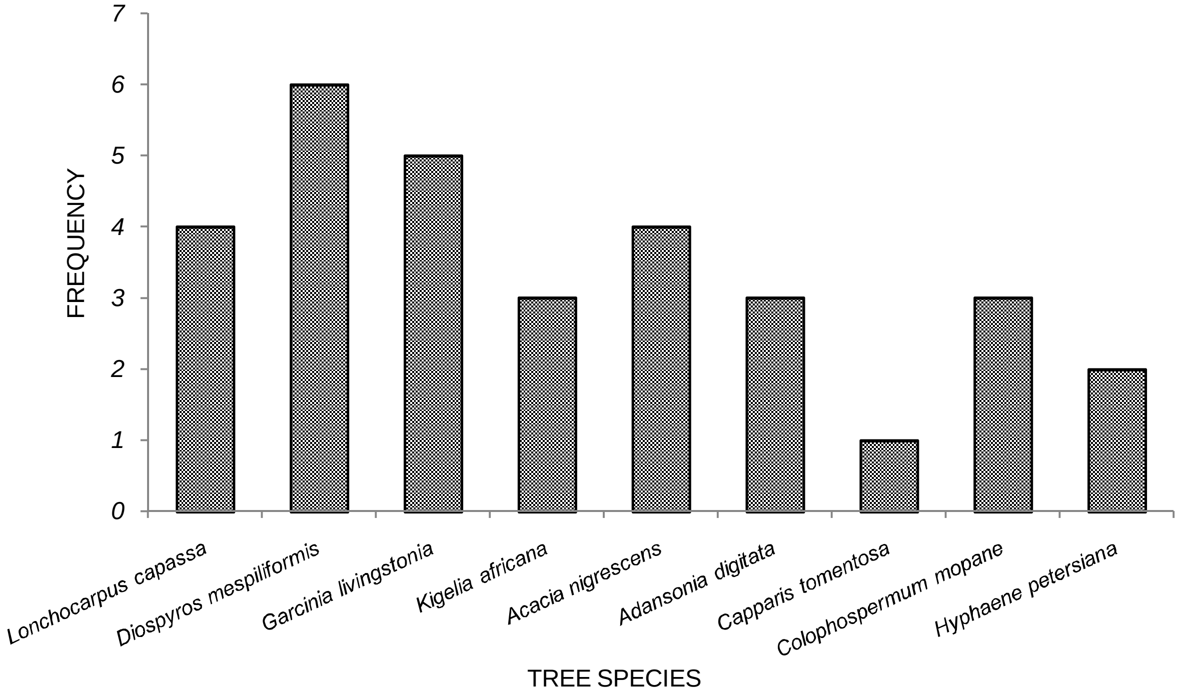

Figure 10: Total number of roost sites in each tree species over the entire study period

Meyer's Parrots were observed to disperse in different directions from activity centres close to the roost trees in pairs or small groups of up to four parrots. Based on observed flight distance, initial dispersal distance from the activity centre was 1–3km. Roosting behaviour was distinctly seasonal, whereby Meyer's Parrots utilized open branches and crooks of trees during the wet season when temperatures remained above 20°C over night, while switching to natural cavities in *A. digitata*, *A. nigrescens*, *C. mopane*, *L. capassa* and *C. imberbe* during the dry, cold breeding season. Summer roosts were found to move constantly and a specific roost tree was not used for more than three consecutive days before being abandoned. Winter roost cavities were much harder to find due to infrequent vocalizations at or near the cavity. In contrast, vocalizations were frequent and often synchronous in activity centres adjacent to roost trees. In the summer non-breeding season (August – February), the primary roosts were typically crooks, crevices or open branches and were relocated every 2.93 days (n = 30; SE = 0.486). Occupation of primary roost sites in the winter breeding season was difficult to monitor due to difficulty in locating these sites, as a result of the lack of vocalizations at the roost cavity. The utilization of these cavities is likely permanent through the whole of winter, whereby occupancy of one nest was recorded at 142 days (Chapter 9).

Mixed-species flocking

Observation of competing frugivores and seed predators at feeding sightings were infrequent and included only 19 species in 15.6% (n = 309) of all feeding sightings (n = 1979) (Table 3). There was a significant negative correlation between percentage mixed-species flocks and percentage available food items consumed by Meyer's Parrots (r_s = -0.454; n = 24; p = 0.026) (Figure 11). Meyer's Parrots had no competing species for 12 of their food items and were the only avian predispersal seed predator in the Okavango Delta. All competing species were frugivores that typically targeted the fruit pulp of fleshy fruits rather than the seed kernels preferred by the parrots (e.g. *D. mespiliformis, G. livingstonia* and *B. discolor*). These species, however, were in direct competition for food resources with the Meyer's Parrot due to utilization of the same time and space. There were 20 diurnal frugivores or facultative seed predators (e.g. Giraffe) observed at feeding sightings during this study (Table 3).

Table 3: Percentage occurrence (%) of competing species observed during feeding bout observations

Common name	Scientific name	%	n
African Green Pigeon	*Treron calva*	26.5	82
Grey Lourie	*Corythaixoides concolor*	20.7	64
Crested Barbet	*Trachyphonus vaillantii*	12.9	40
Burchell's Starling	*Lamprotornus australis*	10.0	31
Long-tailed Starling	*Lamprotornus mevesii*	7.8	24
Black-headed Oriole	*Oriolus larvatus*	4.2	13
Black-eyed Bulbul	*Pycnonotus barbatus*	3.6	11
Chacma Baboon	*Papio ursinus*	3.2	10
Red-faced Mousebird	*Urocolius indicus*	2.6	8
Black-collared Barbet	*Lybius torquatus*	2.6	8
Yellow-billed Hornbill	*Tockus leucomelas*	1.6	5
Red-billed Hornbill	*Tockus erythrorynchus*	1.6	4
Tree Squirrel	*Paraxerus cepapi*	0.6	2
Vervet Monkey	*Cercopithecus aethiops*	0.3	1
Grey Hornbill	*Tockus nasutus*	0.3	1
Wattled Starling	*Creatophora cinerea*	0.3	1
Plum-coloured Starling	*Cinnyricinclus leucogaster*	0.3	1
Glossy Starling	*Lamprotornis nitens*	0.3	1
Bradfield's Hornbill	*Tockus bradfieldi*	0.3	1
Giraffe	*Giraffa camelopardolis*	0.3	1
TOTAL		100	309

Peters' Epauletted Fruit Bats (*Epomophorus gambianus crypturus*) were the dominant nocturnal arboreal frugivores competing for food resources with the Meyer's Parrot, including the following food items: *Ficus sycomorus* figs, *Diospyros mespiliformis* fruit, *Ficus burkei* figs, *Berchemia discolor* fruit, *Garcinia livingstonia* fruit, *Kigelia africana* flowers, and *Adansonai digitata* flowers. Other arboreal nocturnal frugivores and seed predators observed during night walks in riverine forest and *Acacia-Combretum* marginal woodland at Vundumtiki, included: Tree Mouse (*Thallomys paedulcus*), Hairy-footed Gerbil (*Gerbillurus paeba*) and Woodland Dormouse (*Graphiurus murinus*).

Risk of predation

There were no instances of predation during feeding activity; however, predation during the breeding season was recorded, including instances of predation of fledglings by African Fish Eagle (*Haliaeetus vocifer*), Gymnogene (*Polyboroides typus*), Tree Monitor (*Varanus albigularis*) and Little Sparrowhawk (*Accipter minullus*). Predation by Large Spotted Genet *Genetta tigrina* was recorded on nesting female and three nestlings. Meyer's parrots were noted to alarm call and take flight to signal the presence of human beings, most large raptors, African Leopard (*Panthera pardus*), Chacma Baboon (*Papio ursinus*), and Large Spotted Genet. Meyer's Parrots reacted without failure to the aerial and arboreal alarm calls of Tree Squirrels.

Sighting frequency

Mean sighting frequency was 10.32 and 12.14 parrots per transect at Vundumtiki and Mombo over the entire study period respectively. There was a significant difference between the feeding bout frequency per census transect at Vundumtiki and Mombo (Kruskal-Wallis ANOVA: H(1, N= 24) = 10.67575 p = 0.001). There was, however, no significant difference between feeding bout frequencies at Vundumtiki (Kruskal-Wallis ANOVA: H (11, N= 12) =11.0, p = 0.4433) and Mombo (Kruskal-Wallis ANOVA: H(5, N= 6) =5.0, p = 0.416) over a continuous period of time (Bonferonni procedure, significant at $p < 0.017$).

DISCUSSION

Evidence for sedentary life history

Results from this study support the assertion by Wirminghaus (1998) that there is a "significant" Meyer's Parrot population in the Kavango Basin. Meyer's Parrot populations at Vundumtiki and Mombo were stable and free from significant disturbance. The sighting frequency, however, was significantly higher at Mombo than at Vundumtiki, thus indicating that Mombo likely has a higher Meyer's Parrot population than Vundumtiki, probably as a result of a higher carrying capacity. Roosting and socializing flock size was also significantly larger. The habitat mosaic at Mombo is, therefore, likely more suitable to Meyer's Parrots, but both study sites should be considered to be suitable to support stable Meyer's Parrots populations, and thus could function as an ecological benchmark for comparison with other areas. In addition, no significant difference between feeding flock size in the wet and dry seasons indicates that there were no periods of food resource scarcity, patchiness or sparse distribution that warranted additional foraging effort or local migrations or "wandering" in search of food resources.

There is no evidence in the diet of Meyer's Parrots at Vundumtiki and Mombo that would indicate a necessity for any local migration for food resources (Chapter 2). Over the 24 month study period, the sighting frequency per transect month-to-month was not significantly different, thus indicating no net emigration out of or immigration into either of the study areas. Movement data are required for the Meyer's Parrot in order to determine daily flight activity and foraging flight distance.

Evidence for social monogamy and maintenance of "family units"

The findings of this study support social monogamy, in that over 66% of all sightings of Meyer's Parrots in flight were pairs, thus indicating that the basic sub-unit of flocking is likely socially monogamous pairs or "family units" including recent progeny. In addition, over 42% of feeding sightings involved pairs of Meyer's Parrots. Boyes & Perrin (Chapter 9) found that Meyer's Parrots maintain pair-bonds over several breeding seasons; however, there was evidence for the incidence of extra-pair copulations, thus indicating that Meyer's Parrots are socially monogamous. Allo-preening within apparent pair sub-units and family units also supports the findings of Taylor & Perrin (2004).

Communal roosting behaviour

Complex and diverse vocalizations represented in *Poicephalus* parrots are indicative of the importance of socializing and group membership (Taylor 2002). Meyer's Parrots vocalized constantly during feeding activity, thus sharing information on food resource availability. Aggregation during the course of the day was, therefore, likely due to these obligate vocalizations during feeding, thus allowing for gradual aggregation and subsequent use of secondary roosts to avoid midday temperatures over 30°C and facilitate digestive gut passage.

Communal roosting behaviour is central to population dynamics due to its influence on spatial distribution, intra-specific competition and resource utilization, risk of predation, and breeding behaviour

(Ward & Zahavi 1973; Chapman *et al.* 1989). Similar to the Grey-headed Parrot (Symes & Perrin 2003), Meyer's Parrots dispersed in pairs or small flocks of three or four parrots on different flight paths from the roost tree or morning activity centre, thus creating a central place from which they dispersed. If Meyer's Parrots disperse from a roost tree, this creates a central point, thus making them central place foragers (Lair *et al.* 1994). As communal roosting central place foragers, Meyer's Parrots are expected to return to the communal roost (Lair *et al.* 1994). The constant relocation of communal roosts during the wet season is likely a function of food resource utilization and anti-predatory behaviour. Based on movements of individually-marked European Starlings *Sturnus vulgaris*, Caccamise & Morrison (1986) suggested that individuals only leave their own foraging area to come to communal roosts, and the associated feeding areas, when doing so more than compensated for the cost of travelling to the roost. Therefore, it could be that, through a complex network of vocalizations, Meyer's Parrots find a new central place at which to aggregate based on their distribution following a day of wandering during foraging activity. Primary roosting behaviour of Meyer's Parrots, therefore, supports the assumptions of the Foraging Dispersion hypothesis. In addition, mean socializing and roosting flock size was significantly larger than feeding flock size, thus further supporting the Foraging Dispersion hypothesis. There was no evidence in this study that supported information-sharing at the communal roost or associated activity centres, and therefore, the Information Centre hypothesis cannot be used to describe the roosting behaviour of Meyer's Parrots.

The Information Centre and Foraging Dispersion hypotheses are probably not mutually exclusive (Caccamise & Morrison 1986), and therefore, certain birds may switch between the two hypotheses, deriving benefit from both based on spatial and temporal resource abundance and seasonal basal metabolic requirements. Therefore, Meyer's Parrots in sub-optimal environments may use roosts as information centres. For example, in the Seronga area, 40km north-east of Vundumtiki, where Meyer's Parrots are reported to aggregate in flocks of up to 40 parrots on corn and millet fields (Boyes *pers obs.*), it is unlikely that Meyer's Parrots in the surrounding areas disperse from communal roosts prior to raiding these agricultural crops. Further research is required on the roosting behaviour of Meyer's Parrots elsewhere in their range.

Feeding flock size fluctuations

The General Foraging hypothesis, put forward by Caccamise & Morrison (1986), probably functions best to predict feeding flock size fluctuations of *Poicephalus* parrots. Therefore, no significant difference between the feeding flock size in the wet and dry season was likely due to the annual flood arriving during the dry season, thus supporting the atypical fruiting of riverine forest tree species such as *D.*

mespiliformis and *G. livingstonia* during the dry season and early wet season. The significant difference in feeding flock size between Vundumtiki and Mombo supports the hypothesis that feeding flock size is resource-dependent.

Feeding flock size was significantly larger during the breeding season, probably due to cooperative prospecting for and utilization of arthropod larvae incubating in and feeding on pods and fruits in their diet. Boyes & Perrin (Chapter 9: Boyes & Perrin in review c) found that infestation levels of Coleopteron and Lepidopteron larvae parasitizing tree species within the diet of Meyer's Parrots were significantly different between trees. In addition, Derbel *et al.* (2007) found that infestation levels of bruchid beetles *Bruchidius uberatus* (Coleoptera, *Bruchidae*) in *A. tortilis raddianae* seeds vary from one year to the next according to humidity, temperature and rainfall. These bruchids are similar to those consumed by Meyer's Parrots during the breeding season, and this variation demonstrates the necessity to prospect for these arthropod larvae cooperatively, thus resulting in elevated feeding flock sizes during the breeding season.

Feeding flock size was significantly larger at Mombo, thus indicating differences in carrying capacity or spatial distribution of resources between the two study sites. The lack of temporal variation in feeding flock size between 2005 and 2007 at Vundumtiki also demonstrated that feeding flock size is site-specific, and therefore, variable dependent on habitat characteristics and the assumptions of the Foraging Dispersion hypothesis.

Large feeding flocks have only been reported on agricultural crops, and thus are likely a function of anthropogenic habitat changes resulting in highly concentrated seasonal food resources (e.g. agricultural crops). Similarly, Cape Parrots (Wirminghaus *et al.* 2002), Grey-headed Parrots (Symes & Perrin 2003) and Brown-headed Parrots (Taylor & Perrin 2006) have been reported to flock on abundant food items such as agricultural crops (e.g. grain and citrus) and summer fruits (Rowan 1983; Symes & Perrin 2003; Taylor & Perrin 2004). The findings of this study indicate that in healthy Meyer's Parrot populations, such as the Okavango Delta metapopulation, feeding flock size is not governed by resource availability, but rather social cohesion and anti-predatory behaviour.

Importance of predation

Our findings showed that Meyer's Parrots were sensitive to predation risk. No adults were predated during feeding or socializing, thus demonstrating that these measures were successful in mitigating predation risk. Due to low incidence of large flocks over time and across context, it appears that predation risk is not a causal factor of flocking dynamics of Meyer's Parrots, and therefore it is likely that the cost of sharing food resources is less than the anti-predatory benefits of larger feeding flock sizes.

Mixed-species flocking and avoidance inter-specific competition

The influence of inter-specific competition on feeding flock size of *Poicephalus* parrots is poorly studied. Similar to Black-cheeked Lovebirds *Agapornis nigregenis* (Warburton & Perrin 2005), Meyer's Parrots generally foraged in single-species flocks and had few species that they directly competed with regularly. Black-cheeked Lovebirds are granivorous and predominantly ground foraging, and thus predators and competitors are different to an arboreal forager such as the Meyer's Parrot. Black-cheeked Lovebirds, are also considerably smaller than Meyer's Parrots, and thus may benefit from single- and multi-species flocking more than Meyer's Parrots. Therefore, due to the likely insignificance of predation risk to flocking dynamics, Meyer's Parrots probably avoid multi-species flocking.

In the African subtropics and elsewhere, anti-predatory behaviour does not function exclusively between conspecifics and is often inter-specific, whereby several species co-operate at feeding sites to detect and deter potential predators. For example, Chacma Baboon *Papio cynocephalus ursinus*, Impala *Aepycerus melampus* and Banded Mongoose *Mungos mungo* often forage together and react equally to alarm calls from all species (Boyes unpub. data). Our results, however, showed that Meyer's Parrots have a low tolerance for mixed-species flocking. Factors contributing to this avoidance of mixed-species flocking are unclear; however, demonstrated lower predation risk for this arboreal seed predator likely facilitate this preference to feed in single-species flocks. Boyes and Perrin (Chapter 3: Boyes & Perrin in review d; Chpater 4: Boyes & Perrin in review e) found that Meyer's Parrots feed predominantly in the high canopy, thus avoiding competition with primates and large-bodied frugivores (e.g. Hornbills *Tockus spp.*). In addition, Boyes and Perrin (Chapter 2) showed that Meyer's Parrots, preferred unripe fruits when available and had exclusive predispersal access to seeds inside Leguminosae and Combretateae pods, thus allowing them to avoid inter-specific competition.

There was, however, evidence that Meyer's Parrots reacted to and benefitted from alarm calls of squirrels, which were observed on two occasions feeding with Meyer's Parrots. Meyer's Parrots were most frequently observed foraging with African Green Pigeons on *D. mespiliformis* seeds and *F. sycamorus* figs. Other species frequently observed foraging with Meyer's Parrots included the Grey Lourie, Crested Barbet, Burchell's Starling, Long-tailed Starling, Black-headed Oriole and Chacma Baboon. These are all facultative frugivores, and thus one would expect minimal niche overlap with Meyer's Parrots. Numerous nocturnal seed predators were observed at Vundumtiki and Mombo, however, as arboreal seed predators only the Peters' Epauletted Fruit Bat, Tree Mouse and Bushveld Dormouse competed indirectly with Meyer's Parrots for food resources.

There was a significant Chacma Baboon population of between 200 and 250 at Vundumtiki (Boyes unpub. data). Baboons were frequently observed to disturb parrot feeding bouts, thus forcing the parrots to move to smaller, marginal trees. Sightings of parrots feeding with primates were only observed between August and October when feeding on ripe *D. mespiliformis* and *G. livingstonia* fruits. Meyer's Parrots were observed on one occasion to feed on unripe *Acacia erioloba* pods in the same tree as a giraffe. The avoidance of inter-specific competition could be the selection criteria protecting highly productive food trees from seed predation by Meyer's Parrots, whereby dominant facultative frugivores and seed dispersers such as Chacma Baboons and starlings (*Lamprotornus spp.*) could out compete or scare off parrots from a feeding site, thus having likely implications for both primary and secondary dispersal of these trees.

There was a peak in mixed-species flock observations between October and December, thus indicating a slight bottleneck of food resources coinciding with the end of the dry season after the dominant flowering period and prior to the availability of unripe seeds. The significant negative correlation between percentage mixed-species flocks and percentage available food item consumed suggests that inter-specific competition for food resources increases as number of available food items consumed decreases. This also supports the hypothesis that Meyer's Parrot prefer to forage in small single-species flocks.

CONCLUSION

For the majority of the year, Meyer's Parrots in the Okavango Delta probably do not benefit significantly from flocking on food resources, and feeding flocks greater than two or three are probably the result of lingual feeding and opportunistic flocking on favourable food items after dispersion from communal roosts. Communal roosting likely does not facilitate flocking unless the food resources are close to the roost site, but rather functions as anti-predatory defense mechanism and to facilitate even dispersal into habitat with uniformly or sparsely distributed food resources. The primary benefits of roosting were likely anti-predatory and social cohesion. Meyer's Parrots are likely dependent on riverine forest, *Acacia-Combretum* marginal woodland and Mopane woodland for roost sites in the Okavango Delta. They also aggregated more during the breeding season due to their specialist nutritional requirements and the female being reliant on food provisioning by the male parrots. Meyer's Parrots are sedentary in the Okavango

Delta, but the possibility of limited local migrations in other areas (especially the Zimbabwean highlands) should be investigated.

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Chapter 9:

Breeding biology of Meyer's Parrot (*Poicephalus meyeri*) in the Okavango Delta, Botswana[1]

Abstract. Meyer's Parrots *Poicephalus meyeri* are the most abundant and widespread African parrot and the breeding biology of this analogous Poicephalus parrot had not previously been studied. Meyer's Parrots formed socially monogamous pair-bonds maintained over at least four breeding seasons. Breeding pairs established breeding territories up to an estimated 160 ha within which there were 1–6 nest cavities. Twenty-eight nest cavities utilized by Meyer's Parrots were located during intensive searches within the 430ha sample area. Twelve of these nest cavities were utilized by active breeding pairs for nesting, however; only eight of the breeding pairs could be identified using unique yellow-markings on the crown and carpal joint. Individuals were sexed according to parental role at the nest cavity and over 1700 hours of intensive nest observations at six nest cavities was undertaken. Eggs hatched asynchronously, yet nestlings fledged synchronously with similar body size and condition. Social constraints such as inter-specific competition for nest cavities, predation risk and brood parasitism within the context of the Energy Constraints hypothesis likely supported the early incubation that facilitated this asynchrony. Rainfall seasonality and the consumption of parasitic arthropod larvae incubating in and feeding on pods and fruits in their diet were likely significant factors in the timing and synchrony of breeding at population level. Historical records demonstrated a primary breeding season (February–July) and an auxiliary breeding season (September–November) throughout their southern distributional range.

Introduction

Very little, beyond anecdotal reports in the literature, is known about the breeding biology of Meyer's Parrot *Poicephalus meyeri* in the wild (Perrin *et al.* 2002). Comprehensive studies, however, have been undertaken on the breeding biology of the Cape Parrot *P. robustus* (Wirminghaus *et al.* 2001; Symes *et al.* 2004), Rüppell's Parrot *P. rueppellii* (Selman *et al.* 2004), the Grey-headed Parrot *P. fuscicollis suahelicus* (Symes and Perrin 2004), and the Brown-headed parrot *P. cryptoxantus* (Taylor and Perrin

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[1] Formatted for *Emu* – Austral Ornithology, Royal Australasian Ornithologists' Union: Boyes and Perrin (in review) Breeding biology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana.

2006). Preliminary studies have also been done on the Red-bellied Parrot *P. rufiventris* (Massa 1995) and the Yellow-faced Parrot *P. flavifrons* (Boussekey *et al.* 2002). Senegal Parrots *P. senegalus* and Niam-Niam Parrots *P. crassus* remain data deficient (Juniper and Parr 1998).

Wilson (1989) put forward that persistence of a phyletic line through geological time is the key measure of ecological success. Ecological success is, therefore, a function of the number of species in the monophyletic group, occupation of unusual adaptive zones, extent of distributional range, and fluctuations in population size and status (Wilson 1989). As the most abundant and widespread *Poicephalus* parrot (Rowan 1983; Juniper and Parr 1998), understanding the adaptive zone of Meyer's Parrot is central to better understanding their ecological success. Our study gathered evidence to support the hypothesis that the breeding biology of Meyer's Parrot is significantly different from other *Poicephalus* parrots.

All *Poicephalus* parrots studied thus far breed during the dry winter season (Wirminghaus *et al.* 2001; Selman *et al.* 2004; Symes and Perrin 2004; Taylor and Perrin 2006). Cape Parrots, however, breed predominantly at the end of winter and beginning of summer (Wirminghaus *et al.* 2001; Tarboton 2001). Meyer's Parrots are also reported to breed during the dry season in Zimbabawe (*P. m. transvaalensis*), Zambia (*P. m. matschiei*), Malawi (*P. m. matschiei*), Angola (*P. m. matschiei*), and Sudan (*P.m. meyeri*) (White 1965; Rowan 1983; Fry *et al.* 1988; Forshaw 1989; Juniper and Parr 1998; Hockey *et al.* 2005). There are, however, sporadic nesting records for *P. m. transvaalensis* breeding activity between October and January in Zimbabwe (Rowan 1983). *P. m. damarensis* and *P. m. transvaalensis* are reported to overlap in the Okavango Delta likely forming an intermediate. Results from our study and historical nesting records (1918–1996) from South Africa, Namibia and Botswana were used to evaluate breeding seasonality of *P. meyeri damarensis* and *P. m. transvaalensis* in southern Africa for comparison with results from our study.

Monogamous pairs of Cape Parrots (Wirminghaus *et al.* 2001), Grey-headed Parrots (Symes and Perrin 2004), and Brown-headed Parrots (Taylor and Perrin 2006) are reported to breed synchronously. Breeding synchrony has been put forward as the most important factor promoting the evolution of extra-pair mating systems (Birkhead and Biggins 1987; Stutchbury *et al.* 1994; Stutchbury and Morton 1995; Weatherhead 1997; Stutchberry 1998; Stutchbury *et al.* 1998; Schwagmeyer and Ketterson 1999; Peters *et al.* 2003). Extra-pair copulations (EPCs) are, therefore, expected in *Poicephalus* parrots, unless there are mechanisms that minimize opportunity for extra-pair fertilizations (e.g. mate-guarding or female detention (e.g. Hornbills *Tockus spp.*)) (Petrie and Kempenaers 1998; Petren *et al.* 1999). Symes and Perrin (2004) put forward that only a small proportion of a Grey-headed Parrot population actively nest. Therefore, there are likely numerous unpaired, non-nesting males prospecting for extra-pair fertilizations. Females either become fertile after a few years or seek intra-specific brood parasitism opportunities (Sandell and Diemer 1999). Males provision females during egg-laying and incubation in all *Poicephalus* parrots studied thus far (Taylor and Perrin 2006; Symes and Perrin 2004; Wirminghaus *et al.* 2001). Provisioning males are, therefore, away from the nest cavity for long periods of time (depending on food resource availability), providing opportunity for extra-pair fertilizations of synchronously fertile females by non-nesting males. Males likely benefit from EPCs by gaining extra-pair paternity, while the female benefits by acquiring additional genetic diversity (Arnqvist and Kirkpatrick 2005; Spoon *et al.* 2007). Our study tested the hypothesis that Meyer's Parrots are socially monogamous and breeding synchronously within an extra-pair mating system.

Parrots are more insectivorous than initially suspected (Forshaw 1989) and African parrots have consistently been found to actively forage for invertebrates (Selman *et al.* 2002; Wirminghaus *et al.* 2002; Symes and Perrin 2003; Warburton and Perrin 2005; Taylor and Perrin 2006). Boyes and Perrin (Chapter 2: Boyes and Perrin in review a) revealed a dietary switch to arthropod consumption far more dramatic than previously recorded in other *Poicephalus* parrots, whereby arthropod consumption was distinctly seasonal and accounted for 20-72% of the total monthly feeding activity during the breeding season (March – February). Phenotypic changes in gut retention rate, digestive efficiency and hence feeding rate to accommodate dietary switches between seed predation, frugivory and insectivory have been demonstrated in several bird species (Levey and Karasov 1989; Levey and Martinez Del Rio 2001). Arthropod consumption was previously linked with the breeding activity of Rüppell's Parrots (Selman *et al.* 2002) and Grey-headed Parrot (Symes and Perrin 2003), but not with other *Poicephalus* parrots studied thus far (Wirminghaus *et al.* 2002; Taylor and Perrin 2006). Selman *et al.* (2002) put forward that arthropod consumption likely provided additional protein necessary for egg production, chick growth and supplementary metabolic water during the dry season. Infestation rates (within and between trees) and developmental stage of all arthropod larvae in the breeding season diet were estimated from samples taken in the field. We used the relative resource abundance of the pods and fruits parasitized by these larvae over time (Chapter 4: Boyes and Perrin in review b) to estimate larval resource abundance during the breeding season from infestation levels. Our study tested the hypothesis that Meyer's Parrots are dependent on arthropod consumption during the winter breeding season.

Parental effort is the expenditure of parental resources such as time or energy on the care of offspring (Siegel *et al.* 1999). Females of all *Poicephalus* parrots studied thus far, remain in the nest cavity from onset of egg-laying and initiate incubation simultaneously, after which they share the provisioning of nestlings with the male (Wirminghaus *et al.* 2001; Symes and Perrin 2004; Selman *et al.*

2004; Taylor and Perrin 2006). Males are reported to be in attendance throughout the nesting cycle, provisioning the female and nestlings (Wirminghaus *et al.* 2001; Symes and Perrin 2004; Selman *et al.* 2004; Taylor and Perrin 2006). Numerous parrot species initiate incubation before they complete egg-laying, thus facilitating asynchronous hatching (Snyder et al. 1987; Beissinger and Waltman 1991; Gnam 1991; Stoleson and Beissinger 1995; Beissinger *et al.* 1998). Symes and Perrin (2004) put forward that hatching asynchrony occurs in Grey-headed Parrots, but were unable to confirm this. Asynchronous hatching results in significant differences in hatchling size and opens opportunity for avian brood reduction (Stouffer and Power 1991; Stoleson and Beissinger 1997). Our study evaluated putative stimuli for facultative early incubation and assessed the applicability of established hypotheses to hatching asynchrony in *Poicephalus* parrots.

Taylor and Perrin (2004) have suggested the social mechanism behind group dynamics in *Poicephalus* parrots is likely intra-specific association, whereby flocking is a function of the aggregation and dispersal of pair sub-units governed by food resource availability. Brown-headed Parrot pairs showed no special affiliation to other members of the group (except recently hatched progeny), and therefore, will join or leave the flock voluntarily (Taylor and Perrin 2004). On the basis of life-history traits and breeding requirements, Armstrong and Juritz (1996) predicted that cooperative breeding likely occurs in Cape Parrots. Wirminghaus *et al.* (2001), however, found no evidence to support cooperative breeding. Massa (1995) put forward that breeding synchrony within a loose colony was important to the breeding biology of the Red-bellied Parrot, a member of the *P. meyeri* superspecies. Our study evaluated intra-specific interactions and territoriality using individual identification (ID) cards.

Methods

Study area

The Okavango Delta was chosen as our study area because of its significant Meyer's Parrot population (Wirminghaus 1997). Our study was conducted in the area surrounding Vundumtiki Island in the north-eastern Okavango Delta (Figure 1). Vundumtiki is a wilderness area with limited human impact or disturbance to habitat and animal behaviour. Breeding records were also gathered from other areas in the Okavango Delta, including Mombo Camp, Chitabe Camp, Duba Plains and Tubu Tree Camp (Figure 1).

