Nutrient composition of the diet of parent-raised kakapo nestlings

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Abstract The natural diet of the kakapo (*Strigops habroptilus*) is exclusively herbivorous. The bird breeds synchronously with the heavy fruiting or "masting" of certain plant species, including rimu (*Dacrydium cupressinum*), at intervals of 2 – 5 years, and did so in 2002 on Codfish Island (Whenua Hou) in southern New Zealand. Crop contents of kakapo chicks of 10 - 30 and 31 - 43 days of age, and samples of rimu fruit (entire fruit, red aril, green aril and seed) were collected and chemically analysed for dry matter, organic matter, crude protein, fatty acids, amino acids, fibre, simple sugars and minerals. The crop content samples contained predominantly carbohydrates (76 - 81 % by dry wt.), crude protein (7 - 13 %) and fatty acids (6 - 7 %). Entire rimu fruit contained 7.2 % crude protein, 10.9 % fatty acids, and 78 % carbohydrate predominantly of cellulose, hemicellulose and lignin. The red aril, green aril and seed nutrient composition were similar with the exception of the seed fatty acid profile. There was a large degree of similarity in the nutritional composition of the entire rimu fruit and the crop contents, supporting field observations of the time that female kakapo were feeding almost exclusively entire rimu fruit to their chicks. The nutrient profiles provide the first detailed descriptions of the diet of growing kakapo chicks which can guide the development of supplements and artificial rearing diets for this species. The diet of kakapo chicks up to 60 days of age appears to have a low concentration of essential nutrients and high indigestible matter content when compared with other species, consistent with specialised anatomical features and foraging behaviour of this parrot.

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INTRODUCTION

The kakapo (*Strigops habroptilus*) is a large (1.3 - 4.0 kg), flightless nocturnal parrot and one of New Zealand's most endangered endemic birds. Although formerly widespread throughout the country (Holdaway 1989), only 86 birds (41 females: 45 males) are presently (2005) alive on three islands to which they have been relocated since 1975 for protection from introduced mammalian predators. The kakapo has anatomical and behavioural features, and combinations of features, not shared by other parrots making the species highly unique (Powlesland *et al.* 2006). It is the world's largest parrot, has a "lek" mating system (Merton *et al.* 1984), exhibits pronounced sexual dimorphism in body mass (females weigh 30 - 40 % less than males) (Livezey 1992), and has adapted to a cool temperate environment (Higgins 1999). The kakapo is one of the most ancient elements of New Zealand's avifauna and one of the last surviving representatives of a unique avian-herbivore/plant system. The kakapo's breeding strategy, infrequent breeding coupled with solo-parentage and chicks that are vulnerable for many weeks in a nest on the ground, are believed to be the main reason for its decline (Holdaway 1989; Higgins 1999).

The kakapo is exclusively herbivorous, eating a variety of fruits, seeds, leaves, stems and rhizomes (Gray, 1977; Best, 1984; James *et al.* 1991; McNab & Salisbury 1995; Elliott *et al.* 2001; Wilson *et al.* 2006). Its basal metabolic rate is the lowest known for any bird (Bryant 2006) and the bird is able to subsist for long periods on a low-quality diet, which results in adult weights fluctuating markedly, and with seasonal weight changes in excess of 100 % as body fat is stored and mobilized (Higgins 1999). Kakapo have one of the lowest reproductive rates of any bird, breeding in synchrony with the heavy fruiting or "masting" of certain plant species, including rimu (*Dacrydium cupressinum*), and at intervals of two - five years (Henry 1903; James *et al.* 1991; Powlesland *et al.* 1992; Lloyd & Powlesland 1994; Higgins 1999; Elliott *et al.* 2001).

Detailed descriptions of foods consumed by kakapo, as well as changes of incidences of food items in faecal scats have been published (Gray 1977; Best 1984; Trewick 1996; Wilson *et al.* 2006). James *et al.* (1991) determined the diet of adult kakapo in breeding (prior to egg laying) and non-breeding seasons from faecal scat analysis and reported its crude protein

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Table 1 Summary of the four pooled crop content samples from kakapo chicks, Codfish Island, 2002. [1]A number of chicks were sampled twice and are represented in more than one group.

