

Fruiting in two afro-montane forests in KwaZulu-Natal, South Africa: the habitat type of the endangered Cape Parrot *Poicephalus robustus*

JO Wirminghaus¹, CT Downs*, CT Symes and MR Perrin

School of Botany and Zoology, University of Natal, Private Bag X01, Scottsville 3209, Pietermaritzburg, South Africa

* Corresponding author, e-mail: downs@nu.ac.za

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Monthly fruiting data including general fruit-fall of species fruiting, and stage of fruit development and quantity of *Podocarpus* spp. were collected for two southern African afro-montane forests, Hlabeni and Ingeli, over a period of three years. Fruits of the dominant *Podocarpus* species were the most abundant fruit resource at Hlabeni. The percentage of species fruiting (fruit-fall) differed significantly between months for each study site. Peak fruiting period, expressed as a percentage of species in fruit, occurred during winter months (June – August) and was lowest during spring (September – November). Peak fruiting production occurred during winter at Ingeli, but was not signifi-

cantly different between months at Hlabeni. Most of the dominant canopy fruiting species, particularly the *Podocarpus* spp., showed unpredictable fruiting patterns. Fruiting periods were extended (greater than 2 months) in some species including the *Podocarpus* spp. However, total fruit production of some canopy fruiting species differed monthly rather than seasonally. During periods of low fruit production, spring, *Kiggelaria africana* and *Ptaeroxylon obliquum* were available. However, these are not keystone species as they are not a food source for avian frugivores, including Cape Parrots *Poicephalus robustus*.

Introduction

The endangered Cape Parrot *Poicephalus robustus* is a habitat and dietary specialist with a limited range. It is dependant on fragmented afro-montane forest (Low and Rebelo 1996) in South Africa for its survival. This necessitated a detailed study of phenology and fruit production within this forest community.

Despite numerous studies of forest tree phenology, factors which control reproductive phenophases are poorly understood (Bawa *et al.* 1991, Smith-Ramirez and Armesto 1994); including climatic factors (photoperiod, temperature, precipitation), and ecological parameters (competition for pollinators, seed dispersers, and breeding systems see Smith-Ramirez and Armesto 1994). In addition, the long-term relationship of rainfall to phenological patterns remains uncertain (Heideman 1989). Most studies of tropical fruiting phenologies report seasonality as one of the main factors controlling reproduction and phenology, particularly in forests with distinct wet and dry seasons (Howe 1984, Singh and Singh 1992, Murali and Sukumar 1994). Anomalous weather conditions can cause failures of fruit crops and lead to mass starvation of frugivorous vertebrates (Foster 1982). Direct evidence of food limitation in frugivores is scarce for a wide range of forest types (Howe 1984).

Keystone (Gilbert 1980) plant species, can be defined as those plant taxa that produce fruit during periods when other fruit resources are insufficient (Terborgh 1986a, b), in pre-

venting extinction of frugivores that depend on them during periods of resource scarcity (Lambert and Marshall 1991). The concept of pivotal plant species (Howe 1977, 1984) is similar, i.e. species that produce fruit during periods of fruit scarcity. Keystone plant resources are important for the survival of frugivores through periods of general food scarcity (Terborgh 1986a, Levey 1990), especially if these species become rare or confined to special habitats (Howe 1984). Phenological variation at the level of the forest community affects primary consumers which respond to scarcity in various ways including diet switching, seasonal breeding, changes in range use, or migration (Van Schaik *et al.* 1993). Seasonal food scarcity may result in local migration of various species within a habitat mosaic according to the regular seasonal pattern (Karr 1982, Leighton and Leighton 1983, Wheelwright 1983, Wong 1986). Levey (1990) argues for keystone habitats rather than keystone species, particularly when obvious keystone species are lacking.

In southern African forest habitats there are irregular flowering and fruiting of trees, with availability of fruit with these being early, normal or entirely absent during a season, and ranging from very high to entirely lacking, from year to year and within species (Liversidge 1972). Factors affecting seasonal variations in fruit production and fruit ripening are possibly climate, rest period for the plant, unavailability of pollinating agents and insect or animal predation (Liversidge

¹ Deceased

1972). Fruiting patterns are different between forest types (Viljoen 1980, Wirringhaus 1990, Lawes 1991).

