CHAPTER 11.

DIET, KEYSTONE RESOURCES AND ALTITUDINAL MOVEMENT OF DWARF CASSOWARIES IN RELATION TO FRUITING PHENOLOGY IN A PAPUA NEW GUINEAN RAINFOREST

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Abstract
I recorded plant community phenology for three years, classified each fruiting species according to pattern (continually, annually, biennially or one-year fruiting) and documented what cassowaries consumed versus this fruit availability through dung analyses. Dwarf cassowaries are 25 kg ratites whose diet consists of over 91% fruit year-round. Although the study site had aseasonal rainfall, it experienced an annual fruit lean season. During peak fruit periods cassowaries preferred predictable, synchronously fruiting annual and biennial species over continually fruiting species. However, during the lean season they had to rely on continually fruiting species, as they were almost the only fruits available over a 3-4 month period each year at the site. Cassowary diet is much more diverse than that of other specialized frugivores, perhaps because they are non-volant and can consume large quantities of fruit without the ballast limitations experienced by volant frugivores. Fruit availability and cassowary signs at three different altitudes over a 5-month period suggested that some individuals move altitudinally to follow fruit availability. I suggest that these are the females and that males remain to incubate eggs (the lean season is also the incubation season) and live mostly off their fat reserves.

Key words: *Casuarius bennetti*, cassowary, diet, phenology, specialist frugivore

INTRODUCTION

Cassowaries, the largest known specialist frugivores, are flightless ratites. There are three species in the family Casuariidae. *Casuarius casuarius*, the southern cassowary, is found in the remnant rainforests of Australia and in New Guinea; *Casuarius unappendiculatus*, the northern cassowary, is found only in New Guinea; and *Casuarius bennetti,* the dwarf cassowary, also occurs only in New Guinea. The northern and southern cassowaries weigh 50 kg and live from sea level to 500 m

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a.s.l.; the dwarf cassowary weighs 25 kg and lives from 500-3300 m a.s.l. (Beehler, Pratt, & Zimmerman, 1986).

Cassowaries are particularly important to New Guinea's flora because they are probably the only non-human vertebrate large enough to disperse the many large-seeded plant species found on the island. Possible exceptions are Blyth's hornbill, *Rhyticeros plicatus*, and two species of flying fox, *Pteropus neohibernicus* and *Dobsonia moluccensis*. However, the first two species are only found below 1000 m and the dwarf cassowary's range extends to 3300 m (Beehler et al., 1986; Flannery, 1995).

Diet can be studied through direct observation (e.g., Robinson, 1986; Sun & Moermond, 1997), indirect observation (e.g., Oloo, Brett, & Young, 1994), stomach contents (e.g., Poulin, Lefebvre, & McNeil, 1994), stable isotope analysis (e.g., Fleming, Nunez, & Sternberg, 1993), or dung (fecal) contents (e.g., Fleming, 1988). In Australia habituation of southern cassowaries is possible, thus direct observations are possible (e.g., Bentrupperbaumer, 1997); however, in New Guinea cassowaries are widely hunted and thus are extremely shy and difficult to observe. In New Guinea dung analysis is the best method for determining cassowary diet because their droppings are conspicuous, persist for weeks without decay and are unmistakable for any other animal dropping in New Guinea (Mack, 1995). Cassowaries have remarkably gentle gut treatment and most items come through reasonably intact (Crome, 1975a; Stocker & Irvine, 1983; Pratt, 1983). Some fruits do not even lose their pulp (personal observation).

The diet of the southern cassowary has been studied in Australia (Crome, 1975a; Stocker & Irvine, 1983). However, in New Guinea only one relatively small study on the dwarf cassowary has been published (Pratt, 1983). Pratt examined 43 droppings that contained the seeds of 36 fruit species.

The diet of most frugivores is half fruit and half a protein-rich food such as insects (Foster, 1978). Very few animals have diets with over 90% fruit, although this is the usual definition of a specialist (or virtually obligate) frugivore (McKey, 1975; Wheelwright & Orians, 1982; Bell, 1983). Specialist avian frugivores feed their young fruit without supplementing the diet with insects, as do most other birds (Morton, 1973). They typically have a narrower diet than other frugivores, because they specialize on nutrient-rich fruits of families such as Lauraceae and Arecaceae (Snow, 1962; Wheelwright, 1983). The few examples of specialized avian frugivores include oilbirds (Snow, 1962), bearded bellbirds (Snow, 1970) and cassowaries (Crome, 1975a; Stocker & Irvine, 1983; Pratt, 1983). I wanted to find out what percentage of cassowary diet is fruit and if this varies seasonally.

Temporal patterns of fruit availability affect a frugivore's foraging efficiency. This factor is usually overlooked in frugivore studies, though it is a prominent component of nectarivore studies (Caraco, 1980; Real, 1981; Feinsinger, 1987). If the fruits in the diet are temporally and spatially predictable (e.g., they are pulsed annually or biennially, appearing during predictable months on predictable individual plants), an animal can potentially remember this information and can visit plants when they come into fruit without undirected or random searching. If fruit availability is unpredictable (e.g., asynchronously on different individuals), then a frugivore must return to individual plants to see if they have ripe fruits, which may waste foraging time. If the above is true, one could predict that frugivores should prefer predictable annually or biennially fruiting species over unpredictable but continually fruiting species (continual fruiting as a species, but unpredictable at the individual plant level). I wanted to see if cassowaries preferred predictable species over unpredictable species.

Tropical forests typically have peaks and lows of fruits available for frugivore consumption (Terborgh, 1986; Foster, 1982). Even in aseasonal rain forests where temperature and rainfall are fairly constant, fruit supplies are not constant and frugivores face lean times (Leighton & Leighton, 1983). To get through these periods frugivores can 1) expand their home ranges to find more fruiting plants or decrease their range to save energy (van Schaik, Terborgh, & Wright, 1993; Peres, 1994a), 2) emigrate to other areas that have a different phenological schedule (Wheelwright, 1983; Debussche & Isenmann, 1992; Loiselle & Blake, 1991; Loiselle & Blake, 1993), 3) switch to other food items during the fruit scarcity (Garber, 1993; Kaplin, Munyaligoga, & Moermond, 1998; Sun & Moermond, 1997), or 4) live on fat stores (Churchill, 1994). During lean times frugivores generally consume fewer fruit species than in plentiful times because fewer are available (Robinson, 1986; Sun & Moermond, 1997; but see Pyke, Pulliam, & Charnov, 1977); at one site in Peru as few as 12 plant species sustain 80% of the frugivore biomass during the lean season (Terborgh, 1986). I wanted to learn if aseasonal rainforests in Papua New Guinea (PNG) undergo an annual lean season, and if so, what strategies cassowaries use to get through these periods.

To summarize, in this study, I examined plant phenology patterns at Crater Mountain in Papua New Guinea to see if there was a fruit lean season. I examined cassowary droppings over the same three-year period to determine the extent of their dietary specialization on fruits and whether they preferred synchronous, annually or biennially available species over asynchronous, continual ones. I censused droppings and examined dropping content diversity over time in order to assess the birds' response to lean seasons. I learned which plant species sustained cassowaries during the lean season, if cassowaries switched to alternative food items when fruits were not plentiful and/or if they migrated altitudinally in response to fruit availability.

METHODS

Study Site

This study was conducted at the Crater Mountain Biological Research Station (known locally as Wara Sera) within the Crater Mountain Wildlife Management Area (WMA) of Papua New Guinea (6° 43' S, 145° 05' E). The station is 15 km east of Haia, a small village with a landing strip, in Simbu Province. The 400 ha study area ranges in elevation from 850-1350 m a.s.l. and has steep topography. Annual rainfall averages 6.7 m with no predictable wet or dry season (Wright, 1998). Vegetation is very diverse with 228 species > 10 cm DBH on a 1 ha plot (Wright, Jessen, Burke, & Garza, 1997). The surrounding area has a low human population density of about 3,600 people in the 2,700 km^2 Wildlife Management Area (Johnson, 1997). No people live within a one-hour hike of the study area and no hunting or vegetation clearing is permitted within this uninhabited area by agreement of the local people. The site is above the range of other species of cassowaries so that all droppings found can be unambiguously attributed to the dwarf cassowary.

Fruits

Plots-- From June through September, 1990 I delineated 40 plots measuring 50 x 10 m. Plots were randomly placed and oriented within each 200 m section of the trail system throughout the study area. All plots began 5 to 10 m off the trail. Plots were not placed on slopes greater than 75°. In February and March, 1991 I extended all plots to 50 x 20 m and added two more for a total of 4.2 ha.

Timing of Plot Visits-- I visited each plot 7 to 10 times (average 8.5 times) between June, 1990 and March, 1993, or roughly every 4 months (average 1 ha searched per month). Although some individuals could have fruited or flowered during the times I did not visit them, I thought it was more important to have a large sample area to estimate relative species abundance and overall phenology rather than to track a smaller number of individual plants. This timing allowed me to find most if not all of the reproductive events for each plant (either flowers or fruits in some stage). Generally, in tropical rainforests fruiting cycles (presence of ripe fruits) can last from 10 days to 7 months (van Roosmalen, 1985). Although ripe fruit presence can be an ephemeral stage, fruits usually take 3 or more months to develop after the plant flowers (e.g., Lucas & Corlett, 1991; Peres, 1994a). Therefore, by recording the presence of flowers and ripe, unripe, and old (rotten) fruit, I was likely to find all reproductive periods (either beginning, middle, or end) for each plant by examining them once every 4 months. To increase sample size for rare tree species (< 1 individual per ha), I also recorded phenology for individuals of these species found fruiting or flowering along 8.5 km of trails.