Parameter	**Female supplement**		**Female not supplemented**	
Sample group	**S1**	**S2**	**NS1**	**NS2**
Average chick weight (g)	644	1173	885	1115
Average chick age (d)	21.7	38.3	26.8	35.2
Number of nests	5	3	2	4
Number of chicks (♂,♀)[1]	6 (3♂,3♀)	4 (1♂,3♀)	3 (2♂,1♀)	7 (2♂,5♀)
Number of individual samples	8	6	6	7
Sample weight (g as-is)	10.7	9.3	12.4	8.6

content to be only 5.9 g/100 g dry matter during the breeding season and 3.7 g/100 g dry matter during the non-breeding seasons. In addition, James *et al.* (1991) calculated the lipid concentration in the foods to be 3.8 and 2.3 g/100 g dry matter during non-breeding and breeding seasons, respectively. These dietary crude protein and lipid concentrations are barely adequate for egg production and chick growth in other birds.

There is little information on the nutrient requirements of kakapo nestlings. Female kakapo with chicks on Codfish Island (Whenua Hou) predominantly forage in and around rimu trees (DM, pers obs; Trewick 1996), and droppings from two nests containing kakapo chicks on Codfish Island in 1992 contained only fruit and leaves of rimu (Trewick 1996), indicating that chicks receive hydrated masticated material primarily, if not exclusively, from the rimu tree. The present study aimed to obtain estimates of the nutrient composition of the diet of kakapo nestlings by analysis of samples obtained from the crops of chicks, as well as the main food items consumed by female kakapo raising chicks.

MATERIAL AND METHODS

Crop content sampling

When kakapo bred on Codfish Island (Whenua Hou) in 2002, 24 nests were established of which 15 were successful, producing a total of 24 fledglings (Elliott *et al.* 2006). Females tending six of these nests (containing nine chicks) accepted supplementary food, while those tending the other nine nests (containing 15 chicks) did not consume supplementary food while feeding nestlings. Supplementary foods comprised of spirulina-based pellets and raw, organically-grown walnuts, almonds, sweet potato and sweet-corn, all of which were offered *ad lib*.

Body weights of nestlings were recorded nightly for the first four - five weeks following hatching. Thereafter, nestlings were weighed at two - three night intervals until fledging, at 10 - 11 weeks of age. Weights were obtained by placing the chick in a light-weight nylon bag and weighed using "Pesola" spring balance scales.

Crop content samples were collected from nestlings of known age and weight using a 5 mm diameter soft opaque plastic tube attached to the end of a 60 ml syringe. Food spilled by the female while feeding nestlings was also collected when this was found in a fresh state. Twenty crop content samples from a total of 17 chicks from 11 nests were collected. The age of nestlings from which samples were collected ranged from 10 to 43 days (Table 1).

Samples were stored in plastic bags and frozen within an hour of collection. Crop samples were transported frozen to the laboratory, weighed, freeze-dried and reweighed in order to ascertain the total amount of dry matter available for analysis. Crop content samples were then pooled based on whether chicks belonged to a supplementary fed (S) or non-supplementary fed (NS) parent and were aged 10 - 30 d (group 1) or 31- 43 d (group 2), so that there were four samples in total (S1, S2, NS1 and NS2). Samples were pooled in order to obtain sufficient material to allow the various chemical analyses to be conducted. Each of these four freeze-dried pooled crop content samples was ground to a fine powder using a mortar and pestle and stored in a desiccator until chemical analysis.

Rimu fruit collection

Fallen rimu fruit (consisting of a fleshy aril and a seed, weighing in total when ripe approximately 0.1g) was collected using 3 x 3 m sheet plastic collection trays suspended beneath female trees throughout the 2002 breeding period. Bulk sample collection time (7 April 2002) fell within a week of the time when the majority of the crop content samples were collected. As it was unclear what kakapo were consuming, this 'fallen entire fruit' (REF) was split into components of green (unripe) aril (GA), red (ripe) aril (RA), seed (S). Samples of REF, RA, GA and S were freeze-dried, ground using a mortar and pestle and stored at -20ºC until chemical analysis. In order to compare potential changes in chemical composition of the rimu fruit red aril over the breeding season of the kakapo, rimu fruit red aril was also collected on 15 March and 22 April.

Chemical analyses

The ground samples were analysed for dry matter (DM), crude protein, lipid, amino acids, fatty acids, minerals and ash. Selected samples were also analysed for simple sugars, cellulose, hemicellulose and lignin. Dry matter was determined by oven drying at 105 °C while ash was determined by heating the sample to 550 °C for 16 h. Crude protein was determined by multiplying nitrogen by 6.25 with nitrogen determined by the Kjeldahl technique.