Temperate broad-leaved evergreen forests of southern Africa are synonymous with Afromontane forest and are dominated by conifers (*Podocarpus* spp.) (Donald and Theron 1983, Low and Rebelo 1996). The forests are also characterised by the presence of *Apodytes dimidiata*, *Ilex mitis*, *Nuxia congesta*, *Prunus africana*, *Rapanea melanophloeos*, *Halleria lucida*, *Kiggelaria africana*, *Nuxia floribunda*, *Ocotea bullata*, and *Xymalos monospora* (White 1978). This climatic climax forest vegetation found in the KwaZulu-Natal Midlands, South Africa, is also known as Mistbelt mixed *Podocarpus* Forest or afromontane forest (Cooper 1985). It occurs at 1 000–1 500m altitude, on steep, south-facing slopes on dolerite ridges that receive frequent mist in the summer and mean annual rainfall of >1 000mm (Moll 1972). It is the preferred habitat of the Cape Parrot, which has suffered a major population decline and reduction in range (Wirringhaus *et al.* 1999, 2000). Factors contributing to this decline include habitat loss, food shortage, the low reproductive rate, human predation and disease (Wirringhaus *et al.* 1999, 2000).

A survey based on two afromontane forests, Nxumeni and Hlabeni, the latter being the study site for research into the ecology of the Cape Parrot, showed they were generally depauperate with little variation in species composition. They were classified as coarse-grained forests with shade-intolerant species dominating, with sporadic regeneration (Everard 1993). An extraordinary feature of the forest structures was the lack of middle-sized trees, probably the result of past exploitation of timber by colonists and present exploitation of poles by rural populations (Everard 1993). Failed regeneration of *Podocarpus* spp. might negatively impact on Cape Parrots since they feed almost entirely on their fruit, and hole nest in old trees. Assessment of the food resource of the parrots was an integral part of a large conservation biology research programme.

The method used to assess for fruit abundance, as a resource for birds (Blake *et al.* 1990) is critical, since methodological differences may mask changes caused by biological factors such as season, habitat or species (Chapman *et al.* 1994). Seasonal phenological patterns provide few quantitative, comparative data and are of limited value in studies of fruit abundance for bird populations (Blake *et al.* 1990). However, phenological studies may be used to determine fruit production for a subset of species (Blake *et al.* 1990).

The Cape Parrot, *Poicephalus robustus* is dependant on afromontane forest in southern KwaZulu-Natal and the Eastern Cape Provinces, where it feeds predominantly on *Podocarpus* species. (Wirringhaus *et al.* in press). Consequently, the primary aim of this study was to quantify fruit availability for the Cape Parrot in afromontane forests as part of a broader study of its ecology and conservation. Monthly and seasonal phenological patterns of forest fruiting trees, particularly *Podocarpus* species, the preferred diet of Cape Parrots, were determined to assess patterns of fruit availability. It was expected that the fruiting of these species has resulted in periods of fruit scarcity and food shortages. Previously, there have been problems in correlating results from phenological studies with avian demographic owing to

differing time frames (Leighton and Leighton 1983, Wheelright 1983, Blake *et al.* 1990). Consequently fruit production was determined simultaneously with an estimation of the Cape Parrot Population size in this study.

Methods

Study sites

The study sites, Hlabeni and Ingeli Forests, area, altitude and soil type are shown in Table 1.

Fruit-fall production traps

Fruit-fall traps were used in Hlabeni and Ingeli Forests to quantify fruit production of two Afromontane forests. Monthly, seasonal and annual production of fruit, particularly *Podocarpus* spp., were studied. As the total area of the fruit-fall traps was small relative to the total study area, traps were used as an index of fruiting and not of total fruit production. Fruit-fall traps, made of fine-mesh nylon shade-netting (1m x 1m in area, with a mesh size preventing loss of fruit (>0.5mm diameter), but allowing drainage of water) were used. Each trap was weighted to prevent loss of fruit through inversion. Traps (21 at Ingeli, 25 at Hlabeni,) were positioned randomly and set at > 100m apart for independence. Height of traps varied (0.01–1.2m) according to the presence of nearby vegetation, to which the trap was tied with nylon rope. Traps were emptied each month from December 1993 to December 1996. Fruits were collected and weighed after oven drying at 60°C to constant mass. All seed-bearing structures were classified as fruit, and identified to species with the aid of a reference collection, or with reference to plant specimens in the University of Natal Herbarium. Dry mass, number of fruit and fruit size for each species were recorded for 36–37 months for each trap. Nomenclature of the tree species follows Pooley (1993).