Data Collection-- During each plot visit, I thoroughly searched for any signs of plant reproductive activity, using binoculars for the canopy. I put a unique tag number on all angiosperms (herbs, shrubs, vines, trees, epiphytes) that had fruits or flowers within the interior 50 x 10 m strip of the plot (50 x 5 m strip before the plots were extended in early 1991). On the portions of each plot outside this interior strip, I excluded herbs and shrubs (assuming they were more numerous and so should require a smaller sample area). For each plant I recorded its position on the plot, its estimated height, and its DBH at 1.5 m (or above buttresses) if the plant was that tall. If a plant was on the border of the plot, I included it if it was rooted in the plot or, for lianas, if most of the plant was within the plot. I collected a voucher sample for all species and described and illustrated all species in a catalog. Vouchers are deposited at the Forestry Research Institute, Lae, PNG, the University of PNG, Port Moresby, PNG, and the Harvard University Herbarium, Cambridge, USA. During each plot visit, for each marked plant, I counted the number of ripe, unripe, and old fruits on the ground and up to 1.5 m on the plant and ripe, unripe and old fruits above 1.5 m on the plant. Fruits below 1.5 m are accessible to cassowaries. If a canopy crop contained over 100 fruits, I extrapolated using crop subset counts. I also recorded whether or not each plant was producing flowers or buds.

Phenology Classifications-- For species with over five marked individuals (the minimum suggested number for documenting phenology patterns, Frankie et al., 1974), and with observations for at least 11 of the 12 annual months, I classified population phenology pattern according to regularity (sensu Newstrom, Frankie, & Baker, 1994) as: Continual if fruiting or flowering did not have a gap of 4 consecutive months. Annual if there were at least four consecutive months with: 1) no ripe or old fruits, 2) no unripe fruits if fruit diameter was under 15 mm (see below), and 3) no flowers or buds. Biennial if it was like an annual species (fruits available from one to eight contiguous months per year) but fruits were only produced every other year. One-year if it was like an annual species but with fruits produced in only one of the three years of the study. The reason for including unripe fruits for small-fruited plant species (< 15 mm when ripe) and not for large ones in this classification is that unripe small fruits are more likely to ripen in the same month than are unripe fruits of large-fruited species. When measuring fruit diameters for analyses in this section, I measured the entire aggregate for aroids and pipers and the syconium for figs because the entire aggregate/syconium has to mature before the individual fruits can ripen (Wright, 1998). If any individual of a species had any fruits or flowers during a particular month, the species was counted as fruiting or flowering that month for this classification (i.e., these phenology patterns reflect absolute periods, not peak periods).

Analyses-- I calculated the proportion of observed individuals of all species that had ripe fruits for each month of the study. Months with very small sample sizes of observed plants (fewer than 100 plants observed that had been reproductively active at some time during the study) were not included in analyses. Furthermore, if outliers in an analysis had fewer than 200 individuals observed that month (again, reproductively active at some time during the study), then I excluded those outliers from the analysis. I used ANOVAs (with arcsine square-root transformations for proportions) to look for variation by month in ripe fruits. I did the same type of analysis for the proportion of observed species, genera, and families.

I calculated the proportion of plants per species with ripe fruit per month and used a Kolmogorov-Smirnov test to see if annual and biennial species had more predictable fruiting than continual species. I used a Mann-Whitney U test to see if species with continuous fruiting patterns had smaller fruits than those with annual or multi-annual patterns. I used a Chi-square test to see if phenology pattern (continual, annual, or multi-annual) varied with plant form (liana, epiphyte, shrub defined as < 3 m tall, midstory defined as 3-10 m tall, or overstory defined as > 10 m tall). All analyses were done using Systat 7.01 (SPSS, Inc.), Excel 6.0, or according to Sokal and Rohlf (1981).

Cassowaries

Dung Collections-- Dwarf cassowary droppings were collected throughout the study area both on and off trails from May 1990 to May 1993. I quantified the area searched off trails separately from the area searched on trails as the former gives a more unbiased dropping density estimate (Westcott, 1999). Droppings were from at least 2-5 adult-sized birds partially resident in the study area at most times (estimate based on footprints, sleeping areas with fresh droppings, tracking individual birds, and cassowary vocalizations; number varied with time of year). Individual sample size is unavoidably low due to the large home ranges of these ratites, and because the entire study had to be conducted on foot in rough terrain.

I only quantified contents from droppings that were less than one month old to minimize any effects of seed removal by granivores. Studies of *in situ* droppings indicate that seed predators at this site remove very few seeds from cassowary droppings, and instead consume portions of each seed in place, allowing accurate quantifications (A. Mack, personal communication). Estimated dropping age was based on regular observations of the deterioration of known-age droppings. Droppings were recorded for the month in which they were deposited, not the month in which they were found.

Determination of Dung Contents-- Most droppings (68%) were bagged, taken to the research station and then washed individually through a 1 mm screen to detect all contents. Others were left *in situ* as part of concurrent seed dispersal and seedling studies (Mack, 1995, 1998; Mack, Ickes, Jessen, Kennedy, & Sinclair, 1999), but were carefully examined to determine contents (these were minimally disturbed to avoid affecting seedling establishment).

Vouchers of all seed species found in droppings were preserved in 70% ethanol. Fruits and seeds of all angiosperms found in the forest were preserved in 70% ethanol and catalogued in a reference collection of 763 species (Wright, 1998). Seeds in droppings were identified by comparison with this reference collection. I also collected extensive data on fruit morphology for the roughly 400 species that produced fleshy fruits (fruit dimensions, average number of seeds per fruit, etc., Wright, 1998; Mack and Wright, this volume). I used fruit number, not seed number, for all analyses. Fruit number was estimated by dividing the number of seeds of a species found in a dropping by the average number of seeds per fruit for that species; fractions of fruits were rounded up to the nearest whole fruit.

Calculation of Meal Mass-- From the data collected on fresh fruit morphology (Wright, 1998), it was possible to calculate "meal mass" based on the seed content of droppings. Meal mass is defined as the pulp mass from fresh fruits that was consumed to make up each dropping (corrected for seed number per species as above) plus the calculated fresh mass of non-fruit items (fungi, vegetation, etc.) found in that dropping. In other words, meal mass is the mass of fresh food (without the indigestible seed mass) that was consumed to make up a single dropping.

Analyses-- For each analysis I first compared data from collected droppings to *in situ* droppings to see if there was a difference for the factor being investigated. If there was not, then the combined data set was used to increase sample size and to reduce error due to small sample size. If there was a difference for the factor being tested, I checked to see if there was a bias against small or infrequently encountered items (e.g., those that may have been underestimated in *in situ* droppings). Where no bias was found, the data were combined. If a bias was detected, only collected/washed droppings were used.

I used one-way ANOVAs with Tukeys post-hoc tests to test for monthly and yearly differences. All proportional (ratio) data were arcsine square-root transformed. Two-group mean and category distribution differences were tested with Mann-Whitney U and Chi-square tests. For paired directional differences, I used Wilcoxon Signed Rank tests.

Lean Season

Elevational Study-- To see if there was evidence that cassowaries migrate to follow fruit availability, I established two camps (one at 550 m and one at 1450 m elevation) in addition to the main study site at 900 m elevation within the Crater Mountain WMA. The main study area was hill rainforest to lower montane rainforest. The 550 m site ranged from riverine rainforest to hill rainforest and was 10 km southwest of the main study area. The 1450 m site was in lower montane rainforest 6 km north of the main study area. All sites were relatively undisturbed (containing a few old gardens or tree-felling sites).

At each of the three sites I choose random compass bearings in each of three 60 degree arcs set to avoid major topographic features (cliffs, large rivers). I then searched 20 m wide by 600 m long transects along these bearings beginning 50 m from the inception point of the arcs, recording all fruits and fungi found < 1.5 m above ground (within the reach of a dwarf cassowary). I also recorded all cassowary signs (footprints, droppings, nests or sleeping areas) seen on the same 3.6 ha of transects per site.

Transects were searched in 1993 on the following dates: 1450 m: 27-29 January, 16-18 March, 5-7 May; 900 m: 2-9 February, 31 March-2 April, 18-27 May; 550 m: 13-15 February, 23-25 March, 11-12 May. I used a Spearman test to see if there was a positive correlation between fresh cassowary signs (droppings less than one month old, footprints and sightings) on the transects and the number of plants with ripe cassowary fruits at each of the sites during each time period on the transects.