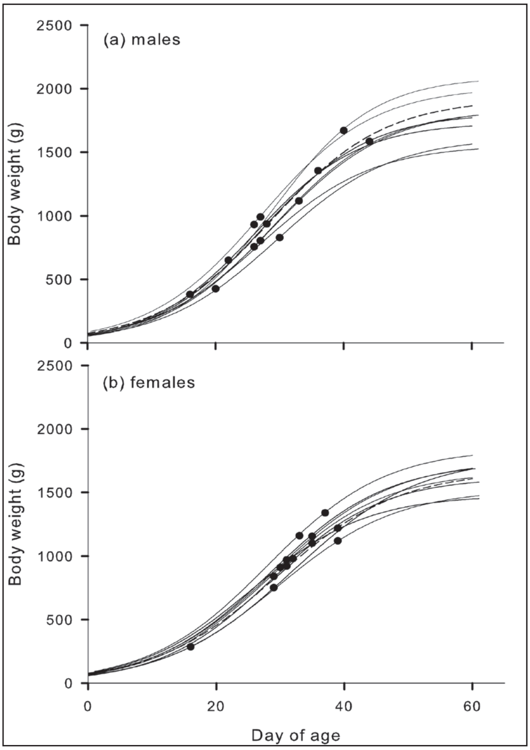

Figure 1 Growth curves of male (a) and female (b) kakapo chicks between days 1 and 60, Codfish Island, 2002. The solid dots represent a crop content sample collection; each solid line is the growth curve for a single chick, and the dotted line the average growth curve for the sampled chicks.

Lipid was analysed using petroleum ether extraction (AOAC 2000). Cellulose, hemicellulose and lignin were calculated from neutral detergent fibre, acid detergent fibre and acid detergent lignin analyses conducted using methodology described by Van Soest (1973) and Van Soest *et al*. (1991). Amino acids were determined by hydrochloric acid hydrolysis followed by high performance liquid chromatography separation with cysteine and methionine oxidation before hydrolysis as described by Hendriks *et al*. (2000). Fatty acids were analysed using gas chromatography (Sukhija & Palmquist 1988), with mineral determination carried out by plasma emission spectrophotometer (Lee 1983). Simple sugars were analysed by a combination of gas chromatography and spectrophotometry according to the method of Englyst *et al*. (1994).

Statistical analyses

The growth rate of the chicks was calculated from day 1 to day 60, and subjected to ANOVA with gender, supplementation of the parent, and the interaction between gender and parent supplementation as variables. One chick was excluded from the growth rate data as it was removed from the nest on day 34 (due to weight loss) and hand-raised. The crop content sample of this chick, obtained at day 23, was included in the pooled crop content sample as its growth at the time of collection was considered normal. The following Gompertz growth curve was fitted to the body weight data of individual chicks using the non-linear procedure in the statistical software package SAS (SAS 1999):

$$LW_t = b_0 + b_1 \cdot e^{-e(-b_2 \cdot (t-b_3))}$$

where LW_t = live weight at time t in grams, b_0 = live weight at time 0 in grams, b_1 = asymptotic maximal weight in grams, b_2 = growth rate, b_3 = time when maximum rate occurred in days, and t = time in days.

Correlation coefficients were determined between the components of the rimu fruit (REF, RA, GA, S) and the four crop content samples for both amino acid and fatty acid profiles. All statistical analyses were performed using SAS and effects were considered significant at a probability of 5 %.

RESULTS

Nestling growth rates

All kakapo nestlings sampled remained healthy and live weights increased throughout the first 60 days of life, with the exception of one bird which was removed at day 34 of age due to insufficient weight gain. The growth curves of the male and female kakapo chicks and the crop content sampling times are presented in Figure 1. The mean (± *se*) growth rate of nestlings (from days 1 to 60) was 31.4 ± 0.8 g/d for males (n = 6) and 27.2 ± 0.6 g/d for females (n = 10) ($P < 0.01$). Supplementation of the parent had no significant effect on the growth rate of the chick. There was, however, a significant interaction between the sex of the chick and supplementary feeding of the parent, with the male chicks growing 32.9 (NS) and 30.0 g/d (S), and the females growing 26.5 (NS) and 28.3 g/d (S) ($P < 0.05$). The mean (± *se*) coefficients of the Gompertz curve model fitted to the body weight data of the chicks used in the present study were (male, female): b_0 = 0.34 ± 25.20, -20.33 ± 31.79; b_1 = 2129 ± 60, 1929 ± 81; b_2 = 0.064 ± 0.003, 0.057 ± 0.004 and b_3 = 24.52 ± 0.43, 25.21 ± 0.61.