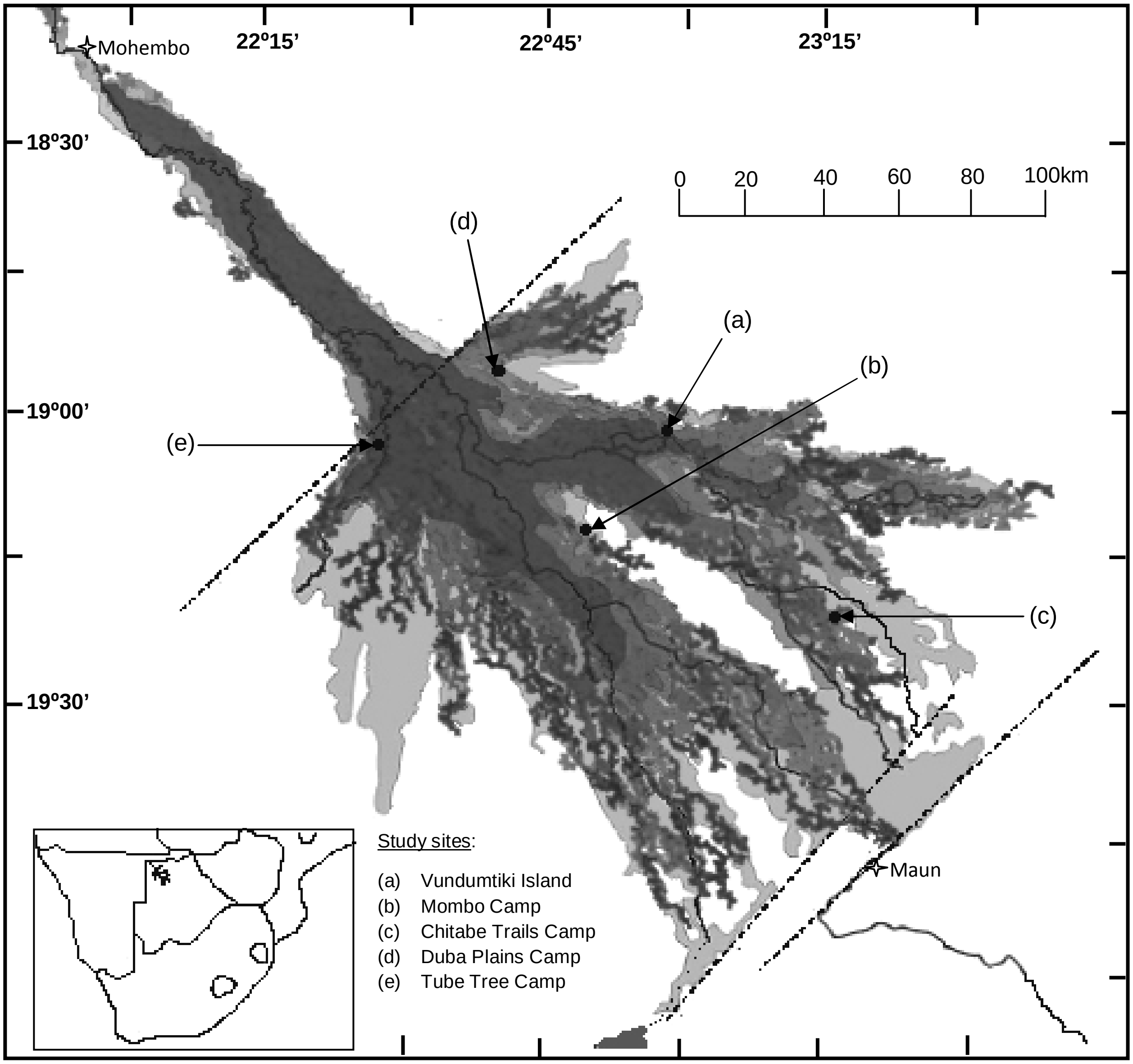


Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

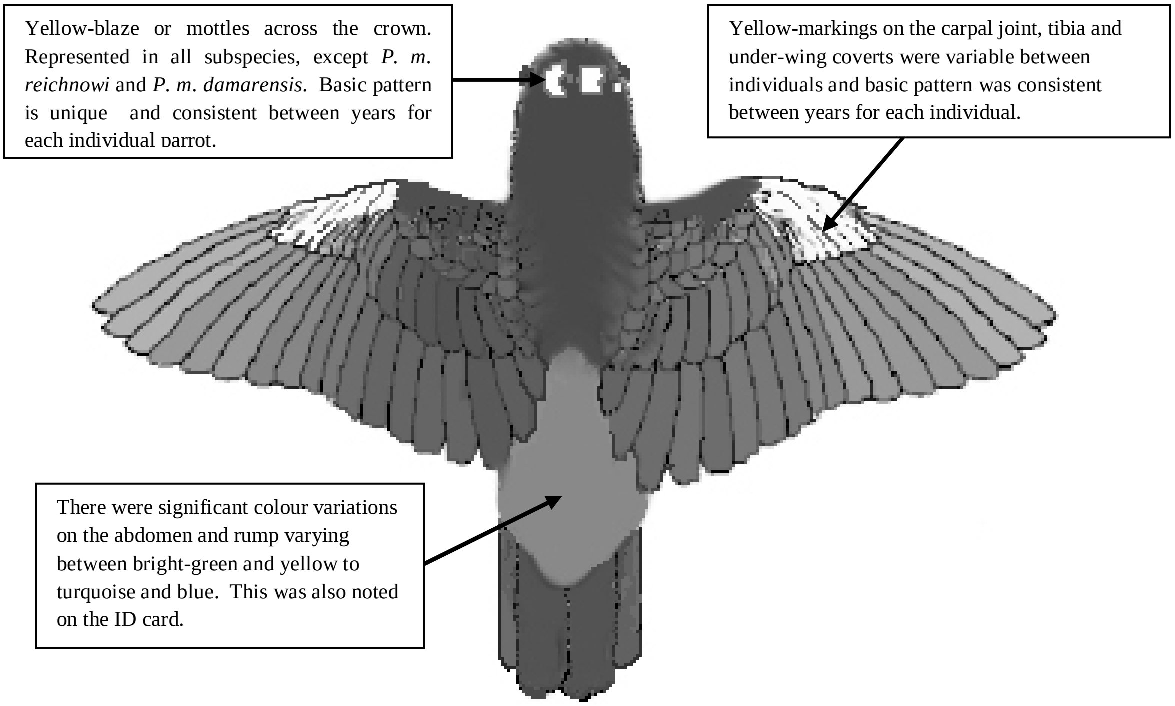
Climatic conditions in the Okavango Delta are distinctly seasonal, comprising a wet season (November-March) and dry season (April-October). Mean annual rainfall is 450–560mm (Ellery *et al.* 2003; Wolski and Savenije 2006). During the annual flood the area covered by water expands from its annual low of 2500–4000km^2 in February–March to its annual high of 6000–12000km^2 in August–September. Arrival of the annual flood lags the rainy season and follows one or two months after the end of rainfall in the region (Gumbricht et al. 2001; Ellery *et al.* 2003).

Questionnaire

Questionnaires were sent out to all Wilderness Safaris Botswana professional guides operating in the Okavango Delta. Respondents were asked to report on breeding seasonality and most important food resources during the breeding season in their area of operation. Respondents were also asked to comment on the re-use of Meyer's Parrot nest cavities by other cavity-nesting bird species during summer.

Individual identification

Meyer's Parrots are sexually monomorphic (Rowan 1983; Juniper and Parr 1998). The bright yellow blaze on the crown is, however, an inconsistent character, varying with age and subspecies (Rowan 1983). Six Meyer's Parrot subspecies are recognized with *P. meyeri damarensis* and *P. m. transvaalensis* reported to overlap in the Okavango Delta (White 1965; Rowan 1983). Probable subspecies were identified using the following criteria: *P. m. transvaalensis* had full yellow blaze on their crown, *P. m. damarensis* had no yellow on their heads, and the intermediate (*P. m. damarensis* x *transvaalensis*) had a mottled or incomplete yellow blaze on their crown (Figure 2) (Rowan 1983).



Yellow-blaze or mottles across the crown. Represented in all subspecies, except *P. m. reichnowi* and *P. m. damarensis.* Basic pattern is unique and consistent between years for each individual parrot.

Yellow-markings on the carpal joint, tibia and under-wing coverts were variable between individuals and basic pattern was consistent between years for each individual.

There were significant colour variations on the abdomen and rump varying between bright-green and yellow to turquoise and blue. This was also noted on the ID card.

Figure 3: Distinctive yellow-markings proven to be unique to every individual Meyer's Parrot

We used the presence and absence of these unique yellow blazes on the crown and carpal joint to individually identify Meyer's Parrot within breeding pairs (Figure 2). We prepared breeding pair identification (ID) cards when visibility was optimal at nest cavities. Following initial identification of the breeding pairs, individuals were sexed in the field based on their breeding roles (e.g. female remained in the nest during egg-laying and incubation) during subsequent visits to the nest cavity. High resolution photographs were taken to facilitate identification in subsequent seasons (when possible). Breeding pairs comprising two *P. m. damarensis* were excluded from the intensive nest observations due to inability to individually identify individuals. These pairs were indentified through association with the nest cavities.

Data collection

Identification of all fruit- and pod-bearing trees potentially used by Meyer's Parrot was done between July 2003 and July 2004. Tree nomenclature followed Van Wyk and Van Wyk (1997) and Palgrave (2002). Rainfall was monitored daily using a rain gauge between January 2004 and July 2007. The extent of the flood was monitored using flow rate data from Mohembo (Figure 1) (Powerserve 2008) and calibrated to the study site by recording first significant increment in water level on a measuring pole in permanent water as the start of the flood.

Food item preferences were monitored five times a week using road transects between August 2004 and July 2005, and February 2007 and July 2007 (Chapter 2).

To standardize spatial distribution the sample area was defined as the area 250m either side of an 8.6km standardized road transect - this constitutes one third of the feeding activity road transect (Chapter 2). Only breeding pairs utilizing natural cavities within this sample area were included. Sample area was subdivided into four, 1.7 km sections along the road transect.

Preliminary fieldwork was conducted between August 2004 and July 2005. Nest cavities were located by following "duetting" vocalizations (i.e. breeding territory announcement) during road transects conducted five times a week during feeding ecology transects (Chapter 2). All breeding activity was recorded, including courtship and copulation, inter- and intra-specific competition (e.g. territorial displays), and predation. All nest cavities associated with Meyer's Parrot breeding activity were inspected by climbing into the tree and using a mounted mirror and LED light to ascertain nesting period. The nesting cycle was separated into the following nesting periods: territorial advertisement and nest preparation; copulation and egg-laying; incubation; hatching; nestling; fledging; and post-fledging. After cessation of breeding by August 2005, a hole was drilled behind the main cavity, when possible, to allow for access to nest contents during the 2007 field season. These holes were sealed with an 8mm PVC disk and painted brown to minimize reflectivity.

Intensive fieldwork was conducted between February 2007 and August 2007. From February to May, we conducted extensive 4-hour bush walks once a week between 06h00 and 11h00 in each section of the sample area (i.e. five times a week). During bush walks we thoroughly investigated each section for Meyer's Parrot nesting and non-nesting activity (e.g. socializing flocks). Non-nesting parrots were those found in socializing flocks (i.e. not feeding) of greater than two parrots after the initiation of the egg-laying and incubation periods. The following data were recorded when breeding pairs were encountered: GPS-coordinate of new nest cavities; identity from ID cards (when possible); activity (e.g. nest preparation, feeding, prospecting for new cavities), nesting period; and notes on nesting behaviour (e.g. posturing and vocalizations). Nest cavities with actively nesting breeding pairs (i.e. containing eggs) were classified as primary nest cavities. Other nest cavities that were prepared and not used, excavated or altered on more than one occasion, or used and then abandoned for the primary nest cavity nearby, were classified as subsidiary nest cavities. When non-nesting parrots were encountered we recorded the following: flock size; activity (i.e. socializing, feeding or resting); time of day; and location and habitat type. On bush walks, all new breeding pairs and nest cavities encountered were GPS-marked and re-visited until nesting period was ascertained and new ID cards compiled.

Intensive nest cavity observations began when female Meyer's Parrots took up permanent occupancy of nest cavity. We conducted 10-hour observations in two 5-hour shifts using volunteer field researchers. Observation period varied according to logistical constraints (e.g. use of research vehicle). All observations were made with a 30x Kowa spotting scope at the maximum sighting distance possible to minimize disturbance of behaviour. Six primary nest cavities with the most identifiable (i.e. contrasting yellow-markings) and good visibility of nest contents (e.g. hole drilled in 2005 field season) were monitored as part of the intensive nest cavity observations (A–E: Table 1). Activity at these nest cavities was separated into three nesting activity class: outside cavity (O), away from cavity (A), and inside cavity (I). ID cards were used until observer could identify male and female without referencing. Exact time of day was recorded every time the nesting activity class changed for male, female or nestlings, or the female or nestling stuck their head out the nest entrance, nestlings vocalized, or an unknown, extra-pair Meyer's Parrot arrived at the nest cavity. Additional information on feeding behaviour, vocalizations, inter-specific interactions, anti-predatory behaviour (e.g. provisioning away from the nest cavity and female vigilance), and nest predation was also recorded. Composition of regurgitate was determined through observation of residue on the nestlings and beak of provisioning adult (where possible samples were taken from the nest entrance). Two nests a day, six days a week, were monitored between March and July. Nest observation was not repeated at a specific cavity until all other cavities were monitored. Nest inspections were conducted once a week prior to the copulation and egg-laying period, after which nest cavities were inspected every second day until no eggs were laid for one week. Nest cavities were then inspected once a week until the first egg hatched, after which inspections were conducted every other day.

All other nest cavities discovered to be active within the sample area were monitored once a week during bush walks for one hour to ascertain nesting period. These nest cavities were, if active, inspected bi-monthly or whenever there was a significant event at one of the primary nest cavities (e.g. hatching or fledging).

Nest cavity and ambient temperature readings

DALLAS Thermochron data loggers (Fairbridge Technologies 2006) were placed inside all six nest cavities monitored during 10-hour nest cavity observations. Temperatures inside primary nest cavities (not under the clutch) were measured every 71 minutes between March and July. Control DALLAS Thermochron data loggers measured temperature fluctuations every 71 minutes outside each of the primary nest cavities.

Predation risk and brood parasitism

During nest inspections, remnants of egg shell, blood or feathers indicated predation by rodents or Large Spotted Genet *Genetta tigrina*, while no sign of predation indicated predation by snakes (e.g. Vine snake *Thelotornis capensis*) (Sorace *et al.* 2000). Following a predation event, we would conduct 10-hour nest cavity observations for three days to record subsequent nesting behaviour (if breeding activity continued).

We recorded all activity of putative brood parasites (especially the Lesser Honeyguide *Indicator minor* and Greater Honeyguide *Indicator indicator*) in the vicinity of active nest cavities and within the sample area. We also introduced one fake white egg made from clay to six active Meyer’s Parrot nest cavities after the first egg was laid to test the reaction of female Meyer’s Parrots. Fake eggs were modeled according to egg dimensions for Meyer’s Parrot reported by Rowan (1983) and Juniper and Parr (1998), and from measurements made in the field (n = 5).

Arthropod larvae availability and infestation levels

We assessed developmental stage of arthropod larvae using a photographic record and daily inspection of samples ($n \approx 100$) of infested pods and fruits held in a controlled environment. These photographs were compared with scanned electron microscopy images of the life cycle of *Bruchidius raddianae* that prey on *Acacia tortilis subsp. raddiana* seeds (Derbel *et al.* 2007).

We gathered samples ($n < 500$) of all pods and fruits parasitized by arthropod diet that occur in the breeding season diet from the canopies of trees utilized by Meyer’s Parrots twice a week between March and June, thus estimating infestation levels within each tree (W_i). On bush walks we sampled pods and fruit ($n = 50$) from five trees of each species twice a week and investigated them for evidence of larval infestation, thus estimating infestation levels between trees (B_i). From these data we estimated total relative resource abundance of arthropod food items at the population level by multiplying the total relative resource abundance of host tree species (T-RRA_i) (Chapter 4) by B_i and W_i.

Data analyses

For analysis, the 2007 breeding season was split into 18 weeks starting on 13 March 2007 and ending 16 July 2007. One breeding pair that achieved fledging was randomly selected for intensive assessment and correlation with ambient nest temperatures measured inside the nest cavity.

Breeding synchrony was evaluated using the corrected breeding synchrony index (SI) forward by Kempenaers (1993). The following equation was used to calculate breeding synchrony at Vundumtiki:

$$\mathrm{SI}_{\mathrm{VTK}} = \frac{1}{6}\sum_{p=1}^{6}\left[\frac{\sum_{i=1}^{tp} f_{i,p}}{tp(F-1)}\right] \times 100$$

$\mathrm{SI}_{\mathrm{VTK}}$ accounted for differences in population size and duration of the fertile period. The index was standardized and thus ranged from 0% when there was no overlap in fertile periods to 100% in a fully synchronous breeding population. The duration of the fertile period was the period from five days before the first egg was laid or the day copulation was first observed (which ever was first) until five days after the last egg was laid (Kempenaers 1993).

Mayfield's estimator (Mayfield 1975) was used to compare nesting success (N_s) between nesting periods, using the following equation:

$$N_s = (1 - \left[\frac{Losses}{Exposure}\right])^{np}$$

The basic units of Mayfield's estimator were "nest days" (Johnson 1979; Hensler and Nichols 1981; Farnsworth et al. 2000). Losses could include all nestlings lost to predation, brood reduction and disease; exposure is the total number of active nest days; and *np* is the number of days in the specific nesting period being investigated (Ndithia and Perrin 2007).

Relative resource abundance of arthropod larvae was estimated by estimating the infestation levels between and within host trees (Boyes and Perrin in press c). We then converted estimates of relative resource abundance of fruits and seeds in host trees (Boyes and Perrin in press c).

Spearman rank correlation (r_s) was used to evaluate the relationship between potential environmental triggers for breeding (e.g. temporal food resource abundance, ambient temperature in nest cavity, and rainfall) and observed breeding activity (e.g. number of clutches or offspring). Wilcoxon Matched Pair Test was used to look for significant difference in parental effort between years, breeding pairs and sexes. Statistical analysis followed Quinn and Keough (2002) and STATISTICA 7.1 (Statsoft 2006).

Results

Questionnaire

The results of 28 questionnaires confirmed the year-round presence of Meyer's Parrot throughout the Okavango Delta. Most respondents were unclear on food resources important during the breeding season, however, three reported *Combretum imberbe*, two reported *Terminalia sericea*, and one reported *Sclerocarya birrea caffra*. Eight respondents confirmed that Meyer's Parrots breed during winter between April and July. Nine respondents, however, reported breeding throughout the year due to nesting records between October and December. One respondent noted that Lilac-breasted Rollers *Coracias caudata* utilized a nest cavity previously occupied by Meyer's Parrots, and another reported re-use by a Woodland Kingfisher *Halcyon senegalensis.*

Analysis of historical nesting records

Historical nesting records demonstrate that Meyer’s Parrots breed during the dry season between March and August throughout southern Africa (Figure 3). There is limited evidence for an auxiliary breeding season during summer, following the first significant rains in November (Figure 3).

In captivity, the incubation period of Meyer’s Parrots is reported to be between 29–31 days and nestling period at between eight to nine weeks (Brickell 1985). A wild pair in a nest box was, however, reported to incubate the eggs for between 27–31 days, and the nestlings were fed by both parents for 13 weeks after hatching before all nestlings fledged together (Brickell 1985).

Over 76% (n = 13) of records during the incubation period were in the winter dry season between April and October. Similarly, over 93% (n = 15) of records during the nestling period were also during the winter dry season. There were, however, significant differences in breeding seasonality between 1918 and 1994.

There was also a significant difference between breeding seasonality in different regions, whereby the Namibian, Angolan, Zimbabwean and South African populations all bred during the winter dry season, while Meyer's Parrots in the Zimbabwean highlands bred during the summer wet season. There was evidence for predation at seven of the nest cavities recorded on nesting records. Failure of eggs to hatch was recorded on six occasions and three abandoned nest cavities were discovered. There was one nesting record in Zimbabwe in 1953 that reports two large unknown eggs that appeared to be those of the Greater Honeyguide *Indicator indicator*.

Adult survival, pair-bonding and territoriality

Yellow-markings were unique to individual Meyer’s Parrots within the study area. According to re-sightings of breeding pairs with ID cards at the same nest cavities in subsequent years, adult survival was high with breeding pairs A and D utilizing the same nest cavities and remaining socially monogamous for four years. Breeding pairs C and E also utilized the same primary nest cavity and remained socially monogamous for at least two years.

Breeding pairs A–F were shown to establish breeding territories of between one and six nest cavities within an area of up to 160 ha (Table 2). Males excavate and maintained all of the nest cavities within the breeding territory, often with the female in attendance. Territorial vocalizations and duetting occurred at primary and auxiliary nest cavities. All sightings were confirmed using ID cards and high resolution digital images (when available).

Inter- and intra-specific breeding territory defence was infrequent. Following the Large Spotted Genet predation event (breeding pair E: NC17), however, an additional breeding pair arrived at the nest cavity and chased the predator away, after which they attacked the, now unpaired, male and usurped the breeding territory.

During the 68 bush walks within the sample area we observed flocks of non-nesting parrots on 22 occasions. Mean non-nesting flock size was 9 ± 0.43 parrots with a maximum flock size of 18. Highest probability of detecting non-nesting flocks was in March 2007 (32%, n = 7), followed by April (27%, n = 6) and May (27%, n = 6). Twenty bush walks were conducted in each of these months (n = 60). These gatherings were confirmed to comprise non-nesting parrots by comparing behaviour with nesting parrots over precisely the same time period. Nesting parrots as 10-hour observations in the study area were either inside the nest cavity (i.e. female) or provisioning the female and/or chicks (i.e. male), and thus did not have time to aggregate in these large flocks. Non-nesting or "singles club" flocks were followed for 85.77 ± 9.60 minutes (n = 22). Upon disbanding pairs were followed on nest inspection forays on three occasions and were found to inspect up to 5 cavities per hour, thus indicating breeding behaviour, but no nesting activity.

There was no separation of subspecies during the breeding season, whereby breeding pairs A – E were all mixed pairs. Overall there were eight *P. m. damarensis* (44%), five *P. m. transvaalensis* (28%), and five intermediates (28%).

Breeding seasonality

We recorded breeding activity at 75 nest cavities during our study, including 28 within the 860 ha sample area along the 8.6 km road transect in the Vundumtiki study area (Table 2), 16 in the Mombo area, 11 in the Tubu Tree area, seven in the Chitabe area, five in the Duba area, and four in the Xigera area (Figure 1). Over 90% (n = 64) of nesting attempts were made from March–July 2005 and 2007 (Figure 4) - this was recognized as the <u>primary breeding season</u>. There was no significant difference between number and timing of clutches in the 2005 and 2007 primary breeding seasons (Wilcoxon Matched Pairs: T = 2.5; Z = 1.68; p-level = 0.093) (Figure 4). Breeding activity outside of the primary breeding season was recorded between October and January at Mombo Camp (n = 3), Tubu Tree Camp (n = 2), and Vundumtiki (n = 2) – this was recognized as the <u>auxiliary breeding season</u>.

Table 1: Breeding territories of eight Meyer's Parrot breeding pairs at Vundumtiki. **Bold** indicates primary nest cavity used for breeding. All other nest cavities are subsidiary.

	Nest cavity		Territoriality	
Breeding pairs	Nest cavity	FAMILY/Species	Distance to primary nest cavity (m)	Size of breeding territory (ha)
A	**NC01**	**LEGUMINOSAE/*Acacia nigrescens***	-	14.25
	NC02	EBENACEAE/*Diospyros mespiliformis*	59	
	NC03	LEGUMINOSAE/*Acacia nigrescens*	228	
	NC04	LEGUMINOSAE/*Colophospermum mopane*	213	
B	**NC05**	**LEGUMINOSAE/*Lonchocarpus capassa***	-	57.82
	NC06	LEGUMINOSAE/*Acacia nigrescens*	290	
	NC07	EBENACEAE/*Diospyros mespiliformis*	246	
	NC08	LEGUMINOSAE/*Acacia nigrescens*	343	
	NC09	LEGUMINOSAE/*Acacia nigrescens*	477	
	NC10	MORACEAE/*Ficus sycomorus*	429	
C	NC11	COMBRETACEAE/*Combretum imberbe*	662	160.16
	NC12	**COMBRETACEAE/*Combretum imberbe***	-	
	NC13	LEGUMINOSAE/*Colophospermum mopane*	714	
	NC14	BOMBACEAE/*Adansonia digitata*	24	
D	NC15	COMBRETACEAE/*Combretum imberbe*	256	20.59
	NC16	**COMBRETACEAE/*Combretum imberbe***	-	
E	**NC17**	**LEGUMINOSAE/*Acacia nigrescens***	-	35.68
	NC18	LEGUMINOSAE/*Acacia nigrescens*	126	
	NC19	LEGUMINOSAE/*Acacia nigrescens*	328	
	NC20	LEGUMINOSAE/*Acacia nigrescens*	337	
F	**NC21**	**LEGUMINOSAE/*Acacia nigrescens***	-	57.55
	NC22	LEGUMINOSAE/*Acacia nigrescens*	428	
G	**NC23**	**LEGUMINOSAE/*Colophospermum mopane***	-	-
H	**NC24**	**LEGUMINOSAE/*Colophospermum mopane***	-	-
I	NC25	LEGUMINOSAE/*Acacia nigrescens*	-	-
No ID	NC26	LEGUMINOSAE/*Acacia nigrescens*	-	-
No ID	NC27	COMBRETACEAE/*Combretum imberbe*	-	-
No ID	NC28	LEGUMINOSAE/*Acacia erioloba*	-	-

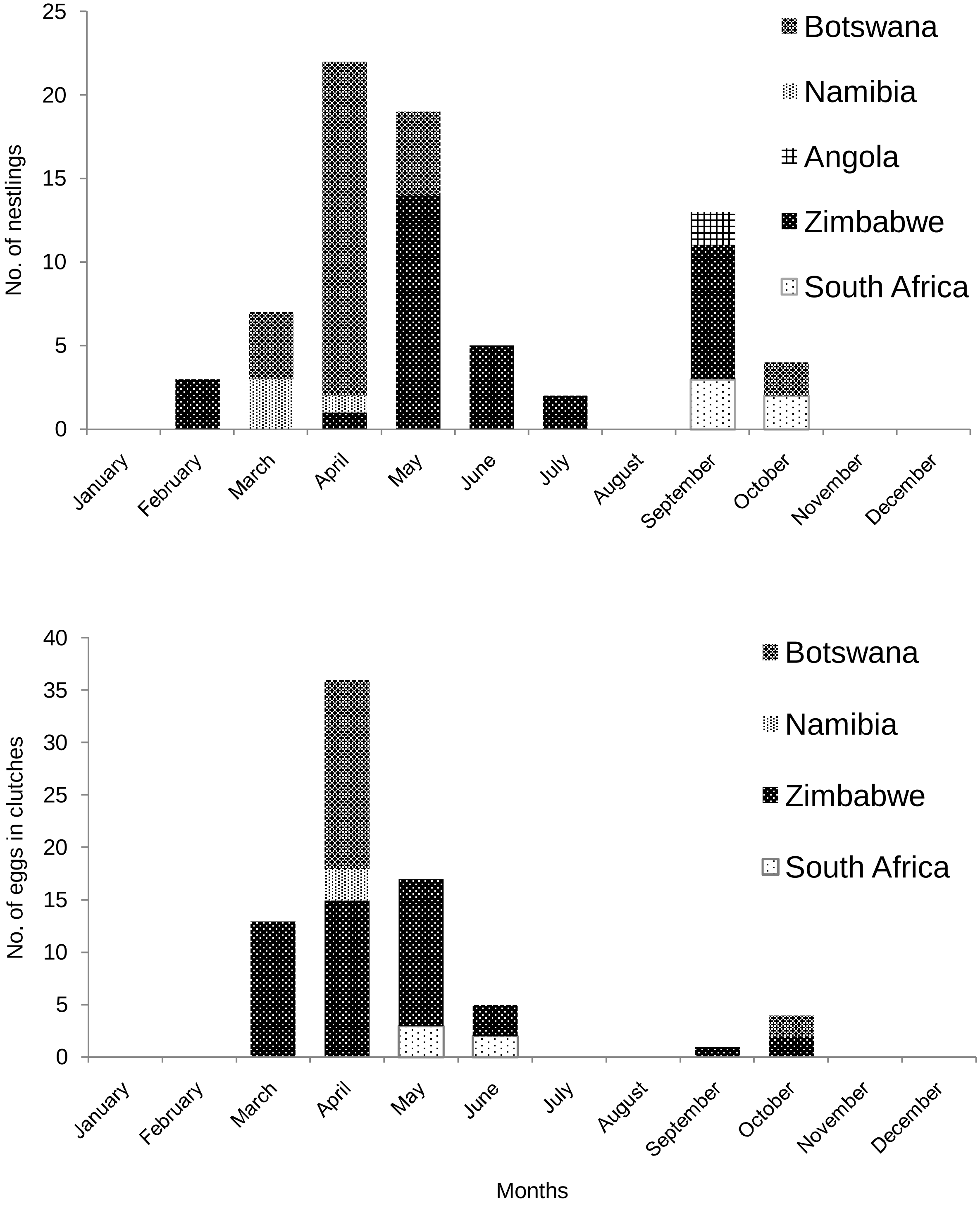


Figure 3: Historical nesting records from South Africa, Namibia, Angola and Zimbabwe (1918–1996)

Table 2: Breeding success and nesting cycle of Meyer’s Parrots during the 2007 breeding season at Vundumtiki

		Breeding success		Nesting cycle							
Breeding pairs		No. of eggs	No. fledged	Territory establishment	Copulation	Days	Laying	Days	Hatching	Days	Fledging
A	NC01	3	3	15 Feb - 24 Mar	25 Mar - 6 Apr	11	1 Apr - 8 Apr	30	1 May - 7 May	51-58	28-Jun-07
B	NC05	3	3	21 Feb - 21 Mar	22 Mar - 27 Mar	5	29 Mar - 7 Apr	30-31	29 Apr - 5 May	55-61	30-Jun-07
	NC06	1	0	21 Feb - 21 Mar	22 Mar - 27 Mar	5	26 Mar - 28 Mar	Disturbed by investigator*			
C	NC11	1	0	29 Feb - 23 Mar	24 Mar - 5 Apr	12	30 Mar - 2 Apr	Disturbed by investigator*			
	NC12	3	3	29 Feb - 23 Mar	24 Mar - 5 Apr	12	3 Apr - 10 Apr	29-30	3 May - 8 May	53-58	1-Jul-07
D	NC16	3	3	4 Feb - 22 Mar	-	-	30 Mar - 4 Apr	28-30	3 May - 8 May	52-57	30-Jun-07
E	NC17	4	0	16 Feb - 28 Mar	-	-	31 Mar - 6 Apr	30-31	1 May - 5 May	Predation**	
F	NC21	3	3	2 Mar - 2 Apr	2 Apr - 10 Apr	8	-	-	3 May - 10 May	49-59	1-Jul-07
G	NC23	3	0	-	-	-	25 Mar - 30 Mar	Predation**			
H	NC24	3	0	12 Feb - 25 Apr	-	-	-	-	1 May - 5 May	54-60	1-Jul-07
Unknown	NC25	3	3	-	-	-	-	-	-	-	27-Jun-07
Mayfield’s estimator	-	-	-	-	-	-	-	0.204	-	0.080	-

*Investigator introduced a fake white egg and females abandoned the nest cavity to resume laying in another nest within the breeding territory.

**Predation of female and three nestlings inside the nest cavity overnight by Large Spotted Genet *Genetta tigrina*.

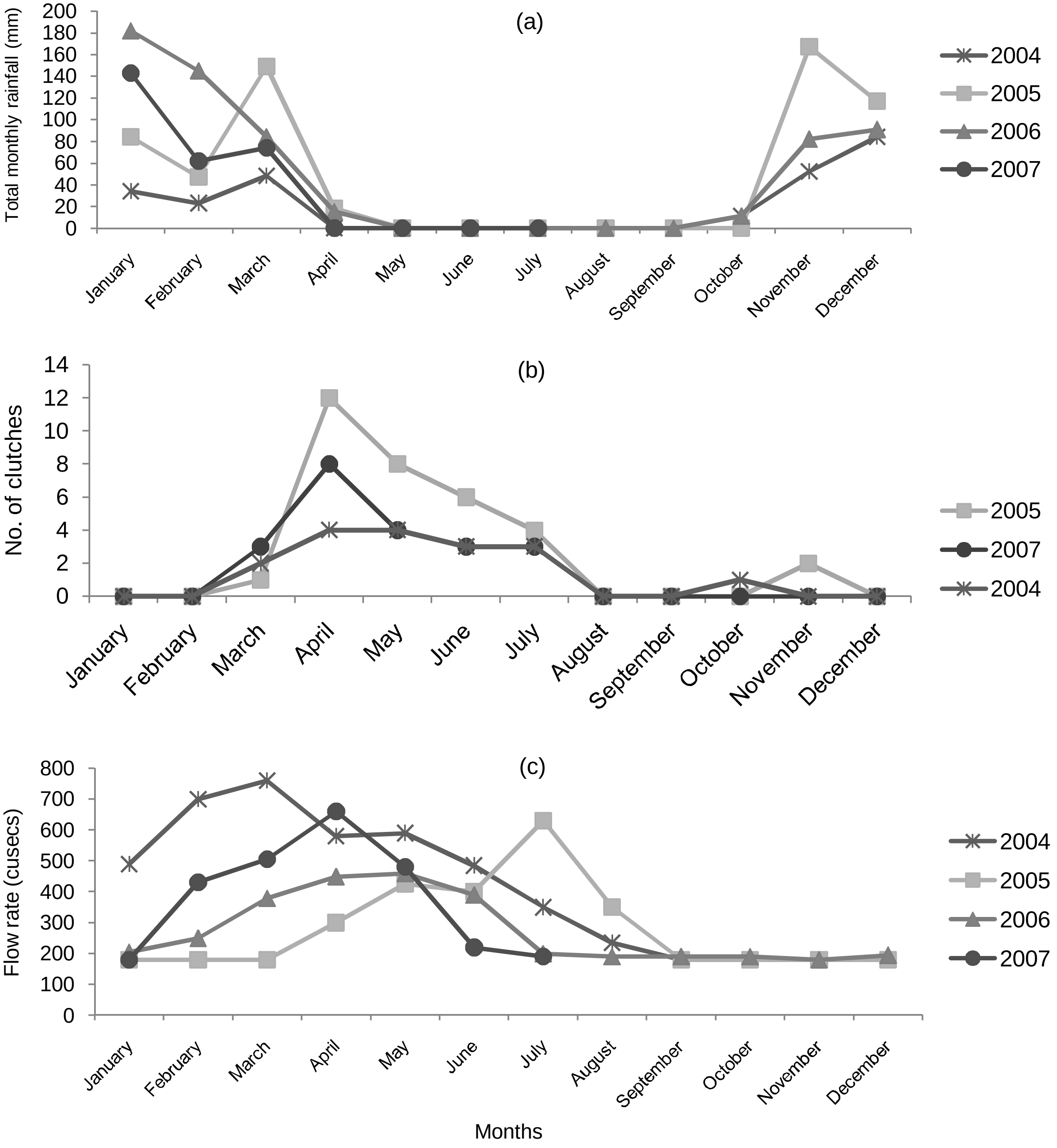


Figure 4: (a) Total monthly rainfall at Vundumtiki study site between 2004 and 2007; (b) No. of clutches recorded within the sample area at Vundumtiki during 2004, 2005 and 2007 field seasons; (c) Mean flood flow rate at Mohembo corrected to delay in flooding at Vundumtiki.