RESULTS

Fruits

Sample Size—Although different transects and numbers of transects were examined each month of the study, I attempted to evenly distribute elevational representation in all monthly samples. I searched an average of 11.7 transects (1.17 ha) per month for each of the 30 months sampled (range 1-32, SD = 6.8). The following sample sizes apply for all of the phenological data presented below. Of the over 7000 marked plants that were reproductive during the study period, I examined from 132 to 3159 individuals in each of 30 months (mean = 1572, SD = 906) and from 59 to 412 species (mean = 256, SD = 102). I examined from 41 to 199 genera in each of 30 months (mean = 132, SD = 44) and from 25 to 78 families (mean = 60, SD = 13). Because I was testing for annual patterns I used the monthly values from different years as the dependent variable in ANOVA analyses. October, 1992 had a small sample size of observed plants and was eliminated from analyses.

Monthly fruit availability-- The proportion of observed individuals with ripe fruit varied by month (ANOVA, F11,17 = 3.76, P = 0.007; Figure 1). June had a significantly greater proportion of plants with ripe fruits than March or December (Tukey's P = 0.007, P = 0.018, respectively). The proportion of observed species with ripe fruit also varied by month (ANOVA, F11,18 = 2.71, P = 0.03). June had a significantly greater proportion of species with ripe fruits than December (Tukey's P = 0.045). Neither the proportions of observed genera or families with ripe fruits differed by month (Genera: ripe: F11,18 = 1.95, P = 0.10; Families: ripe: F11,18 = 1.21, P = 0.35).

Phenology Patterns-- Of 178 species with recorded phenology patterns, Crater Mountain had at least 8 biennial and 1 supra-biennial fruiting species (5% of the community, 12% of overstory tree species). All but one (Elaeocarpaceae) fruited together in even-numbered years (two Clusiaceae and one each in Anacardiaceae, Gnetaceae, Lauraceae, Meliaceae, Arecaceae, and Rosaceae). A few individuals of these species produced small crops during off years; however, these crops were insubstantial (less than 10% of main-year crops).

Species with continual fruiting patterns had smaller fruits than species with annual or biennial fruiting patterns (Mann Whitney U = 2094, n1 = 107 species, n2 = 58 species, P = 0.001). Phenology patterns varied with plant form ($\chi^2 = 41.3$, df = 4, $P < 0.001$, n = 165 species). Although lianas and epiphytes had roughly equal numbers of continual and annual fruiting species, shrubs and midstory trees had more continual than annual species. Conversely, overstory trees had more annually than continually fruiting species.

A greater proportion of individuals of species with annual and biennial phenology patterns had ripe fruit at the same time than individuals of species with continuous fruiting patterns (K-S = 0.34, n = 50 annual and biennial species and 121 continual species, $P < 0.001$). Individuals of annual and biennial species had ripe fruits more predictably than individuals of continual species.

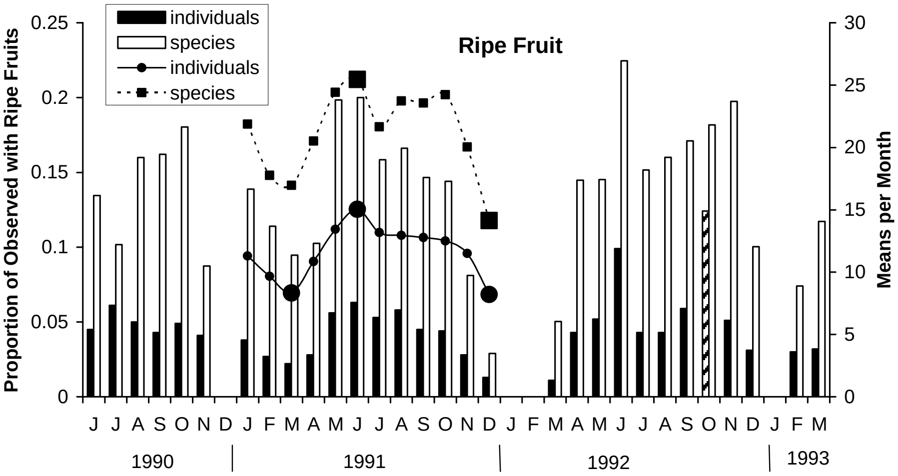

Figure 1. The proportion of observed individuals and species per month that had ripe fruit (bars) along with the means for each month for the three year period (lines) expressed as the arcsine-transformations of the proportions; i.e., the values used in ANOVA analyses. The large squares and circles represent months with significant differences. The striped bar (October 1992) represents a small sample of under 150 individuals that was an outlier in the analysis and so was excluded. December 1990, January and February 1992 and January 1993 were not sampled.

Lean Season-- An annual lean fruit season from December through March is evident not only in the numbers of species fruiting, but also in the amounts of ripe fruit and pulp mass available to consumers (Figure 2). Years of biennial masting (1990 and 1992) are also evident by the greater fruit mass produced. Annual and biennial species fruited almost entirely during the peak fruiting season so that continuous fruiting species were almost all that was available during the lean season (Figure 3).

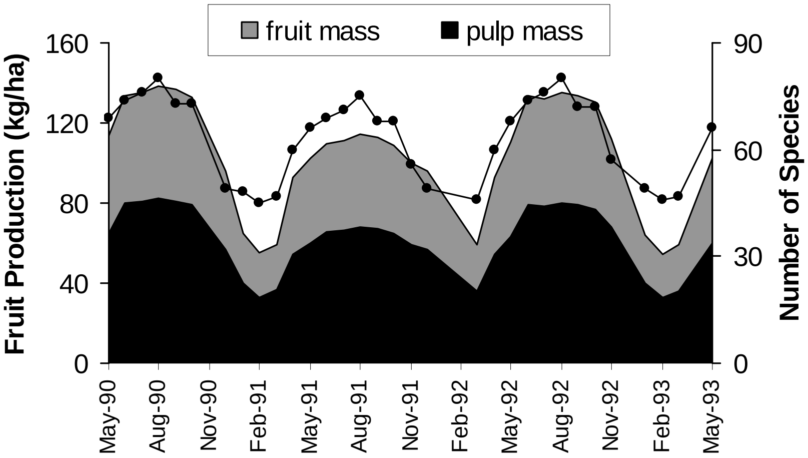

Figure 2. The minimum available fruit mass (seeds included) and pulp mass (seeds excluded) produced per ha per month of the study and the number of species (line with dots) from which these fruits came. Areas are not stacked; they are overlapping, thus the gray area represents seed mass. Not included are: species with seeds < 1 mm in diameter, with densities less than 1 per ha, with all fruits inaccessible to terrestrial frugivores (held above 1.5 m until rotted) and with non-fleshy fruits. The annual crop for each species was evenly divided among all possible months of its fruiting season so that each fruit produced was counted in only one month. This even distribution tends to level out peaks and troughs, thus the observed peaks and troughs are conservative representations.

Cassowaries

Sample Size and Dropping Age-- I analyzed a total of 855 droppings; of these 583 (68%) were collected and sieved and 272 were left *in situ.* Average dropping age was 7.4 days for all droppings (range 0-30 days, SD = 7.1 days) and 6.5 days (range 1-30 days, SD = 6.2 days) for collected droppings.

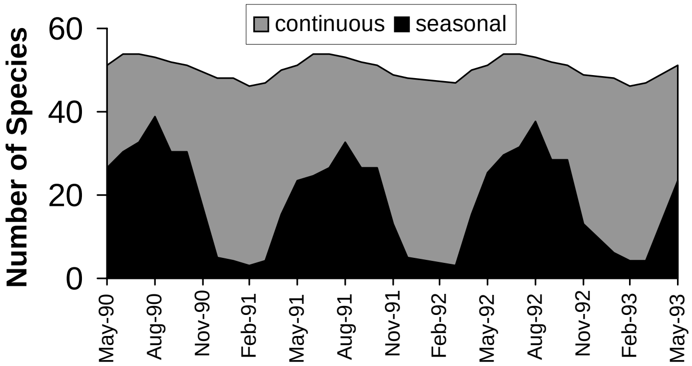

Figure 3. The number of species that have continuous fruiting versus the number that have seasonal fruiting (annual, biennial or one-year) for each month of the study. Areas are not stacked; they are overlapping. Not included are: species with seeds < 1 mm in diameter, with densities less than 1 per ha, with all fruits inaccessible to terrestrial frugivores (held above 1.5 m until rotted) or with non-fleshy fruits.

Diet Diversity-- Dung content types refer to different fruit species or to categories of non-fruit items that cassowaries consumed (e.g., beetles, snails, etc.). Remains of 192 fruit species plus mammals, birds, snakes, snails, crabs, beetles, fig wasps, maggots, parasitic worms, fungi, ferns, 1 cm diameter fibrous green stems, bark, branches, sago fibers, flowers and rocks were found in droppings (see Wright, 1998 for further detail).

Non-fruit components accounted for between 0% and 9% of total meal mass each month (Figure 4). Fungi and vertebrates were the most important non-fruit items taken (by mass) and they were taken throughout the year. Rocks were ingested more often than non-fruit plant material or invertebrates. The proportion of non-fruit mass in the diet did not differ between months ($F(11,20) = 2.24$, $P = 0.06$) or years ($F(3,28) = 2.30$, $P = 0.1$; Figure 4). Of the 192 fruit species found in the cassowary diet, 57 (30%) had three or fewer occurrences in droppings over the three year period. Unripe fruits were taken year-round, but very rarely.