Nutrient composition of crop samples

The gross nutrient composition (including sugars) of the four crop content samples is presented in Table 2, amino acid profile in Table 3 and fatty acid profile in Table 4. The dry matter content of the samples was approximately 15%, with the exception of the NS1 sample which had a dry matter content of 30 %. Organic matter was similar between the four samples at approximately 95 %. Amino acid nitrogen content was similar for three of the samples (1.21 - 1.47 %) with the exception of S1 which was 39 - 61 % higher. In the supplementary-fed group (S1 and S2), the crop content samples from the younger chicks contained overall higher concentrations of amino acids compared

Table 2 Gross nutrient composition (%) of pooled crop content samples of kakapo chicks in two age groups (1 = day 10-30, 2 = day 31-43) from nests of supplementary-fed (S) and non supplementary-fed (NS) females.

Component	**Female supplemented**		**Female not supplemented**	
Sample group	**S1**	**S2**	**NS1**	**NS2**
Fresh sample (%)				
Dry Matter	15.26	16.99	29.83	15.47
Dry matter basis (%)				
Organic matter	95.44	95.65	94.99	94.98
Crude protein	12.73	(7.93)[a]	9.17	(7.55)
Amino acid N	2.04	1.27	1.47	1.21
Non amino acid N[b]	0.20	-	0.34	-
Total fatty acids	6.66	6.70	7.73	7.89
Carbohydrates[c]	76.06	81.01	78.09	79.55
Fructose	-	7.36	-	6.49
Glucose	-	5.20	-	3.46
Sucrose	-	0.00	-	0.00
Maltose	-	0.32	-	0.32

[a] Values between brackets are estimates from amino acid N values and the corresponding percentage of the contribution of non amino acid N to total N of the previous time period.
[b] Total nitrogen minus amino acid nitrogen.
[c] Calculated as organic matter – (crude protein + total fatty acids).

Table 3 Amino acid profile (g /100 g DM) of pooled crop content samples of kakapo chicks in two age groups (1 = day 10-30, 2 = day 31-43) and from nests of supplementary-fed (S) and non supplementary-fed (NS) females.

Amino acid	**Female supplemented**		**Female not supplemented**	
Sample group	**S1**	**S2**	**NS1**	**NS2**
Aspartic acid	1.442	0.993	0.964	0.931
Threonine	0.495	0.293	0.325	0.262
Serine	0.654	0.401	0.452	0.383
Glutamic acid	2.338	1.346	1.515	1.279
Proline	0.740	0.442	0.453	0.377
Glycine	0.622	0.424	0.455	0.388
Alanine	0.713	0.441	0.485	0.407
Valine	0.783	0.482	0.529	0.436
Isoleucine	0.653	0.398	0.430	0.356
Leucine	1.062	0.613	0.681	0.576
Tyrosine	0.484	0.267	0.288	0.220
Phenylalanine	0.615	0.368	0.415	0.351
Histidine	0.493	0.289	0.318	0.274
Lysine	0.812	0.456	0.503	0.439
Arginine	1.007	0.768	1.213	0.799
Cysteine	0.283	0.184	0.198	0.203
Methionine	0.387	0.164	0.198	0.174

to the other groups, which was consistent with the higher crude protein value recorded for this group. The amino acid profiles were highly similar between the four groups (Table 3). The amino acids present in the highest concentrations were glutamic acid, aspartic acid, leucine and arginine. The total fatty acid content between the four samples was also similar and ranged from 6.66 to 7.89 g/100 g dry matter. Of the fatty acids, palmitic (C16.0), oleic acid (C18:1 cis) and linolenic acid (C18:3) were present in the highest concentrations (Table 4). The carbohydrate fraction of the crop content sample, calculated by difference, was similar between all groups and made up 76 - 81 % of the dry matter.

Nutrient composition of rimu fruit

The nutrient composition of the three red aril samples collected on 15 March, 7 April and 22 April were similar (data not shown). Thus only the data of the early April sample are presented in detail to allow direct comparison with the composition of the other rimu fruit fractions collected at

Table 4 Fatty acid profile (mg/g DM)of pooled crop content samples of kakapo chicks in two age groups (1 = day 10-30, 2 = day 31-43) and from nests of supplementary-fed (S) and non supplementary-fed (NS) females. (b.d. = below detection limit of the assay).