Breeding synchrony

Over the 2007 breeding season, Meyer's Parrots bred synchronously between 21 March 2007 and 1 July 2007 with a breeding synchrony index (SI) value of **79.26%** (Table 3). In addition, there was no significant difference in the nesting cycles of the males in breeding pairs A and F over 18 months (N = 54; T = 512.0; Z = 0.311; p-level = 0.755). Similarly, there was no significant difference in the nesting cycles of the females in breeding pairs A and F (N = 54; T = 420.0; Z = 0.875; p-level = 0.381). Similar relationships were found between breeding pairs B, C, D and E.

Environmental constraints

The primary breeding season coincided with the cessation of rainfall and the arrival of the annual flood (Figure 4). During 2007, there was a significant negative correlation between monthly rainfall and number of eggs or nestlings in all nest cavities each month (n = 7; r_s = -0.867; t(n-2) = -3.89; p-level = 0.011). Flood regime had no direct impact on breeding biology.

Arthropod larvae consumed by Meyer's Parrots during the breeding season, included the following: Red Marula caterpillar *Mussidia nigrivenella* (Lepidotera, *Pyralidae*) feeding on *Sclerocarya birrea caffra* fruit; bruchid beetle larva *Caryedon spp.* (Coleoptera, *Bruchidae*) feeding on seed inside *Combretum hereroense* and *Terminalia sericea* pods; bruchid beetle larva *Bruchidius uberatus* (Coleoptera, *Bruchidae*) feeding on seed inside *Acacia erioloba* pods, and an unknown owlet moth larva (Lepidoptera, *Noctuidae*) feeding on seed inside *Colophospermum mopane* pods (Table 4; Figure 4).

The unknown owlet moth larvae (Lepidoptera, *Noctuidae*) and Red Marula caterpillars were both observed to pupate shortly after feeding by Meyer's Parrots was first reported. Bruchid larvae in *T. sericea*, *C. hereroense* and *A. erioloba* all maintained constant size throughout the sample period. Bruchids inside *Terminalia sericea* pods were demonstrated to pupate outside the pod (Figure 6a) and emerge in November (Figure 6b).

They were all available during the egg-laying and incubation periods and bruchid larvae in *C. hereroense* were available for the longest period (Figure 7(a)). There was a significant positive correlation between relative weekly resource abundance of bruchid beetle larvae incubating in *C. hereroense* and weekly feeding activity on this food resource (Chapter 2) over 18 weeks (r_s = 0.47; t(n-2) = 2.16; p-level = 0.047). Similarly, there was a significant positive correlation between relative resource abundance of Red Marula caterpillars feeding on *S. birrea caffra* fruit pulp and observed feeding activity (r_s = 0.74; t(n-2) = 4.42; p-level < 0.001). Meyer's Parrots also tracked the relative resource abundance of an unknown owlet moth (Lepidoptera, *Noctuidae*) incubating in and feeding on *C. mopane* pods (r_s =

0.83; t(n-2) = 6.06; p-level < 0.001). There was, however, no significant correlation between feeding activity and relative resource abundance of bruchid beetle larvae in *T. sericea* pods during the breeding season ($r_s = -0.28$; t (n-2) = -1.17; p-level = 0.259) (Figure 7).

Social constraints

There were 26 cavity-nesting bird species observed in the study area (Table 4). Over 80% (n = 23) of the Meyer’s Parrot nest cavities located in the Vundumtiki study area were subsequently re-used by other cavity-nesting birds species, including nine species in 25 nesting events (Table 4). There was one instance, when two bird species, Woodland Kingfishers and Lilac-breasted Rollers, bred successfully in a Meyer’s Parrot nest cavity (NC04) during the 2005 summer breeding season.

Inter-specific competition for nest cavities during the breeding season was limited due to inactivity of all other cavity-nesting bird species and absence of migratory cavity-nesting species (e.g. Woodland Kingfisher). Meyer Parrots were, however, chased away from potential nest cavities by Burchell’s Starlings *Lamprotornis australis* in February. Meyer’s Parrots were also observed to directly compete with Lilac-breasted Rollers for a nest cavity in an *Acacia erioloba* tree in October prior to the auxiliary breeding season.

During incubation, the female stuck her head out the nest hole every time there was a sound outside (e.g. foraging animals or disturbance by investigator), indicating sensitivity to predation risk inside the nest cavity. Predation events on adults were, however infrequent, whereby only one female, from breeding pair D (Table 1), was killed by a Large Spotted Genet at nest cavity NC17 during the 2007 primary breeding season (Table 2). This predation event included the loss of three eggs and a chick. In addition, there was an unconfirmed snake predation event during the incubation period (breeding pair G (NC23) (Table 3). During the 2005 primary breeding season, Tree Monitor *Varanus albigularis* and Gymnogene *Polyboroides typus* preyed on three nestlings each, while a Fish Eagle *Haliaeetus vocifer* preyed on fledglings near the nest cavity.

Mayfield’s estimator predicted nest failure probabilities of 0.204 and 0.080 for the incubation and nestling periods respectively (Table 2).

Table 3: Arthropod larvae predated upon by Meyer's Parrots, infestation rates and relative resource abundance, and Spearman's Rank Correlations for observed feeding activity and food resource abundance

			Infestation rate				
			Within tree		Between trees		Overall
FAMILY/Species	Part parasitized	Arthropod	n	Mean±SE	n	Mean±SE	
COMBRETACEAE							
Combretum hereroense	Seed in pod (below)	Bruchid Beetle larva *Caryedon spp.* (Hemiptera, Bruchidae)	3790	0.23 ± 0.02	193	0.95 ± 0.03	0.22
Terminalia sericea	Seed in pod (Fig. 6)	Bruchid Beetle larva *Caryedon spp.* (Hemiptera, Bruchidae)	2745	0.23 ± 0.05	136	0.38 ± 0.06	0.09
LEGUMINOSAE							
Colophospermum mopane	Seed in pod (below)	Unknown Owlet moth larva (Lepidoptera, Noctuidae)	8733	0.053 ± 0.008	150	0.84 ± 0.05	0.04
EBENACEAE							
Sclerocarya birrea	Fruit pulp (below)	Red Marula caterpillar *Mussidia nigrivenella (Lepidotera, Pyralidae)*	831	0.51 ± 0.08	55	0.75 ± 0.13	0.38

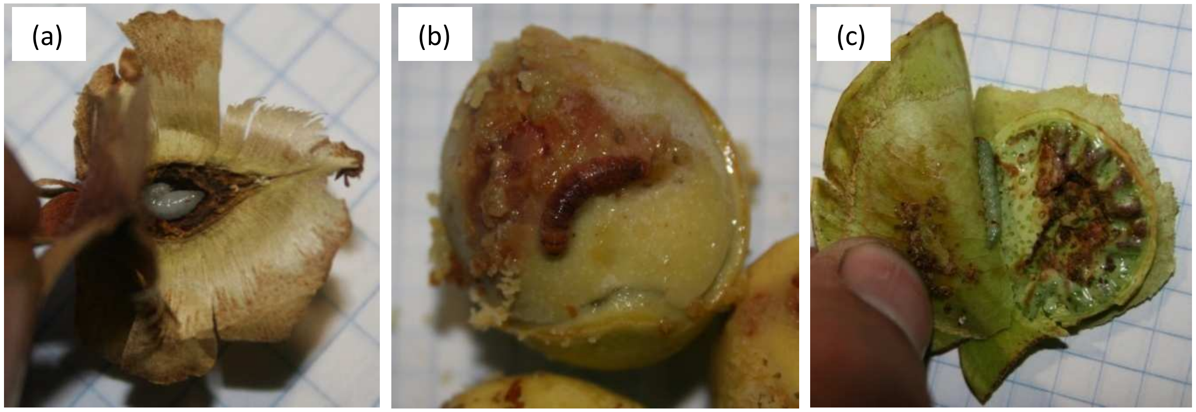


Figure 5: Arthropod food items consumed during the primary breeding season (a) Bruchid Beetle *Caryedon spp.*; (b) Red Marula caterpillar *Mussidia nigrivenella*; (c) Unknown Owlet moth (Lepidoptera, *Noctuidae*)

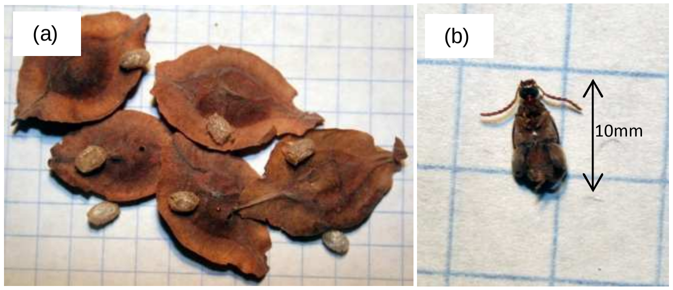


Figure 6: (a) Bruchid beetle *Caryedon spp.* cocoons hatched from larvae feeding on *T. sericea* pods; (b) Adult bruchid beetle *Caryedon spp.*

Table 4: Other cavity-nesting bird species observed within the sample area at Vundumtiki. ( ) indicate number of Meyer's Parrot nest cavities subsequently utilized by this species.

FAMILY	Species	Common name
STRIGIDAE	*Otus senegalensis*	African Scops Owl
	O. leucotis	White-faced Owl
	Glaucidium perlatum	Pearl-spotted Owl
	G. capense	Barred Owl
HALCYONIDAE	*Halcyon senegalensis*	Woodland Kingfisher(1)
	H. chelicuti	Striped Kingfisher
CORACIDAE	*Coracias caudata*	Lilac-breasted Roller(2)
	C. naevia	Purple Roller
	Eurystomus glaucurus	Broad-billed Roller(1)
PHOENICULIDAE	*Phoeniculus purpureus*	Red-billed Woodhoopoe(5)*
	Rhinopomastus cyanomelas	Scimitar-billed Woodhoopoe
BUCEROTIDAE	*Tockus nasutus*	Grey Hornbill
	T. erythrorhynchus	Red-billed Hornbill
	T. leucomelas	Southern Yellow-billed Hornbill
LYBIIDAE	*Lybius torquatus*	Black-collared Barbet(3)*
	Trachyphonus vaillantii	Crested Barbet(6)*
PICIDAE	*Campethera bennettii*	Bennett's Woodpecker
	C. abingoni	Golden-tailed Woodpecker
	Dendropicos fuscescens	Cardinal Woodpecker*
	Thripias namaquus	Bearded Woodpecker*
PARIDAE	*Parus niger*	Southern Black Tit(1)
STURNIDAE	*Cinnyricinclus leucogaster*	Plum-coloured Starling
	Lamprotornis australis	Burchell's Starling(4)
	L. mevesii	Long-tailed Starling(2)
	L. nitens	Glossy Starling
BUPHAGIDAE	*Buphagus africanus*	Yellow-billed Oxpecker

*denotes species known to breed sporadically during winter

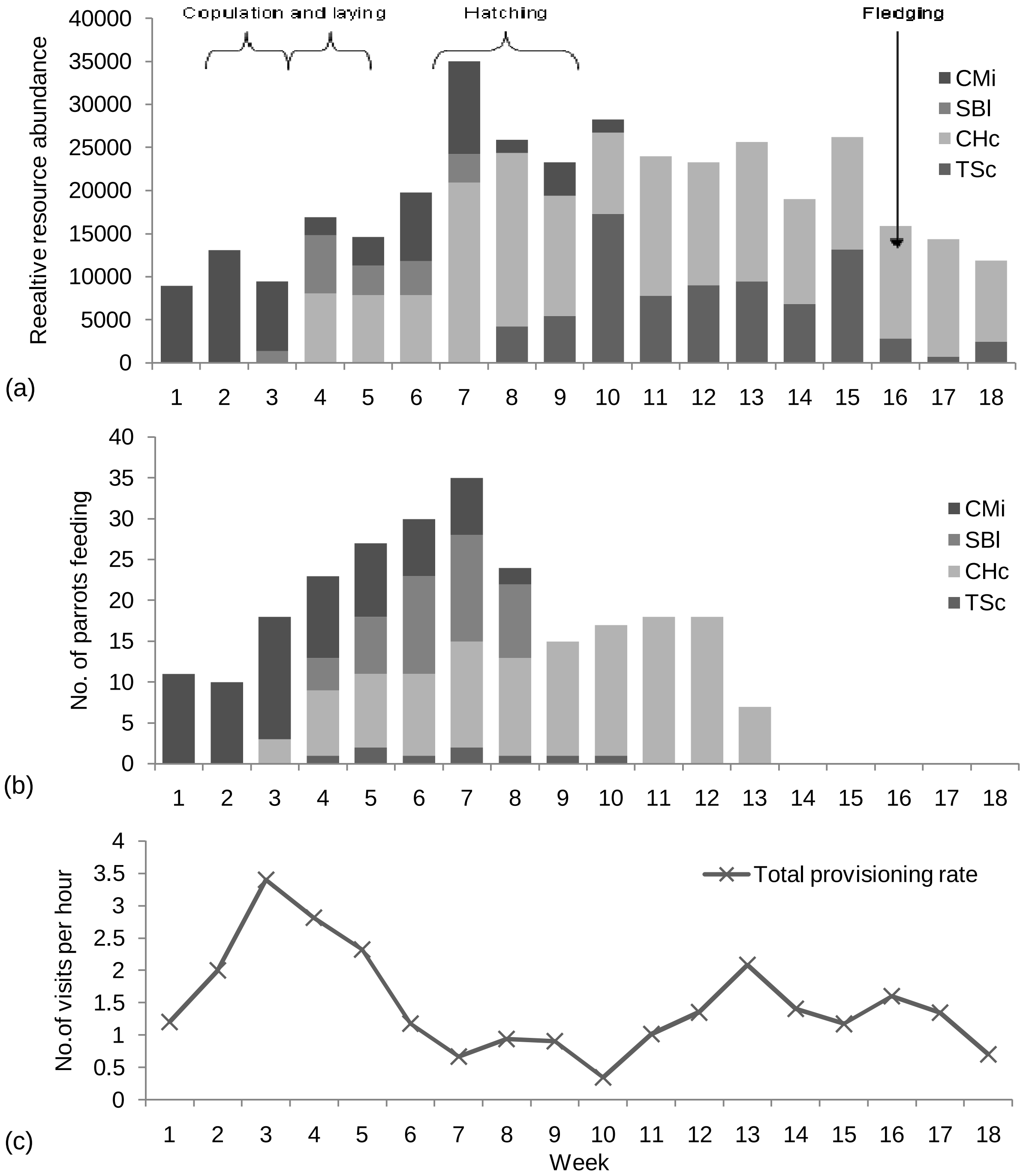


Figure 7: (a) Total relative resource abundance of parasitic Coleopteron larvae incubating in *C. hereroense* (CHc) and *T. sericea* pods (TSc), and Lepidopteron larvae incubating in *C. mopane* and feeding on *S. birrea caffra* fruits (SBl); (b) Number of parrots observed feeding on these food resources (Boyes and Perrin *in press* a); (c) Overall provisioning rate of male and female to the nest cavity over the nesting cycle.

Nesting cycle

At Vundumtiki, the sample area of 860 ha along the 8.6 km road transect was searched thoroughly, yielding 28 nest cavities utilized by 12 breeding pairs (Table 2). Over 1700 hours of nest observations were recorded between March 15 and July 14. Due to no significant difference in breeding behaviour between breeding pairs A–F and a very high breeding synchrony index value, we randomly selected breeding pair A for the analysis of parental effort and nestling behaviour.

There were distinct sex-based parental roles in each nesting period, whereby the female was responsible for all incubation and nesting effort, while the male was solely responsible for provisioning the female and nestlings until Week 10, after which the female shared provisioning (Figure 7).

Nest advertisement and preparation

Meyer's Parrots initiated breeding activity synchronously in early to mid-February with territorial displays (e.g. "arch-angelling" and posturing by males) and "duetting" (i.e. synchronized vocalizations) by breeding pairs at prospective primary nest cavities (Table 2). These "duetting" or territorial vocalizations were unique to the contact and feeding calls recorded during our study (Boyes unpub. data). Territorial vocalizations peaked in the early morning and late afternoon. Conflict was infrequent and only observed on three occasions. Breeding pairs prepared nest cavities by removing any plant material or animal waste together with wood chips. All auxiliary nest cavities within the breeding territory were excavated further and prepared for breeding (i.e. cleaned) during this period. Territorial advertisement and nest preparation continued until the end of March when copulation began and females took up permanent residence in their nest cavities for egg-laying and incubation. Males regurgitated a mixture of seed pulp and arthropod larvae to female throughout this period.

Copulation, egg-laying and incubation periods

Copulation occurred between March 20 and April 15 (Table 2). Five copulation events were witnessed during the study period. All of these were within 100m of the nest cavity of known (i.e. with ID cards) breeding pairs. Copulation events observed were all between breeding pairs. Copulation was precluded by complex courtship displays by the male, whereby male walked up and down the perch frequently head-bobbing and doing wing extensions (e.g. arch-angelling). The male typically mounted the female by stepping onto her back, then lowering his tail to one side of her raised tail and making cloacal contact 10–20 times before moving his tail to the other side and repeating cycle.

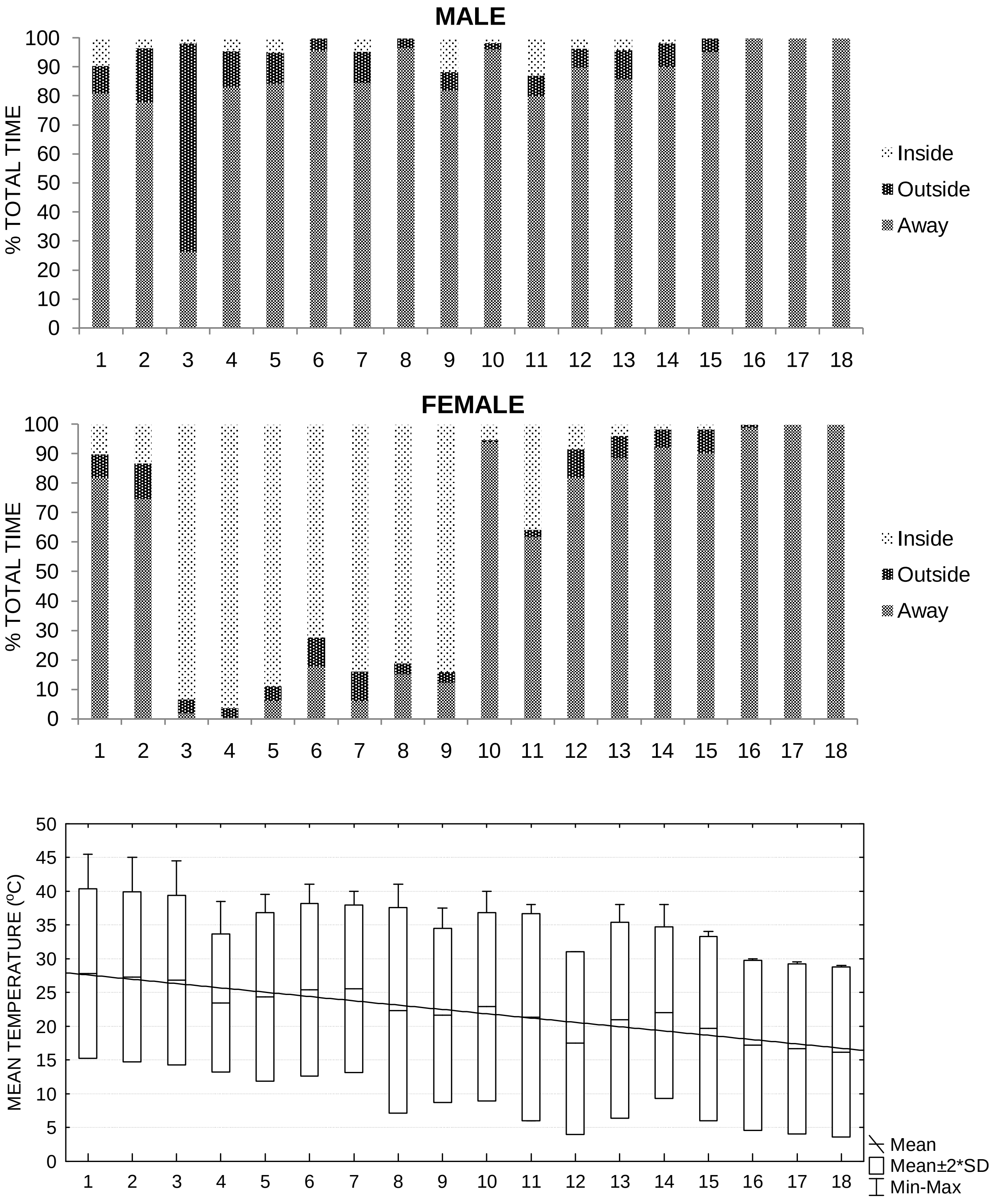


Figure 8: Breeding roles of male and female (Breeding pair A), and mean weekly temperatures (ºC) inside the nest cavity (not under brood) at NC01

Copulation bouts lasted for 20.6 ± 1.21 minutes ($n = 5$) and a cloacal contact rate of 64.2 ± 3.23 contact or flicks per minute was recorded. The female received several regurgitations before consenting. All regurgitate provisioned to the female over this period comprised entirely of insect larvae. On one occasion, the breeding pair was followed and observed to copulate in a nearby tree.

Mean egg-laying period was 8.8 ± 1.46 days ($n = 8$). Eggs were typically laid every other day over this period. Mean clutch size was 3.3 ± 0.17 eggs ($n = 9$). Mean incubation period was 30.2 ± 0.29 days ($n = 10$). Between weeks 3–9 females remained inside the cavity for 72–93% of the observation period (Figure 7). There was a dramatic increase in the amount of time the male spent outside the nest in week 3, while the female was fertile and laying eggs. Female only left the cavity to receive arthropod regurgitate from the male.

The influence of temperature fluctuations inside the nest cavity on the nesting behaviour of female was significant, whereby there was a significant positive correlation between the amount of time spent outside the cavity during incubation and nest cavity temperature ($n = 9$; $r_s = 0.767$; $t(n\text{-}2) = 3.16$; p-level = 0.016). There was, however, no significant correlation between the amount of time spent with her head at the entrance and nest cavity temperatures ($n = 9$; $r_s = 0.150$; $t(n\text{-}2) = 0.40$; p-level > 0.05) (Figure 7). In addition, females stuck their head out the hole every time there was a disturbance outside the nest cavity, indicating that this behaviour was the product of anti-predatory behaviour and not nest temperature regulation. During incubation there was a significant positive correlation between provisioning rate by male to incubating female and rejection rate by female ($n = 9$; $r_s = 0.714$; $t(n\text{-}2) = 2.5$; p-level = 0.046), whereby she ignored the calling of the male at the entrance of the hole (Figure 8). The female was only provisioned at the nest cavity during egg-laying; otherwise she was provisioned away from the cavity (Figure 8). The male typically landed in a tree near the nest cavity and vocalized to alert the female, after which she left the nest cavity to receive regurgitate in the adjacent tree or elsewhere. Composition of regurgitate was almost exclusively a creamy, white paste of arthropod parts. There was no evidence of plant material in regurgitate. The females return to the nest cavity was silent.

During the copulation and egg-laying periods, we observed what we assumed to be additional nest attendants (e.g. fledglings from the previous breeding season) on two or three times a day. These parrots vocalized outside of the nest in a similar fashion to the male from the breeding pair. The female would then emerge and leave the nest with this parrot, presumable to receive regurgitate. Extra-pair visitations to the nest cavity occurred at a rate of 0.1–0.12 visits per hour (Figure 8). After the egg-laying period, these additional nest attendants no longer visited the nest.

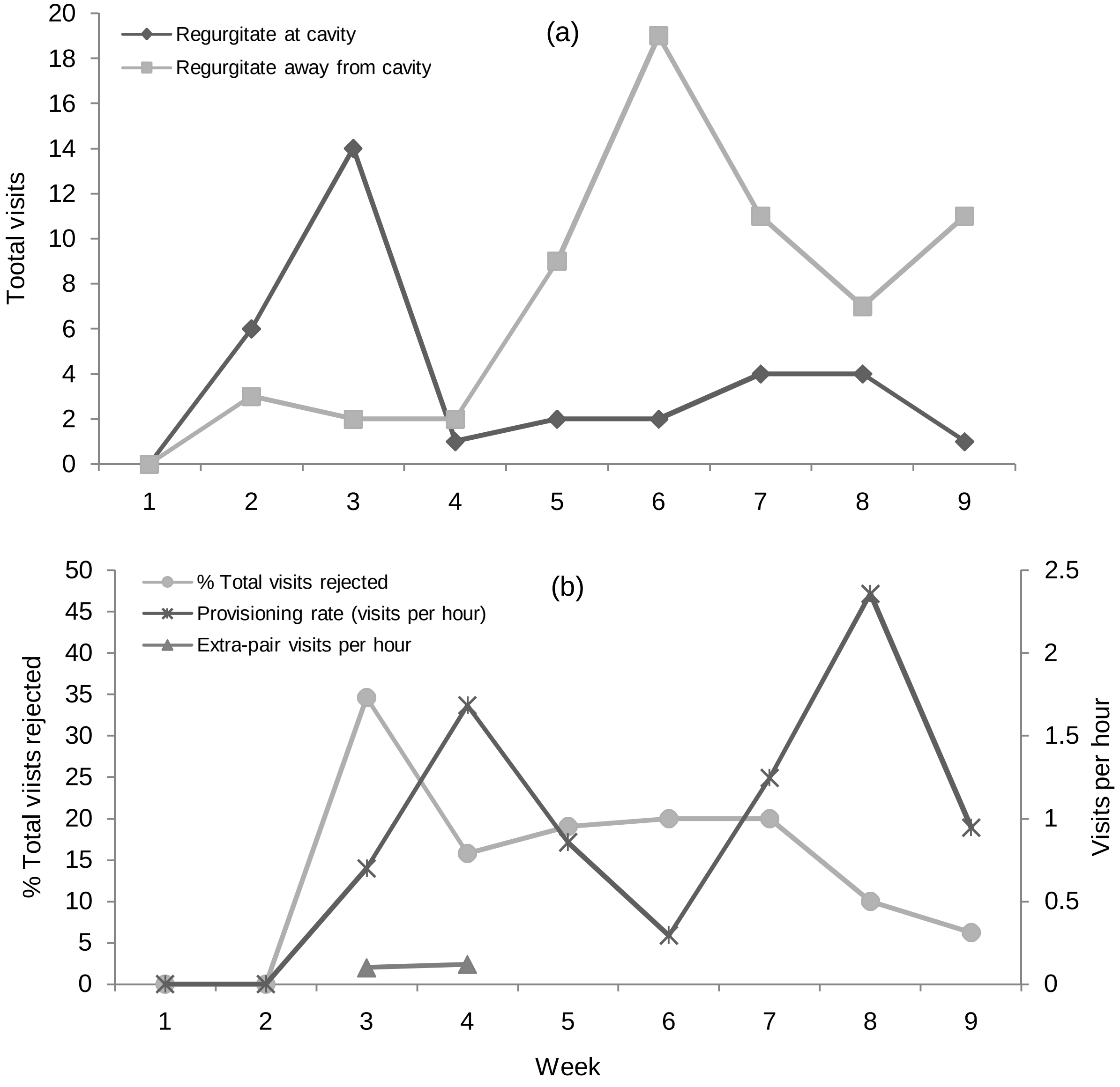


Figure 9: (a) Number of provisioning events at and away from nest cavity; (b) Provisioning rate by paired male, percentage total visits rejected and incidence of extra-pair visits; during copulation and egg-laying period (Week 3 and 4) and incubation period (Weeks 5–9)

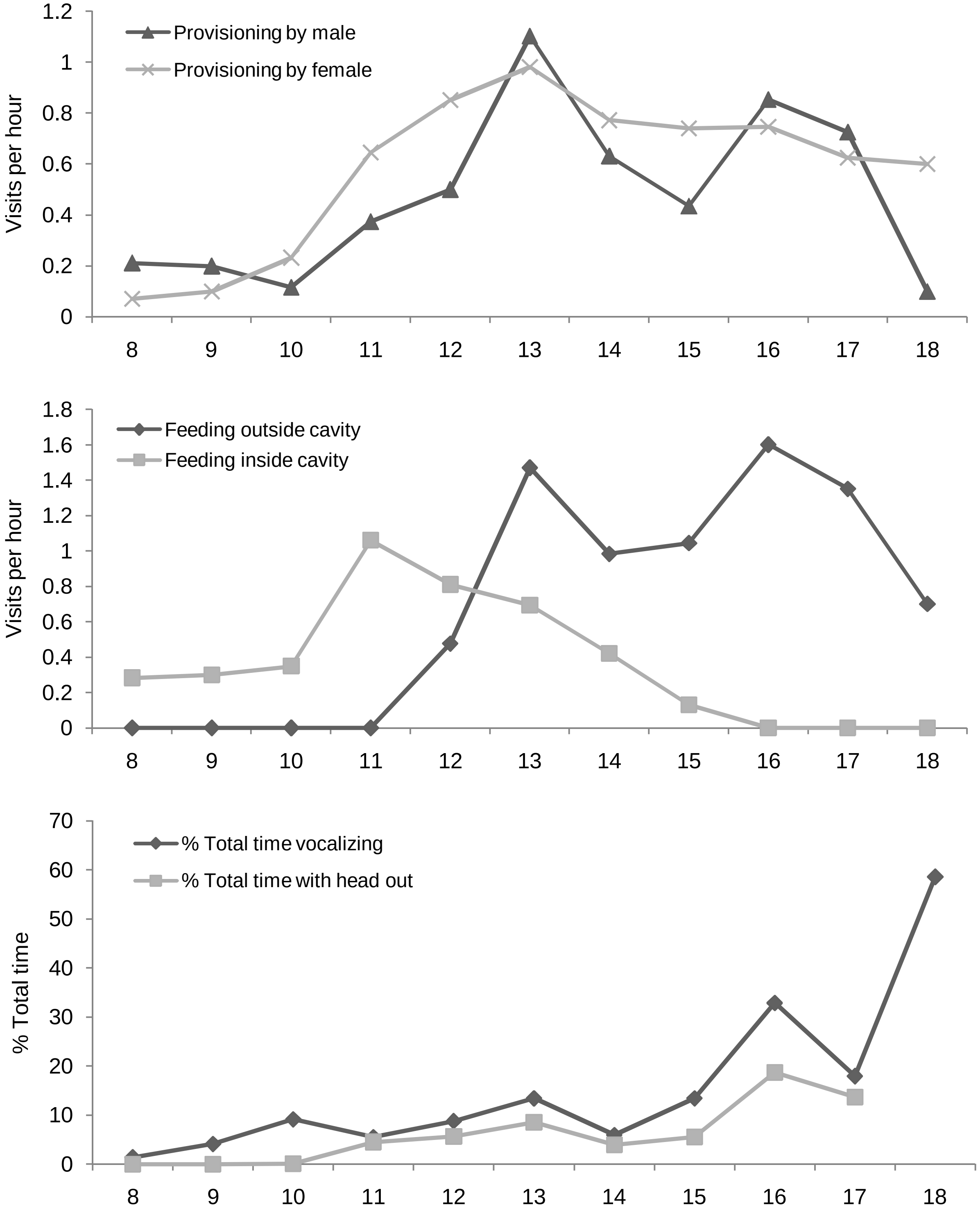


Figure 10: Provisioning rate of male and female, location of regurgitation bouts, and percentage total time spent with their heads out of the nest cavity entrance

There was no direct evidence of brood parasitism, however, Lesser Honeyguides were observed to be active and prospecting in the vicinity of active nest cavities on 12 occasions. All six fake white Meyer's Parrot eggs were destroyed and rejected by the female Meyer's Parrot within 24 hours of placement in the clutch (Figure 11).

Figure 11: Fake white Meyer's Parrot egg rejected and destroyed by female Meyer's Parrot during egg-laying period

Hatching and nestling periods

Both female and male assisted in hatching, as blood and albumen was observed on their beaks after being inside the nest cavity during the hatching period in week 8. Hatching was asynchronous, whereby eggs were hatched every second day for approximately a week (Table 2). A total of 28 eggs were laid during our study and only two failed to hatch. Upon hatching of the last chick there was a pronounced difference in body size and development. Females remained in the nest cavity until week 10 before leaving to assist the male in provisioning the nestlings (Figure 8). Both socially monogamous parents shared the provisioning of the nestlings equally (Figure 9(a)). Between Week 10 and Week 12, nestlings were fed predominantly inside the nest cavity and "begging" vocalizations were minimized. After week 12, the nestlings became a lot more vocal at the nest and regurgitation was predominantly at the nest cavity entrance (Figure 9(b)). There was a significant positive correlation between percentage total observation time spent at the entrance of the nest cavity by nestlings and percentage total time spent begging ($n = 9$; $r_s = 0.898$; $t(n-2) = 6.1$; p-level < 0.001) (Figure 9(b)).