Plant Families in Cassowary Diet-- Fruits of 39 plant families were found in droppings; twelve of these families accounted for at least 15% of meal mass during some month of the study (Figure 5). I used combined dropping contents (collected and *in situ*) when calculating monthly family meal mass percentages, as there were no differences between collected and *in situ* average family meal mass data sets (Chi-square tests, $P > 0.1$). The only exceptions (July 1990 and June 1991) were due to large, common fruits, and not to small or rare fruits, as would be expected if it were a bias due to being left *in situ.*

Clusiaceae, Pandanaceae, and Moraceae were taken year-round during every year of the study (Figure 5). During the lean season Clusiaceae and Pandanaceae plus Arecaceae (palms) were consistently important and in 1993 Moraceae was also important. Combretaceae and to a lesser extent Anacardiaceae were taken from March or April through September of every year. They are important during the late lean season. Apocynaceae was consistently important from September through December, covering part of the early lean season.

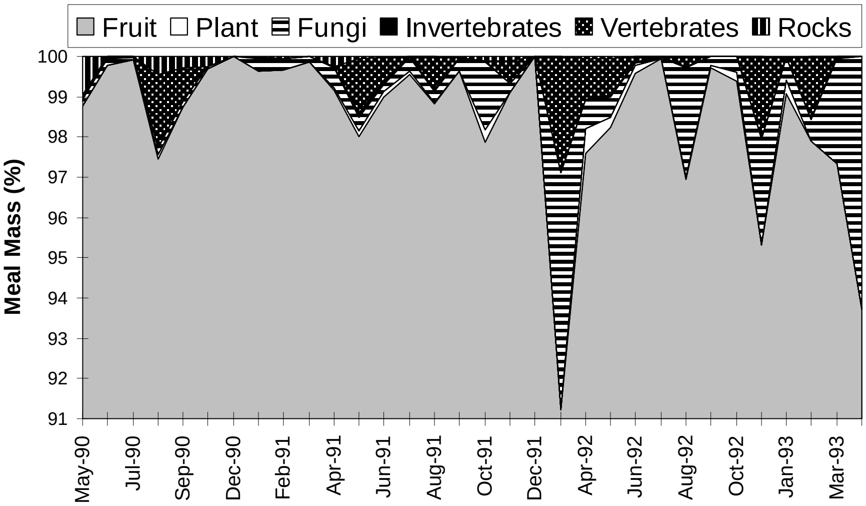

Figure 4. Cassowary diet over a three year period. Note that the Y axis begins at 91%; cassowary diet was at least 91% fruit year-round over the full three year period.

Consumption of Lauraceae, and to a lesser extent Meliaceae, peaked during the plentiful season (May through August) in 1990 and 1992, probably representing a regular biennial phenological cycle (Figure 5). Although some Lauraceae fruits were taken at other times (including the same time period in 1991), they were not a major component of the diet during those times. During the peak fruiting period of May through September in odd-numbered years the dietary mainstays were Clusiaceae, Pandanaceae, Moraceae, Combretaceae, Anacardiaceae and Myrtaceae (note the similarity to the lean season mainstays).

During the lean season patterns could not easily be identified. Different plant families were eaten in different amounts during different years, suggesting that fruit availability is more unpredictable during this time than during the rest of the year (Figure 5). For example, from January through March 1991 Clusiaceae was extremely important; in 1992 Combretaceae fruited early and it dominated the diet during this period; and in 1993 Moraceae was important. Lauraceae was important in the cassowary diet from May through September during even-numbered years, but not in odd-numbered years when a variety of other families, including the year-round fruiters, increased in prominence in the cassowary diet.

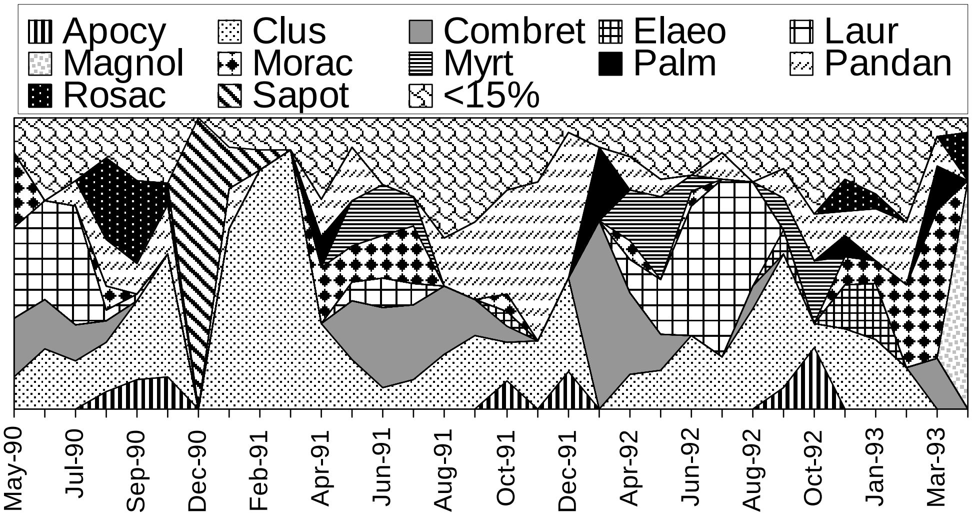

Figure 5. Proportions of each family that accounted for > 15% of the pulp mass ingested in at least one month of the study. Families that accounted for < 15% were pooled. Apocy = Apocynaceae, Clus = Clusiaceae, Combret = Combretaceae, Elaeo = Elaeocarpaceae, Laur = Lauraceae, Magnol = Magnoliaceae, Morac = Moraceae, Myrt = Myrtaceae, Palm = Arecaceae, Pandan = Pandanaceae, Rosac = Rosaceae, Sapot = Sapotaceae.

Plant Species in Cassowary Diet-- Over the entire study period fruits of ten species accounted for 55% of the total meal mass (fruit pulp and non-fruit item mass) of all droppings and 30 species accounted for 82% (Table 1). Although fungi are not among the 30 most important items by meal mass, fungi accounted for 16% of the items found in all droppings. Fungi plus nine fruit species accounted for 68% of the total items in droppings; fungi, vegetation, *Pandanus* flowers and 27 fruit species accounted for 87%. *Pandanus sp.* 5 and *Terminalia complanata* are notable for being in the top five species for both meal mass and overall frequency.

Each month the top 5 species accounted for 49-100% of the meal mass and of the frequency of items in droppings, although the same species did not always overlap in the lists of meal mass and frequency (see Wright, 1998). The biennial peaks of Lauraceae (Figure 5) were mainly caused by *Cryptocarya sp.* 2 although other Lauraceae species that fruited annually were also taken in larger quantities in even-numbered years. The extreme importance of Clusiaceae during the lean period of 1991 (Figure 5) was due to the continually fruiting *Garcinia latissima*, which was eaten during all periods of every year and which accounted for 17% of the meal mass of all droppings over the three-year study (Table 1).

Table 1. The top thirty items in the cassowary diet by meal mass (see methods for definition) and by number of items over the entire study period (sample size = 855 droppings from May 1990 through May 1993). Total percentage of top ten, twenty and thirty items is given at top of table.

Meal Mass	10 = 54.6% 20 = 72.5%	30 = 81.6%		**Number of Items**	10 = 67.5% 20 = 80.4%	30 = 87%	
Family	**Genus**	**species**	**%**	**Family**	**Genus**	**species**	**%**
Clus	*Garcinia*	*latissima*	17.2	Fungi	bracket fungi		15.7
Pandan	*Pandanus*	*penicillatum*	6.7	Pandan	*Pandanus*	sp. 5	12
Laur	*Cryptocarya*	sp. 2	5.6	Myrt	*Syzygium*	sp. 2	10.2
Pandan	*Pandanus*	sp. 5	5.4	Rosac	*Prunus*	*gazelle-peninsulae*	7.6
Combret	*Terminalia*	*complanata*	4.8	Combret	*Terminalia*	*complanata*	7.2
Apocyn	*Cerbera*	*floribunda*	3.4	Anacard	*Dracontomelon*	*dao*	3.6
Combret	*Terminalia*	*impediens*	3.1	Pandan	*Pandanus*	sp. 3	3.5
Laur	*Endiandra*	sp. 2	3.1	Magnol	*Elmerillia*	*tsiampacca*	3.1
Myrt	*Syzygium*	sp. 3	2.7	Laur	*Cryptocarya*	sp. 2	2.5
Rosac	*Prunus*	sp. 2	2.6	Arecac	?3		2.1
Anacard	*Dracontomelon*	*dao*	2.4	Rosac	?1		1.9
Clus	*Garcinia*	sp. 2	2.2	Arecac	?1		1.6
Clus	*Garcinia*	*celebica*	2.1	Elaeo	*Elaeocarpus*	sp. 2	1.4
Myrt	*Syzygium*	sp. 2	1.8	Morac	*Ficus*	1-2 cm figs	1.4
Laur	*Endiandra*	sp. 5	1.7	Elaeo	*Elaeocarpus*	*sphaericus*	1.3
Morac	*Ficus*	1-2 cm figs	1.7	Laur	*Endiandra*	sp. 5	1.3
Prot	*Helicia*	sp. 1	1.7	Combret	*Terminalia*	*impediens*	1.2
Clus	*Mammea*	*grandifolia*	1.6	Rosac	*Prunus*	sp. 2	1
Morac	*Ficus*	3 cm figs	1.4	Sapot	*Burckella*	sp. 1	1
Meliac	*Aglaia*	*mackiana*	1.3	Morac	*Ficus*	3 cm figs	0.8
Clus	*Garcinia*	cf. *assugu*	1.2	Clus	*Garcinia*	*latissima*	0.8
Sapot	*Burckella*	sp. 1	1	Vegetation	ferns, stems		0.8
Elaeo	*Elaeocarpus*	sp. 2	1	Morac	*Ficus*	*trachypison*	0.7
Rosac	*Prunus*	*gazelle-peninsulae*	1	Clus	*Garcinia*	cf. *assugu*	0.7
Pandan	*Pandanus*	*papuanus*	0.9	Rub	*Psychotria*	sp. 1	0.7