Phenological studies

Fruits of *Podocarpus* spp. are the preferred diet of Cape Parrots. Monthly and seasonal phenological patterns of *Podocarpus* spp. were therefore studied at Hlabeni and Ingeli using the classical method of recording flowering and fruiting activity (Frankie *et al.* 1974, Blake *et al.* 1990). A series of *Podocarpus falcatus* (Thunb.) R. Br. Ex Mirb, *P. henkelii* Stapf ex Dallim. Jacks, and *P. latifolius* (Thunb.) R. Br. Ex Mirb, trees were chosen randomly and individually marked. Reproductive activity of the trees was recorded monthly from February 1994 to December 1996. Since fruits remained on the trees for long periods, a shorter inter-sample period was unnecessary. Quantity of fruits (ranked; 0 =

Table 1: Summary description of study sites.

| | Hlabeni | Ingeli |
|---------------------|------------------------|------------------------|
| Grid reference | 29°50'40"S, 29°40'28"E | 30°32'22"S, 29°40'32"E |
| Area (ha) | 410 | 752 |
| Altitude (m a.s.l.) | 1 727 | 1 324 |
| Soil type | dolerite | dolerite |

none, 1 = 1–10, 2 = 11–100, 3 = 101–1 000, 4 = 1 001–10 000, 5 = >10 000) and stage of fruit development on the tree (fruit stage) (0 = zero fruit, 1 = setting, 2 = unripe, 3 = ripe, 4 = moribund) was recorded visually.

Analysis

Analysis of variance (ANOVA), T-tests and linear regressions were conducted with Statistica (Statsoft, Tulsa, OK, USA) computer software.

Results

Fruiting patterns of forest species

Species recorded in fruit-fall traps are shown (Table 2) together with average fruit diameter. Monthly occurrence of each fruiting species, expressed as a percentage (37 months at Hlabeni and 36 months at Ingeli respectively) are presented (Figure 1). Species that produced no fruit in the fruit-fall traps during the study were ignored. Thirty and 34 fruiting species were recorded at Hlabeni and Ingeli respectively; Hlabeni had 4 species that produced fruit in > 75% of the monthly samples namely: *Celtis africana*, *P. falcatus*, *P. latifolius* and *P. henkelii* ie. a dominance of *Podocarpus* spp. Ingeli had 5 species producing fruit in > 75% of the study period: *P. henkelii*, *C. africana*, *Cryptocarya woodii*, *Kiggelaria africana* and *Ocotea bullata*. The dominant deciduous species in both forests were *C. africana* and *Calodendrum capense*.

Mean monthly cumulative fruit production, was expressed as dry mass (Figure 2) which does not account for differences in fruit size. However, as large fruit are favoured by large vertebrate frugivores (e.g. *Podocarpus* spp. and *K. africana*), this illustrates when availability of these preferred fruits is low (potential crunch periods). Monthly total cumulative fruit production, expressed as dry mass, differed significantly temporally during the study period at Ingeli and Hlabeni (ANOVA, df = 35, F = 1.92; df = 36, F = 0.70, P < 0.05 respectively). When analysed seasonally (December–February = summer, March–May = autumn, June–August = winter, September–November = spring), cumulative fruit production at Ingeli differed significantly (ANOVA, df = 3, F = 4.40, P < 0.05) between the seasons with greater fruit production recorded in autumn and winter. However, cumulative fruit production at Hlabeni did not differ significantly seasonally (ANOVA, df = 3, F = 0.18, P > 0.05). For each forest there was spatial and temporal variation in fruit production, shown by the presence or absence of fruit in individual fruit-traps, and changes in monthly dry mass of fruit. Fruits of the dominant *Podocarpus* spp. were the most abundant fruit resource.