Fatty acid	Female supplemented		Female not supplemented	
Sample group	S1	S2	NS1	NS2
C 8:0 caprylic	2.01	2.04	2.28	2.28
C 10:0 capric	0.47	b.d.	0.47	0.94
C 12:0 lauric	0.74	1.04	0.66	2.38
C 14:0 myristic	0.72	0.93	0.66	0.69
C 16:0 palmitic	19.39	24.17	23.22	23.26
C 16:1-trans palmitelaidic	0.15	0.21	0.18	0.22
C 16:1-cis palmitoleic	0.03	b.d.	0.05	0.05
C 17:0 margaric	0.24	b.d.	0.28	0.31
C 18:0 stearic	2.84	b.d.	3.39	3.26
C 18:1-trans elaidic	0.15	1.46	0.19	0.00
C 18:1-cis oleic	22.42	25.75	26.85	27.02
C 18:2-trans linolaidic	0.26	b.d.	b.d.	b.d.
C 18:2-cis linoleic	4.20	b.d.	4.87	5.94
C 18:3 linolenic	10.82	7.54	13.06	11.79
C 20:0 arachidic	0.30	3.40	0.41	0.39
C 20:1-cis eicosenoate	0.76	0.24	0.24	0.08
C 22:0 behenate	0.16	0.27	0.25	0.12
C 22:1-cis erucic	0.18	b.d.	0.21	0.20
C 24:0 lignoceric	0.73	b.d.	0.04	b.d.
C 24:1 nervonic	b.d.	b.d.	b.d.	b.d.
Total fatty acids	66.59	67.04	77.31	78.92

Table 5 Gross nutrient composition (%) of entire rimu fruit and three components.

Component	Entire fruit	Green aril	Red aril	Seed
Fresh sample (%)				
Dry matter	34.02	30.84	31.91	65.04
Dry matter basis (%)				
Organic matter	95.82	95.12	97.16	95.70
Crude protein	7.23	7.17	5.88	9.10
Amino acid N	0.96	0.97	0.77	1.22
Non amino acid N	0.19	0.18	0.17	0.23
Total fatty acids	10.90	6.30	12.82	23.43
Carbohydrates[a]	77.69	81.65	78.47	63.16

[a]Calculated as organic matter – (crude protein + total fatty acids).

Table 6 Carbohydrate composition (g /100 g DM) of entire rimu fruit. Carbohydrates calculated as 100 – (crude protein + total fatty acids + ash).

Component	Entire fruit
Carbohydrates	77.69
Starch	4.47
Cellulose	17.34
Hemicellulose	10.59
Lignin	30.63
Total Sugars	6.45
Fructose	4.06
Glucose	1.98
Sucrose	0.42
Maltose	0.00

the same time. The entire rimu fruit, red aril, green aril and seed gross nutrient composition is presented in Table 5. The crude protein content in the REF was 7.23 %, while 10.90 % of the dry matter consisted of fatty acids (Table 5). Most of the other components (GA, RA, Seed) were similar in composition with the exception of the seed which contained more than twice the concentration of fatty acids (23.43 %). The carbohydrate content of the entire fruit was 78 %, with 75 % of this being composed of cellulose, hemicellulose and lignin (Table 6). Fructose, glucose and sucrose made up 6.5 % of the dry matter content of the fruit while no maltose was detected. The amino acid profiles were similar between components (Table 7). The amino acids present in the highest concentrations were glutamic

Table 7 Amino acid profile (g /100 g DM) of rimu samples.

Amino Acid	Entire fruit	Green aril	Red aril	Seed
Aspartic acid	0.664	0.698	0.518	0.795
Threonine	0.265	0.305	0.213	0.255
Serine	0.320	0.370	0.256	0.395
Glutamic acid	0.919	0.770	0.599	1.374
Proline	0.383	0.389	0.353	0.384
Glycine	0.344	0.375	0.279	0.376
Alanine	0.360	0.398	0.295	0.395
Valine	0.406	0.440	0.347	0.428
Isoleucine	0.316	0.342	0.259	0.366
Leucine	0.490	0.527	0.398	0.569
Tyrosine	0.231	0.258	0.195	0.242
Phenylalanine	0.311	0.299	0.224	0.402
Histidine	0.218	0.223	0.195	0.276
Lysine	0.401	0.466	0.373	0.388
Arginine	0.513	0.382	0.371	0.948
Cysteine	0.143	0.151	0.109	0.155
Methionine	0.121	0.123	0.100	0.159

Table 8 Fatty acid profile (mg / g DM) of rimu samples (b.d. = below detection limit of the assay).