Morac	*Artocarpus*	sp. 1	0.9	Pandan	*Pandanus*	*penicillatum*	0.6
Clus	*Garcinia*	sp. 1 cf. *maluensis*	0.8	Clus	*Litsea*	sp. 1	0.6
Logan	*Neubergia*	*corynocarpa* ssp. 2	0.8	Pandan	*Pandanus*	flowers	0.6
Pandan	*Pandanus*	*limbatus*	0.8	?	catalog #	DW1146	0.6
Myrt	*Syzygium*	sp. 7	0.7	Cunon	*Schizomeria*	sp. 1	0.5

During each year's lean season eight fruit species (of five families) formed the core of the observed cassowary diet (they were available during each lean season) (Appendix 1). During the plentiful season, when fruits were most readily available, nine fruit species (of six families) were taken in appreciable quantities every year of the study and an additional six species were taken every even-numbered year (Appendix 1).

Eight droppings from cassowary chicks were found. These could be identified because they were much smaller than adult droppings, had only small items within them and often had juvenile footprints near them and larger droppings and prints from the parent were nearby. They contained seeds from 19 plant species (13 families) plus fungi; all of the items consumed were items also eaten by adults (Wright, 1998).

Seasonality of Fruits in Diet-- Of the 192 fruit species eaten, 39 species (20%) were annual. Eight species (4%) were biennial; 7 in 90/92 and 1 in 91/93. Forty-eight species (25%) were continual, and ninety-nine species (52%) were one-year only (see Wright, 1998).

One-way ANOVAs (with months as the categorical factor and meal mass proportions (arcsine transformed) for each year as the dependent variable) showed that annual fruits accounted for a larger proportion of the meal mass from April through October than from December through February ($F(11, 20) = 2.84$, $P = 0.02$, Tukey's $P < 0.05$ for May > February; Figure 6). Continual fruits made up a higher proportion of the diet from December through March than from April through October ($F(11, 20) = 3.44$, $P = 0.008$, Tukey's $P < 0.05$ for December > May, June, July; Figure 6).

Biennial fruits in 1990 and 1992 made up a larger proportion of the diet in June, July and August than from October through April ($F(9,6) = 4.27$, $P < 0.05$, but no Tukey's $P < 0.05$ due to the small sample size of 1 to 2 years sampled per month) and were virtually missing from 1991 and 1993 (Figure 6). The study ended in May 1993 and so biennially pulsed species for 1991 and 1993 may have been classed as one-year species in 1991 if they fruited after the end of the study in 1993. However, in 1991 one-year fruits were also in low abundance from June through December (Figure 6), so even if some of these were biennials, 1991-1993 biennials would still be rare (much rarer than 90-92 biennials). The proportion that one-year fruits contributed to meal mass varied by month (F(11,20) = 3.11, P = 0.01), but no discernable pattern was apparent (Tukey's P > 0.05).

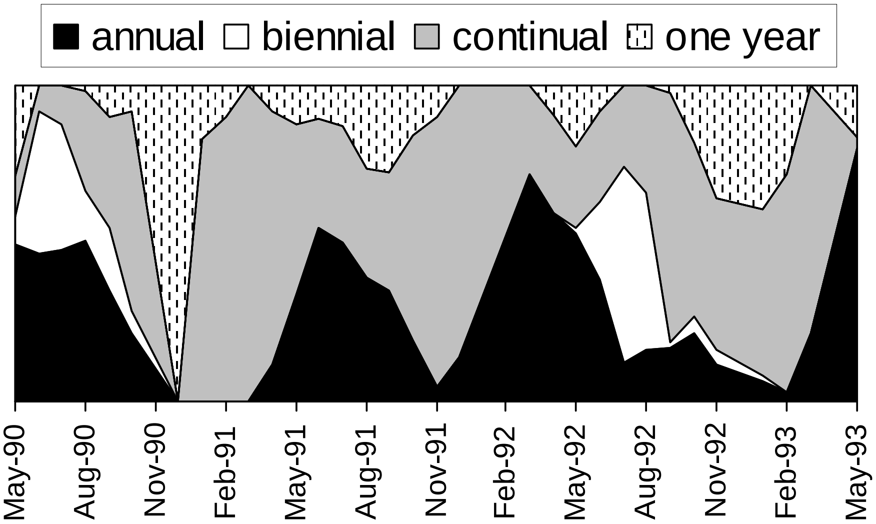

Figure 6. Proportions of annual, biennial, continual or one-year fruits that were included in the meal mass for each month of the study.

In summary, in December, January, and February 80-100 % of the meal mass for cassowaries consists of continual species that fruit year-round but unpredictably on individual plants. In March, April, and May the proportion of annual fruits increases, but continual fruits are still important (these two types make up over 90% of the meal mass). In June, July, and August during even-numbered years, biennial fruits become important (15-50% of meal mass), but annual and continual fruits are also still important; during odd-numbered years, annual and continual fruits are taken in roughly equal proportions (90% total, no biennials). During September, October, and November, the proportions of biennial and annual fruits begin to dwindle and the proportion of continual fruits increases.

These patterns may result because fruits of seasonal species (annual, biennial, and one-year) are more available from May through September than during the lean season (Wright, 1998). However, a greater proportion of seasonal species were eaten than were available in 29 months, and this was true in only 3 months for continually fruiting species (Sign test P < 0.05; Figure 7). Cassowaries take more seasonally fruiting species than expected by availability alone, but are unable to do this during the lean season when continually fruiting species are almost all that is available.

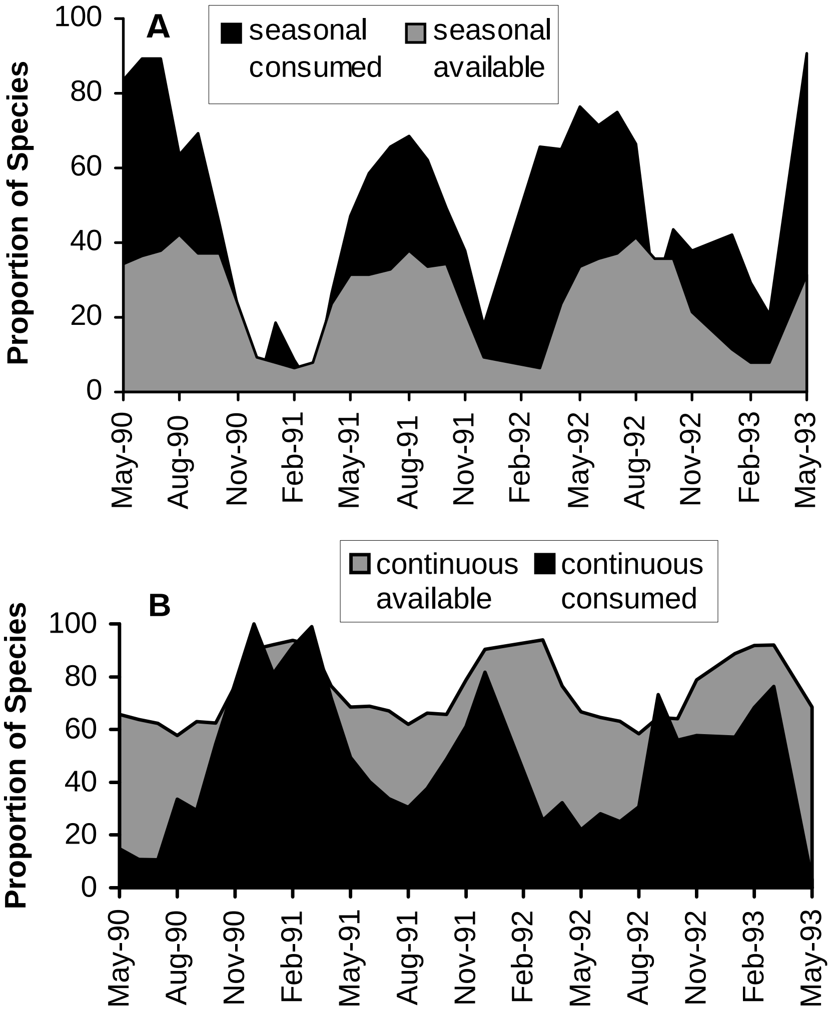

Figure 7. The proportion of species that were seasonal fruiters (annual, biennial or one-year) (in graph A) and continual fruiters (in graph B), and the proportion of these species types that were consumed by cassowaries. The gray areas of the two graphs (available species) add up to 100% and the black areas of the two graphs (consumed species) add up to 100%. A greater proportion of seasonal species were eaten than were found on the transects (available) and a lower proportion of continual species were eaten than were available throughout the study period.