Meyer's Parrot nestlings were light grey in colour, and thus perfectly camouflaged to the colour of dead, sun-bleached *Acacia nigrescens, C. imberbe* and *C. mopane* bark and wood – nest hole was more difficult to differentiate when nestling had head at entrance. There was also a significant positive correlation between total resource abundance of arthropod larvae and total provisioning rate to the nest cavity (including male and female) over 18 weeks ($r_s = -0.51$; $t(n-2) = -2.40$; p-level $= 0.029$) (Figure 5(c)). Regurgitate was still a creamy, white paste of arthropod larvae until week 11, after which there was more and more evidence of seed material (e.g. *C. imberbe* seed pulp).

Fledging and post-fledging periods

Fledging period started when nestlings began to spend most of their time vocalizing at the nest cavity entrance (Figure 10). From week 13, regurgitate was predominantly a yellow paste comprising *C. imberbe* seeds. There was no evidence of arthropod parts or larvae in regurgitate in week 14. Male provisioning rate declined considerably prior to fledging in week 16 (Figure 10(a)). Fledging was synchronous between June 28 and July 1 in all primary nest cavities and there was no apparent difference in the size or strength on the wing of the fledglings.

The post-fledging period was characterized by the male and female provisioning the fledglings within an area of approximately 2–5 ha around the nest cavity. Male and female provisioning rates prior to fledging resumed on day two and there was no significant change during the first two weeks of the post-fledging period. Fledglings did not re-enter the nest cavity following fledging, however, they did use the nest tree as a gathering point for regurgitation by the parents. Fledglings were observed to roost in "nursery" trees, usually dense foliage of *Kigelia africana*, *Diospyros mespiliformis* or *Garcinia livingstonia*. First signs of feeding independently were on unripe *D. mespiliformis* fruits on day six after fledging. They were also observed to feed on the *K. africana* fruits, and chew on bark, leaves and wood. Whilst the parents were foraging, the chicks remained silent and motionless, often sleeping in dense foliage.

Discussion

Atypical winter breeding seasonality

Winter breeding seasonality is atypical in southern Africa, whereby all cavity-nesting bird species breed during the summer months, with the notable exceptions of the Red-billed Woodhoopoe *Phoeniculus purpureus*, Black-collared Barbet *Lybius torquatus*, Crested Barbet *Trachyphonus vaillantii*, Bearded Woodpecker *Thripias namaquus* and Cardinal Woodpecker *Dendropicus fuscescens* that are reported to breed occasionally in winter in their southern African range (Tarboton 2001; Hockey *et al.* 2005).

According to Tarboton (2001) and Hockey *et al.* (2005), there are 57 cavity-nesting bird species in southern Africa, including seven primary excavators, 13 predominantly secondary cavity-nesting species, 32 species that utilize natural cavities, and five that nest in clay embankments. Of which 45 are represented in the Okavango Delta, including 29 small-bodied cavity-nesting bird species likely to compete with Meyer's Parrots for nest cavities within the nest web (Martin and Eadie 1999; Aitken *et al.* 2001). Over 80% of Meyer's Parrot nest cavities were re-used by other cavity-nesting bird species during summer, including the Crested Barbet, Red-billed Woodhoopoe, Black-collared Barbet, Burchell's Starling and Meve's Starling *Lamprotornis mevesii*. All of these are powerful insectivores (i.e. high energy with strong beaks), and therefore, likely able to displace Meyer's Parrots from nest cavities. Inter-specific competition for Meyer's Parrot nest cavities during summer is, therefore, likely an important selection mechanism for the winter breeding seasonality of Meyer's Parrots.

Ingold (1996; 1998) demonstrated that a high proportion of Northern Flickers *Colaptes auratus* were forced to delay breeding due to competition from European Starlings *Sturnus vulgaris*, thus having a significant effect on their reproductive success at the population level. Koenig (2003) also recognized starlings as aggressive cavity-nesters that usurped cavities from other bird species, resulting in adverse effects on their breeding biology. Meyer's Parrots were observed to compete with Burchell's Starlings and seemingly postponed nest preparation and territorial advertisement until the cessation of breeding by this large, aggressive cavity-nesting bird species. Cape Glossy Starling *Lamprotornis nitens* and Burchell's Starlings were aggressive towards Rüppell's Parrots when nesting (Selman *et al.* 2004). Competition with Burchell's Starlings and other larger secondary cavity-nesting bird species (e.g. Lilac-breasted Rollers) likely dictates onset of territory establishment and nest preparation in the Vundumtiki area. Competition for Meyer's Parrot nest cavities could be due to the modifications Meyer's Parrots make to their adopted nest cavities (i.e. long entrance, large cavity and clean interior) (Chapter 11: Boyes and Perrin in review c).

Preference for arthropod food resources during egg-laying and preferential mobilization of endogenous protein reserves suggest that increased protein requirements of nesting female birds are physiologically important during the breeding effort (Robbins 1981; Selman and Houston 1996; Houston 1997; Cottam *et al.* 2002). Robbins (1981) estimated that the daily cost of egg production to wild birds varied between species from 37–216% of normal daily energy metabolism and from 86–230% of daily protein requirements. Therefore, it is likely that birds with high metabolic costs for egg production and incubation have synchronous breeding seasons according to the Food Availability hypothesis put forward by Lack (1967), whereby birds time their breeding effort to coincide with the season of maximum food availability each year.

Although seeds contain high concentrations of crude protein, they are usually deficient in several essential amino acids which are critical for reproduction (Hawley 1997; Arnot and Perrin 1999). Banjo *et al.* (2006) found Coleopteran and Lepidopteron larvae to be high in crude protein and essential amino acids, vitamins A and vitamin C, as well as calcium, iron and magnesium, which are all important in egg production. The only other source of animal protein was endogenous protein reserves (e.g. muscle). The only evidence in our study that dilutes the importance of arthropod larvae in the breeding biology of

Meyer's Parrots is the high rejection rate during the incubation period, thus indicating that females are, at least in part, dependent on endogenous protein reserves and are highly sensitive to predation risk, and therefore, choose to reject provisioning opportunities. Costs of incubation during winter are probably very high due to low temperatures, and therefore, arthropod larvae are likely a significant source of supplementary protein necessary for egg production, chick growth, the maintenance of female condition, and supplementary metabolic water during the dry season. For males, the consumption of Red Marula caterpillars and energy-rich *S. birrea caffra* fruit pulp in the early breeding season may function to maintain muscle condition during this high cost period.

Bruchid Beetle larva inside *C. hereroense* pods were the most important food resource during the breeding season, as they formed the primary constituent of regurgitate to incubating females and nestlings from egg-laying to the beginning of the fledging period. Our findings corresponded with those of Derbel *et al.* (2007) on the life cycle of *Bruchidius raddianae* that preyed on *Acacia tortilis subsp. raddiana*. Based on comparison with photographs of *B. raddianae* larval instars (Derbel *et al.* 2007), it is clear that Meyer's Parrots target the third instar larvae of *Bruchidius spp.*, which develops in April. According to Derbel *et al.* (2007), the larval stage last for six weeks, after which the larvae pupate in July. Therefore, our study demonstrated that Meyer's Parrot track the temporal food resource abundance and developmental stage of Coleopteran and Lepidopteron larvae incubating inside and feeding on seeds inside pods and fruits in their diet. It is likely that Meyer's Parrots synchronize egg-laying and incubation with the period of highest arthropod larvae availability. Derbel *et al.* (2007) found that infestation levels of *A. tortilis raddianae* seeds by bruchids vary from one year to the next according to humidity, temperature and rainfall. In our study, despite more intensive sampling there were fewer nest attempts recorded during 2007 than there were recorded in 2005, which had significantly higher rainfall – 445mm (2005) and 338mm (2007) between November the previous year and March. In the absence of a direct comparison of infestation levels between years, this indicates that Meyer's Parrots initiated fewer nesting attempts due to lower rainfall and resultant decline in infestation levels. Therefore, during periods of low annual rainfall and relative humidity, Meyer's Parrots may have lower fecundity. Arthropod larvae are likely an important, yet unpredictable cue for breeding, thus supporting the hypothesis that endogenous protein reserves and arthropod larvae likely interact in determining individual fecundity. Provisioning of females with arthropod larvae during courtship and copulation period by males together with territorial vocalizations are likely important in the synchronization of the breeding effort at the population level, as observed during this study.

Meyer's Parrots have the widest distributional range of any African parrot, exceeding that of the African or Rose-ringed Parakeet *Psittacula krameri* and Red-faced Lovebird *Agapornis pullarius* (Juniper and Parr 1998), and therefore, their phyletic line has demonstrated its ability to out compete other *Poicephalus* parrots for space and resources over geological time. Bruchid beetles parasitize Leguminosae and Combretaceae pods throughout subtropical Africa (Ernst *et al.* 1990; Miller 1996; Derbel *et al.* 2007), and thus exclusive access to this cryptic resource of protein-rich arthropod larvae during the winter breeding season may facilitate this apparent ecological advantage over other *Poicephalus* parrots in subtropical Africa. Seeds from the host trees of these arthropod larvae are, however, reported in the breeding season diets of Rüppell's Parrots, Brown-headed Parrots and Grey-headed Parrots. Further investigation is, therefore, required to ascertain whether these *Poicephalus* parrots prey on the arthropod larvae that parasitize these tree species throughout Africa.

Nest predation is a primary cause of nest failure in many birds and an important factor in the life history evolution of secondary cavity-nesting bird species (Eddington and Eddington 1972; Martin 1996; Martin and Clobert 1996; Brightsmith 2005; Muchai and du Plessis 2005). Our study recorded predation of a breeding female and the loss of 25% of the offspring. Further research is required on the seasonality of predation risk to cavity-nesting species in the Okavango Delta; however, predation risk is probably higher during summer due to increased breeding activity of predators (e.g. Large Spotted Genet and Gymnogene) over this period (Skinner and Smithers 1990). Increased parental activity at the nest increases predation risk (Dunn 1977; Muchai and du Plessis 2005; Sorace *et al.* 2000) and Meyer's Parrots demonstrated high levels of vigilance at the nest cavity and cryptic provisioning behaviour by avoiding regurgitation events at the nest cavity. Meyer's Parrots are long-lived, socially monogamous non-passerines, and therefore, adult survival is very important. Winter breeding seasonality increases the probability that female Meyer's Parrots survive the egg-laying and incubation period when they are permanently in the nest cavity.

Rainfall is known to be a stimulus for initiating breeding in arid-zone birds (Lloyd 1999). In our study, however, there was significant lag time, whereby rainfall between November and January influenced arthropod infestation levels which only became available to Meyer's Parrots at the third instar larval stage of *Bruchidius spp.*. Radford and du Plessis (2003) found that Red-billed Woodhoopoes had significantly lower nesting success in the wet breeding season, with 25% of the variation in fledging success explained by the total rainfall in that period. Wet conditions were shown to reduce nesting success by reducing the amount of food delivered to the nestlings and flooding of the nest cavity (Radford and du Plessis 2003). It is, therefore, reasonable to assume that, when possible, cavity-nesting bird species avoid breeding during wet periods. However, breeding cannot occur without suitable food resources outside of the wet season (Stutchbury and Morton 2005). As a result, we demonstrated a significant negative correlation between monthly rainfall and total number of clutches, whereby the influence of rainfall was indirect and likely linked to declining food resource availability (e.g. insects and ripe fruits) for other cavity-nesting bird species and subsequent cessation of their breeding activity (often in Meyer's Parrot nest cavities). Consumption of arthropod larvae protected inside Combretaceae and Leguminosae pods enables Meyer's Parrots to breed during the dry season when other cavity-nesting bird species, which are predominantly insectivorous, experience a food resource bottleneck.

Our findings support the hypothesis that the breeding seasonality of Meyer's Parrots is dependent on the interrelationship of inter-specific competition for Meyer's Parrot nest cavities during summer, likely reduced predation risk during winter, and resource abundance fluctuations of arthropod larvae. Based on the findings of Boyes and Perrin (Chapter 2) and this study, breeding during the auxiliary breeding season is likely in response Pssillid beetle and fig wasp larval resource abundance, and availability of suitable nest cavities.

Breeding synchrony and possible extra-pair copulations (EPCs)

All *Poicephalus* parrots studied thus far demonstrate high breeding synchrony during winter Wirminghaus *et al.* 2001; Selman *et al.* 2004; Symes and Perrin 2004; Taylor and Perrin 2006). Breeding synchrony, regardless of the facilitation mechanism (e.g. vocalizations or food quality), requires breeding stimuli such as rainfall (Lloyd 1999), food availability (Lack 1967; Eikenaar *et al.* 2003), or social constraints (e.g. inter-specific competition for nest cavities (Aitken *et al.* (2002) or predation risk (Morton 1971)). Our study supports the hypothesis that the stimuli for breeding synchrony are the cessation of rainfall, the availability of arthropod larvae, and delaying breeding until the cessation of nesting activities by other large cavity-nesting bird species (e.g. Burchell's Starling).

The facilitation mechanism are unclear, however, synchronization of breeding at the local population level necessitates synchronous female fertility (Stutchbury and Morton 1995; Weatherhead 1997; Weatherhead and Yezerinac 1998; Yezerinac and Weatherhead 2002). Meyer's Parrots are intrinsically social (Holyoak and Holyoak 1972) and utilize communal roosts outside the breeding season. Therefore, socializing at activity centres near communal roosts (Chapter 8: Boyes and Perrin in review d), followed by subsequent territorial vocalizations or "duetting" by breeding pairs likely facilitate synchronous territory establishment and initiation of copulation at the population level. An additional mechanism that likely supports synchronous female fertility is provisioning of females by pair-bonded males thus enabling females to measure arthropod food resource availability and abundance (i.e. through provisioning rate).

The application of molecular genetics techniques has revealed that birds are rarely sexually monogamous, with extra-pair offspring found in approximately 90% of species (Griffith *et al.* 2002). Even among socially monogamous species over 11% of offspring are the result of extra-pair paternity (Griffith *et al.* 2002). Our study demonstrated that extra-pair Meyer's Parrots provisioned pair-bonded females during the egg-laying period, but did not confirm extra-pair fertilizations. These were unlikely to be offspring from the previous season, as visitations ceased during the incubations period and these parrots were never observed in the vicinity when the male was at the nest cavity.

Based on frequent sightings of large flocks non-nesting Meyer's Parrots it appears that, similar to Symes and Perrin (2004) observed in the Grey-headed Parrot, at least 50% of the local population was non-nesting. If the Therefore, there are likely numerous unpaired males seeking extra-pair fertilizations by soliciting fertile, synchronously nesting females with arthropod regurgitate. In addition, to circumstantial evidence, there is evidence of EPCs in the nesting behaviour of Meyer's Parrots, whereby males exhibit mate-guarding behaviour. Mate-guarding is the primary mechanism used by males to mitigate the risk of extra-pair copulations (Ritchison and Klatt 1994; Pinxten and Eens 1997). In our study, breeding males perched outside the nest cavity for over 70% of time during the copulation and egg-laying period, seeming to invest all their time in mate-guarding and provisioning the female. Whittingham (1993) noted similar behaviour in male Red-winged Blackbirds *Agelaius phoeniceus*, whereby they decreased mating (i.e. seeking extra-pair copulations) and somatic (i.e. maintenance activities) effort during provisioning of nestlings. Provisioning rate by male Meyer's Parrots to females also peaked during the egg-laying period, after which it declined significantly and then increased gradually until the female left the nest cavity to assist in provisioning the nestlings (Figure 7). Although speculative, this decline in provisioning rate may represent males withholding parental effort due to suspicion of non-paternity of offspring. It is, however, more likely, due to the high rejection rate, that females prioritize, as far as possible, the minimization of predation risk over energetic and nutritional requirements during incubation. Meyer's Parrots also have the longest copulation bout time of any African parrot studied thus far (Warburton and Perrin 2005). Breeding pairs typically mounted for over 20 minutes and made genital contact over 1300 times, repeated several times a day. This represents significant energy expenditure by the male likely to minimize opportunity for EPCs.

Spoon *et al.* (2007) suggest that extra-pair copulations facilitate mate switching in cockatiels and that behavioural compatibility is important in mate retention. Our study, however, supports the hypothesis that Meyer's Parrots maintain socially monogamous pair bonds over at least four years within an extra-pair mating system. Mitochondrial DNA sequence data are required to ascertain the degree to which territoriality, mate-guarding, and prolonged and frequent copulation, mitigate extra-pair copulations in Meyer's Parrot populations (Yamagishi *et al.* 1992).

Early incubation and hatching asynchrony

Asynchronous hatching is common to all *Poicephalus* parrots (Wirminghaus *et al.* 2001; Selman *et al.* 2004; Symes and Perrin 2004; Taylor and Perrin 2006). The Brood Reduction hypothesis (Ricklefs 1965; Mock 1994; Mock and Forbes 1994), the oldest and most widely accepted hypothesis for asynchronous hatching, predicts differences between synchronous and asynchronous broods only when food resources are limited. It operates when food resources availability is variable over time (Stoleson and Beissinger 1997). Stoleson and Beissinger (1997) recognized the mortality of the smallest offspring as an adaptive adjustment of brood size to fit parental ability (Stoleson and Beissinger 1997). Although, intuitively anticipated, there was no evidence of brood reduction during our study. Both parents were observed to enter the nest cavity throughout the nestling period likely to provision the last-hatched nestling. There is also no evidence of brood reduction in Rüppell's Parrots (Selman *et al.* 2002) and Grey-headed Parrot (Symes and Perrin 2003) as both in both cases nestlings were found dead with food material in their crops, thus indicating that chicks did not die due to starvation or sibling competition, but rather disease or inadequate dietary intake. All nestling mortality recorded in *Poicephalus* parrots are due to predation, environmental constraints (e.g. rainfall and ambient temperature) and energetic constraints (i.e. field metabolic rate during breeding effort) (Selman *et al.* 2004; Symes and Perrin 2004; Symes *et al.* 2004). Krebs and Magrath (2000) demonstrated that nesting Crimson Rosella *Platycercus elegans* adults distributed food equally within broods, whereby females provisioned the last-hatched chick preferentially, only preferring the first-hatched chick when the whole brood was hungry. CCD video footage from inside the nest cavity is required to evaluate this dynamic in Meyer's Parrots. We, therefore, examined putative environmental (e.g. temperature) and social (e.g. predation risk and intra- and inter-specific competition) constraints that likely encourage early onset of incubation.

Jordan (2001) noted that, for parrots, when temperature of 36.9–37.5°C was used constantly, most psittacine eggs hatched in the same amount of time they would if incubated by the female. In our study, nest temperatures inside the nest cavity were consistently below this range, thus necessitating constant incubation effort by female Meyer's Parrots. Constant occupation of the nest cavity by female parrots also minimizes their energetic expenditure during egg-laying and decreases the cost of egg production (Waltman and Beissinger 1992). Breeding during winter is, therefore, central to early onset of incubation in an often restricted number of nest cavities (Chapter 10: Boyes and Perrin in review e; Chapter 11).

The incubation period is a potential energy bottleneck for altricial birds (Nilsson 1994; Wiebe and Martin 2000; Wiebe 2007), whereby, as per the Energetic Constraints hypothesis (Slagsvold 1986), the amount of time a bird allocates to incubation is likely to be limited by energetic constraints (Eikenaar *et al.* 2003). Therefore, if food is abundant, energetic constraints may be reduced and incubation attendance may increase. Eikenaar *et al.* (2003) suggested that females less constrained by the need to forage may start incubating before clutch completion. Meyer's Parrots adhere to the assumptions of the Energetic Constraints hypothesis, as males are responsible for provisioning the female, thus providing the energetic opportunity to initiate incubation early and thus minimize exposure to predation risk in the nest cavity.

Numerous authors have recognized the importance of social constraints on early onset of incubation and resultant asynchronous hatching, including intra- and inter-specific competition, predation and brood parasitism (Lombardi *et al.* 1989; Beissinger and Waltman 1991; Beissinger 1996), often prioritizing these above environmental and energetic constraints to early incubation. The Limited Breeding Opportunity Hypothesis (Beissinger and Waltman 1991; Beissinger 1996) puts forward that asynchronous hatching over an extended period and incubation initiation on the first egg is in response to protecting the nest cavity from conspecifics (e.g. nest destruction and usurpation). Nest usurpation by conspecifics was not observed during our study, and therefore, either breeding opportunities (i.e. nest cavity availability) are not restricting or nest-guarding, territorial defence and territory advertisement by males and females are effective in mitigating the threat of intra-specific nest usurpation. Low breeding population and highly-specialized nest cavity requirements (Chapter 10) both support the assumptions of the Limited Breeding Opportunity Hypothesis (Beissinger and Waltman 1991; Beissinger 1996). The Egg Protection Hypothesis (Bollinger *et al.* 1990; Bollinger and Gavin 2004), on the other hand, states that females start incubation from the first egg to protect them from predation and inter-specific competition. Mayfield's estimator for nesting success (Mayfield 1975), however, indicated that during our study predation risk was highest in the hatching and nestling periods. This was still comparatively low, thus indicating that either predation risk was low or was successfully mitigated. Meyer's Parrots are reported to live for 50 – 60 years in captivity (Low 1992). Therefore, these long-lived parrots, likely focus on minimizing adult mortality during nesting, as they have multiple nesting opportunities during their lifetime. Therefore, the Nest Failure hypothesis put forward by MacGrath (1988) better explains early initiation of incubation and resultant asynchronous hatching as it promotes rapid fledging and minimizes female exposure to predation risk during incubation and nestling period.

Greater and Lesser Honeyguides are the only brood parasites that parasitize clutches in nest cavities in the Okavango Delta (Hockey *et al.* 2005). Both species have eggs of comparable size and appearance to Meyer's Parrot eggs (Tarboton 2001; Hockey *et al.* 2005). These brood parasites breed predominantly during the summer months with limited overlap with Meyer's Parrots (Hockey *et al.* 2005). Lesser Honeyguides were active in the vicinity of Meyer's Parrot nest cavities, and therefore, were considered potential brood parasites. In addition, Meyer's Parrots instantly rejected and destroyed fake white eggs introduced to established clutches, thus demonstrated recognition of risk of brood parasitism by females.

Our study supports the hypothesis that Meyer's Parrots effectively mitigate risk of brood parasitism, and that the Brood Parasitism Hypothesis (Lombardi *et al.* 1989; Beissinger 1996) and clutch-guarding hypotheses (Beissinger and Waltman 1991; Beissinger 1996) likely influence their nesting cycle and hatching synchrony.

Territoriality and limited breeding population

Poicephalus parrots studied thus far (Wirminghaus *et al.* 2001; Symes and Perrin 2004; Selman *et al.* 2004; Taylor and Perrin 2006) have demonstrated no evidence to support territoriality, thus indicating either a lack of territoriality, avoidance of conspecifics at known territorial boundaries, or efficient communication of occupancy and avoidance of confrontation (Selman *et al.* 2004). Selman *et al.* (2004) put forward that territoriality may be restricted to the nest tree, as Rüppell's Parrots were observed to nest in neighboring trees. Rüppell's Parrots did, however, employ mechanisms (e.g. specific flight path to nest tree) to avoid confrontation (Selman *et al.* 2004). Our study, however, demonstrated that Meyer's Parrots are territorial during the breeding season and there is no cooperation or mutual benefit (e.g. dilution of predation risk) between socially monogamous breeding pairs. This is significant in that it raises several questions about the life history evolution of Meyer's Parrots. Male Meyer's Parrots partially excavating nest cavities and maintaining a nesting territory of up to six nest cavities is indicative of a polygynous mating system (Slagsvold and Lifjeld 1994), whereby one male supports several females through nesting. This relationship is functional when the commodity provided by the male is the nest (e.g. *Ploceus* spp. weavers), however, it becomes dysfunctional when the male is responsible for provisioning the females. Therefore, we put forward the Additional Options hypothesis to explain the breeding territories of Meyer's Parrots, whereby a socially monogamous male Meyer's Parrots establishes a territory with several nest cavities at varying levels of readiness for nesting so as to provide additional nesting options during the critical egg-laying period. This was observed twice when due to the addition of a fake white egg to the clutch, the female abandoned the nest to initiate egg-laying at another nest within the breeding territory within three days.

The confirmed population breeding population within the sample area was 16 parrots, whereby 8 different breeding pairs were confirmed to nest within the 430 ha sample area. A minimum non-nesting population of 18 non-nesting parrots was confirmed to frequent the sample area, judging from the maximum flock size of non-nesting Meyer's Parrots. Therefore, at least 50% of the local population was non-nesting and aggregated into these "singles clubs" during the copulation and nest territory establishment periods in March and April. Limiting the breeding population is seemingly dysfunctional, as the resultant low fecundity at the population level would appear to be mal-adaptive. Based on the findings of this study, however, we demonstrate that adult survival of this long-lived non-passerine is central to their breeding biology, and it is, therefore, likely that male Meyer's Parrots only start nesting after several seasons prospecting for extra-pair copulations and nest cavities (i.e. adolescence), while females compete for available males with suitable nest cavities or prospect for intra-specific brood parasitism opportunities before they establish a socially-monogamous pair-bond with a male that has a safe nest cavity that suites her specifications. Although anticipated there was, however, no evidence to support intra-specific brood parasitism in Meyer's Parrot. Mitochondrial DNA sequence data are required to ascertain the possible incidence of extra-pair maternity (Yamagishi *et al*. 1992).

According to Boyes and Perrin (Chapter 11) there are no primary excavators (e.g. barbets and woodpeckers) that excavate nest cavities that are deep enough for utilization by Meyer's Parrot, and project that it takes up to five years to sufficiently excavate nest cavities during the winter dry season when highly competitive insectivorous (e.g. rollers) and carnivorous (e.g. owls) are inactive. Meyer's Parrot populations, are therefore, dependent on relatively few productive breeding females, and thus avoidance of predation risk and avoidance of inter-specific competition during summer for nest cavities is important in their breeding biology. Nest poaching (i.e. for the wild-caught bird trade) or loss of established nest cavities due to deforestation likely have a significant impact on their reproductive output at population level. Sustainable harvesting of eggs from *Poicephalus* parrot nest cavities, as put forward for neotropical parrots (Beissinger and Bucher 1992).

Future research

Cavity-nesting forest specialists, such as *Poicephalus* parrots and woodpeckers, are likely threatened by deforestation and habitat loss in the African subtropics (Chapter 12: Boyes and Perrin in review f), and therefore, further research is required on the interactions between species and ecological processes that support the production of dead wood suitable for nesting (Chapter 10). Further research is also required to confirm higher predation risk for cavity-nesting bird species during summer. Most importantly, mitochondrial DNA sequence data are required to confirm the incidence of EPCs and ascertain the degree to which territoriality, mate-guarding, and prolonged and frequent copulation, mitigate extra-pair copulations in Meyer's Parrot populations (Yamagishi *et al.* 1992). This data could also be used to check for the incidence of intra-specific brood parasitism. Finally, a comparative research project on Coleopteran and Lepidopteron larvae incubating in and feeding on fruits and pods in the diets of Poicephalus parrots must be undertaken at a different location.

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Chapter 10:

Nest tree preferences of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana[1]

There is a dichotomy in *Poicephalus* parrot nesting behaviour, whereby members of the *P. meyeri* superspecies complex demonstrate generalists nest tree preferences, while the *P. robustus* superspecies complex includes nest tree specialists. All *Poicephalus* parrots, however, likely have specialist nest tree characteristic preferences (i.e. tree height, diameter and condition). A modified Hurlbert's niche breadth index demonstrated that Meyer's Parrot *Poicephalus meyeri* are nest tree generalist. Although specific nest tree preferences were significantly different between tree species utilized by Meyer's Parrots, Meyer's Parrots preferred large trees greater than 14m in height that were in relatively poor condition. Comparison of nest tree characteristics (n = 75) and availability of tree species (n = 1129) within a representative sample of the Okavango Delta indicates that Meyer's Parrots track suitable nest cavity availability in the different forest habitat types at the landscape level. This generality between tree species is demonstrated in their regional nest tree preferences within the Okavango Delta and the rest of their distributional range. Coupled with non-random nest cavity preferences and low breeding population size, *Poicephalus* parrots are likely threatened, more than other cavity-nesting bird species, by drastic changes in African forest habitat structure and extent.

Introduction

Numerous studies have been conducted on nest cavity preferences of cavity-nesting bird species (Mannan *et al.* 1980; Inouye *et al.* 1981; Muldal *et al.* 1985; Welsh and Capen 1992; Ingold 1991; Li and Martin 1991; Merila and Wiggins 1995; Lawler and Edwards 2002; Giese and Cuthbert 2003; Martin *et al.* 2004). Few studies, however, have been done on the nest tree characteristics and ecological context of nest cavities utilized by cavity-nesting bird species (Bednarz *et al.* 2004). Our study gathered baseline data on the nest tree characteristics and ecological context of Meyer's Parrot *Poicephalus meyeri* nest cavities. Here we also evaluated nesting habitat characteristics for comparison with nest tree preferences to determine whether nest tree preferences are non-random.

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[1] Formatted for *Ostrich* – Journal of African Ornithology, Birdlife South Africa, NISC, Grahamstown, South Africa: Boyes and Perrin (in press). Nest tree preferences of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana.

Meyer's Parrots have the widest distributional range of any African parrot, exceeding that of the Rose-ringed Parakeet *Psittacula krameri* and Red-faced Lovebird *Agapornis pullarius* (Snow 1978, Juniper and Parr 1998). They are distributed throughout subtropical Africa with strongest associations with riverine forest communities, dry *Acacia*-*Combretum*/*Brachstegia* woodlands, and secondary growth around cultivation (Snow 1978; Tarborton 1980; Forshaw 1989, Juniper and Parr 1998; Chapter 3: Boyes and Perrin in review a). Meyer's Parrot is the smallest of the *Poicephalus* parrots and forms a superspecies with Rüppell's Parrot *P. rueppellii*, Brown-headed Parrot *P. cryptoxanthus*, Senegal Parrot *P. senegalus*, Red-bellied Parrot, and Niam-Niam Parrot *P. crassus* (Rowan 1983; Juniper and Parr 1998; Massa 2000). Comprehensive studies have been undertaken on the nesting ecology of the Cape Parrot *P. robustus* (Wirminghaus *et al.* 2002; Symes *et al.* 2004), Grey-headed Parrot *P. fuscicollis suahelicus* (Symes and Perrin 2004), Rüppell's Parrot (Selman *et al.* 2004) and Brown-headed Parrot *P. cryptoxanthus* (Taylor and Perrin 2006).

Cape Parrots utilize *Podocarpus henkelii* and *P. falcatus* snags almost exclusively for nesting (Wirminghaus *et al.* 2001; Symes *et al.* 2004). Similarly, Grey-headed Parrots, which along with Brown-necked Parrots *P. fuscicollis fuscicollis* and Jardine's Parrots *P. gulielmi* form the *P. robustus* superspecies with Cape Parrots, specialized in nesting in *Adansonia digitata* trees (Symes and Perrin 2004). Therefore, the *P. robustus* superspecies complex includes nest tree specialists. Both Rüppell's Parrots (Selman *et al.* 2004) and Brown-headed Parrots (Taylor and Perrin 2006) utilized over eight tree species during long-term studies of their nesting ecology, and thus could be considered to be nest tree generalists in the areas studied. These relationships are likely auto-correlates of habitat structure and composition within their distributional range. Secondary cavity-nesting bird species are limited by the availability of suitable nest cavities, which depends on the availability of dead wood, the rate of excavation by primary excavators (e.g. woodpeckers), inter- and intra-specific competition with other secondary cavity-nesters, and the rate of loss of excavated cavities (e.g. fire, natural pruning or wind damage) (Martin and Holt 1997; Aitken *et al.* 2002). Therefore, we investigated the degree of specialization in nest tree utilization using a modified Hurlbert's standardized and expanded niche breadth index (β_i) (Colwell and Futuyma 1971; Hurlbert 1978).

Niche breadth is the variance in resource use by a species, and can be estimated by measuring the uniformity of the distribution of conspecifics among resource states within the resource matrix (Colwell and Futuyma 1971). A resource matrix is a table formed by using different competing species as rows and resource states as columns. Resource states are subdivisions within a heterogeneous habitat considered individually (e.g. nest tree species) or grouped on the basis of similarity (e.g. forest habitat types) (Hurlbert 1978). Colwell and Futuyma (1971) observed that relative resource abundance among resource states should provide adequate information on the ecological distinctness of resource states. Estimated total number of nest cavities for each species (M_{ij}) was thus used in the weighted expansion of the resource matrix ($k = 10000$), thus accounting for error caused by nonlinearity and ecological inequality of spacing among resource states (Colwell and Futuyma 1971). We tested the hypothesis that Meyer’s Parrots are nest tree generalists similar to the other members of the *P. meyeri* superspecies complex.