Fatty acid	Entire fruit	Green aril	Red aril	Seed
C 8:0 caprylic	1.76	1.25	2.28	0.69
C 10:0 capric	0.46	0.42	0.43	b.d.
C 12:0 lauric	0.31	0.30	2.05	b.d.
C 14:0 myristic	0.77	0.65	1.12	b.d.
C 16:0 palmitic	19.96	20.55	43.17	8.407
C 16:1-trans palmitelaidic	0.12	0.14	0.36	b.d.
C 16:1-cis palmitoleic	0.05	0.04	0.09	b.d.
C 17:0 margaric	0.20	0.21	0.24	b.d.
C 18:0 stearic	1.92	1.44	2.31	3.130
C 18:1-trans elaidic	0.18	b.d.	b.d.	b.d.
C 18:1-cis oleic	21.88	25.40	52.47	23.94
C 18:2-trans linolaidic	b.d.	b.d.	b.d.	b.d.
C 18:2-cis linoleic	16.51	6.39	15.14	43.79
C 18:3 linolenic	43.83	5.810	6.99	154.12
C 20:0 arachidic	0.38	0.05	0.70	b.d.
C 20:1-cis eicosenoate	0.12	0.06	0.27	0.26
C 22:0 behenate	b.d.	0.19	0.07	b.d.
C 22:1-cis erucic	0.10	0.07	0.14	b.d.
C 24:0 lignoceric	0.06	0.08	0.10	b.d.
C 24:1 nervonic	0.42	b.d.	0.22	b.d.
Total fatty acids (%)	10.90	6.30	12.82	23.43

acid, aspartic acid, leucine and arginine. The fatty acid data (Table 8) showed similar profiles for the REF, RG and GA, with the highest levels of palmitic (C16:0), oleic (C18:1 cis), linoleic (C18:2 cis) and linolenic (C18:3) acid. The seeds contained higher concentrations of linoleic and linolenic compared to the other three components. The rimu samples showed similar profiles for all of the minerals measured (Table 9). The ratio of calcium : phosphorous in the rimu fruit was high ranging from 4.7:1 (RA) to 7.8:1 (GA).

The correlation coefficients between the crop content samples and the various rimu components are presented in Table 10. Correlation coefficients between REF and the crop content samples ranged from 0.62 to 0.76 for the fatty acids, and 0.94 to 0.99 for amino acids. All correlations were significant ($P < 0.05$). The overall highest correlations for amino acids and fatty acids within rimu fruit component were obtained for the REF and GA components, respectively.

DISCUSSION

Nestling growth

The chicks from this study grew on average at a rate of 31.4 g/d (male) and 27.2 g/day (female). The mean (± *se*) growth rates of kakapo chicks (days 1 - 60) raised

Table 9 Mineral content (mg/g DM) of the rimu samples (Fe, Zn, Mn, Cu measured at µg/g DM).

Mineral	Entire fruit	Green aril	Red aril	Seed
Calcium (Ca)	8.42	7.54	4.94	10.22
Phosphorous (P)	1.11	0.97	1.06	1.67
Potassium (K)	3.68	4.89	3.99	3.16
Sulphur (S)	1.19	1.28	1.15	1.32
Magnesium (Mg)	1.21	1.47	0.92	1.17
Sodium (Na)	1.41	2.35	1.63	0.65
Iron (Fe)	37.4	36.9	34.3	41.1
Zinc (Zn)	25.1	23.4	22.0	39.1
Manganese (Mn)	309	354	245	379
Copper (Cu)	5.8	6.4	5.9	6.8

Table 10 Correlation coefficients between crop content samples and rimu fruit components for amino acids and fatty acids.