The percentage of fruiting species, of those collected throughout fruit-fall, differed significantly between months for each study site (T-test, Hlabeni, df = 36, t = 9.9; Ingeli, df = 35, t = 10.53, P < 0.05). Peak fruiting, expressed as the percentage of species in fruit, occurred during winter months but was lowest during spring (Figure 3). Monthly number of canopy fruiting plants (trees and climbers) (mean ± SD) was 11.1 ± 3.0 (37.0%, n = 37) and 12.9 ± 3.6 (38.0%, n = 36) for

Table 2: Fruiting species monitored (with abbreviations used) and fruit size at Ingeli and Hlabeni Forests

| Species | | Fruit size (mm) |
|-------------------------------------|-----|-----------------|
| <i>Acacia melanoxylon</i> * | am | |
| <i>Apodytes dimidiata</i> | ad | 6 x 3 |
| <i>Behnia reticulata</i> | br | |
| <i>Buddleja salviifolia</i> | bs | |
| <i>Calodendrum capense</i> | cc | 60 x 60 |
| <i>Calpurnia aurea</i> | cau | 50–100 x 13–19 |
| <i>Carissa bispinosa</i> | cb | 10–16 x 4–6 |
| <i>Celtis africana</i> | caf | 13 x 13 |
| <i>Combretum kraussii</i> | ck | 20 x 15 |
| <i>Cryptocarya woodii</i> | cw | 15–20 x 15–20 |
| <i>Dalbergia obovata</i> | do | 90 x 18 |
| <i>Dioscorea sylvatica</i> | ds | |
| <i>Diospyros whyteana</i> | dw | 20 x 20 |
| <i>Eugenia zuluensis</i> | ez | 13 x 13 |
| <i>Ficus craterostoma</i> | fc | 5–10 x 5–10 |
| <i>Halleria lucida</i> | hl | 10 x 10 |
| <i>Harpephyllum caffrum</i> | hc | 25 x 13 |
| <i>Hippocratea africana</i> | ha | |
| <i>Kiggelaria africana</i> | ka | 20 x 20 |
| <i>Maytenus mossambicensis</i> | mm | 13 x 13 |
| <i>Ocotea bullata</i> | ob | 10–20 x 10–20 |
| <i>Podocarpus falcatus</i> | pf | 13 x 13 |
| <i>Podocarpus henkelii</i> | ph | 25 x 20 |
| <i>Podocarpus latifolius</i> | pl | 10 x 10 |
| <i>Ptaeroxylon obliquum</i> | po | 20 x 15 |
| <i>Rapanea melanophloeos</i> | rm | 5 x 5 |
| <i>Rhoicissus rhomboidea</i> | rr | 10 x 10 |
| <i>Riocreuxia torulosa</i> | rt | |
| <i>Rothmannia capensis</i> | rc | 70 x 70 |
| <i>Scolopia mundii</i> | smu | 10 x 10 |
| <i>Scutia myrtina</i> | sm | 8 x 8 |
| <i>Secamone frutescens</i> | sf | |
| <i>Secamone gerrardii</i> | sg | |
| <i>Solanum giganteum</i> | sg | 10 x 10 |
| <i>Solanum mauritianum</i> * | sm | |
| <i>Strophanthus speciosus</i> | ss | 180 x 15 |
| <i>Trichocladus ellipticus</i> | te | small |
| <i>Trimeria grandifolia</i> | tg | 5 x 3 |
| <i>Vepris lanceolata (undulata)</i> | vu | 5 x 5 |
| <i>Xymalos monospora</i> | xm | 10–15 x 10–15 |
| <i>Zanthoxylum davyi</i> | zd | 5 x 5 |

*alien spp.

Hlabeni and Ingeli respectively. Peak fruiting occurred during winter months at Ingeli.