Nest cavity formation and subsequent utilization by cavity-nesting species functions within a complex inter-relationship between biotic (e.g. primary excavators, fungi and tree species) and abiotic (e.g. rainfall, humidity and wind) factors that facilitate cavity-nesting communities (Aitken *et al.* 2002; Bednarz *et al.* 2004; Martin *et al.* 2004). Few studies, however, have considered the role of disturbance agents (e.g. African elephants *Loxodonta africana* and hot fires) in the formation of deadwood suitable for use in nest cavity excavation. Jackson and Jackson (2004) put forward that cavity excavation by Red-cockaded Woodpeckers *Picoides borealis* was likely influenced by the dispersal dynamics of fungi. Heinl *et al.* (2007) showed that, in the Okavango Delta, Botswana, large trees in high fire frequency areas had significantly lower canopy cover, thus indicating poor condition and potential opportunity for fungal infection or natural pruning of part of the canopy (Horton and Mannan 1988; Blanc and Walters 2007). Heinl *et al.* (2007) also found that changes in water level had a significant impact on forest ecology and tree mortality in riverine forest and *Acacia-Combretum* woodlands. Furthermore, Okello *et al.* (2007) put forward that African Elephants are an important source of tree mortality in burned areas. We, therefore, investigated the frequency of probable ecological processes resulting in dead wood targeted for nest cavity excavation. Wirminghaus (1997) put forward that the Meyer’s Parrot population in the Okavango Delta is the most significant in southern Africa. Here we investigate the probable role the disturbance regime in the Okavango Delta in supporting this significant Meyer’s Parrot population.

Methods

Study area

The Okavango Delta was chosen as our study area because of its significant Meyer’s Parrot population (Wirminghaus 1997). Our core study area, where habitat assessments and intensive Meyer’s Parrot nesting surveys were conducted, surrounded Vundumtiki Island in the north-eastern Okavango Delta (Figure 1). Vundumtiki is a wilderness area with limited human impact or disturbance to habitat and animal behaviour. In addition, we surveyed Meyer’s Parrot nest cavities at Mombo Camp from August

2005–January 2006). We also compiled nesting records from the following Wilderness Safaris Botswana camps: Chitabe Trails, Duba Plains, Xigera and Tubu Tree (Figure 1).

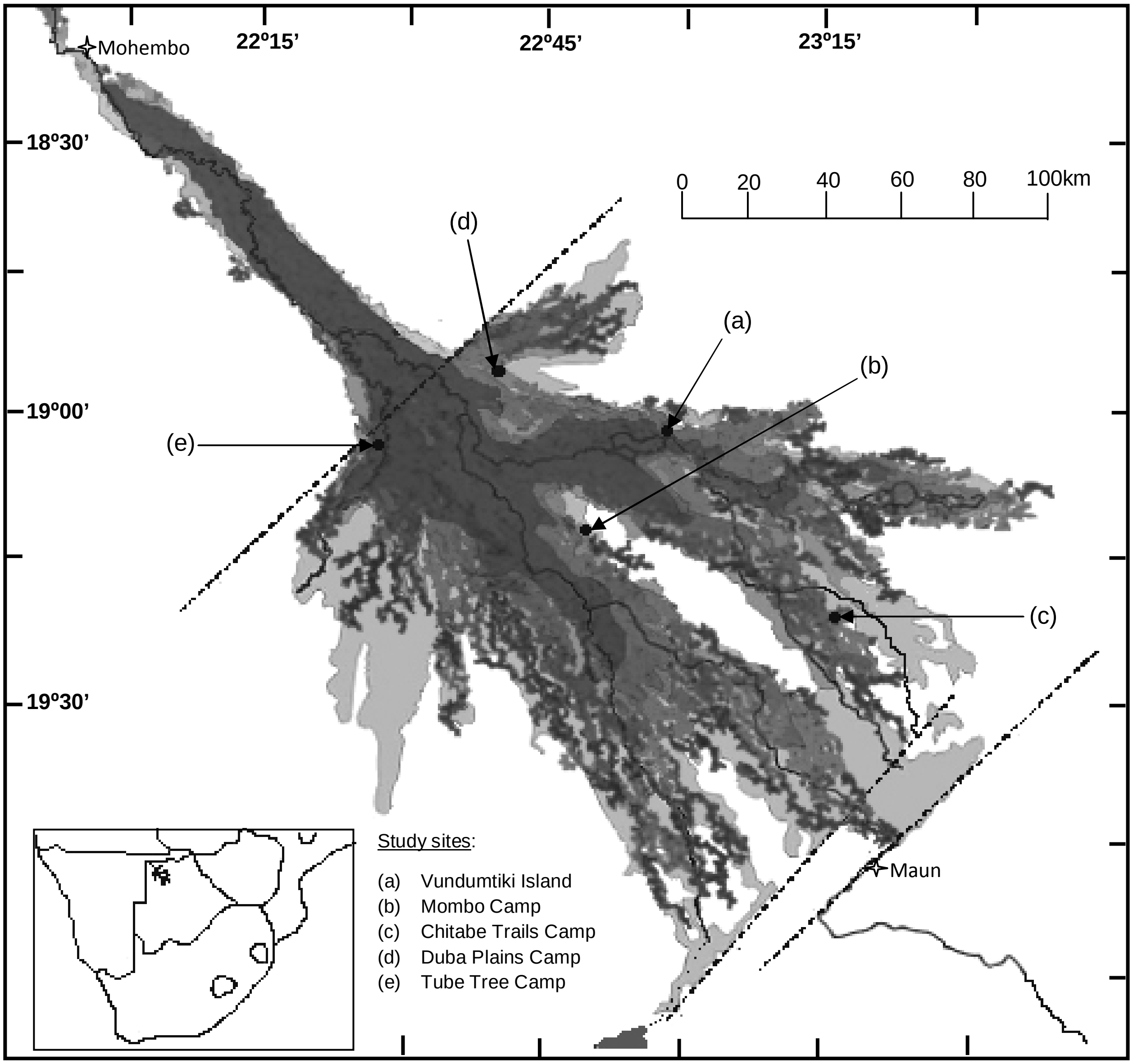


Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

Climatic conditions in the Okavango Delta are distinctly seasonal, comprising a wet season (November–March) and dry season (April–October). Mean annual rainfall is 450–560mm (Ellery *et al.* 2003; Wolski and Savenije 2006). During the annual flood the area covered by water expands from its annual low of 2500–4000km^2 in February–March to its annual high of 6000–12000km^2 in August–September. Arrival of the annual flood lags the rainy season and follows one or two months after the end of rainfall in the region (Gumbricht *et al.* 2001; Ellery *et al.* 2003).

Analysis of historical nesting records

Historical nesting records from the Nest Record Card Scheme (NERCS) were provided by the Avian Demography Unit (University of Cape Town) and Birdlife South Africa.

Data collection

A preliminary survey was conducted from January 2004–January 2006 at Vundumtiki (Jan'04–July'05), Mombo (Aug'05–Jan'06), Chitabe Trails (Jan'06), Xigera (Jan'06), Tubu Tree (Jan'06) and Duba Plains (Jan'06). At Vundumtiki and Mombo, we located Meyer's Parrot nest cavities while conducting standardized feeding activity road transects, five days a week. Breeding pairs prospecting for or establishing breeding territories (Chapter 9: Boyes and Perrin in review b) were located by following "duetting" or territorial vocalizations until nest cavity located and GPS-marked (Garmin Etrex; Garmin 2006). Nest cavities were subsequently inspected and the following nest tree characteristics recorded: tree species, tree height, diameter at breast height (DBH), and crown condition (CC). CC was estimated using subjective visual assessment, and scored in increments of 0.1 between 0 and 1, whereby 0 represents a snag (i.e. dead tree) and 1 represents a full healthy, productive canopy. Tree nomenclature followed Van Wyk and Van Wyk (1997) and Palgrave (2002). Nest cavities were visited daily or as often as possible, until the nesting period was ascertained, after which the cavity was visited bi-monthly to the most advanced nesting period. The nesting cycle was separated into the following nesting periods: territorial advertisement and nest preparation; copulation and egg-laying; incubation; hatching; nestling; fledging; and post-fledging.

An intensive study of the Vundumtiki study area was conducted between February 2007 and July 2007. To standardize spatial distribution, the sample area was defined as an area 250m either side of an 8.6km standardized road transect. Only breeding pairs utilizing nest cavities within this sample area were included. Sample area was subdivided into four, 1.7 km sections along the road transect. From February to May, we conducted extensive 4-hour bush walks between 06h00 and 12h00 once a week in each section of the sample area. Nest tree characteristics of all nest cavities located during this intensive study were measured for comparison with habitat assessments within the sample area.

We also identified the probable disturbance agents responsible for the dead wood in which the cavity excavated. We used the following criteria: (a) If the tree trunk had visible signs of elephant tusk marks or the cambium was stripped off longitudinally, we assumed elephant disturbance; (b) If there were signs of drastic habitat change due to water level or soil salinity fluctuations (MacCarthy 2006; Bauer-Gottwein *et al.* 2007) (e.g. mortality of under-storey and other surrounding trees), we assumed shifting floodwaters disturbed the forest community; and (c) If there was evidence of fire damage (e.g. burned wood or bark), we assumed that fire had caused the initial disturbance to the nest tree. We also investigated the incidence of secondary infections, including fungal attack (e.g. Turkey Tail *Coriolus versicolor*), Coleopteran bark beetles, termites, ants, and natural pruning (i.e. natural removal of lower branches). If there were no signs of primary disturbance to tree and one of the above indicators of poor condition or secondary infections were considered to be the primary agent in producing dead heartwood utilized for nest cavities. For analysis, probable disturbance agents were classified as primary and secondary disturbance agents based on chronology and outcome of disturbance.

Habitat assessment

Habitat descriptions followed Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000). Total habitat area of each forest habitat type identified within the sample area was estimated by measuring the total distance along the road transect line corresponding to the different forest habitat types up to 250m either side of the road. Thirteen (300x20m) habitat line transects were conducted within the sample area (Bullock & Solis-Magallenes 1990, Chapman *et al.* 1994, Renton 2001). Each habitat transect was mapped and the transect line was maintained using a Garmin Quest (Garmin 2006). We used a stratified sampling design within which three resource abundance line transects were dispersed in each forest habitat type to obtain a representative sample of resource availability (Renton 2001). Due to homogeneity and high stand density of *Lonchocarpus nelsii* sandveld only one transect was done in this forest habitat type. Due to heterogeneity of *Acacia*-*Combretum* woodland, this forest habitat type was further stratified to include *Acacia*-*Combretum* woodland dominated by *Combretum imberbe*, *Combretum hereroense* and *Acacia nigrescens*. Similarly, dry Mopane woodland was stratified to include dry Mopane woodland dominated by trees under 4m in height (i.e. scrub Mopane), above 4m in height (i.e. cathedral Mopane) and with multiple-storeys. Total number of trees of each species were counted on each transect and a habitat conversion factor (H_{ij}) used to estimate total number of nest trees in each habitat type (X_{ij}). H_{ij} was calculated by dividing the total forest habitat area within the sample area by the total area of habitat line transects in each forest habitat type. We also recorded the tree species, tree height, diameter at breast height (DBH), and crown condition (CC).

Due to the difficulties in locating nest cavities on habitat transects, we climbed 30 large trees (i.e. DBH > 100cm) of five different tree species to investigate incidence of nest cavities in tree of varying degree of disturbance. We assessed *Acacia nigrescens*, *Combretum imberbe*, *Colophospermum mopane*, *Diospyros mespiliformis* and *Ficus sycomorus* using trees of varying crown conditions (i.e. from snag (0) to full canopy (1)).

Data analyses

We counted the number of nesting attempts in each tree species during the study period to evaluate the degree of specialization in nest cavity preferences. Relative abundance of each tree species within the sample area was used to expand the resource matrix (k = 10 000). The following equation for the modified Hurlbert's expanded and standardized niche breadth index (β_i) was used:

$$\beta_\mathrm{i} = \left[\frac{1}{\sum_\mathrm{j}\left(10000 \times \frac{\mathrm{N}_{ij}}{\sum_i d_j k \times \mathrm{N}_{ij}}\right)}\right]\left[\frac{1}{9999}\right]$$

Where: N_{ij} is the total number of nesting attempts in tree species j over time period i; and $d_j k$ is the proportion of the total available nest cavities represented in tree species j multiplied by k = 10000.

For β_i, a value close to 0 indicates nest tree specialization, and a value tending to 1 indicates broader nest tree preferences (Hurlbert 1978). Relative resource abundance among resource states should provide adequate information on the ecological distinctness of resource states (Colwell & Futuyma 1971).

Kolmogorov-Smirnov (K-S) and Lilliefors tests were used to test for normality. One-way ANOVA was used to test for significant differences between nest tree characteristics between tree species. Spearman rank correlations (r_s) were used to test for significant correlations between crown condition and incidence of cavities in different tree species. Statistical analysis followed Quinn and Keough (2002) and STATISTICA 7.1 (Statsoft (USA) 2006).

Results

Historical nesting records (1918–1996)

Historical nesting records from Zimbabwe, Zambia, Namibia, Angola, South Africa and Botswana were tabulated (Table 1). There were distinct regional differences in nest tree utilization by Meyer's Parrot, whereby *Brachystegia spiciformis* (n = 15), *Acacia galpinii* (n = 3) and *Entrandrophragma caudatum* (n = 1) were utilized exclusively in Zimbabwe, *Pterocarpus angolensis* (n = 2) was used exclusively in Zambia, and *Hyphaene petersiana* was only used in Botswana (Table 1). *Colophospermum mopane*, *Adansonia digitata* and *Ficus sycomorus* were also utilized in Zimbabwe, and there was one nesting record in a *Brachystegia spiciformis* in Angola (Table 1).

Table 1: (a) Summary of Meyer's Parrot nest cavities discovered during the Meyer's Parrot Project in the Okavango Delta; (b) Summary of historical records (1918–1996) in Zimbabwe, Zambia and Botswana (there were no tree species reported in the Namibian and South African historical nesting records)

(a)

Okavango Delta (2003 – 2008)

FAMILY/Species	Vundumtiki	Mombo	Tubu Tree	Xigera	Chitabe	Duba	TOTAL
LEGUMINOSAE/*Acacia nigrescens*	12	8	6	2	4	2	34
LEGUMINOSAE/*Colophospermum mopane*	6						6
COMBRETACEAE/*Combretum imberbe*	5	1	1		2	2	11
BOMBACEAE/*Adansonia digitata*	1	2	2		1		6
MORACEAE/*Ficus sycomorus*	2						2
EBENACEAE/*Diospyros mespiliformis*	2			2		1	5
LEGUMINOSAE/*Acacia erioloba*	1		1				2
LEGUMINOSAE/*Lonchocarpus capassa*	1					1	2
ARECACEAE/*Hyphaene petersiana*		5	2				7
TOTAL	30	16	12	4	7	6	75

(b)

Historical nesting records (1918 – 1996)

FAMILY/Species	Zimbabwe	Zambia	Botswana
CAESALPINIACEAE/*Brachystegia spiciformis*	15		
LEGUMINOSAE/*Acacia galphinii*	3		
MORACEAE/*Ficus sycomorus*	1		
MELIACEAE/*Entandrophragma caudatum*	1		
LEGUMINOSAE/*Acacia nigrescens*	1		
LEGUMINOSAE/*Colophospermum mopane*	1		
BOMBACEAE/*Adansonia digitata*	1		
FABACEAE/*Pterocarpus angolensis*		2	
ARECACEAE/*Hyphaene petersiana*			1
TOTAL	23	2	1

Nest tree preferences

Seventy-five Meyer's Parrot nest cavities were located in the Okavango Delta during our study, of which over 40% (n = 31) were in *A. nigrescens* trees, followed by almost 15% (n = 11) in *C. imberbe*, 12% (n = 9) in *C. mopane*, over 9% (n = 7) in *H. petersiana*, 8% (n = 6) in *A. digitata*, 7% (n = 5) in *D. mespiliformis*, and almost 3% (n = 2) each for *A. erioloba*, *L. capassa* and *F. sycomorus* (Table 1).

The modified Hurlbert's expanded and standardized niche breadth index (β_i) value was 0.701. There was a significant difference between tree condition (ANOVA: F(8, 64) = 2.18; p-level = 0.040), DBH (ANOVA: F(7, 60) = 16.20; p-level < 0.001) and tree height (ANOVA: F(8, 64) = 5.63; p-level < 0.001) between tree species. *Adansonia digitata* was omitted from the DBH analysis due to a mean DBH of 473 ± 126.82 cm (Figure 2). Meyer's parrots preferred large nest trees that were in relative poor condition (Figure 2).

Habitat assessment

All forest habitat types outlined by Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000) were recorded at in the Vundumtiki study area (Table 2) and/or the Mombo, Xigera, Chitabe or Tubu Tree areas. *Hyphaene petersiana* woodland was observed at Mombo, Xigera, Tubu Tree and Chitabe. *Terminalia sericea* sandveld was recorded at all study sites, *Acacia tortilis* sandveld was sampled at Mombo, *Acacia erioloba sandveld* was represented at Vundumtiki, and *Ficus verruculossa* was sampled along the channels at Vundumtiki and Xigera. *Terminalia sericea* sandveld and *A. erioloba sandveld* were excluded from sample area for intensive study at Vundumtiki due to high aridity during the dry winter breeding season and logistical difficulties in surveying these areas regularly.

Over 62% (n = 47) of Meyer's Parrots nest cavities recorded in the Okavango Delta were in dry *Acacia-Combretum* woodlands, followed by 20% (n = 15) found in riverine forest, 11% (n = 8) in *H. petersiana woodland*, and 7% (n = 5) in dry Mopane woodland. Over 93% (n = 57) of nest cavities were on ecotones, which were usually the disturbed contact zones between *Acacia-Combretum* woodland and riverine forest, *Acacia-Combretum* woodland and *D. lycoides* marginal woodland, or forest habitat (esp. Acacia-Combretum woodland) on the edge of floodplains or seasonally-flooded grasslands.

At Vundumtiki: We conducted 13 habitat transects, including 1124 trees, to estimate nest tree availability within the sample area (Figure 3), as well as the DBH, height and tree condition profiles for each forest habitat type (Figure 4).

Nest cavity availability

At Vundumtiki there was a significant negative correlation between crown condition of trees with DBH >100cm and number of nest cavities discovered across all five tree species (rs = -0.986; t(n-2) = 7.55; p-level = 0.005). All tree species utilized for nesting were the most abundant tree species in the habitat mosaic. There was, however, no significant correlation between nest tree availability and utilization (r_s = 0.454; n = 8; t(n-2) = 1.25; p-level = 0.258) (Figure 5).

Table 2: Projected number of trees and potential nest cavities in each forest habitat type within sample area at Vundumtiki

Habitat type	Within sample area			Habitat description
	Total area (ha)	Stand density (stems/ha)	Projected no. of trees (n)	
Riverine forest	29	128	3676	Closed canopy dominated by *Diospyros mespiliformis*, *Garcinia livingstonia, Berchemia discolor*, *Ficus sycomorus* and *Kigelia africana*.
Acacia-Combretum woodland	133	102	13510	Dominated by *A. nigrescens*, *Combretum imberbe*, *C. hereroense and Adansonia digitata.*
Diospyros lycoides woodland	23	207	4747	Homogenous *D. lycoides lycoides* on silty alluvium (often ecotone between habitat types)
Mopane woodland	43	106	4574	Dominated by *Colophospermum mopane* with *Combretum imberbe* and *A. nigrescens* interspersed.
Lonchocarpus nelsii sandveld	10	161	1647	Homogenous *L. nelsii* on deep sand, with *Acacia erioloba* and *Terminalia sericea* interspersed.

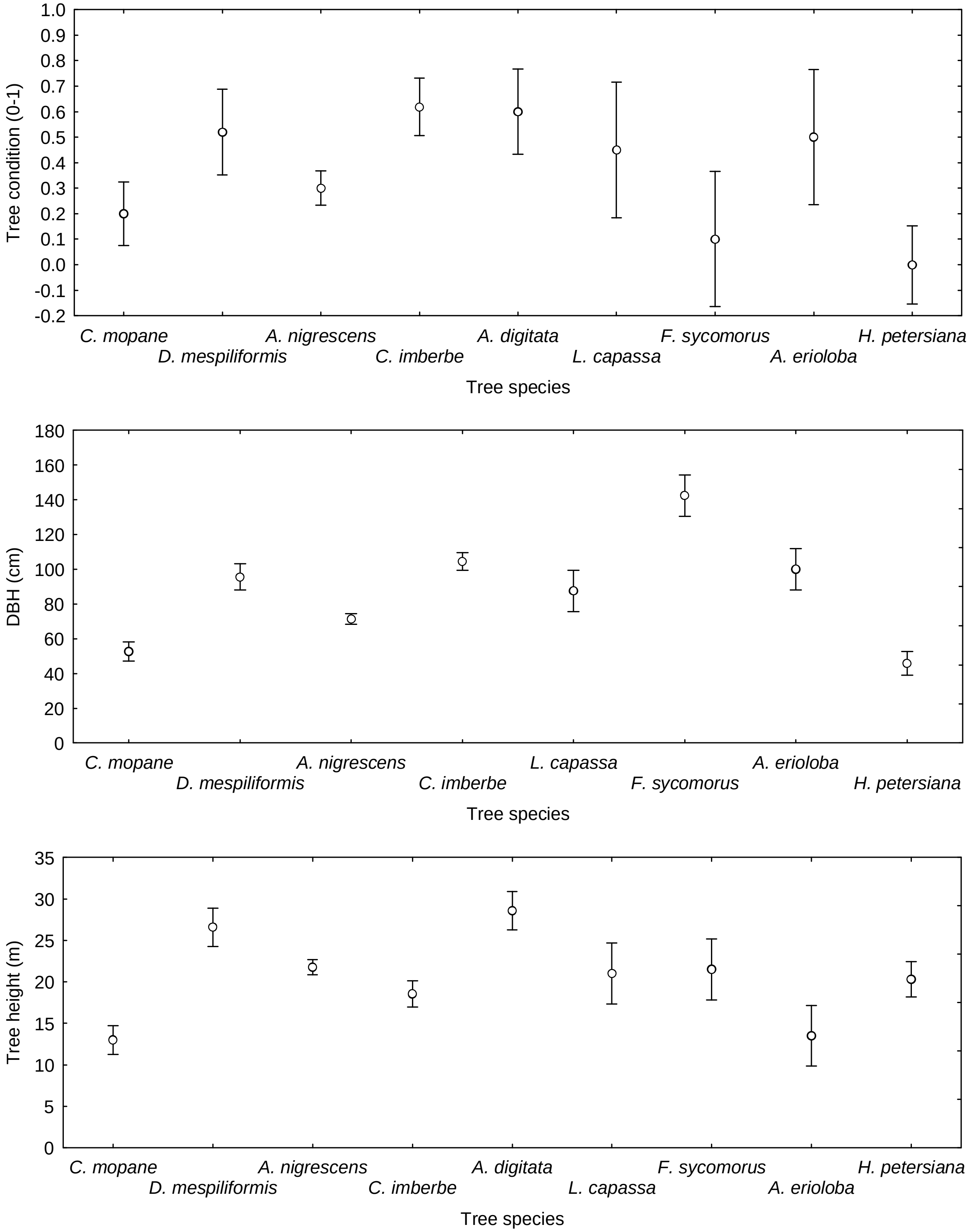


Figure 2: Nest tree preference system: (a) Tree condition (0-1) (Mean ± SE); (b) DBH (cm) (Mean ± SE); and (c) Tree height (m) (Mean ± SE) of all nest cavities utilized by Meyer's Parrots

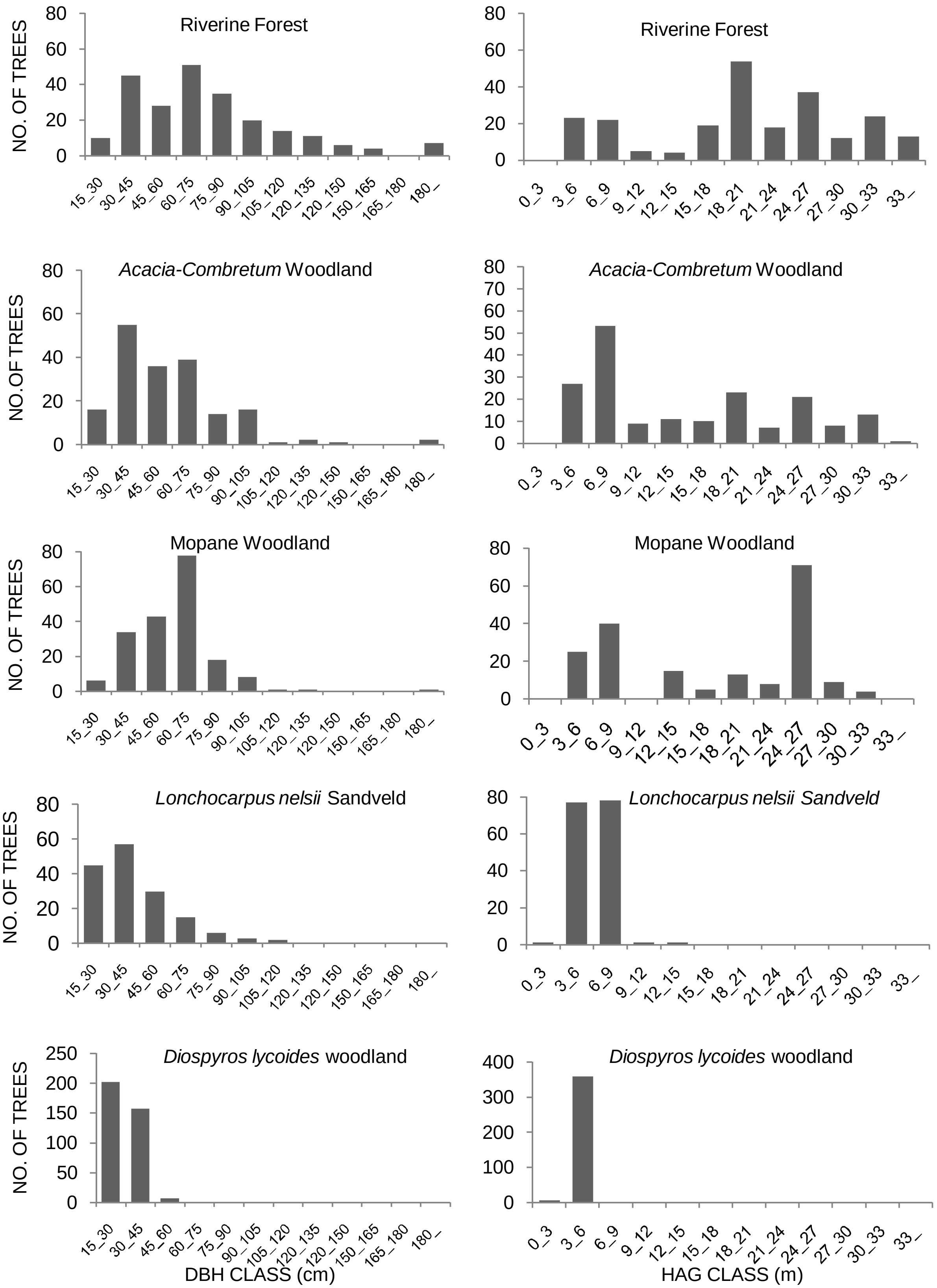


Figure 3: DBHOB and HAG class distributions for forest habitat types identified in the Vundumtiki study area

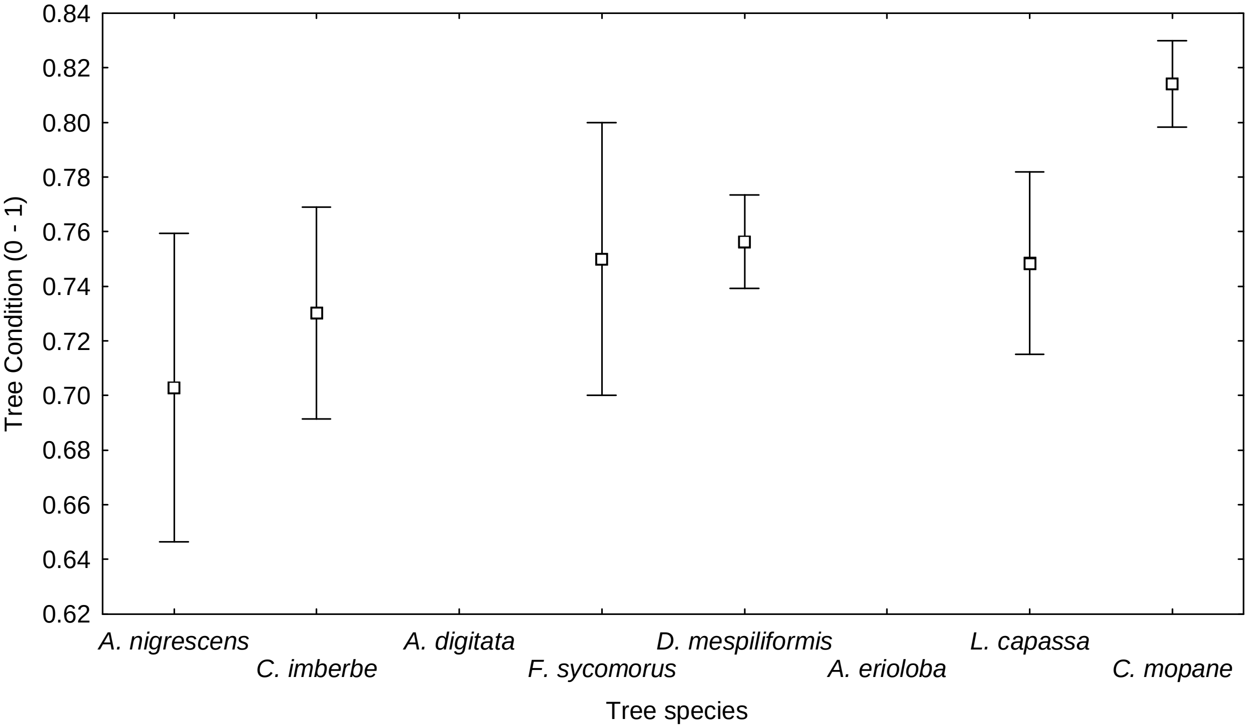


Figure 4: Tree condition (Mean ± SE) of tree species utilized by Meyer's Parrots located within the habitat transects (300m x 20m) (n = 1129)

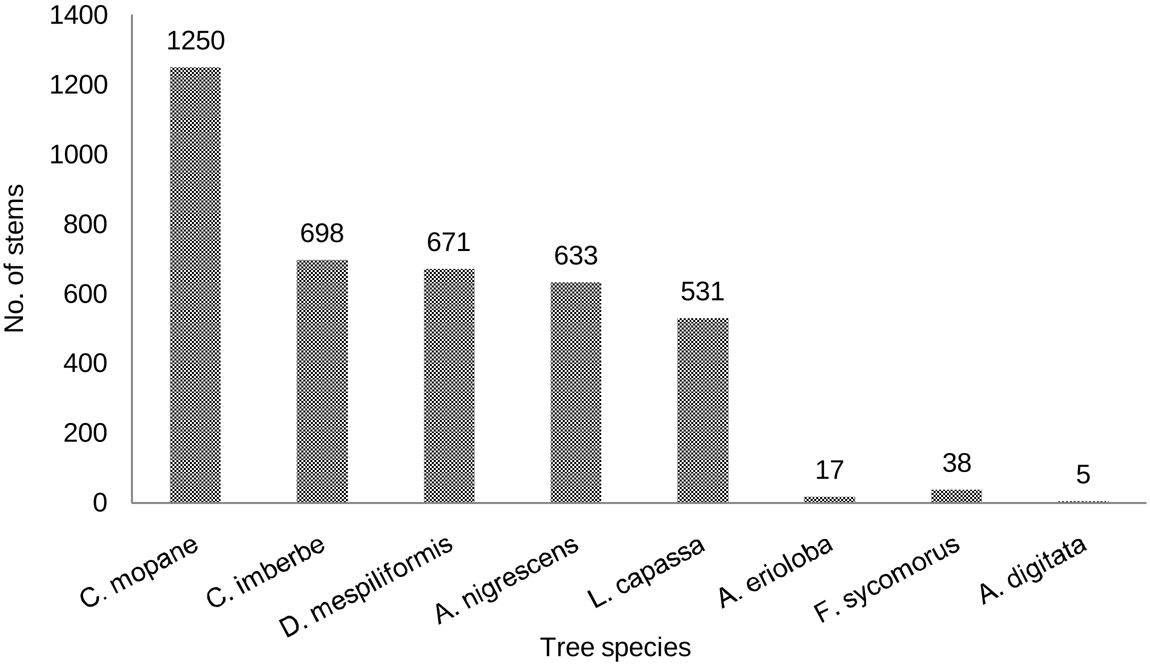
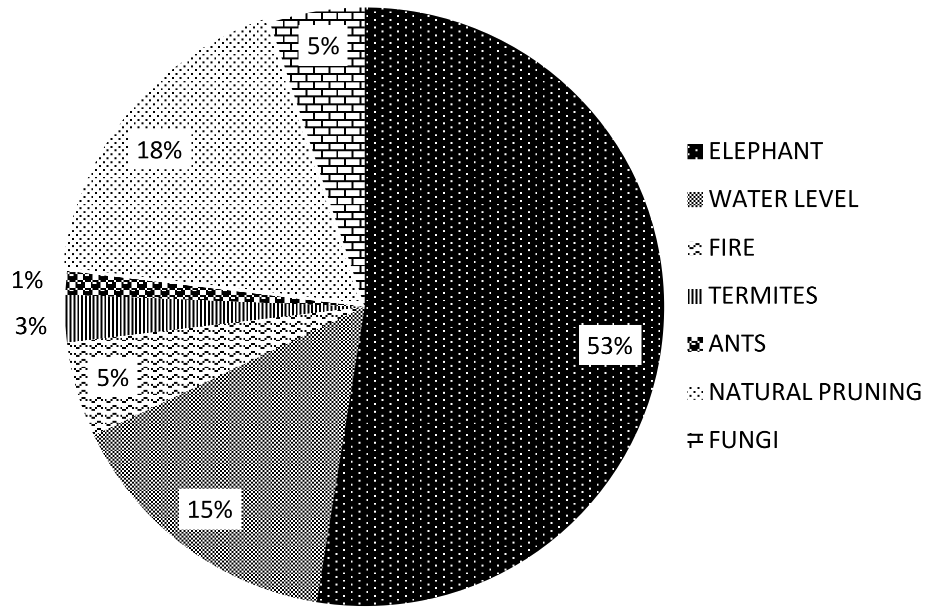


Figure 5: Estimated number of standing trees of tree species utilized for nesting by Meyer's Parrots within the sample (≈430ha) at Vundumtiki

(a) Primary disturbance agents:



(b) Secondary disturbance agents (subsequent to above):

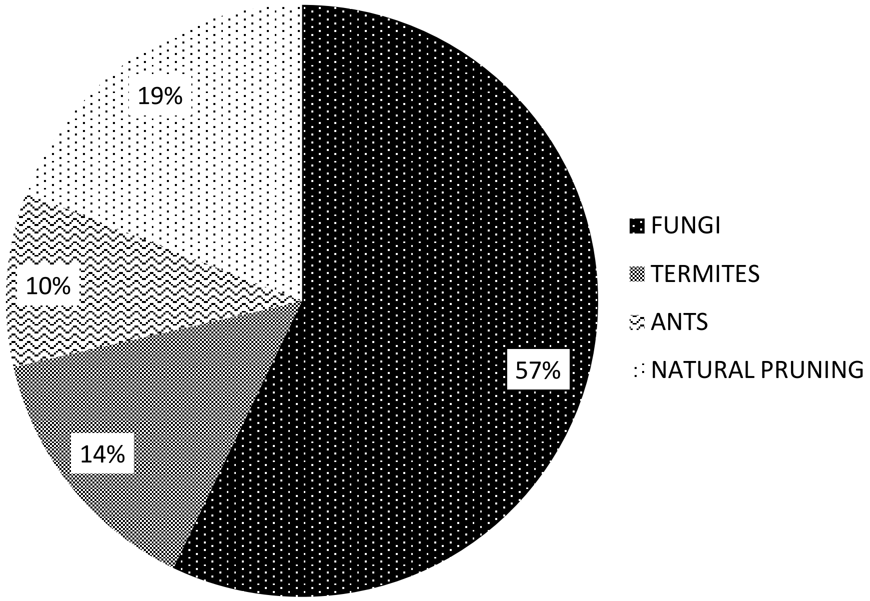


Figure 6: Ecological context of Meyer's Parrot nest cavities: (a) Primary disturbance agents responsible for initial disturbance; (b) Secondary disturbance responsible for subsequent decline in tree condition.