Sample group	Entire fruit	Green aril	Red aril	Seed
S1	0.98, 0.75[1]	0.92, 0.98	0.92, 0.96	0.95, 0.41
S2	0.99, 0.62	0.92, 0.97	0.94, 0.96	0.97, 0.24
NS1	0.94, 0.76	0.82, 0.98	0.88, 0.96	0.99, 0.41
NS2	0.98, 0.74	0.89, 0.98	0.92, 0.97	0.98, 0.38

[1] Amino acid and fatty acid correlation, respectively.

between 1991 and 2005 (excluding chicks sampled in the present study) were 29.8 ± 0.8 g/day for males ($n = 8$) and 26.5 ± 1.5 g/d for females ($n = 9$) (G. Elliott pers. comm.). Thus, the chicks from which crop content samples were collected grew at similar rates to chicks in other years and there was no effect on growth from the crop content sampling procedure. Males grew significantly faster than females, and as a result males reached a higher body weight at 60 days of age (Fig. 1). The slope obtained from the Gompertz curve fitted to the growth data also showed a significant effect of sex ($P < 0.01$) on the growth of the chicks with the slope for female chicks 0.057 ± 0.003 and 0.064 ± 0.004 for the male chicks. The maximum growth rate of male (50.1 g/day) and female (40.4 g/day) chicks occurred around day 25 with males weighing 783 g and females 710 g.

Breeding and mast fruiting

Kakapo must have an abundant and enduring food source of suitable quality in order to breed successfully (Higgins 1999). A number of authors (Henry 1903; James *et al.* 1991; Powlesland *et al.* 1992; Lloyd & Powlesland 1994; Elliott *et al.* 2001) have observed the association between kakapo breeding behaviour and the heavy fruiting ("masting") of certain plants. Lloyd & Powlesland (1994) commented that, on Stewart Island, the only adequate food to promote kakapo breeding was the periodic prolific fruiting of two species of podocarp, rimu and pink-pine (*Halocarpus biforme*). On nearby Codfish Island (Whenua Hou) rimu trees are present but not pink pine. For kakapo to have developed this breeding association, predictors of an upcoming super-abundance in food would be required. Lloyd & Powlesland (1994) pointed towards the development of green ovules on rimu trees during the middle of the year as a potential trigger for the subsequent breeding of kakapo the following autumn.

During 2001-02 on Codfish Island (Whenua Hou) there was a super-abundance of ripe rimu fruit available to the birds. Four previous rimu fruit mastings had occurred in the region since 1981 but each time the fruit crop failed before ripening (Merton *et al.* 2002). During March - April 2002 when the kakapo nestlings were being raised, the rimu fruit remained on the trees and ripened for the first time since 1981.

The female kakapo rearing chicks in the present study were observed during the collection of the crop content samples to forage almost excessively in and around rimu trees. A similar field observation was made by R. Buckingham (reported in Trewick 1996), and Trewick (1996) reported that faecal material collected in April 1992 from two Codfish Island nests with kakapo chicks contained only remains of rimu fruit and leaves. Since no other plant material was found in the collected faeces, clearly female kakapo on Codfish Island identify rimu fruit and leaves as the most suitable food item for chick growth.

This foraging behaviour appears to be unique during the chick-rearing period as adult kakapo on Codfish Island (Whenua Hou) consume a variety of food items throughout the year (Wilson *et al.* 2006). On Little Barrier Island, however, female kakapo were found to have provided chicks with a range of foods including kauri (*Agathus australis*) and rata (*Meterosideros albiflora*) leaves, Blechnaceae fern frond, *Dracophyllum* sp. but primarily artificial supplementary foods (Trewick 1996). Although faecal scat analyses to identify individual food items provided to chicks were not conducted, the concurrent field observations as well as a previous report in the literature provide strong evidence that the kakapo chicks in the present study would have received predominantly rimu food.

Nutrient analyses

The analysis of crop content samples to measure nutrient intake has been carried out previously with grey-faced petrels (*Pterodroma macroptera*) (Hendriks *et al.* 2000) in order to formulate model rearing diets for these birds. One potential bias in the methodology applied in the present study, and by Hendriks *et al.* (2000), is the fractionation of dietary components or nutrients within the crop or proventriculus. The crop is considered to function as a temporary storage organ where food is moistened and little digestion occurs whereas the proventriculus secretes HCl and pepsin for digestion (Klasing 1998). Although samples taken from the crop would be less likely to be fractionated, it cannot be excluded that digestive enzyme of parental origin was present in the samples which may have caused some fractionation of nutrients.

As expected, there was a large degree of similarity in the nutritional composition of the rimu fruit and the crop content composition, providing further evidence that the females were feeding predominantly, if not exclusively, rimu fruit to the chicks. Most of the variation (88 - 98 %) in the crop content amino acid composition of the different samples was explained by the REF rimu sample. Likewise, the RA component of the rimu fruit explained 92 - 94 % of the variation in the crop fatty acid profile. The latter suggests that young kakapo chicks were being fed almost exclusively on either the entire rimu fruit or the females were choosing the red aril component of the fruit to feed the chicks. Field observations (by DM) indicate kakapo fed on the fruits and seeds (but ejected the seed husk) and, at times, leaves, which is supported by the results of this study. However, more detailed information is needed on which parts from the rimu tree are consumed by female kakapo nursing chicks before studies into the digestibility of dietary nutrients of chicks should be conducted.