When the patterns of monthly fruiting of each species, expressed as total monthly dry mass, was compared at Ingeli it showed that *C. africana*, *Combretum kraussii*, *Halleria lucida*, *K. africana*, *O. bullata*, *P. henkelii*, *Scutia myrtina* and *Xymalos monospora* differed significantly (ANOVA, df = 35, P < 0.05 respectively). Similarly, at Hlabeni *C. africana*, *P. falcatus*, *Ptaeroxylon obliquum*, *S. myrtina*, *Strophanthus speciosus*, *Vepris lanceolata* and *X. monospora* differed significantly in monthly fruit production (ANOVA, df = 36, P < 0.05 respectively). When analysed at a seasonal level fruit production in *C. capense*, *Carissa bispinosa*, *C. africana*, *P. henkelii*, *S. speciosus*, *Xymalos monospora* *H. lucida* and *O. bullata* differed significantly

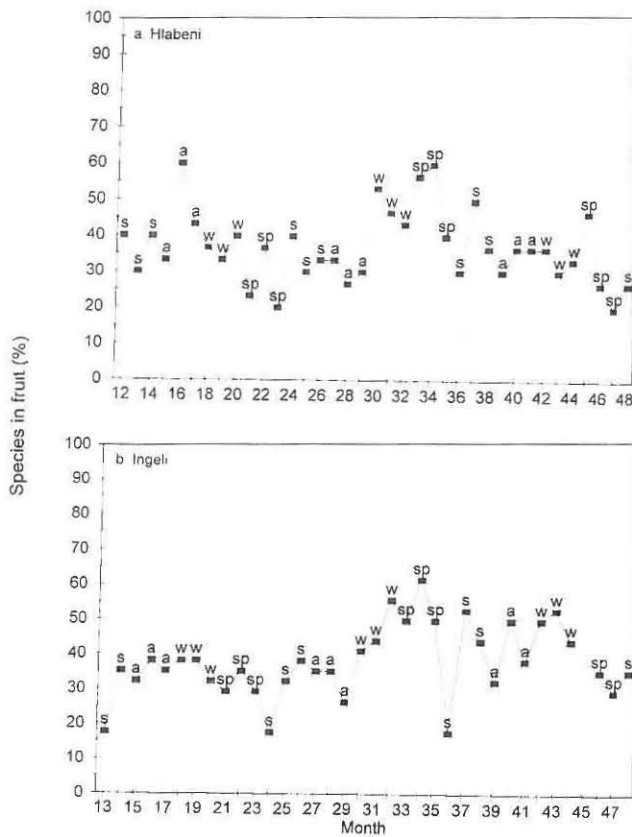


Figure 3: Peak fruiting expressed as a percentage of species in fruit, a. for Hlabeni and b. Ingeli where s = summer, a = autumn, w = winter, and sp = spring

Smallwood 1982). Wirminghaus (1990) recorded that monthly variation in fruit-fall results from heavy production of a few dominant species (usually < 5) which is confirmed by the results of the present study. Similarly in Gabon, eight species accounted for the variability in fruit availability (Tutin and Fernandez 1993).

Generally, Hlabeni forest is *P. falcatus*-dominated (Everard 1993). Areas with moist, flat, gentle slopes were dominated by species type *P. henkelii*, while higher, drier, exposed areas that received orographic mist were dominated by a second climax type, *P. falcatus* (Moll and Woods 1971). The secondary gradient is a successional gradient with species including *Kiggelaria africana*, *Zanthoxylum davyi* and *Xymalos monospora* being dominant, which are later replaced by *Podocarpus* spp. (Moll and Woods 1971). These canopy tree species were represented in monthly fruit collected in fruit-fall traps at Hlabeni and Ingeli in the present study. However, unpredictable and patchy monthly and seasonal variation in fruit production of dominant fruiting trees was recorded. Visual assessments of the fruiting condition of marked individual *Podocarpus* spp. corroborated this.

Afromontane forests in southern Africa which have had little logging are dominated by *Podocarpus* spp., which form