Lean Season

Fewer Droppings-- Although the mass of droppings did not differ through time (Wright, 1998), droppings were less abundant within the study area from October through April than during the rest of the year, coinciding with the fruit lean season. There were 40% fewer droppings per hectare from October to April than from May to September each year (Figure 8; one-way ANOVA looking for differences between months F = 6.33(11, 80), $P < 0.001$). August had more droppings per hectare than all months except for May, July, and September (Tukey's $P < 0.05$).

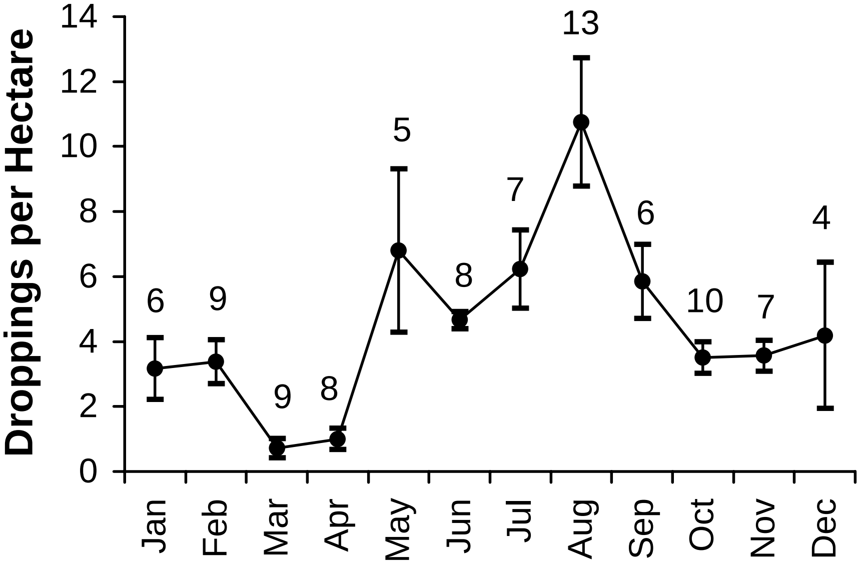

Figure 8. The mean and standard error of the number of droppings found per hectare searched off-trail during the study period. The number of hectares sampled per month is shown above each error bar. The graph combines data from all years.

Fewer Items per Dropping-- Collected droppings contained more content types (different fruit species or categories of non-fruit contents) per dropping than *in situ* droppings (n = 855, Mann Whitney U = 43923, $P < 0.001$); therefore, I used only collected droppings to determine the number of content types per dropping. The 583 collected droppings contained a total of 56,279 individual items (fruits and non-fruit items) which represented from 1 to 24 content types (fruit or non-fruit taxa) per dropping (mean = 6.2, SD = 3.2). Droppings collected in January contained fewer content types than those collected in April and September (5.1 versus 7.4 and 7.3), and March also had fewer content types than April, May, August, September, and

November (3.5 versus 7.4, 6.3, 6.5, 7.3 and 6.7; one-way ANOVA F(11, 571) = 3.64, $P < 0.001$, Tukey's $P < 0.05$). Overall, droppings collected in January through March, the fruit lean season, tended to have fewer content types than those collected in April through November, and with 30 droppings collected per month most content types were found (Figure 9).

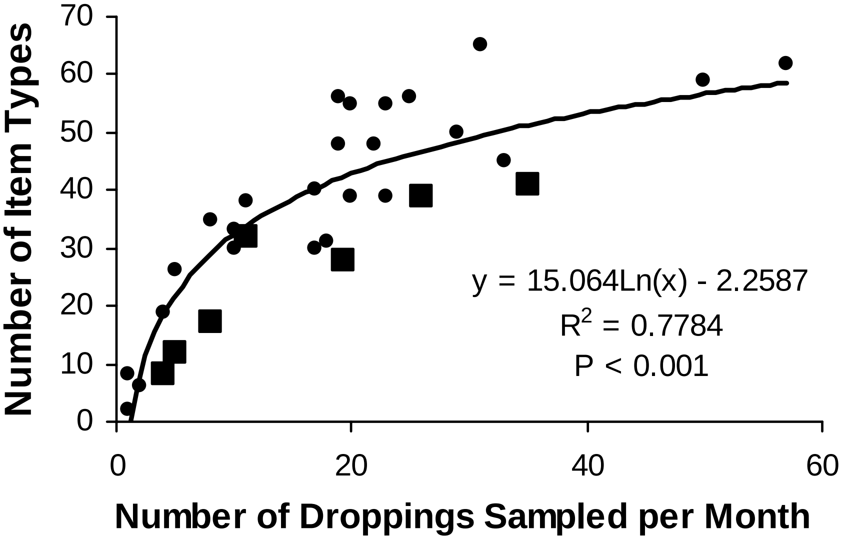

Figure 9. The number of item types (fruit and non-fruit) found in month-long samples of droppings as the number of droppings in those samples increase. The data fit a logarithmic curve. Square data points are from the main lean season (January through March).

Seasonal Altitude Shifts-- Over the three elevations and five months examined, the number of plants with ripe cassowary fruits on the transects was positively correlated with the number of cassowary signs observed on the transects (Spearman $r = 0.862$, $P = 0.001$, $n = 9$ pairs). Furthermore, there were fewer plants with ripe cassowary fruits and fewer cassowary signs at the study site (900 m) during Jan/Feb and March than in May, the beginning of the plentiful season (Figure 10).

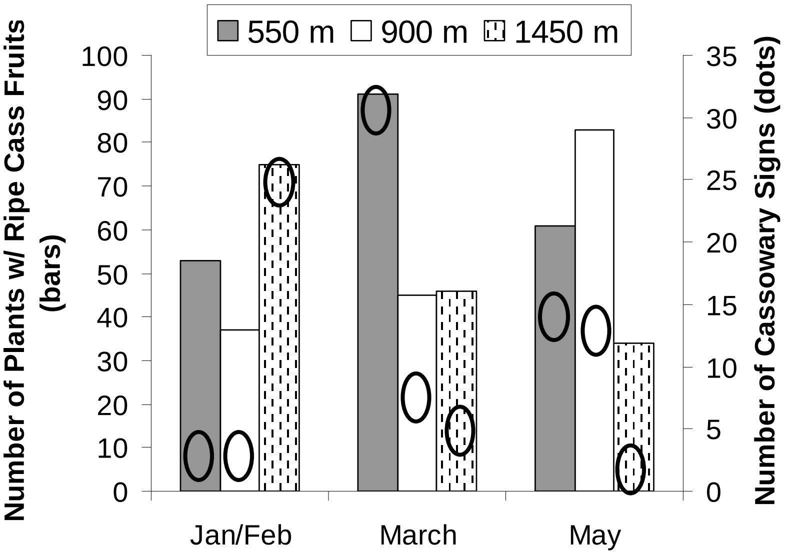

Figure 10. Cassowary fruit availability (includes only fruits cassowaries are likely to consume) versus cassowary signs (fresh droppings, tracks or actual sightings) on 3.6 ha transects over a 5 month period at three different elevations in 1993.

DISCUSSION

Cassowaries as Specialist Frugivores

Dwarf cassowary diet consisted of over 91% fruit pulp year-round over a three year period. During most months the figure was closer to 98%. Specialized frugivores are sometimes defined by what they feed their young. Using some definitions, quetzals would not be considered specialist frugivores even though the parents are obligate frugivores, because chicks are fed mostly insects, snails, and lizards with only 20-35% of their diet being fruit (Wheelwright, 1983). Oilbirds and bearded bellbirds would be considered specialist frugivores by all definitions because they feed their young strictly fruit (Bosque & Parra, 1992; Snow, 1962; Snow, 1970). Juvenile cassowaries appear to eat at least 90% fruit (based on dropping contents, Wright, 1998). Cassowaries are the largest known specialist frugivore in the world.

Many heavily frugivorous bird species rely on particular plant families that are rich in nutrients (e.g., Lauraceae, Arecaceae). Quetzals feed mostly on Lauraceae (greater than 80% of the fruit taken by frequency or mass) (Wheelwright, 1983); fruit pigeons eat 88% Lauraceae and Araliaceae fruits (Crome, 1975b; Frith, Crome, & Wolfe, 1976); Arecaceae, Lauraceae, and Burseraceae accounted for 99% of the diet of oilbirds in Trinidad over a four year period (Snow, 1962); and Lauraceae and Burseraceae accounted for 89% of the diet of bearded bellbirds (Snow, 1970).