Ecological context of Meyer's Parrot nest cavities

All nest cavities were in dead wood resulting from disturbance (e.g. elephant, water level fluctuations, fungal attack, termite or ant infestation, and fire) or natural pruning (i.e. natural shedding of lower branches resulting in dead wood) (Figure 6). Significantly, elephant disturbance was observed in over 56% (n = 42) of trees containing Meyer's Parrot nest cavities, followed by natural pruning (25%; n = 19) and fungal attack (21%; n = 16) (Figure 6). Natural pruning and fungal attack were observed frequently, but almost always in addition to elephant, water or fire disturbance.

Discussion

Nest tree preference system

Meyer's Parrots were recorded to utilize 18 different tree species for nesting in their southern African range, of which 15 were hardwood species. An additional 18 nest trees are anticipated in southern Africa, and several others elsewhere in the range commensurate with local habitat composition and characteristics. Regional differences are, therefore, apparent, whereby *Brachystegia spiciformis* and *Acacia galpinii* are preferred in Zimbabwe, and *Pterocarpus angolensis* is likely preferred in Zambia. Local differences were noted in the Okavango Delta, where *Colophospermum mopane* was only utilized for nesting when available in the Vundumtiki area and *Hyphaene petersiana* was only utilized at Mombo and Tubu Tree. The modified Hurlbert's expanded and standardized niche breadth index (β_i) confirmed that, based on relative availability of nest cavities between tree species, that Meyer's Parrots were nest tree species generalist at Vundumtiki, whereby tree species was insignificant in comparison to tree size and nest cavity characteristics (Chapter 11: Boyes and Perrin in review c). In addition, there was no significant correlation between nest tree availability and utilization, thus indicating the existence of a disparity in nest cavity availability in each tree species, preferences between tree species (e.g. thorns or no thorns), and/or differences in the probability of a specific tree species having nest cavities suitable for use by Meyer's Parrots.

Our study was representative of forest habitat types in the Okavango Delta system, as all forest habitat types outlined by Ellery and Ellery (1997), Roodt (1998) and Ellery *et al.* (2000) were sampled for nesting activity during the primary breeding season (Chapter 9). At Vundumtiki, all nesting activity occurred in *Acacia-Combretum* woodland, riverine forest and dry Mopane woodland communities, thus highlighting the importance of multi-storey habitat structure with a high canopy and established large trees. Therefore, Meyer's Parrots show distinct preference for old growth forest communities, including trees of between 100 and 500 years old (Boyes unpub. data), and are expected to utilize nest cavities in the most abundant hardwood tree species with regional highest availability of large trees (i.e. DBH > 50cm) with high canopies (i.e. > 13m). Due to the lack of nesting records in *D. lycoides* marginal woodland, *Terminalia sericea* sandveld, and *Lonchocarpus nelsii* sandveld, it seems that nesting habitat preferences are governed by habitat structure, whereby Meyer's Parrots prefer habitat types such as *Acacia*-*Combretum* woodlands, riverine forest, dry Mopane woodlands and *Brachystegia* woodlands with established high canopies. Comparison of mean nest tree DBH and height with the availability of these parameters within the habitat mosaic indicated that nest tree preferences of Meyer's Parrots were non-random, as trees of the preferred DBH and height (Figure 2) were not the most abundant in the habitat mosaic. Nest tree characteristics preferred by Meyer's Parrots were significantly different in each species, however, all represented trees that were significantly older than the surrounding trees. Therefore, utilization of a specific tree could be a function of age, whereby older trees have a higher probability of being disturbed by elephants, changes in water level or biotic agents (e.g. fungi).

Similarities with closest congeners in southern Africa

Ruppell's Parrot and the Brown-headed Parrot are the closest congeners to Meyer's Parrot in southern Africa, forming part of the *P. meyeri* superspecies complex. Rüppell's Parrots occur in dry Acacia woodlands with *A. digitata* (Rowan 1983; Selman *et al.* 2004). Brown-headed Parrots, on the other hand, prefer low altitude forest communities which include *A. digitata* (Rowan 1983; Taylor and Perrin 2006). Rüppell's Parrot had five nest trees in common with Meyer's Parrot, and is reported to nest in twelve additional tree species, including *A. erioloba*, *C. imberbe*, *A. tortilis*, *A. digitata* and *A. nigrescens* (Vincent 1944; Rowan 1983; Namibian Nest Record Scheme 1996; Selman *et al.* 2004). All nest trees were >37.8cm in diameter with very few large trees (i.e. >70cm) (Selman *et al.* 2004). No nest cavities were <3m, however, very few were >7.5m (Selman *et al.* 2004). Brown-headed Parrots had four nest tree species in common with Meyer's Parrots and also demonstrated a preference for nest cavities >6m above the ground (Taylor and Perrin 2006). *Adansonia digitata* was the only tree species common to all three members of the *P. meyeri* superspecies complex. Results from our study support the hypothesis that all members of the *P. meyeri* superspecies complex are nest tree generalist, preferring specific nest tree characteristics but showing no specific preference for nest tree species.

Ecological processes that support cavity availability

Meyer's Parrots are "weak cavity excavators" (Aitken *et al.* 2002; Chapter 11), and thus are predominantly dependent on the productivity of primary excavators (e.g. Bearded Woodpecker

Dendropicos namaquus) for nest cavity availability in a given area. Productivity of primary and weak excavators is dependent on the availability of dead wood (Aitken *et al.* 2002; Bednarz *et al.* 2004), thus linking disturbance agents (e.g. African elephants and fire) with the nesting ecology of cavity-nesting bird species. At Vundumtiki, we demonstrated that disturbance of trees by African elephants was the most important causal factor in the production of deadwood suitable for cavity excavation in the habitat mosaic. Elephants typically stripped off longitudinal sections of bark off *C. mopane* and *A. nigrescens* trees, thus causing either the entire tree or part of the canopy to die off. The distribution of Meyer's Parrot nest cavities was roughly correlated with the annual migration route of the elephants back into the Okavango Delta each year in April (*Boyes unpub. data*). Current range conditions for elephants, however, have restricted their movements and eliminated opportunity for emigration, resulting in local population densities detrimental to the concurrent phase of vegetation (Herremans 2008). This has resulted in drastic reduction to riverine forest Acacia-Combretum woodland communities along the Chobe River, and has likely had a significant reduction in Meyer's Parrot populations in the area.

Natural pruning and fungal attack were most likely secondary infections resulting from significant disturbance elephants, fluctuating water levels and fire. Further research is required on the relationship between African elephants and cavity-nesting bird communities throughout subtropical Africa.

Conclusion

Prerequisites for Meyer's Parrot nesting activity in a given geographical area likely include the following: (a) Large hardwood trees prone to disturbance by African Elephants, fungal attack, fire, and changing soil conditions (e.g. *A. nigrescens*, *C. mopane*, *B. spiciformis*, *A. galphinii*, *E. caudatum* and *P. angolensis*); (b) Suitable primary excavators (e.g. Bearded Woodpecker); and (c) Suitable resource of arthropod larvae parasitizing fruits and pods in close proximity to nest trees (Chapter 9). Therefore, prime locations for Meyer's Parrot nesting activity include dry savanna woodlands prone to fire disturbance, riverine forest communities prone to disturbance by fluctuating water levels and changes in water course, and dry Mopane, *Brachystegia* and *Acacia-Combretum* woodland communities prone to disturbance by African elephants. Therefore, the Okavango Delta, which is a casebook study of disturbance ecology represents an important area the conservation of the Meyer's Parrot metapopulation and cavity-nesting species in subtropical Africa. *Poicephalus* parrots likely require a disturbance regime commensurate with the establishment of trees over 50cm in diameter and 7–10m in height.

Nest trees preferred by Meyer's Parrots are poorly protected in their southern African range, whereby only *Adansonia digitata* and *D. mespiliformis* are protected in Botswana (Botswana Forest Act 1981), and *A. digitata*, *C. imberbe* and *Acacia erioloba* are protected in South Africa (Biodiversity Act 2004).

Further research is required on the reaction of Meyer's Parrots to reduced availability of old growth woodlands containing large hardwood tree species prone to disturbance and nest cavity development (e.g. natural pruning). The rapid decline in Cape Parrot populations due to the selective removal of *Podocarpus spp.* trees from within their distributional range is indicative of the potential threat of drastic forest habitat alteration at landscape level (Perrin *et al.* 2002). As a nest tree generalist, Meyer's Parrots will likely persists in an area until the forest habitat structure changes and large tree are no longer available. More research is required on their interaction with other cavity-nesting species and their reaction to drastic alteration of forest habitat.

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Chapter 11:

Nesting ecology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana[1]

Boyes, R.S., Perrin, M.R. and Mpofu, Z. (in review). Nesting ecology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. – *J. Avian Biol.*

Poicephalus parrots are widespread long-lived, secondary cavity-nesting forest specialists that usually have restricted nesting populations. The aspects of their nesting ecology that restrict their breeding success are, however, unclear. Meyer's Parrots *Poicephalus meyeri* were demonstrated to be weak cavity excavators that modify nest cavities excavated by woodpeckers and barbets. Nest cavity preferences of Meyer's Parrot were non-random, whereby they preferred nest cavities that were north-facing, downward-inclining, deeper than 600mm, higher than 10m above the ground, and had a nest hole aperture of between 50mm and 70mm. North-facing nest cavities were demonstrated to receive significantly more warmth than other cardinal point orientations, downward-inclining cavity entrances likely had anti-predatory benefits and sheltered Meyer's Parrots from wind and rain, and a depth of >600mm protected them from nest predation by Gymnogene *Polyboroides typus*. Only 4.5% of 200 random nest cavities within the sample area not already occupied by Meyer's Parrots were commensurate with their nest cavity preferences, indicating that a significant restriction in cavity availability likely maintains the limited nesting population.

Boyes, R.S., Perrin, M.R. and Mpofu, Z., Research Centre for African parrot conservation, School of Biological and Conservation Sciences, University of KwaZulu-Natal, South Africa, Private Bag X01, Scottsville, 3201

Very little, beyond historical nesting records and anecdotal reports in the literature, is known about the nesting ecology of Meyer's Parrot *Poicephalus meyeri* in the wild (Perrin *et al.* 2002). Meyer's Parrots have the widest distributional range of any African parrot, exceeding that of the Rose-ringed or African Parakeet *Psittacula krameri* and Red-faced Lovebird *Agapornis pullarius* (Rowan 1983; Juniper and

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[1] Formatted for *Journal of Avian Biology*, Nordic Society Oikos: Boyes, R.S., Perrin, M.R. and Mpofu, Z. (in review). Nest tree preferences of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana.

Parr 1998). They are distributed throughout subtropical Africa with strongest associations with riverine forest and associated dry *Acacia-Combretum* or Miombo woodlands (e.g. *Brachystegia* woodlands), and secondary growth around cultivation in areas associated with these forest habitat types (Snow 1978; Tarboton 1980; Forshaw 1989, Juniper and Parr 1998; Chapter 3: Boyes and Perrin in review a). Boyes and Perrin (Chapter 10: Boyes and Perrin in review b) demonstrated that Meyer's Parrots are nesting tree generalists, whereby nest tree species was insignificant. Meyer's Parrots did, however, show distinct preferences for large hardwood trees (e.g. *Acacia nigrescens* and *Brachystegia spiciformis*), *Adansonia digitata* and *Hyphaene petersiana* prone to disturbance (Chapter 10). Our study determined to gather baseline data on the nest site characteristics of Meyer's Parrot for comparison with the frequency of these nest cavity parameters within the habitat mosaic.

Comprehensive studies have been undertaken on the nesting ecology of the Cape Parrot *P. robustus* (Wirminghaus *et al.* 2001; Symes *et al.* 2004), Rüppell's Parrot *P. rueppellii* (Selman *et al.* 2004), Grey-headed Parrot *P. fuscicollis suahelicus* (Symes and Perrin 2004), and Brown-headed parrot *P. cryptoxantus* (Taylor and Perrin 2006). Preliminary studies have also been done on the Red-bellied Parrot *P. rufiventris* (Massa 1995) and Yellow-faced Parrot *P. flavifrons* (Boussekey *et al.* 2002). Senegal Parrots *P. senegalus* and Niam-Niam Parrots *P. crassus* remain data deficient (Juniper and Parr 1998). Our study tested the hypothesis that the nesting ecology of Meyer's Parrots is significantly different from other *Poicephalus* parrots.

Nest cavity characteristics, including nest cavity orientation, nest entrance inclination and cavity size, influence nest temperature fluctuations (Hooge *et al.* 1999; Wiebe 2001) and susceptibility to disturbance by heavy rainfall (Radford and du Plessis 2003). Non-random orientation and inclination of nest cavities has been noted by several studies (Inouye *et al.* 1981; Peterson and Grubb 1983; Korol and Hutto 1984). Inclination of the nest cavity entrance likely influences the amount of light and heat entering the cavity and the risk of rainfall disturbing the nest contents (Brightsmith 2005). Numerous studies focusing on nest cavity characteristics have been conducted on cavity-nesting bird species (Mannan *et al.* 1980; Inouye *et al.* 1981; Muldal *et al.* 1985; Welsh and Capen 1992; Ingold 1991; Li and Martin 1991; Merila and Wiggins 1995; Lawler and Edwards 2002; Giese and Cuthbert 2003; Martin *et al.* 2004). Benefit from specific nest cavities likely results from the interrelationship of several social and environmental factors, including predation risk (Eddington and Eddington 1972; Martin 1996; Martin and Clobert 1996; Li and Martin 1991; Brightsmith 2005; Muchai and du Plessis 2005), local food availability (Lack 1967), temperature (Hooge et al. 1999; Wiebe 2001), parasite load (Tomas *et al.* 2007), rainfall seasonality (Radford and du Plessis 1998), and fungal rot (Jackson and Jackson 2004). Inouye *et al.* (1981) reported that nest entrance orientations of Gila Woodpeckers

Melanerpes uropygialis were non-random, thus supporting the hypothesis that such orientation serves to reduce energetic costs of nesting birds, whereby north-facing nests may reduce water loss in hot summer months, while warmer south-facing nests may reduce energy expenditure in the winter. Ours study measured the temperature fluctuations at each of the cardinal points around active Meyer's Parrot nest cavities, thus demonstrating the relationship between compass orientation and nest temperature fluctuations over the entire breeding season. Our study, therefore, tested the hypothesis that the orientation of Meyer's Parrot nest cavities was non-random.

Primary excavators generally excavate a new cavity for nesting each year, likely to reduce predation risk and because new cavities have fewer parasites or debris (Aitken *et al.* 2002). Secondary cavity-nesters, by definition, must use existing cavities for successful reproduction, whereby the presence of suitable nest cavities is considered to limit population size (Holt and Martin 1997). Therefore, for secondary cavity-nesting species, the extent of nest-site limitation depends on the number of cavities available in relation to the demand (Holt and Martin 1997). Phylogenetic analyses of parrots show that secondary cavity-nesting is the ancestral state for this taxon and there have been multiple transitions to both primary tree cavity nesting and termitaria nesting (Brightsmith 2005). All nests utilized by the *Poicephalus* parrots studied comprehensively thus far have been in excavated or natural cavities in large trees (Massa 1995; Boussekey *et al.* 2002; Symes *et al.* 2004; Symes and Perrin 2004; Selman *et al.* 2004; Taylor and Perrin 2006). Red-bellied Parrots *P. rufiventris* have, however, been reported to utilize both termitaria (e.g. *Macrotermes spp.*) and excavated cavities (Fry *et al.* 1988; Juniper and Parr 1998). Evidence of excavation activities (e.g. modifying the nest entrance or removing wood chips from the cavity) have only been observed in Rüppell's Parrot and Meyer's Parrot (Vincent 1944; Rowan 1983; Selman *et al.* 2004). Selman *et al.* (2004) also noted that Meyer's Parrots may be responsible for a disproportionate amount of the excavation effort in their nest cavities. We, therefore, assessed Meyer's Parrot nest cavity characteristics for comparison with nest cavities excavated by primary excavators resident in the study area to evaluate Meyer's Parrot excavation effort. We also monitored excavation rates for thirteen Meyer's Parrot nest cavities over the 2007 breeding season to corroborate their status as secondary cavity-nesters or weak cavity excavators (Aitken *et al.* 2002).

Methods

Study area

The Okavango Delta was chosen as our study area because of its significant Meyer's Parrot population (Wirminghaus 1997). Our core study area, where habitat assessments and intensive Meyer's Parrot nesting surveys were conducted, surrounded Vundumtiki Island in the north-eastern Okavango Delta (Figure 1). Vundumtiki is a wilderness area with limited human impact or disturbance to habitat and animal behaviour. In addition, we surveyed Meyer's Parrot nest cavities at Mombo Camp from August 2005 – January 2006. We also compiled nesting records from the following Wilderness Safaris Botswana camps: Chitabe Trails, Duba Plains, Xigera and Tubu Tree (Figure 1).

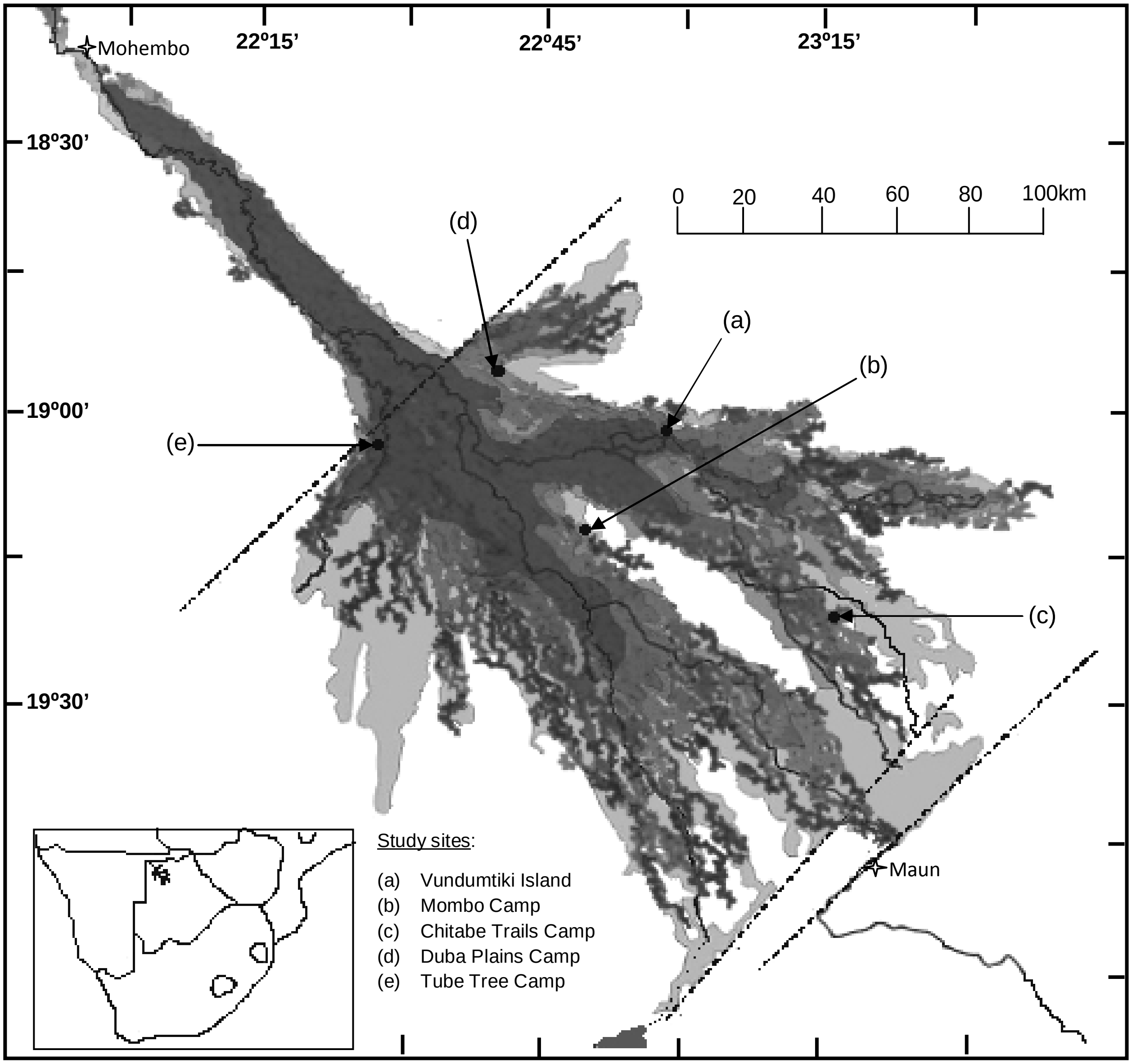

Figure 1: Map of the Okavango Delta showing area of inundation during flood season and location of Vundumtiki and Mombo

Climatic conditions in the Okavango Delta are distinctly seasonal, comprising a wet season (November–March) and dry season (April–October). Mean annual rainfall is 450-560mm (Ellery *et al.* 2003; Wolski and Savenije 2006). During the annual flood the area covered by water expands from its annual low of 2500–4000km^2 (February–March) to its annual high of 6000–12000km^2 (August–September). Arrival of the annual flood lags the rainy season and follows one or two months after the end of rainfall in the region (Gumbricht *et al.* 2001; Ellery *et al.* 2003).

Analysis of historical nesting records

Historical nesting records from the Nest Record Card Scheme (NERCS) were provided by the Avian Demography Unit (University of Cape Town) and Birdlife South Africa.

Data collection

A preliminary survey was conducted from January 2004–January 2006 at Vundumtiki (Jan'04–July'05), Mombo (Aug'05–Jan'06), Chitabe Trails (Jan'06), Xigera (Jan'06), Tubu Tree (Jan'06) and Duba Plains (Jan'06). At Vundumtiki and Mombo, we located Meyer's Parrot nest cavities while conducting standardized feeding activity road transects, five days a week. Breeding pairs prospecting for or establishing breeding territories (Chapter 9: Boyes and Perrin in review c) were located by following "duetting" or territorial vocalizations until nest cavity located and GPS-marked (Garmin Etrex; Garmin 2006).

Nest cavities were subsequently inspected once during and once following the breeding season. Trees were climbed using an 8m ladder and professional climbing equipment. During nest inspections the following data were recorded: height above ground (HAG); cavity entrance compass orientation; entrance dimension (H x W); entrance inclination, cavity depth until the first significant change in direction (D1), angle of descent into the nest cavity (α), and depth from bend to the bottom of the nest chamber (D2) (Figure 2). During the nest inspection after the breeding season we measured all parameters to check for changes due to modifications by Meyer's Parrots during the breeding season. If access to the nest cavity was impossible, a spotting scope was used to estimate the height and width of the cavity entrance by measuring the diameter at breast height (DBH) and diameter highest point possible to estimate taper. Then we compared the width and height of the nest entrance to the width of the tree at that height (corrected for taper) using a 30x Kowa spotting scope.

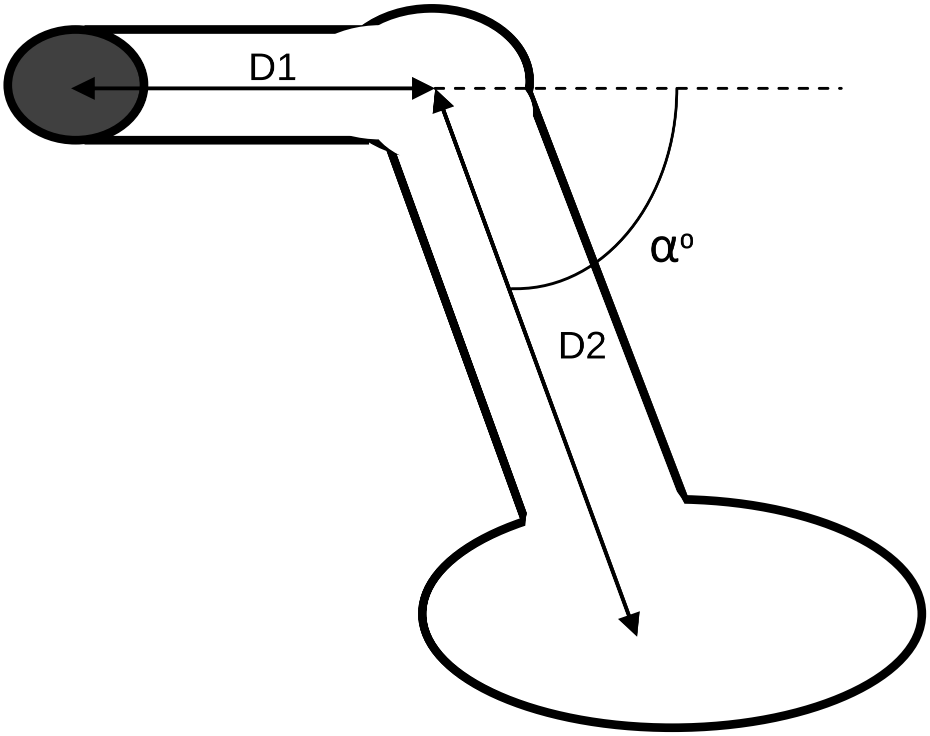

Figure 2: Nest cavity measurements (Total depth of nest cavity = D1 + D2)

An intensive study of the Vundumtiki study area was conducted between February 2007 and July 2007. To standardize spatial distribution, the sample area was defined as an area 250m either side of an 8.6km standardized road transect. Only breeding pairs utilizing nest cavities within this sample area were included. The sample area was subdivided into four, 1.7 km sections along the road transect. From February to May, we conducted extensive 4-hour bush walks between 06h00 and 12h00 once a week in each section of the sample area. Nest cavity characteristics of all nest cavities located during this intensive study were measured for comparison with habitat assessments within the sample area.

Cardinal point experiment

DALLAS Thermochron data loggers (Fairbridge Technologies 2006) were covered in heavy, thermally-inert canvas to protect them from disturbance by Chacma Baboons *Papio ursinus* and attached in north, south, east and west compass orientations around an active nest cavity to measure temperature fluctuations in these compass positions.

Log missions were initiated on 18 May 2007 and stopped on 6 July 2007.

Results

Historical nesting records (1918–1996)

Only 12% (n = 3) of nest cavities recorded were natural cavities, while the rest were excavated cavities. Three nesting records put forward woodpeckers as probable primary excavators and one put forward the Black-collared Barbet *Lybius torquatus*. One nesting record confirmed that the nest cavity had previously been occupied by a Bearded Woodpecker *Dendropicos namaquus*. There were three nesting records that reported hole aperture, whereby all had a width of between 6 and 6.5cm and one had a cavity entrance height of 7.5cm. Height above ground was very variable throughout their range in southern Africa, ranging from 2.5m to 12m. The mean HAG was 6.77 ± 0.75m (n = 18). Total depth of nest cavities recorded in nesting records was 82.3 ± 14.73cm (n = 6), but was typically between 55cm and 65cm. Nest preparation typically involved a thin layer of soft wood chips at the base of the nest cavity, while one nest cavity had at least 35cm of wood chips at the bottom and had a terrible odour.

Nest cavity preferences

Meyer's Parrots preferred nest cavities with moderate cover over the entrance over 10m above the ground (Table 1). The mean nest cavity entrance height was 6.86 ± 0.25m (n = 73) with a mean width of 5.6 ± 0.12cm (n = 73). There was a significant difference between height above ground of nest cavities in different tree species (ANOVA: F(8,64) = 4.74; $p < 0.001$) (Figure 3). There was also a significant difference between nest hole areas (i.e. height x width of entrance) in different tree species (ANOVA: F(8,64) = 3.25; $p = 0.004$) (Figure 3). There was, however, no significant difference in the total depth (i.e. D1 + D2) of nest cavities in different tree species (ANOVA: F(8,36) = 1.63; $p = 0.151$) (Figure 3).

Over 40% (n = 29) of nest cavities were in snags (i.e. dead tree trunk) or branches, while over 57% (n = 41) were in nest cavities excavated in knots resulting from branches breaking off the living trees. Only 3% (n = 2) were in the crook between two branches of a living tree in poor condition. In addition, 64% (n = 46) of nest cavities were in dead wood in branches, while only 36% (n =26) were established on the trunk of the tree. Over 90% (n =65) of nest cavities had one entrance hole, the remaining 10% (n = 7) having two entrances. Meyer's Parrots preferred nest cavities that were downward inclining (Figure 4) and north-facing (Figure 5).

Table 1: Nest cavity characteristics: Cover from sun at entrance (0-1), nest cavity entrance dimensions (cm), and depth and angle of excavated cavities. (Mean ± SE).