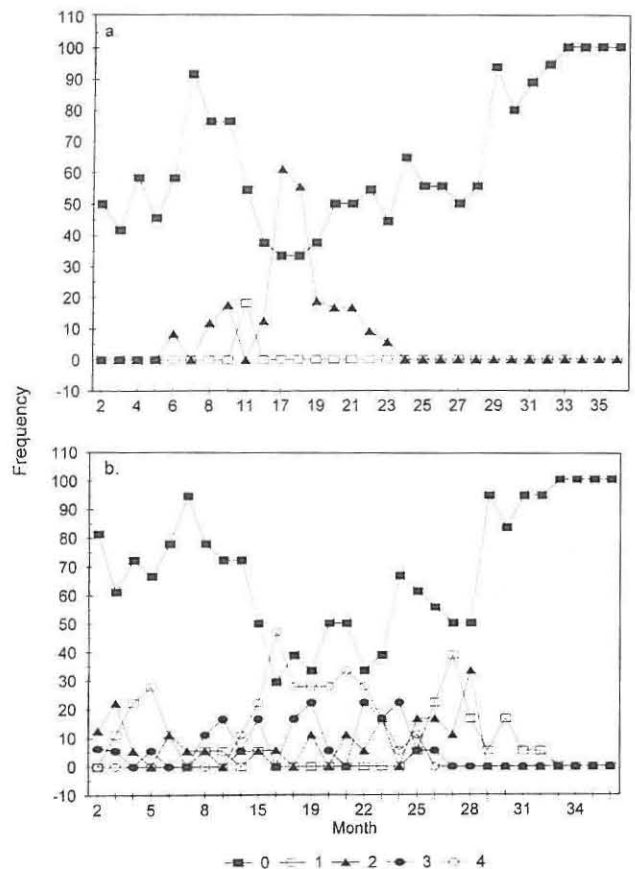


Figure 4: Fruiting of *P. falcatus* at Hlabeni (n = 20) where a. is stage (0 = zero fruit, 1 = setting, 2 = unripe, 3 = ripe, 4 = moribund) and b. is fruit quantity (ranked; 0 = none, 1 = 1–10, 2 = 11–100, 3 = 101–1 000, 4 = 1 001–10 000, 5 = >10 000)

the climax community (Rycroft 1944, Moll and Woods 1971). Their fruit are the preferred food of the endangered Cape Parrot (Wirminghaus *et al.* in press). In the forests of the southern Cape, *Podocarpus falcatus* and *P. latifolius* are widespread and at high densities (Geldenhuys 1993). The former has a low recruitment rate, producing a heavy fruit with a fleshy epimatium enclosing the seed, protective tissue (sclerotesta), and little endosperm reserves (Geldenhuys 1993). The latter have a high recruitment rate, producing a light fruit composed predominantly of a fleshy receptacle, no woody sclerotesta, and ample reserve food for the embryo (Geldenhuys 1993). Furthermore *P. falcatus* is a 1-year life cycle type of *Podocarpus* spp. with ripe seeds shed 12–13 months after pollination (Osborn 1960) resulting in long periods of fruit availability, but not showing seasonal trends.

Miconia centrodesma growing in Costa Rican lowland forest gaps also has long fruiting episodes, and produces large fruit crops that supply resident frugivores with fruits during periods of general fruit scarcity (Levey 1990). Similarly, *Podocarpus* spp. in afromontane forests have extended fruiting episodes, produced large fruit crops and fruit more frequently, providing food for Cape Parrots for much of the year.