Cassowaries have a more varied diet when compared to most specialized frugivores (Figure 11). Crome (1975a) found that double-wattled (southern) cassowaries in Australia also depend on Lauraceae fruits (20% of diet), but that Myrtaceae, Arecaceae, and Elaeocarpaceae are also important; these four families accounted for 70% of the diet over a 2.5 year period. At 1600 m a.s.l. in Papua New Guinea, Pratt (1983) found that dwarf cassowaries consume appreciable quantities of Himantandraceae, Clusiaceae, Rubiaceae, Cunoniaceae, Arecaceae, and Meliaceae in addition to Lauraceae. In my cassowary study population, Lauraceae was very important in even-numbered years during periods of peak fruit abundance, but during other times it was not important in the cassowary diet. It took seven plant families to account for only 50% of the fruits consumed by dwarf cassowaries in the present study.

Most other specialized frugivores are relatively small-bodied and volant. Cassowaries are large-bodied and non-volant. Fat storage is not a problem for cassowaries and so they can potentially consume large quantities of carbohydrate (and store it as fat) to get the other nutrients (e.g., protein) that they need. Volant frugivores cannot use this strategy and so must be more selective about what they eat; oilbird chicks consume so many carbohydrates to get the protein they need that they cannot fly because they are too fat (Snow, 1962; Thomas, Bosque, & Arends, 1993). Flightlessness and size may explain the wider diversity of plant families' fruits that cassowaries consume compared to other specialized frugivore species.

Unpredictability of Cassowary Diet

Cassowaries did prefer annually or biennially fruiting species over continually fruiting species as predicted. During plentiful periods, when both were available, they ate more of the predictable annuals and biennials than were proportionally available. This allows cassowaries to diversify their diet and to go to the same plants that they can rely upon year after year to have fruits during certain months of the year. However, even with this preference for predictable fruit species, cassowary diet was still extremely variable from year to year in addition to season to season. A large proportion of plant species only fruited in one year of the three year study and these accounted for roughly 20% of the diet. Biennial fruiters accounted for 40% of the diet when they were available. Furthermore, even though continually fruiting species were consistently taken during the lean seasons, different species were more readily available and thus consumed more than others during different years. The extreme complexity of the fruiting phenology patterns is duplicated in the cassowary diet. Even after a three year study it is difficult to find any patterns (Figure 5).

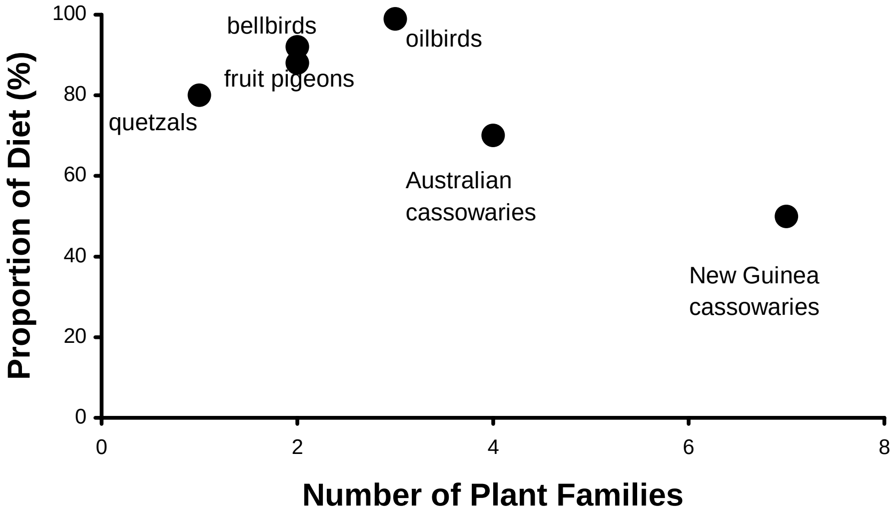

Figure 11. The diet diversity of various specialized frugivores; the greater diversity of cassowary diet may be because they do not fly. This means they can eat large quantities of fruit without calorie restrictions to get the nutritents they need instead of having to choose exceptionally nutrient-rich fruits to avoid weight gain. Data are from Wheelwright, 1983; Crome, 1975b; Frith, Crome, & Wolfe, 1976; Snow, 1962; Snow, 1970; Crome, 1975a; and this study.

Cassowaries during the Lean Season

Even though the rainfall at Crater Mountain is aseasonal and unpredictable, there is an annual predictable dearth of fruit from December through March. During this time cassowaries ate some acorns and even ate branches; they did not eat these items during other times of the year.

Diversity of cassowary dropping contents declined during the lean season. Droppings contained 40% fewer food types both within individual droppings and overall from January through March than from April through November (Figure 9, Table 2). Lean season diet for frugivores is often narrow. Capuchin and squirrel monkeys rely on figs almost exclusively during lean times (Robinson, 1986; Terborgh, 1986). Figs and palms are mainstays for many frugivores during seasonally lean periods because these plants usually have continual phenology patterns at the population level (e.g., Peres, 1994b; Kinnaird & O'Brien, this volume). Likewise, although cassowaries preferred annually fruiting species, they depended upon continually fruiting species like figs, *Garcinia latissima*, *Pandanus spp.*, and some species of palm in the lean season. As a group, these families could be considered keystone resources for cassowaries and perhaps other frugivores in mid-elevation Papua New Guinean rainforests. It appears that despite the huge dietary diversity, a few species may be inordinately important for cassowary survival.

Crome (1975a) also found a fruit lean season for cassowaries in February and March in Australia and Pratt (1983) documented a cassowary fruit lean season from April to December at Mt. Missim in New Guinea (the opposite of our study area). Both detected fewer cassowary droppings during the lean season.

The lower number of droppings found from October through April at our study site implies that cassowaries are either migrating from the area during the lean time (December through March), increasing home range size dramatically, fasting and subsisting on stored fat and muscle, or some combination of the above. Locals report that there is a resident population of cassowaries in the study area, but that other individuals migrate altitudinally to follow fruit availability. My results are consistent with partial migration. Cassowary signs (droppings and foot-tracks on random transects, not trails, Westcott, 1999) were positively correlated with fruit availability at three elevations. When fruits were scarce in the lowlands, cassowary signs were also scarce; in the same month fruits were plentiful in the highlands and so were cassowary signs. A few months later the pattern reverses. This suggests altitudinal migration. However, because some droppings and tracks were present year-round in the main study area, all cassowaries probably do not migrate.

Males probably remain in year-round territories where they incubate and raise chicks. We found chick and adult tracks together from July through January in our study area (cassowaries are polyandrous so the adult tracks were most likely male, Crome, 1975a). January through April is the incubation season at our site, and males probably fast during much of this period. Emus, *Dromaius novaehollandiae*, the sister group to cassowaries (Noble, 1991), fast for 56 days during incubation (Davies, 1974). In Australia, Crome (1975a) found that male southern cassowaries did not come to feeding stations during their 47-53 day long incubation periods, but returned afterwards with their newly hatched chicks. Male southern cassowaries are known to fast for up to 50 days during incubation in Australia (Bentrupperbaumer, 1997). If males are going to fast during incubation, it is advantageous to do so during the lean season.

Female cassowaries, on the other hand, do not have chick-rearing and incubation duties; furthermore their fat stores may already be reduced by egg-laying once the lean season begins. Emus require 26 days to produce a single yolk and they lay the egg 10 days later (time to produce albumen and shell; Carey, 1996). If cassowaries use similar time periods, females are producing yolks just after the end of the fruiting season in December, presumably using fat stores. Once they have laid the eggs they probably need to migrate to find food to replenish their reserves. It seems that dwarf cassowaries may have a mixed strategy involving year-round residency by males, who partially subsist on fat stores in the lean season, and female migrants that track fruit availability altitudinally. However, at this point we can only speculate. It is extremely difficult to capture adult cassowaries in New Guinea for radio tracking and the extreme topography makes telemetry a real challenge for long-ranging species. A promising new method we may use in future studies involves comparing the DNA from epithelial cells in droppings from different sites. If this works, it could verify and track individual movements over time, allowing documentation of any altitudinal migrations. However, even this will not be easy as we would be looking for the proverbial one dropping out of one thousand found and analyzed over many square km in rugged terrain.

Many animals store fat during plentiful times to get them through lean times (Robinson, 1986; Bruno & Lovari, 1989; Churchill, 1994). Animals with variable food resources put on greater fat reserves than animals with predictable, reliable food sources (Ekman & Hake, 1990; Biebach, 1996). The fruit base at Crater Mountain is certainly variable, and cassowaries can accumulate several centimeters of fat. Fat may reduce maneuverability in predator escape (Biebach, 1996) and flight, but cassowaries do not have natural predators (except for humans) and are non-volant. Emperor penguins fast for 60 days during incubation periods (Cherel, Charassin, & Handrich, 1993; Cherel, Robin, Heitz, Calgari, & LeMaho, 1992), and it appears that male cassowaries do the same (Bentrupperbaumer, 1997; Crome, 1975a). Male emus have lower metabolic rates than female emus, perhaps because of their 8 week fasting incubation period (Maloney & Dawson, 1993), which females do not endure. Ratites as a group have 35% lower basal metabolic rates than other non-passerine birds (Maloney & Dawson, 1993); this may aid survival during the fruit lean season.