		Hole area (cm^2)		Total Depth (cm)		
Tree species	Cover (0-1)	Height (cm)	Width (cm)	D1 (cm)	α (º)	D2 (cm)
Acacia nigrescens	0.47 ± 0.08 (31)	6.19 ± 0.26 (31)	5.38 ± 0.16 (31)	12.94 ± 1.42 (19)	59.25 ± 3.19 (20)	53 ± 4.75 (19)
Combretum imberbe	0.76 ± 0.11 (11)	7.65 ± 0.73 (11)	5.84 ± 0.42 (11)	10 ± 2.32(5)	48.33 ± 6.79 (6)	45.17 ± 6.94 (6)
Colophospermum mopane	0.15 ± 0.086 (9)	7.57 ± 0.4 (9)	5.91 ± 0.22 (9)	60 ± 7.96 (6)	51.5 ± 5.78 (6)	8.25 ± 0.75 (4)
Hyphaene petersiana	0 ± 0 (6)	5.58 ± 0.18 (6)	5.56 ± 0.17 (6)	4.2 ± 0.58 (5)	53 ± 4.64 (5)	54.8 ± 3.77 (5)
Adansonia digitata	0.72 ± 0.15 (5)	8.78 ± 1.36 (5)	5.06 ± 0.55 (5)	11 ± 1 (3)	51.67 ± 4.41 (3)	52.33 ± 8.19 (3)
Diospyros mespiliformis	0.52 ± 0.10 (5)	5.44 ± 0.48 (5)	5.4 ± 0.51 (5)	14 ± 10 (2)	45 ± 10 (2)	67.5 ± 12.5 (2)
Acacia erioloba	0.45 ± 0.05 (2)	6.5 ± 0.5 (2)	5.65 ± 0.35 (2)	-	-	-
Ficus sycomorus	0.1 ± 0.1 (2)	10.25 ± 2.75 (2)	6.6 ± 0.6 (2)	20.5 ± 8.5 (2)	55 ± 10 (2)	77.5 ± 14.5 (2)
Lonchocarpus capassa	0 ± 0 (2)	9.5 ± 4.5 (2)	7.5 ± 1.5 (2)	-	-	-

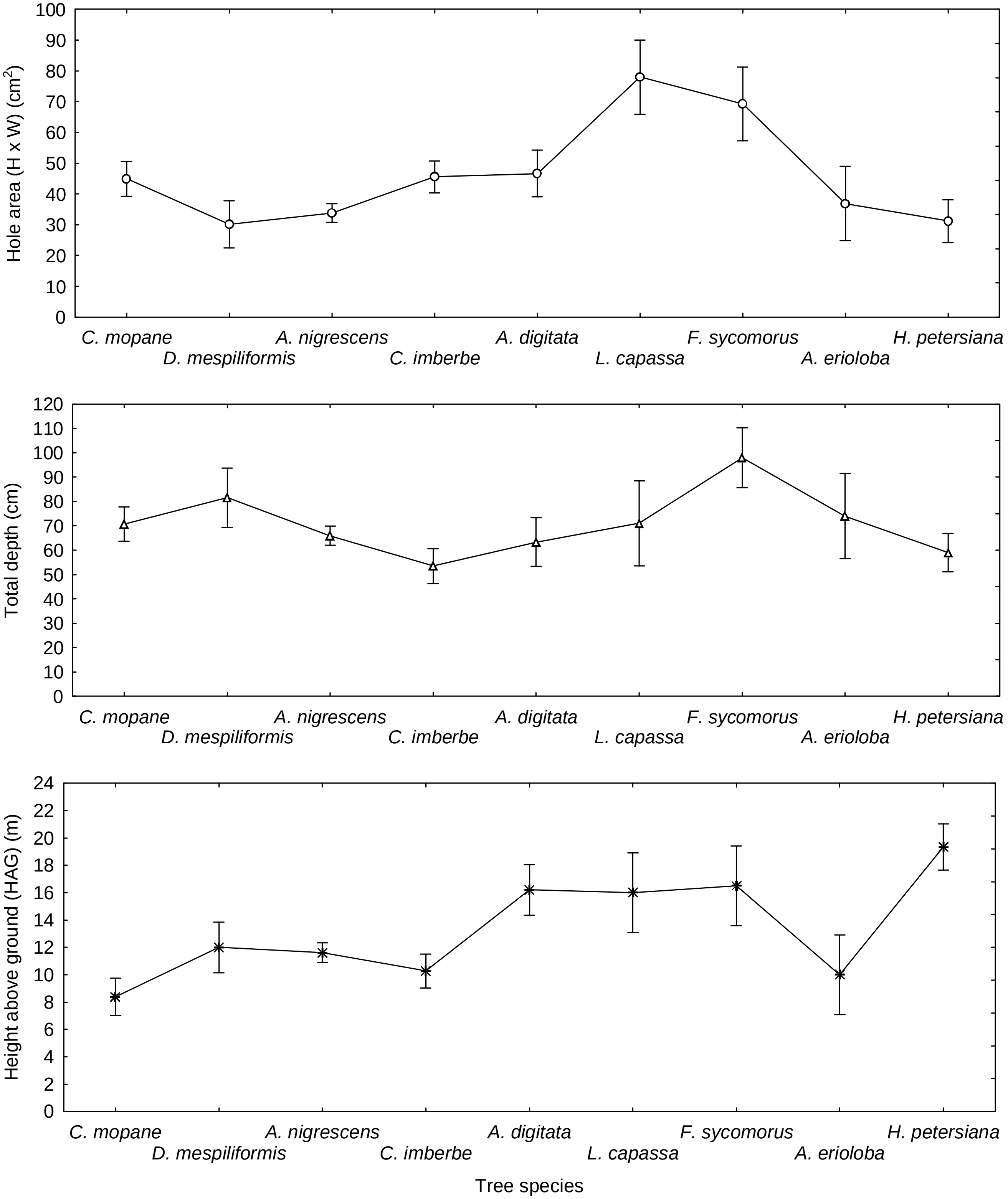

Figure 3: Nest cavity preferences: Hole area (cm^2), total depth (cm) and height above ground of Meyer's Parrot nest cavities in different tree species. Vertical line represent ± SE.

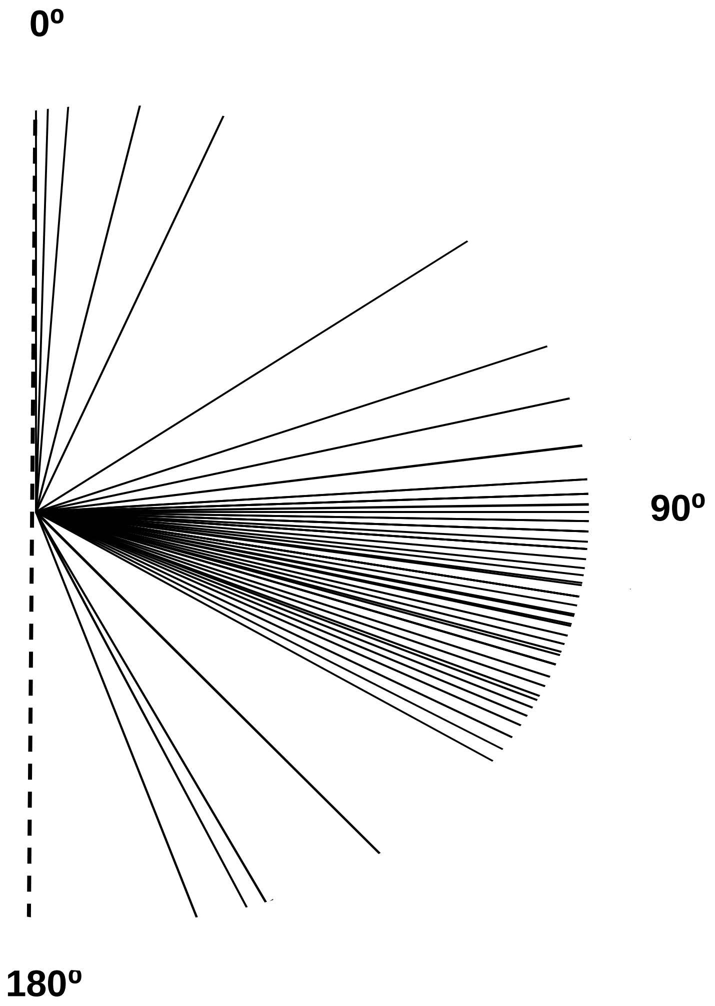

Figure 4: Incline (°) of Meyer's Parrot nest cavity entrances from 0° (directly up to the sky) to 180° (directly to the ground) (n = 75)

Nest cavity availability

The compass orientation of nest cavities were evenly distributed between 0° and 360°, however, 58% (n = 116) were south-oriented (i.e. between 90° and 270°) (Figure 5). Based on nest cavity preferences measured during our study, only 4.5% (n = 9) of nest cavities were suitable for Meyer's Parrots (Figure 6). Over 80% (n = 163) of nest cavities in the sample were excavated by primary excavators (e.g. woodpeckers or barbets). Only 49% (n = 98) of potential nest cavities that were investigated yielded signs of occupation during the summer breeding season.

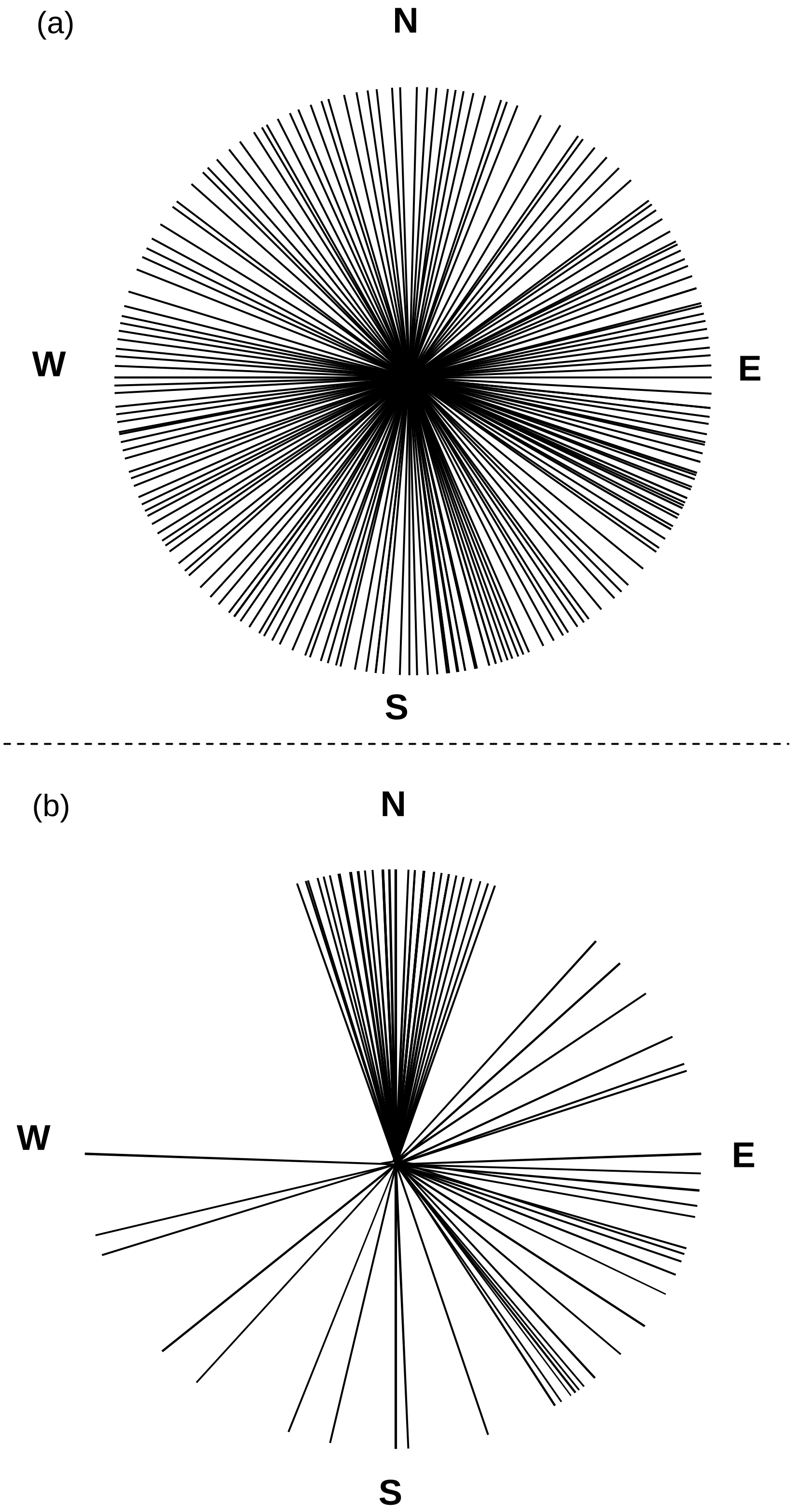

Figure 5: (a) Compass orientations of nest cavities within a random sample (n = 228) of nest cavities from the sample area at Vundumtiki; (b) Compass orientations of Meyer's Parrot nest cavities measured during study (n = 72).

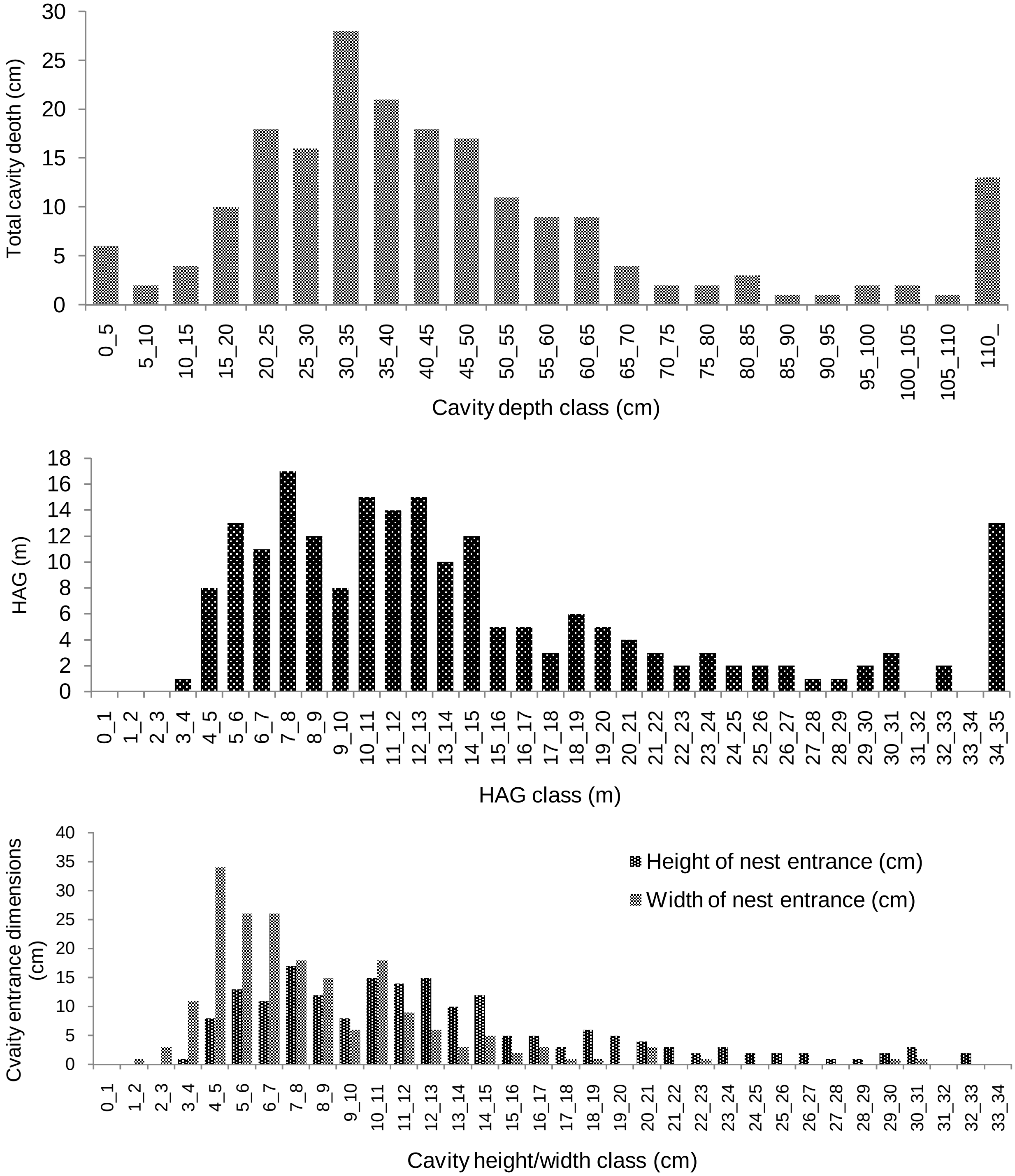

Figure 6: Relative frequency of different height above ground (HAG) classes (a), total cavity depth (including D1 and D2) (b) and nest entrance height and width classes (c) within a sample of 200 nest cavities within the sample area.

Nest-building behaviour and commensal excavators

There were signs of modification by Meyer's Parrots in all nest cavities, whereby most cavities had beak marks radiating from the nest cavity entrance, evidence of enlarging the cavity entrance, and evidence that the cavity had been further excavated. In particularly old nest cavities there were signs of smoothing due to extended use and nutrient streaks down the side of the tree indicating leaching of waste materials from the cavity over subsequent summer seasons. There was evidence of excavation during the 2007 primary breeding season for 8 of 13 nest cavities monitored. Mean excavation rate was 4.54 cm per season with a maximum excavation rate of 18 cm in one season observed at in a nest cavity in the branch of an *Acacia nigrescens* tree. Meyer's Parrots were observed actively excavating nest cavities on five occasions. All of these instances involved breeding pairs that had been individually sexed and identified during 10-hour nest cavity observations (Chapter 9). At each sighting the male excavated the nest cavity alone, while the female was either absent or in an adjacent tree. Males were strong excavators and were able to enter the cavity and emerge several minutes with several wood chips. There were no signs that these parrots were feeding on wood-boring Coleopteran larvae.

Six potential excavators were identified in the study area, including: Black-collared Barbet *Lybius torquatus*; Crested Barbet *Trachyphonus vaillantii*; Bearded Woodpecker *Thripias namaquus*; Golden-tailed Woodpecker *C. abingoni*; Bennett's Woodpecker *Campethera bennettii*; and Cardinal Woodpecker *Dendropicos fuscescens*. Crested Barbet utilized Meyer's Parrot nest cavities for nesting during summer (n = 6), while Black-collared Barbet were only noted to do this on three occasions. Bearded Woodpeckers, Crested Barbets and Black-collared Barbets were the most frequently sighted primary excavators.

Cardinal point experiment

Temperature readings from each of the cardinal points were significantly different (ANOVA: F (3, 8188) = 120.26, $p < 0.001$). Overall the mean temperature at the nest entrance was highest (T_a = 21.96°C; n = 2048) for N-facing nest cavities, followed by W-facing (T_a = 21.58°C), E-facing (T_a = 19.15°C) and S-facing (T_a = 17.46°C) (Figure 7). As would be expected temperatures were highest in E- and N-facing orientations in the early morning and W-facing entrances in the late afternoon (Figure 7).

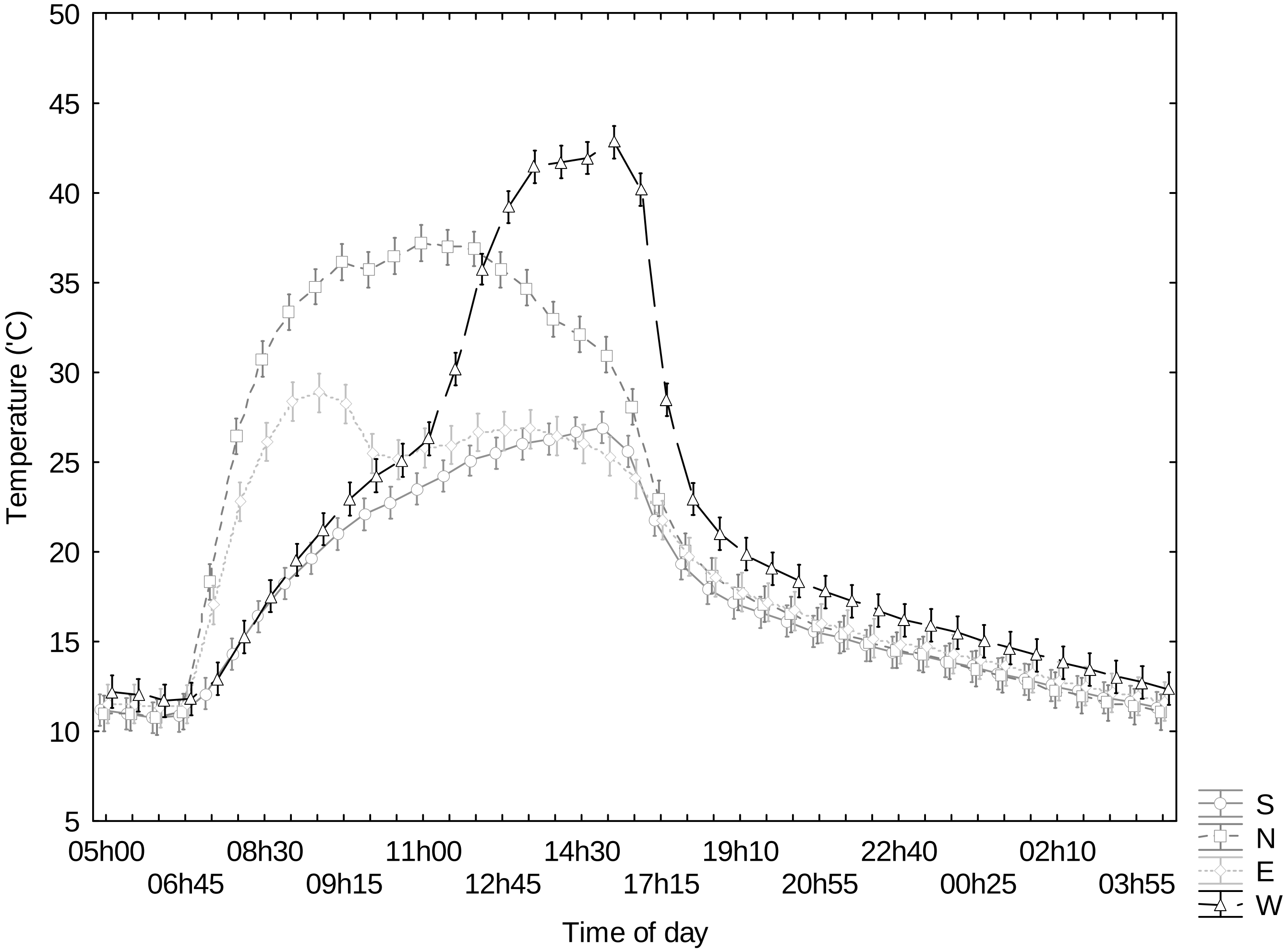

Figure 7: Cardinal point experiment: Ambient temperature fluctuations of north- (N), south- (S), east- (E) and west-facing (W) nest cavities between

Discussion

Non-random nest cavity preferences

Although Meyer's Parrots were found to be nest tree generalists (Chapter 10), which indicates adaptability and utilization of a wide range of nest tree species. Individual utilization of nest cavities was specialized and non-random, whereby they preferred cavities that were north-facing, downward inclining, deeper than 600mm, higher than 10m above the ground, and had a nest hole aperture of between 50mm and 70mm.

The preference for north-facing nest cavities was significant and we hypothesize that in the southern hemisphere north-facing nest cavities minimize energy expenditure during winter.

Furthermore, our cardinal point experiment supported this energy expenditure hypothesis for nest entrance orientation, whereby temperatures at the nest cavity entrance were significantly higher with north-facing orientation. The predominant wind direction during the breeding season was SSE (Boyes unpub. data), and therefore, N-facing nest cavities would be best sheltered from the effects of wind chill during winter. Selman *et al.* (2004), however, found no preference for nest cavity orientation in Rüppell's Parrot. This was likely due to the low availability of nest cavities in their natural habitat (Selman *et al.* 2004). Our study demonstrates that given the opportunity winter breeding populations of Meyer's Parrots will likely select N-facing nest cavities to minimize energy expenditure.

Radford and du Plessis (2003) found that nest cavities with downward-facing entrances were more likely to be successful than those with an inclination between 0° and 90°. This was due to reduced food provisioning rate by adults to nestlings and nest flooding during periods of excessive rainfall (Radford and du Plessis 2003). Meyer's Parrots, however, breed predominantly during winter when rainfall is not a consideration in the Okavango Delta. Selman *et al.* (2004) also found that Rüppell's Parrot demonstrated no preference for the inclination of the nest cavity entrance, likely due to restricted nest cavity availability. Meyer's Parrots, however, showed a distinct preference for downward-facing nest cavities. Downward-facing nest cavities likely assist with nest defense by restricting access to snakes and other predators. Radford and du Plessis (2003), however, found no evidence to support a relationship between anti-predatory considerations and preference for downward-facing nest cavities. Downward-facing nest cavities likely benefit from reliance on ambient temperatures and not direct sunlight, which during the middle of the day could cause heat stress to chicks. Based on the preference for nest cavities deeper than 60cm, however, it is likely that effective insulation maintains a stable micro-climate, thus reducing the significance of ambient temperatures in nest cavity inclination preferences. Ambient nest temperatures inside Meyer's Parrot nest cavities were very consistent over time indicating effective insulation from low ambient temperatures in the early morning (Chapter 9). Ar *et al.* (2004) observed that hypoxia may become a problem for cavity-nesting birds during the breeding season. Wiebe (2007), however, found that oxygen levels inside occupied nest cavites were not significantly lower than ambient levels. Gymnogenes *Polyboroides typus* were observed frequently in the study area and were reported to prey on one Meyer's Parrot nest cavity during our study (Chapter 9). Gymnogenes have a tarsal joint that flexes in all directions, thus allowing it to remove nestlings from shallow nest cavities (Hockey *et al.* 2005). Chacma baboons *Papio ursinus* have been reported to prey on eggs in nest cavities (Skinner and Smithers 1996). In addition, Meyer's Parrots preferred nest cavities with a angle (α) of between 45° and 60° downward from the horizontal (Figure 2), further supporting the notion that this is in reaction to the risk of potential predators reaching in and removing the trapped nest contents. The findings of Selman *et al.* (2004) concure with nest box prescriptions put forward by Manning (1996), whereby Rüppell's Parrots in the wild prefer a tilt inside the nest cavity of 35° from the horizontal. Predation risk was demonstrated to be an important consideration of nesting female Meyer's Parrots (Chapter 9), and thus it is likely that preference for deep nest cavities is linked to anti-predatory behaviour.

Nest cavity availability is limiting

Cavity availability is restricted by rate of excavation achievable by primary excavators, subsequent cavity re-use by these excavators, rate of natural cavity loss, and territoriality and competition among secondary cavity-nesters (Holt and Martin 1997). Differences between Meyer's Parrot nest cavity characteristics and those of nest cavities available in the study area meant that only 4.5% of nest cavities were suitable for Meyer's Parrots. This is likely an important contributing factor to the low breeding population (Chapter 9) and limited number of active Meyer's Parrot nest cavities in the study area (Chapter 10). It seems that, as long-lived cavity-nesting bird species, Meyer's Parrots prioritize adult survival over nesting, and thus likely do not initiate nesting activity until preferred nest cavities become available.

Secondary cavity-nester or primary excavator?

Secondary cavity-nesting bird species are characteristically opportunistic in their cavity adoption behaviour (Holt and Martin 1997; Aitken *et al.* 2002) and due to the likely requirements of Meyer's Parrots to excavate the nest cavity further over several breeding seasons the probability of directly linking Meyer's Parrot nest cavities with primary excavators over three breeding seasons was very low.

Bearded Woodpecker nest cavities are usually 3–5m above the ground with a characteristically oval nest entrance (77mm x 55mm) and a mean cavity depth of 380mm (300–500mm) (Tarboton 2001). Golden-tailed Woodpecker nest cavities are typically 2m above the ground with a smaller entrance hole (50mm x 53 mm) and cavity depth of 200–380mm (Tarboton 2001). Bennett's Woodpecker nest cavities are normally 2–4m above the ground with an entrance hole of 55mm x 60mm and cavity depth of 230–460mm (Tarboton 2001). The smallest woodpecker represented was the Cardinal Woodpecker that excavated nest cavities between 1–3m above the ground with an entrance hole of 44mm x 37mm and cavity depth of approximately 190mm (Tarboton 2001). Crested Barbet excavates nest cavities with an entrance hole of 45–50mm in diameter between 1.5 and 4.5m above the ground, entering the stem at a right angle and descending to a depth of 30–400mm (Tarboton 2001). Black-collared Barbets also excavate nest cavities about 1–4m above the ground with an entrance diameter of 35–40mm and an overall depth of approximately 300mm (Tarboton 2001). Nest cavity characteristics of all these primary excavators fall within the range of utilization by Meyer's Parrots; however, Meyer's Parrots consistently preferred deeper nest cavities, higher up in the tree. It is likely that this poor correlation with the nesting behaviour of primary excavators resulted in only 4.5% of available nest cavities located within the sample area being compatible with the recorded nest cavity preferences of Meyer's Parrots. Therefore, all indications are that Meyer's Parrots should be classified as weak excavators (Aitken *et al.* 2002)

Similar to Rüppell's Parrot, which enlarged the holes of Acacia Pied Barbet *Lybius leucomelas* (Selman *et al.* 2004); Meyer's Parrots were demonstrated to modify nest cavities to be deeper and wider. This may have been to produce new nesting material each season (i.e. moist wood chips at the bottom of the nest), but due to significant increases in cavity depth due to excavation by Meyer's Parrots recorded during one breeding season, it seems that excavation is with the intention of actively modifying these cavities to their preferences.

Noting that Meyer's Parrots were shown to modify existing nest cavities, it seems that Meyer's Parrots could utilize cavities excavated by any of these primary excavators – probably selecting those excavated higher in the canopy. Meyer's Parrots demonstrated the ability to further excavate nest cavities, and thus nest cavity depth restrictions are insignificant. Nesting records from Zimbabwe, however, noted the Bearded Woodpecker as the previous occupant of a Meyer's Parrot nest cavity, thus establishing the only direct link with a primary excavator. Bearded Woodpeckers, Crested Barbets and Black-collared Barbets were the most frequently sighted primary excavators in the Okavango Delta. In addition, Selman *et al.* (2004) observed that Rüppell's Parrots predominantly utilized nest cavities excavated by Bearded Woodpecker. Hockey et al. (2005) put forward that Meyer's Parrots re-use barbet nest cavities. Further research is required on the nesting ecology of primary excavators in the African subtropics to understand this interaction. It is, however, likely that Meyer's Parrots opportunistically usurp barbet or woodpecker nest cavities, excavate them further for one or two breeding seasons, while utilizing another nest cavity within their breeding territory (Chapter 10).

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Chapter 12:

Conservation biology of Meyer’s Parrot *Poicephalus meyeri* (Cretzschmar) 1827 Kordofan[1]

Summary

Meyer’s Parrot *Poicephalus meyeri* has the widest trophic niche and distributional range of any *Poicephalus* parrot studied thus far, and therefore, is expected to be more robust to macroclimatic (e.g. climate change), ecological (e.g. deforestation and influx of exotic species) and historical (e.g. population growth, poverty and social unrest) factors that influence population status in a given area. African deforestation rates are, however, so high that all *Poicephalus* parrot metapopulations are likely under threat. Range reduction has been recorded in all *Poicephalus* parrots studied and surveyed in southern Africa. Most records of the population status of other *Poicephalus* parrots pre-date the chronic loss of forest cover in over 20 range states, resulting in 12 out of 18 range states undergoing significant habitat loss. Meyer’s Parrots have three ecological weaknesses that make them vulnerable to habitat loss, including the low nesting population, specialist nest tree and cavity requirements, and their strong affinity for riverine forest and associated dry *Acacia*-*Combretum*/*Brachystegia* woodlands. Meyer’s Parrots need to be classified as data deficient or near-threatened until a continent-wide survey of the population status of all African parrots and other cavity-nesting forest specialists has been undertaken. The wild-caught bird trade should also be halted until the sustainability of this trade has been evaluated and the relevant information made available.

Introduction

The derivation of a conservation plan for Meyer’s Parrot *Poicephalus meyeri* is complicated by the wide distributional range of this species across subtropical Africa, the paucity of data on their population status and distribution, and the logistical difficulties in surveying remote areas within their range (Wilkinson 1998). At present, Meyer’s Parrots are classified as Least Concern with respect to the IUCN Red List of Threatened Species (Birdlife International 2008), and therefore, are considered widespread and abundant (IUCN 2001). This classification is applicable to the Meyer’s Parrot population in the Okavango Delta, Botswana, because of high sighting frequencies and distribution throughout the system

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[1] Formatted for *Bird Conservation International*, Birdlife International, Cambridge, U.K.

(Wirminghaus 1997; Chapter 2: Boyes and Perrin in review a). In Southern Africa, however, Ruppell's Parrots *P. rueppellii* (Selman 1998; Selman *et al.* 2000), Brown-headed Parrots *P. cryptoxanthus* (Taylor 2002; Boyes unpubl. data), Cape Parrots *P. robustus* (Downs 2000,2005; Perrin 2005) and Meyer's Parrots (Rowan 1983; Boyes unpub. data) have all recorded significant range reduction and population decline over the last 25 years (Wilkinson 1998). Both habitat loss (e.g. Cape Parrot) and wild-caught bird trade (e.g. Ruppell's Parrot) have facilitated these declines (Wilkinson 1998; Selman *et al.* 2000; Perrin 2005). There is no evidence that Meyer's Parrots are able to adapt to the urban or agricultural landscapes, beyond becoming a crop pest in areas associated with significant protected areas, indigenous forest or undeveloped river valleys (e.g. Luangwa Valley) (Rowan 1983; Boyes 2006a). Therefore, the population status of Meyer's Parrots and other *Poicephalus* parrots is likely linked to the carrying capacity and compatibility of suitable forest habitat with specialist ecological requirements (e.g. food resources and nest cavities).

Two primary threats to the population status of Meyer's Parrots were reviewed in this study, including habitat loss and the wild-caught bird trade (Collar and Juniper 1992). Deforestation rates in African countries are twice that of the rest of the world, whereby the continent loses over 4 million hectares of forest cover every year (UNEP 2008). Logging, land conversion to agriculture and settlement, wildfires, cutting of firewood and charcoal, and civil unrest are the primary causes of African deforestation (Kelatwang and Garzuglia 2006). All of these are primarily driven by population growth, poverty and climate change (UNEP 2008). Between 1975 and 2005 over 75 000 wild-caught Meyer's Parrots and almost 1 million *Poicephalus* parrots were recorded in international trade (UNEP-WCMC CITES Trade Database 2005).