Differences in availability of ripe and unripe fruit were not

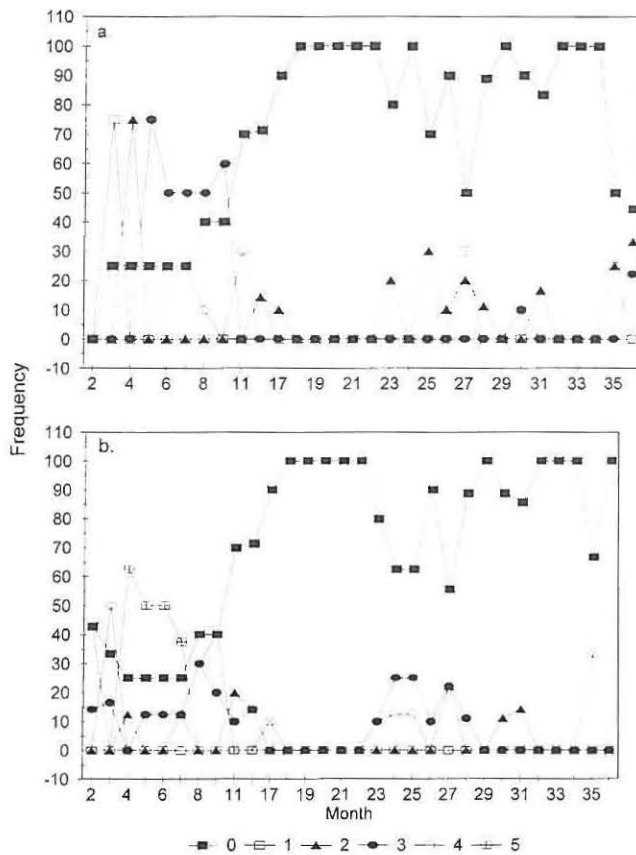


Figure 5: Fruiting of *P. latifolius* at Hlabeni ($n = 10$) where a. is stage (0 = zero fruit, 1 = setting, 2 = unripe, 3 = ripe, 4 = moribund) and b. is fruit quantity (ranked; 0 = none, 1 = 1–10, 2 = 11–100, 3 = 101–1 000, 4 = 1 001–10 000, 5 = > 10 000)

analysed. Most birds prefer ripe fruits (Blake *et al.* 1990) but feed on unripe fruits, particularly when food is scarce (Foster 1977). However, unripe fruits are preferred by Cape Parrots as they usually select the kernels of fruits (Wirringhaus *et al.* in press).

Monthly and Seasonal variation in fruit-fall production

Quantification of fruit production was important in determining food availability for the Cape Parrot. Newstrom *et al.* (1994) found that tropical forest tree phenology differed from temperate phenology. In the former, the nature of the pattern changed temporally and patterns varied widely over the geographic range of a species than in temperate species (Newstrom *et al.* 1994). Similarly, total fruit production of each fruiting species differed temporally and spatially in the two temperate afro-montane forests of the present study. Furthermore, the forests differed in dominant fruiting species; however, for both afro-montane forests studied, spring was a period of fruit shortage.

In adjacent South African coastal forests, which are occasionally exploited by Cape Parrots when food resources fail elsewhere, fruiting occurs throughout the year with a distinct peak in fruit production occurring in the dry season and a low

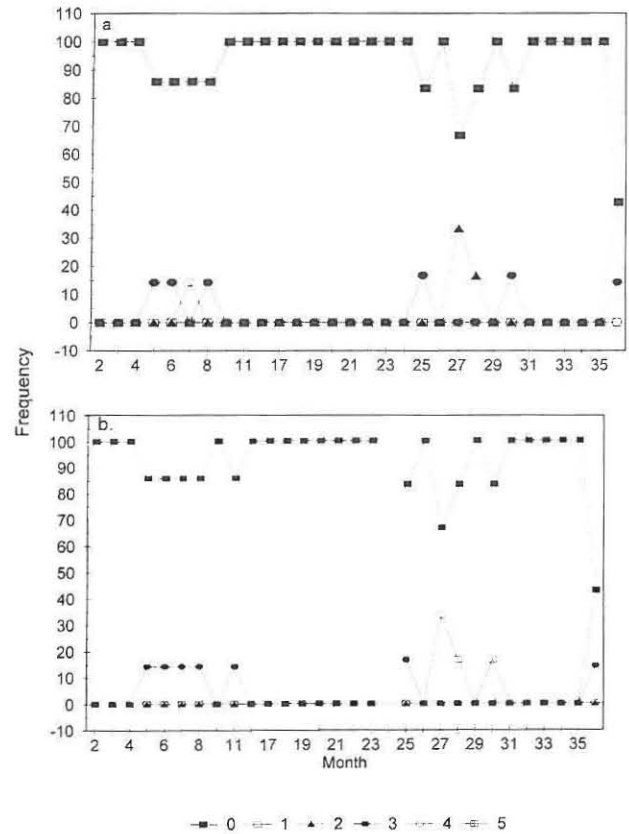


Figure 6: Fruiting of *P. henkelii* at Hlabeni ($n = 8$) where a. is stage (0 = zero fruit, 1 = setting, 2 = unripe, 3 = ripe, 4 = moribund) and b. is fruit quantity (ranked; 0 = none, 1 = 1–10, 2 = 11–100, 3 = 101–1 000, 4 = 1 001–10 000, 5 = > 10 000)