Conservation Aspects

The southern cassowary and the northern cassowary (*C. casuarius* and *C. unappendiculatus*) are both on the IUCN Red List 1 for threatened animals (IUCN, 2002). *Casuarius bennetti*, the dwarf cassowary, is on the Red List 3 for near threatened animals (IUCN, 2002). In New Guinea, all three cassowary species are still avidly hunted for trade, food and feathers and have been extirpated from much of their natural range through hunting and habitat destruction. Juvenile cassowaries are especially vulnerable to human predation because they come to human whistles that sound like the calls their parent makes. Each individual cassowary disperses hundreds of seeds daily, many too large to be moved by any other animal. Without cassowaries to move seeds back uphill, the range of many fleshy fruited plant species would shrink to valley bottoms in the rugged New Guinea terrain (Mack, 1995). If these flightless birds do indeed depend on annual altitudinal migrations to sustain their populations, we need to be aware of this fact when designing reserves. Furthermore, because of the tremendous seasonal and yearly variation in their diet, we need to ensure that the full diversity of fruiting flora is kept intact if we wish to sustain cassowary populations, and especially those continuous fruiters that fill the lean season gap.

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Appendix 1. The seasons that the top five items per month (for percentage of meal mass and/or for frequency eaten) were consumed (sample size = 855 droppings). In other words, in at least one month of the three year study period, these items were important in cassowary diet. The phenology pattern is given after the item name (A = annual, B = biennial, C = continual, OY = one-year only). Thus if an item is found under the lean season and it is A or C, it can probably be relied upon every year during that season. If it is B, it is taken every other year; if it is OY, it was taken only one year of the study (it may only fruit every three or more years). The first letter indicates importance by mass or by frequency (M or F), then comes the rank that month (1-5 with 1 being highest importance), then comes month, then year. Sample period is May 1990 through May 1993.

Family	**Item**	**Phen**	**Sep-Nov (border)**	**Dec-Feb (lean)**	**Mar-May (lean / border)**	**Jun-Aug (plenty)**
Anacardiaceae	*Dracontomelon dao*	A	M3S91, F1S91, F4S92		F5My90, F5A91, F5Mr92, M4Mr92	F2A90, M4A90, F2Jn90, F2Jn91, M3Jn91, F3Jy91, M5Jy91, F3A91, F3Jy92
	Semecarpus papuanus?	B				M4Jn90
Apocynaceae	*Cerbera floribunda*	A	M4S90, M2O90, M4O91, M2O92	M3D91		
Arecaeae	*Calyptrocalyx* sp. 1	C			F5Mr91, M5Mr91, M3Mr92, M4Mr93	
	Unknown sp. 1	C		F3J91, F5F91, F5F93	F4My90, F4My91, F5A92	F4Jn90
	Unknown sp. 3	C		F5D91, F5J91, F1F91,	F1Mr91, M2Mr91, F1A91, M4A91, F2Mr92, M2Mr92, F2Mr93, M5Mr93	
Clusiaceae	*Calophyllum* cf. *goniocarpum*	C	F5O90			

	Calophyllum laticostratum	OY	F5S90			
	Garcinia cf. *assugu*	C	M5S92, M3N92, F5N92			
	Garcinia celebica	A	M3N91	M5D91		
	Garcinia latissima	C	M3S90, M1O90, M1S92, M4N92	M2D9, F4D91, M1J91, M1F91, F4F91, M1J93	M4My90, M1Mr91, F3Mr91, M1A91, M3A92, M5My92, M2Mr93, M5My93, F4My93	M3A90, M2Jn92, M2Jy92, M2A92
	Garcinia sp. 1 cf. *maluensis*	C		M3F93		
	Garcinia sp. 2	OY	M1S91, F5S91, M5N91			M3A91
	Mammea grandifolia	B				M2Jn90, M2Jy90, F5Jy90, M5Jn92, M4A92
Combretaceae	*Terminalia complanata*	A	F3S91		M3My90, F2My90, M1My91, F2My91, M1Mr92, F3Mr92, M1A92, F2A92, M2My92, F2My92, F4Mr93	M5Jn90, F1Jn90, F2Jy90, M1Jn91, F1Jn91, M1Jy91, F1Jy91, F2A91
	Terminalia impediens?	A	M4S91		M5My90	M5Jy90, F4Jy90, M1A91, M3A92, F5A92
Cunoniaceae	*Schizomeria* sp. 1	A				M5A91, F4A91
Elaeocarpaceae	*Elaeocarpus nouhuysii*?	B		M2J93		
	Elaeocarpus sp. 5 cf. *sepicanus*	C	F3O92, F4N92			
	Elaeocarpus sphaericus	C	M1N92, F2N92	F2J93		
	Elaeocarpus sp. 2	A	F3O91, F3N91, M4S92, F2S92, M5O92, F4O92	F2D91		

Gnetaceae	*Gnetum* sp. 1	B	M5O90			
Lauraceae	*Cryptocarya* sp. 2	B				M3Jn90, F5Jn90, M4Jy90, F3Jy90, M3Jn92, F2Jn92, M1Jy92, F1Jy92, M1A92, F2A92
	Endiandra sp. 2	A			M2My90, M1Jn90, M4A92, M4My92	M4Jn91, M1Jn92, M4Jy92
	Endiandra sp. 5	A				M1Jy90, F1Jy90, M4Jn92, F1Jn92
	Litsea sp. 1	A				F3Jn90, M5Jy92, F2Jy92
Loganiaceae	*Neubergia corynocarpa* ssp. 2	C	M5S91		M3A91	M4A91
Magnoliaceae	*Elmerillia tsiampacca*	A			F3My90, F4My92, M1My93, F1My93	
Meliaceae	*Aglaia mackiana*	B				M3Jy90, M5A92
	Aglaia sp. 3	A				F5Jn92
Menispermiaceae	*Chlaenandra ovata*	A	M3O92, F5O92			
Moraceae	*Artocarpus* sp. 1	A				M4Jy91
	Ficus spp.	C	F4O91, M5N92	M5F91, M5J93, M1F93, F3F93	M1My90, F1My90, M2A91, F4A91, M2My91, F5My91, M1Mr93, F3Mr93	M5Jn91, F4Jn91, M2Jy91, F5Jy91
Myrtaceae	*Syzygium* sp. 2	A	F2S90, F2O90		F3My91, M2A92, F1A92, M1My92, F1My92	F3Jn91
	Syzygium sp. 3	C	M2S92, M1O92	M5J91	M4My91	M2Jn91, M3Jy91
	Syzygium sp. 7	A			M3My92	
Pandanaceae	*Pandanus papuanus*	C			M4Mr91, M3My91, M3Mr93	
	Pandanus penicillatum	C	M2S91, M2O91,	M4D91, M4J91,	M5My91, M5A92	M2A90, M2A91

			M1N91, F4N91	M3F91, M4J93, M5F93		
	Pandanus limbatus	C			M4My93, F5My93	M3Jy92, F4Jy92
	Pandanus sp. 3	A		F3D91	M5A91, F3A91, F3My92, F5Mr93	F2Jy91, F1A91, F3Jn92
	Pandanus sp. 5	C	M5S90, F3S90, M3O90, F1O90, F4S91, M1O91, F2O91, M2N91, F1N91, M3S92, F1S92, M4O92, F1O92	M1D91, F1D91, M3J91, F1J91, F3J93, F4F93	M3Mr91, F2Mr91	F4A90
Proteaceae	*Helicia* sp. 1	A	M3O91, F5O91, M4N91, F5N91			
Rosaceae	*Prunus* sp. 1	B	M2S90, F1S90			M5A90, F1A90, F4A92
	Prunus sp. 2	A	M1S90, F4S90, M4O90, F4O90, M2N92			M1A90, F3A90
	Unknown sp. 1	OY	F3N92	F1J93	M2My93, F3My93	
Rubiaceae	*Psychotria* sp. 1				F4Mr92	
Sapotaceae	*Burckella* sp. 1	OY		M2J91, F2J91, M2F91, F3F91		
	Payena sp. 1	C		F1D90		
Unknown	Catalog DW166	A	F3O90			
	Catalog DW176	C		M4F91		
	Catalog DW890	OY	M5O91			
	Catalog DW1146	OY				F3A92
	Catalog DW1159	OY				F5Jy92
	Catalog DW1189	OY	F5S92			
	Catalog DW1255	OY		M3J93, F5J93		
	Catalog DW1270	OY		M2F93, F1F93		
Non-Fruit	Bracket Fungi	C	F2S91, F1O91, F2N91,	F2D90, F4J91, F2F91,	F4Mr91, F3A91, M5Mr92,	F5A90, F5Jn91, F4Jy91,

			F3S92, F2O92, F1N92	F4J93, F2F93	F1Mr92, F3A92, F5My92, F1Mr93, M3My93, F2My93	F5A91, F4Jn92, F1A92
	Pandanus flowers	OY			F1My91	
	Vegetation-- ferns, stems	C			F4A92	