Habitat loss in forest communities has been identified as a primary factor threatening avian species survival (Collar *et al.* 1994). Davidar *et al.* (2001) highlighted the value of keystone forest habitat types and the requirement to identify and protect these plant communities. Species-habitat associations are important in conservation planning and management for identifying the potential impacts of habitat change on species survival (Brown & Stillman 1993, Marsden and Fielding 1999). To this end numerous studies have been undertaken on the habitat associations of Psittaformes (Bryant 1994, Gilardi & Munn 1998, Marsden and Fielding 1999, Robinet *et al.* 2003, Evans *et al.* 2005). However, no research, beyond anecdotal descriptions in the literature has been done on the habitat associations of African parrots (Perrin *et al.* 2000). This study evaluated the habitat associations and behavioural ecology of Meyer's Parrot to correlate ecological processes (e.g. niche specialization) with current threats to population status.

Methods

Data on forest cover from up-to-date satellite images were reviewed for evidence of threat to Meyer's Parrots and other *Poicephalus* parrots (UNEP 2008). The UNEP-WCMC CITES Trade Database was reviewed to evaluate past and future threat posed by the wild-caught bird trade to species survival of all *Poicephalus* parrots. Wild-caught trade data for *Agapornis* lovebirds and African Grey Parrots *Psittacus erithacus* were also evaluated. The feeding ecology (Chapter 2), breeding biology (Chapter 9: Boyes and Perrin in review b), nesting ecology (Chapter 10: Boyes and Perrin in review c; Chapter 11: Boyes and Perrin in review d), habitat preferences (Chapter 3: Boyes and Perrin in review e), food resource tracking (Chapter 4: Boyes and Perrin in review f), and trophic niche metrics (Chapter 5: Boyes and Perrin in review g) were reviewed for evidence of phenotypic plasticity or vulnerability to drastic habitat changes and wild-caught bird trade.

Results and discussion

Paucity of data on population status

Global population and population trends of Meyer's Parrots and other African parrots have not been quantified (Birdlife International 2008), and the majority of commentary on their population status is out-dated to the point of place names being redundant (Vincent 1944; Mackworth-Praed and Grant 1952, 1962, 1970; Irwin 1956; Traylor 1965; White 1965; Urban and Brown 1971; Fry *et al.* 1988; Lewis and Pomeroy 1989; Wirminghaus 1997; Wilkinson 1998). Most of these records pre-date the rapid deforestation over the last ten to fifteen years (UNEP 2008). Based on the review of current data on population status and distributional range, Meyer's Parrots and other *Poicephalus* parrots, should be classified as data deficient within the IUCN Red List Categories and Criteria (IUCN 2001). Up-to-date records of the population status and ecology of all *Poicephalus* parrot populations represent a conservation priority, especially in data deficient species (e.g. Yellow-faced Parrots *P. flavifrons* and Niam-Niam Parrots *P. crassus*) and historically heavily-traded species such as Senegal Parrots *P. senegalus* (UNEP-WCMC CITES Trade Database 2005).

Rapid deforestation threatens species survival

Deforestation rates have slowed since the 1990s (Kelatwang and Garzuglia 2006), however, commercial logging, illegal charcoal production, cutting for fuelwood, and conversion of forest habitat to agriculture or monoculture agro-forestry (e.g. oil palms) maintain the highest deforestation rates in the world

(Kelatwang and Garzuglia 2006; UNEP 2008). All Meyer's Parrots range states are experiencing net loss of forest cover (UNEP 2008). Of these Zimbabwe and Uganda had deforestation rates of over 15% per annum between 2000 and 2005 (UNEP 2008), and thus could lose all primary forest cover within 10 years at current rates. Botswana, Zambia, Tanzania and Ethiopia also have significant deforestation rates (i.e. 1–15% per annum). Deforestation rates in Kenya are comparatively low, but primary forest cover has been reduced to less than 2% (UNEP 2008). Most records on the population status of *Poicephalus* parrots pre-date 1990, and if *Poicephalus* parrots are dependent on primary hardwood forest communities, population declines commensurate with forest habitat loss in these range states are expected. According to the IUCN Red List categories and criteria, and inferred population size reduction of ≥50% over the last 10 years indicates that a species is vulnerable (IUCN 2001). At deforestation rates of 15% this loss occurs within 5 years, thus indicating that cavity-nesting hardwood forest specialists such as Meyer's Parrots are likely threatened at several locations within their range. It is projected that within the next 10 years several African countries may only have small forest patches dispersed within a disturbed landscape (UNEP 2008). Loss of keystone habitat resulted in the Cape Parrot population declining to under 1000 individuals (Wirminghaus et al. 2000, 2001; Downs 2000, 2005, 2006).

In this study, Meyer's Parrots were strongly associated with established riverine forest galleries and associated *Acacia*-*Combretum* woodlands (Chapter 3), whereby collectively these habitat types are likely keystone to the persistence of Meyer's Parrots in a given area. Riverine forest galleries and the associated *Acacia*-*Combretum* woodlands provide their nesting and roosting opportunities, and majority of seasonal food resources important to Meyer's Parrots (e.g. seeds from fruits, Combretaceae and Leguminosae pods, figs and arthropod larvae) (Chapter 2; Chapter 9). In addition, Meyer's Parrots feed almost exclusively in the high canopy over 20m (Chapter 4) and specialize in nesting in large hardwoods (e.g. *Acacia spp.* and *Combretum spp.*) over 100cm in diameter (Chapter 10), and therefore, are likely dependent on old-growth primary forests over 100 – 150 years old (Ellery *et al.* 2000; Boyes unpub. data). Habitat assessments in the Okavango Delta demonstrated that large trees preferred by Meyer's Parrots (e.g. *Combretum imberbe* and *Acacia nigrescens* trees over 100cm in diameter) were infrequent in the habitat mosaic. Similar to the Cape Parrot (Symes and Downs 2000; Perrin 2005), removal of these trees from the habitat mosaic due to the illegal charcoal industry and commercial logging would likely cause gradual population decline. Nesting specificity was compounded by the low incidence of suitable nest cavities in suitable hardwood trees, whereby only 4.5% of nest cavities measured in the Okavango Delta corresponded with the non-random nest cavity preference of Meyer's Parrots (Chapter 11). Nest trees preferred by Meyer's Parrots are poorly protected in their southern African range, whereby only *Adansonia digitata* and *D. mespiliformis* are protected in Botswana

(Botswana Forest Act 1981), and *A. digitata*, *C. imberbe* and *Acacia erioloba* are protected in South Africa (Biodiversity Act 2004).

Meyer's Parrots have the widest trophic niche of any *Poicephalus* parrot (Chapter 5). There is, however, no evidence to support the assumptions of the Ecological Specialization Hypothesis put forward by Gaston and Lawton (1990), Pomeroy and Ssekabiira (1990) and Brandle and Brandl (2001) (Chapter 5). Therefore, it is unlikely that the wide distribution of Meyer's Parrots is facilitated by phenotypic plasticity to macroclimatic (e.g. climate change) and historical (e.g. population growth, social unrest and deforestation) factors that influence population status and distributional range. Meyer's Parrots are the smallest *Poicephalus* parrot (approximately 2.5 times smaller than Cape Parrots) (Rowan 1983) and thus have considerably lower absolute protein and energy requirements (Koutsos et al. 2005). Boyes and Perrin (Chapter 5) found a significant negative correlation between body size and extent of distributional range, whereby the smaller the *Poicephalus* parrot, the wider the distributional range. Therefore, the wide distribution of Meyer's Parrots is more likely due to their ability to persist in the most widespread forest habitats in central and eastern sub-Saharan Africa, rather than phenotypic plasticity and resultant high tolerance for disturbance.

Riverine forests and associated dry tropical forest communities (e.g. *Brachystegia* woodlands and dry *Acacia-Combretum* woodlands) likely facilitates their wide distribution and establishment of six sub-species along the Kavango and Zambezi basins, Great Rift Valley system, and across the Nile Valley towards Lake Chad in the Sahel (Figure 1). These are the most significant rivers and associated catchments in southern and eastern Africa, and likely function as "conservation corridors" facilitating gene flow between subspecies at contact zones such as the Okavango Delta (i.e. *P. meyeri damarensis* x *P. m. transvaalensis*). The speciation of *Poicephalus* parrots and other forest non-passerines can be explained by the hypothesis of "forest refugia" (Diamond & Hamilton 1980; Crowe & Crowe 1982), whereby it is likely that during climatic vicissitudes Meyer's Parrots remained in river valleys, Brown-headed Parrots in coastal forest refugia, and Rüppell's Parrots in a forest refuge in southern Angola identified by Crowe and Crowe (1982). This interrelationship between their distribution and macroclimatic conditions supports the hypothesis that Meyer's Parrots populations will disappear from an area if suitable forest habitat disappears. The conservation of riverine forest communities is thus paramount to the persistence of Meyer's Parrots throughout their range and they are likely the sources of meta-populations. At present, Meyer's Parrot populations are likely retreating to river valleys and catchments throughout their range.

P. meyeri subspecies	Date (Taxonomist): Location	Distributional range
P. m. meyeri ○	1827 (Rüppell): Kordofan (Sudan)	Broadly distributed across the northern part of the distributional range in NE Cameroon, S Sudan, Central African Republic and W Ethiopia
P. m. saturatus ☽	1901 (Sharpe): North Ankole (Uganda)	Distributed throughout Uganda, W Kenya, Rwanda, Burundi, and W Tanzania.
P. m. matschei △	1898 (Neumann): Dodoma District (Malawi)	Distributed throughout Tanzania into N Malawi, SE Kenya, SE Democratic Republic of Congo and Zambia.
P. m. reichnowi ✡	1898 (Neumann): Malange (N Angola)	Distributed throughout N and C Angola and adjacent regions in Democratic Republic of Congo.
P. m. damarensis ☆	1899 (Neumann): Damaraland (SW Africa)	Restricted to S Angola, N and C Namibia, and NW Botswana.
P. m. transvaalensis ✧	1899 (Neumann): N Transvaal (South Africa)	Distributed throughout Zimbabwe, NE Mozambique, NE Botswana, and far N South Africa.

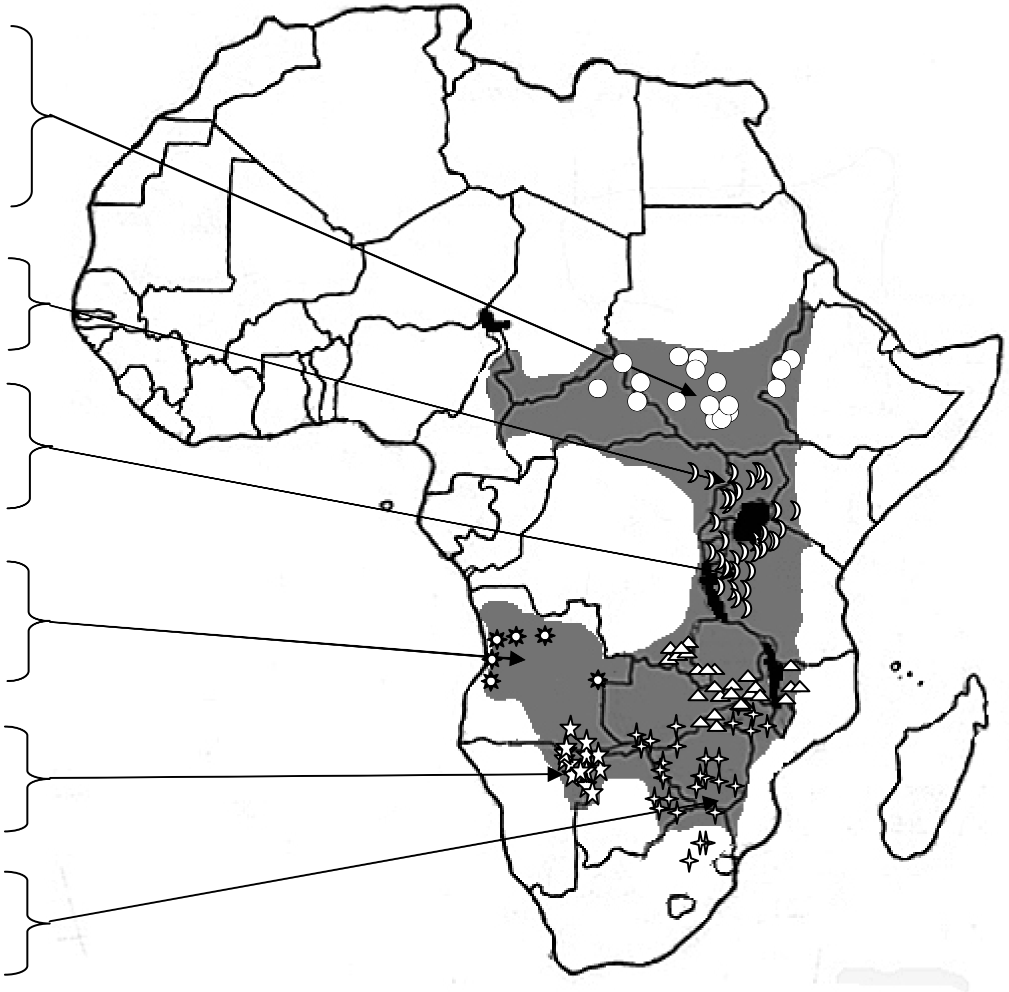

Figure 1: Distribution of Meyer's Parrot subspecies according to historical records and logging locations of all *P. meyeri* skins kept at the British Zoological Museum at Tring, U.K. Subspecies symbol for sampling location for each skin is under subspecies trinomial (n = 124).

Based on the analysis of up-to-date satellite images, the Meyer's Parrot subspecies populations most threatened by deforestation are *P. m. matschei* in Tanzania, Malawi, and Kenya, *P. m. saturatus* in Uganda, and *P. m. transvaalensis* in Zimbabwe and South Africa (Figure 1). Surveys of these range states yielded Meyer's Parrot sighting frequencies between 10 and 20 times less than the Okavango Delta (Boyes unpub. data). Figure 1 represents the distributional range of Meyer's Parrots as per historical records (Vincent 1944; Mackworth-Praed and Grant 1952, 1962, 1970; Irwin 1956; Traylor 1965; White 1965; Urban and Brown 1971; Fry *et al.* 1988; Lewis and Pomeroy 1989) and the sampling locations of 183 Meyer's Parrot skins at the Natural History Museum at Tring (Tring, United Kingdom) collected between 1852 and 1951 (Boyes unpub. data). Range reduction is likely occurring in the north-western part of their distributional range in Chad, northern Central African Republic and western Sudan, where increased climate change has resulted in the desertification of vast, previously forested areas (UNEP 2008). In addition, there incidence in areas of Mozambique, Malawi, Uganda, Zimbabwe, Angola, Zambia, Kenya, and the Democratic Republic of Congo, also needs to be confirmed due to massive habitat conversion and degradation in these countries (Figure 1).

Wild-caught bird trade and UNEP-WCMC CITES Trade Database

According to the UNEP-WCMC CITES Trade Database (2005) over 3 million African parrots have been removed from the wild, including almost 1 million *Poicephalus* parrots, over 850 000 *Agapornis* lovebirds, over 1.2 million African Grey Parrots, and over 11 000 *Coracopsis* parrots from Madagascar (Table 1). The wild-caught bird trade is, therefore, a significant threat to the species survival of African parrots in the wild, regardless of current population levels.

Since 1975, the majority of *Poicephalus* parrots exported from Africa were wild-caught, most notably Meyer's Parrot with captive-breeding deficit of almost 75 000 and the Senegal Parrot with 98% of the almost 830 000 parrots exported being from wild populations (Table 1). Similarly, 93% of the over 1.3 million African Grey Parrots traded were wild-caught (Table 1). There has seemingly been no attempt to source these African Parrots from captivity, even though they are both increasing in popularity in private collections (Perrin 1999). African Grey Parrots (Low 1992; Clark 2001), Meyer's Parrots (Brickell 1985) and Senegal Parrots (Low 1992; Brickell 1997) are easily bred in captivity, thus indicating that the wild-caught bird trade is likely driven by profiteering and not market demand (Collar and Juniper 1992; Beissinger and Bucher 1992a,b). The only feasible alternative source to wild African parrot populations is aviculture, and therefore, the development of avicultural techniques and market access is central to the conservation of wild African parrot populations.

Table 1: UNEP-WCMC CITES Trade Database for *Poicephalus*, *Agapornis*, *Coracopsis* and *Psittacus* between 1975 and 2005 (UNEP-WCMC CITES Trade Database 2005). () indicate a captive-breeding deficit created by poor contribution of aviculture to international trade.

African Parrots	Scientific Binomial	Wild-caught (n)	Captive-bred (n)	Gross exports (n)	Captive-breeding deficit
Meyer's Parrot	*Poicephalus meyeri*	76562	2136	78698	(74426)
Niam-Niam Parrot	*P. crassus*	400	6	406	(394)
Brownheaded Parrot	*P. cryptoxanthus*	13268	682	13950	(12586)
Cape Parrot	*P. robustus**	14923	1338	16261	(13585)
Senegal Parrot	*P. senegalus*	811408	17554	828962	(793854)
Jardine's Parrot	*P. guilielmi*	48313	5793	54106	(42520)
Ruppell's Parrot	*P. rueppellii*	173	6031	6204	5858
Red-bellied Parrot	*P. rufiventris*	25766	1824	27590	(23942)
Yellow-faced Parrot	*P. flavifrons*	9	139	148	130
African Grey Parrot	*Psittacus erithacus*	1225102	88665	1313767	(1136437)
Lesser Vasa Parrot	*Coracopsis nigra*	6294	199	6493	(6095)
Greater Vasa Parrot	*Coracopsis vasa*	4733	587	5320	(4146)
Black-cheeked Lovebird	*Agapornis nigrigenis*	686	26000	26686	25314
Black-collared Lovebird	*A. swindernianus*	409	0	409	(409)
Black-winged Lovebird	*A. taranta*	38	0	38	(38)
Fischer's Lovebird	*A. fischeri*	586446	830228	1416674	243782
Grey-headed Lovebird	*A. canus*	116132	7278	123410	(108854)
Lillian's Lovebird	*A. lilianae*	11752	9912	21664	(1840)
Masked Lovebird	*A. personatus*	55356	677721	733077	622365
Peach-faced Lovebird	*A. roseicollis*	53705	1188674	1242379	1134969
Red-faced Lovebird	*A. pullarius*	33847	1914	35761	(31933)

Relevance of feeding ecology to conservation biology

Rainfall seasonality and the consumption of parasitic arthropod larvae incubating in and feeding on pods and fruits in their diet were likely significant factors in the timing and synchrony of breeding at population level (Chapter 9). Rainfall also has a significant influence on the nesting success of cavity-nesting bird species due to nest flooding and reduced provisioning rate (Radford and du Plessis 2003). It is, therefore, reasonable to assume that, when possible, cavity-nesting bird species avoid breeding during wet periods. Stutchbury and Morton (2005) observed that breeding cannot occur outside of the wet season unless there is suitable food resource available during the dry season.

In the Okavango Delta, there was a significant negative correlation between monthly rainfall and total number of clutches, whereby the influence of rainfall was indirect and likely linked to declining food resource availability (e.g. insects and ripe fruits) for other cavity-nesting bird species and subsequent cessation of their breeding activity (often in Meyer's Parrot nest cavities). Consumption of arthropod larvae protected inside Combretaceae and Leguminosae pods enables Meyer's Parrots to breed during the dry season when other cavity-nesting bird species, which are predominantly insectivorous, experience a food resource bottleneck. Our findings support the hypothesis that the breeding seasonality of Meyer's Parrots is dependent on the interrelationship of inter-specific competition for Meyer's Parrot nest cavities during summer and resource abundance fluctuations of arthropod larvae in their diet during the early breeding season (i.e. egg-laying, incubation and early nesting periods). Therefore, Meyer's Parrots are likely very sensitive to disturbances such as unnaturally hot fires (i.e. poor land management) and aerial pesticides that may influence arthropod larvae infestation levels.

Possible conservation tools to mitigate threats to species survival

Conservation tools identified as potentially useful in the conservation of Meyer's Parrots and other *Poicephalus* parrots include the following:

(a) Census technique: Conservation planning requires a comprehensive knowledge of the ecology and status of a species, thus allowing for the development of management prescriptions that accommodate all ecological and habitat requirements (Wilkinson 1998, Snyder *et al*. 2000). Meyer's Parrots have green under-parts, are arboreal and very skittish. Therefore, to ensure the highest probability of detection without flushing them, thus risking subsequent double-counting, line transects should be conducted when Meyer's Parrots are stationary and vocalizing most frequently (Chapter 7: Boyes and Perrin in review h). They are lingual feeders (i.e. vocalize involuntarily during feeding activity) and the probability of detecting a feeding Meyer's Parrot was over three times greater than detecting socializing or resting parrots, and over 5 times greater than detecting parrots in flight (Chapter 7). In addition, the probability of observing a Meyer's Parrot feeding between 08h30 and 11h00 was between two and three times higher than at any other time of day (Chapter 7). Therefore, population estimates should be derived from survey counts of feeding Meyer's Parrots between 08h30 and 11h00. Feeding activity between 08h30 and 11h00 was not significantly influenced by seasonal temperature fluctuations, rainfall, flood regime, food resource availability or change in location, and therefore, will likely provide a useful index of relative abundance between different sites and over time (Chapter 7). Population density estimates should be gathered between August and January in southern Africa when the majority of the population is not breeding, as females are absent during the majority of the breeding effort. Future work on one of the other *P. meyeri* subspecies, however, is required to test the applicability of these prescriptions to different study populations. These prescriptions likely apply to Brown-headed Parrots and Ruppell's parrots, however, below certain population levels sighting frequency may be too low for viable inferences concerning population level. Further research is required on the Red-bellied Parrot, Niam-Niam Parrot and Senegal Parrot before prescriptions can be adapted for these species.

(b) <u>Sustainable harvesting practices</u>: In Africa, the social (e.g. poverty and unrest), cultural (e.g. utilitarianism) and political (e.g. legislation and governance) obstacles put forward by Beissinger and Bucher (1992) as prerequisites to the sustainable harvesting of parrots are too significant for use of this practice as a conservation tool. In addition, the application of the conservative sustained-harvest model to African parrots is impossible due to inability to effectively sex and age these species in the field. Given the demonstrated low breeding turnover and ecology of these long-lived, cavity-nesting forest specialists, it is unlikely that sustainable harvesting could to be an economically viable. Based on the low breeding population observed in Meyer's Parrot in the Okavango Delta (Chapter 9), all current harvesting quotas for African parrots from the wild are unsustainable until proven to be otherwise. For example, harvesting quotas for Senegal Parrots and African Parakeets in Senegal were 12 000 live parrots each (CITES 2008). Regardless of the source populations, this level of off-take is unlikely to be sustainable given our knowledge of their breeding biology. The development of aviculture in both source and market countries is the only way the international pet trade can sustainably be provided with African parrots. UNEP-WCMC CITES Trade Database demonstrate that international trade in African parrots is driven by economics of the wild-caught vs. the captive-bred bird trade, whereby although more convenient the trade in captive-bred parrots is not as profitable as trade in wild-caught parrots (Wright *et al.* 2001).

(c) Nest boxes: Nest box trials in natural habitat of Cape Parrots and Meyer's Parrots have failed to yield positive results (Downs 2005; Boyes 2008a,b). During the 2007 field season of the Meyer's Parrot Project 105 nest boxes of varying designs were dispersed along four representative forest habitat transects in the Okavango Delta (Boyes unpub. data). After two breeding seasons, only two nest boxes have been included in Meyer's Parrot nesting territories, however, they were never utilized for breeding (Figure 2). Due to the apparent failure of nest boxes as a conservation tool to overcome reduced nest cavity availability due to forest habitat alteration (e.g. logging), conservation authorities need to concentrate on mitigating threats such as the wild-caught bird trade and deforestation.

Figure 2: Nest box incorporated into Meyer's Parrot nesting territory.

(d) Artificial snags: Conservationist should now test the efficacy of artificial snags (e.g. palm stems or dead hardwood trees supported by metal frame of over 10m in height, thus more effectively accommodating the specialist nest tree preferences of Meyer's Parrots (Chapter 10), while providing the ideal nest cavity characteristics as per Chapter 11.

Future research on African parrots

Future research on African parrots needs to centre on the lesser-known *Poicephalus* parrots and the African Grey Parrot. Both the African Grey Parrot and Senegal Parrot are near-threatened by the wild-caught bird trade, and thus urgently require our attention before populations decline below levels useful to empirical scientific research. African conservation authorities need to establish ecological benchmarks for cavity-nesting bird species vulnerable to deforestation by motivating research on the ecological processes (e.g. disturbance regime (Chapter 10) and nest web dynamics (Aitken *et al.* 2002). Future research needs to include analyses of food resource relationships (Chapter 4), nest tree preferences (Chapter 10) and habitat associations (Chapter 3).

Conclusion

If deforestation continues, local conservation authorities and CITES need to ensure that the wild-caught bird trade does not compound the problem. Meyer's Parrots and other *Poicephalus* parrots need to be re-classified as near-threatened or data deficient (IUCN 2001) until further research has been conducted on the behavioural ecology of lesser-known *Poicephalus* parrots (e.g. Yellow-faced Parrot *P. flavifrons* and the African Grey Parrot). National and regional conservation authorities and ministries responsible for the environment need to coordinate into a continent-wide African parrot and forest bird survey, targeted at regions where deforestation and wild-caught bird trade have been most severe. It is likely that several subspecies, populations and sub-populations of African parrots are already endangered (e.g. Cape Parrots and the Meyer's Parrot population in South Africa).

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Appendix I. Food items, acronyms, fruit characteristics, standing relative resource abundance (S-RRA$_i$) and total feeding activity over 12 months

			Fruit characteristics			Within sample area			August 2004 - July 2005	
FAMILY	Species	Food item	Fruit size (LXB)	Colour	Colour value	Structure	No. of trees	S-RRA$_i$	Total feeding bouts	%
Ripe seeds from fleshy fruits										
EBENACEAE	*Diospyros mespiliformis*	DMr	24x22	Yellow	60	Canopy	2782	21500	131	5.3
BIGNONIACEAE	*Kigelia africana*	KAr	750x150	Light brown	60	Canopy	309	2050	111	4.5
EBENACEAE	*Diospyros lycoides*	DLr	13x20	Red	135	Homogenous	6475	2648	83	3.4
CLUSIACEAE	*Garcinia livingstonia*	GLr	15x12	Orange	90	Canopy	722	3711	73	3.0
RHAMNACEAE	*Berchemia discolor*	BDr	19x10	Red	135	Canopy	123	278	52	2.1
ANACARDIACEAE	*Sclerocarya birrea*	SBr	50x30	Yellow/brown	65	Canopy	311	1152	48	1.9
MYRTACEAE	*Ziziphus mucronata*	ZMr	10x10	Red	135	Understorey	105	51	32	1.3
APOCYNACEAE	*Carissa edulis*	CEr	9x11	Red	135	Understorey	532	58	10	0.4
Ripe seeds from woody pods										
COMBRETACEAE	*Combretum imberbe*	CIr	15x15	Yellow	60	Canopy	2387	4979	195	7.9
COMBRETACEAE	*Terminalia sericea*	TSr	30x22	Purple	180	Homogenous	3250	2466	82	3.3
CAESALPINIACEAE	*Guibourtia coleosperma*	GCr	32x15	Light brown	80	Canopy	197	1065	68	2.7
LEGUMINOSAE	*Acacia nigrescens*	ANr	140x15	Brown	85	Canopy	2235	4469	56	2.3
LEGUMINOSAE	*Lonchocarpus capassa*	LCr	160x36	Light brown	80	Canopy	1854	1965	44	1.8
LEGUMINOSAE	*Burkea africana*	BAr	65x26	Light brown	80	Canopy	198	667	18	0.7
LEGUMINOSAE	*Albizia harveyi*	AlHr	155x32	Light brown	80	Understorey	76	42	17	0.7
LEGUMINOSAE	*Acacia tortilis*	ATr	200x7	Brown	85	Homogenous	38	261	8	0.3
LEGUMINOSAE	*Lonchocarpus nelsii*	LNr	85x16	Light brown	80	Homogenous	21563	3942	6	0.2
Unripe seeds from fleshy fruits										
EBENACEAE	*iospyros mespiliformis*	DMun	21x18	Green	0	Canopy	2782	21500	210	8.5
BIGNONIACEAE	*Kigelia Africana*	KAun	45x28	Light green	10	Canopy	309	2050	61	2.5
CLUSIACEAE	*Garcinia livingstonia*	GLun	12x13	Green	0	Canopy	722	3711	47	1.9
EBENACEAE	*Diospyros lycoides*	DLun	11x19	Green	0	Homogenous	6475	2648	47	1.9
RHAMNACEAE	*Berchemia discolor*	BDun	17x8	Green	0	Canopy	123	278	15	0.6
MYRTACEAE	*Ziziphus mucronata*	ZMun	10x7	Green	0	Understorey	105	51	8	0.3
Unripe seeds from woody pods										
LEGUMINOSAE	*Acacia erioloba*	AEun	125x65	Green	0	Canopy	589	786	43	1.7
BOMBACEAE	*Adasonia digitata*	ADun	90x18	Light green	10	Canopy	76	1124	26	1.1

LEGUMINOSAE	*Acacia nigrescens*	ANun	85x14	Green	0	Canopy	2235	4469	26	1.1
LEGUMINOSAE	*Burkea Africana*	BAun	45x19	Green	0	Canopy	198	667	15	0.6
LEGUMINOSAE	*Lonchocarpus capassa*	LCun	100x28	Green	0	Canopy	1854	1965	8	0.3
Fruit pulp only										
MYRTACEAE	*Syzigium guineense*	SGfr	20x10	Light purple	170	Canopy	37	90	1.3	1.3
Seeds and pseudocarp from Moraceae										
MORACEAE	*Ficus sycamorus*	FS	30x26	Red	135	Canopy	82	1187	208	8.4
MORACEAE	*Ficus burkei (thonningii)*	FB	15x12	Light green	10	Canopy	117	1540	91	3.7
Nectar and pollen from flowers										
BIGNONIACEAE	*Kigelia Africana*	KAf	75	Purple	180	Canopy	309	2050	141	5.7
LEGUMINOSAE	*Acacia nigrescens*	ANf	90x15	Light yellow	65	Canopy	2235	4469	74	3.0
BOMBACEAE	*Adasonia digitata*	ADf	120	White	130	Canopy	76	1124	17	0.7
LEGUMINOSAE	*Acacia erioloba*	AEf	15x15	Bright yellow	60	Canopy	589	786	11	0.4
LEGUMINOSAE	*Lonchocarpus nelsii*	LNf	3x4	Muave	150	Homogenous	21563	3942	11	0.4
Insect larvae and products (e.g. exudate)										
COMBRETACEAE	*Combretum hereroense*	CHc	N/A	N/A	N/A	Understorey	5905	2514	108	4.4
LEGUMINOSAE	*Colophospermum mopane*	CMl	N/A	N/A	N/A	Homogenous	3538	18380	88	3.6
COMBRETACEAE	*Terminalia sericea*	TSc	N/A	N/A	N/A	Homogenous	3250	2466	72	2.9
EBENACEAE	*Sclerocarya birrea*	SBl	N/A	N/A	N/A	Canopy	311	1152	35	1.4

Appendix II. International seminars on the Meyer's Parrot Project and the Okavango Delta

1. April 2006: Seminar on the Meyer's Parrot Project and Okavango Delta as part of the Distinguished Lecturer Series of the Cooperative Institute for Research into the Environmental Sciences (CIRES) at the University of Colorado, Boulder.

2. July 2006: Seminar on the Meyer's Parrot Project and Okavango Delta as part of the Wildlife Management Lecture Series of the Department of Environmental Science, Policy and Management (ESPM) at the University of California, Berkeley.

3. November 2006: Seminar on the Meyer's Parrot Project and Okavango Delta at the Wildlife Conservation Society (Bronx Zoo), New York.

4. November 2006: Seminar on the Meyer's Parrot Project and Okavango Delta at the Edward Grey Institute for Ornithology (University of Oxford).

5. November 2006: Seminar on the Meyer's Parrot Project and Okavango Delta at University of Cambridge for UNEP-WCMC, Fauna & Flora International and Birdlife International.

6. September 2008: Seminar on the Meyer's Parrot Project and Okavango Delta at WildCru (University of Oxford).

Appendix III. Popular publications

1. Boyes, R.S. 2005. The Meyer's Parrot – An African Parrot. *PsittScene*, 17(4): 14-15. November 2005.

2. Boyes, R.S. 2006. The Meyer's Parrot of the Okavango Delta. *Parrots*, April 2006: 42–47.

3. Boyes, R.S. 2006. Meyer's Parrot Project: Conserving a common parrot in Africa. *BirdTalk*, September 2006.

4. Boyes, R.S. 2006. Meyer's Parrot – A German parrot in Africa. *Papageien*, 8 (2006): 16–21.

5. Boyes, R.S. 2008. On life in Africa: Interview with a parrot researcher. World Parrot Trust. *Pssitascene*, February: 6–10.

6. Boyes, R.S. 2006. The Meyer's Parrot of the Okavango Delta. *Babbler – Journal of Birdlife Botswana*, April 2006: 42–47.

7. Boyes, R.S. 2008. Fruitful endeavours: Observations of Meyer's Parrots in the Okavango Delta. *Africa Birds & Birding*, February/March: 41–46.

8. Boyes, R.S. 2008. No competition: generalist feeding behaviour of a habitat niche specialist. Wingspan, May: 61-66.

9. Boyes, R.S. 2008. Beobachtungen zur Brutbiologie von Goldbugpapageien. *Papageien*. 11(2008): 388–393.