in the early wet season (Frost 1980, Lawes 1991). There is a temporal segregation in the fruiting season of different species (Frost 1980). Similarly, in a southern afro-montane forest (Knysna) total fruit production peaked during winter (June) although fruits were produced irregularly by some tree species, causing unpredictable fluctuations in food availability (Koen 1992). In the present study, some individual trees fruited prolifically at one season and not at all the following year. Furthermore, monthly fruit production studies of species of *P. latifolius* and *P. falcatus* has shown production of fruit in winter with peak densities varying annually (Koen 1992). Fruit of the latter species was rare and in some years none was produced (Koen 1992). Results of the present study were similar, with *P. latifolius* and *P. falcatus* fruit being produced in winter, with annual variation in peak densities.

Determination of supra-annual cycles of fruit production are difficult. In Gabon, three year rhythms were found in some species and there was much interannual variation in fruit crop size (Tutin and Fernandez 1993). Fruit-fall traps measure fruit fall and represent an indirect estimate of fruit presence but not an accurate estimate of fruit abundance (Blake *et al.* 1990, Chapman *et al.* 1994). How patterns of

fruit fall reflect patterns of absolute fruit abundance remain undetermined (Blake *et al.* 1990).

Tropical forests are considered to be stable, however, they show a degree of seasonality, dependant on rainfall not latitude (Boinski and Fowler 1989). Phenology of canopy trees of a tropical deciduous forest in Mexico showed annual reproduction for most populations, with sub-annual intervals correlated with rainfall anomalies (Bullock and Solis-Magallanes 1990). Many species responded to rainfall so their phenology appeared to be driven by water availability, although other species were probably limited by photoperiod (Bullock and Solis-Magallanes 1990). In temperate afro-montane forests it was expected that rainfall would affect fruit production, but no direct correlation was found. Photoperiod appears to affect deciduous species which are more seasonal in fruit production than other canopy fruiting species. Tutin and Fernandez (1993) found that minimum temperature during the dry season also influences fruit crop production.

Food availability

Food availability is the basis of several hypothesis formulated to explain various biological patterns in several studies (Hutto 1990) including timing of annual cycles, diet, mating system, clutch size, reproductive success, population size, and geographic distribution. In South America, predictable fruit production of several palm nut and *Ficus* species are important to frugivorous vertebrates during periods of fruit scarcity (Terborgh 1986a). However, other studies have shown that *Ficus* species are not staple foods of vertebrate frugivores during periods of food shortage (Gautier-Hion and Michaloud 1989, Wirminghaus 1990, Lawes 1991).

In a Bornean lowland tropical rain forest, preferred fruit types were highly seasonal and varied in abundance annually (Leighton and Leighton 1983). Birds (including psittacine seed predators) with specialised diets of large-seeded fruits with lipid-rich flesh emigrated when food resources became scarce (Leighton and Leighton 1983). Local densities of the frugivore species varied directly with food abundance, but their ranging systems varied (huge, but fixed home ranges; local migration, nomadism) (Leighton and Leighton 1983). Intra-forest movement data for Cape Parrots has shown seasonal preferences for particular parts of the forests, and occasionally even certain trees (Wirminghaus *et al.* in press).

In Barro Colorado 38% of 164 resident bird species eat fruits (Willis 1980), while in Nigerian forests about 46% of canopy fleshy fruits are dispersed by 180 species of vertebrates (Jones 1955, 1956). Frugivores are important for the dispersal of the fruits and seeds of many tree species found in tropical rainforest, and a large proportion of vertebrates found there are frugivorous (Frankie *et al.* 1974, Terborgh 1980, 1986a, b, Chapman *et al.* 1994). By comparison, southern African afro-montane forests have only a few species of resident frugivorous mammals and these are unimportant in fruit dispersal (Wirminghaus 1990). Similarly, numbers and species of resident avian frugivores are low compared with forests in the tropics and only a few of these species are important in fruit dispersal. This may reflect the

unpredictable food availability of these forests, but further studies of fruiting availability and population numbers of frugivores in southern African forests are required. During periods of low fruit production, spring, *Kiggelaria africana* and *Ptaeroxylon obliquum* were available. However, these are not keystone species as they are not a food source for avian frugivores, including Cape Parrots.

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