James *et al.* (1991) estimated the nutrient composition of the diet of adult kakapo during the breeding and non-breeding season from the nutrient composition of plant species consumed by kakapo on Stewart Island and from faecal cuticle analyses. Although there may be a number of potential inaccuracies in reconstructing a diet from the intake and composition of individual ingredients, these authors reported that the diet of adult kakapo during the non breeding season contained a dietary crude protein content of 37 g/kg dry matter. They estimated the dietary crude protein content during the breeding season was 39 or 59 g/kg dry matter depending on the availability of pink pine and mänuka (*Leptospernum scoparium*) fruiting bodies. These maintenance values are in line with the higher dietary crude protein concentration (7.6 - 12.7 %) of growing chicks found in the present study. Diets for growing animals should contain approximately 1.5 - 3 times the amount of protein compared to adult maintenance diets in order to achieve normal growth rates and as such the estimates by James *et al.* (1991) and those provided in the present study are consistent with observations in other animal species.

The carbohydrate fraction of the entire rimu fruit made up 78 % of the dry matter with 75 % of the carbohydrate fraction composed of the indigestible carbohydrates cellulose, hemicellulose and lignin. The starch content was only 4.5 % of the dry matter content of the entire rimu fruit. Similarly the carbohydrate content of the crop content ranged 75 - 80 % of the dry matter. It is unlikely that kakapo would be able to obtain significant amounts of energy from the carbohydrate fraction of the entire fruit.

Kakapo have been reported to have a well defined crop, proventriculus, muscular gizzard and no vitelline diverticulum or caeca (Kirk *et al.* 1993). In order to obtain significant amounts of energy from the indigestible carbohydrate fraction of the rimu fruit, some specialised anatomical or physiological adaptation would be required such as a rumen, large caeca, large colon or intestinal enzyme activity (cellulase, hemicellulase or lignase). The kakapo, however, has no specialised anatomical adaptations to its gastrointestinal tract to facilitate fermentation (Kirk *et al.* 1993), such as caeca, which are associated with a herbivorous diet (McLelland 1989) although the obvious crop and the fact that the gizzard is larger than the proventriculus in kakapo could be regarded as an intestinal adaptation to a fibrous diet (Kirk *et al.* 1993). Although this has not been investigated, it is unlikely that there would be significant cellulase, hemicellulase and lignase activity in the intestine which would make a significant contribution to the overall energy requirements of kakapo.

In order to obtain sufficient nutrients and energy from a diet that contains over 55 % indigestible carbohydrates, the herbivorous kakapo would need to consume large quantities of vegetation. Kakapo, however, have a specialised tongue (with keratinised lobe) which fits closely into the palate, and a prominent pharyngeal pad, making it well suited to grind and squeeze juices from vegetable matter (Kirk *et al.* 1993). Gray (1977; see Butler 2006) has described the kakapo's characteristic method of feeding, involving the chewing of fibrous plant material, ingestion of the juices and soft portions, and ejection of the indigestible residue as "chews" (Kirk *et al,* 1993). This behaviour would extract more digestible nutrients from what otherwise should be regarded a low nutritional quality or highly indigestible food.

The ratio of calcium : phosphorous in the rimu samples was relatively high, ranging from 4.7:1 to 7.8:1. Although insufficient crop content sample was available to allow a mineral analysis, the mineral composition of the REF sample (believed to be consumed by kakapo chicks) can be expected to closely match the crop content mineral profile. The REF sample had a calcium to phosphorus ratio of 7.6:1 which is well outside the range of calcium to phosphorus ratios of 2:1 to 3:1 for growing birds considered to be optimal for proper absorption and metabolism (Robbins, 1993). The ratios of Ca:P in laying hens are up to 12:1 (NRC 1994). The chicks in the present study, however, did not develop "rickets", a condition caused by an imbalance of calcium to phosphorus (Klasing 1998) indicating that either kakapo can tolerate high dietary Ca:P ratios or the calcium in the rimu fruit may not be highly available. James *et al.* (1991) reported a calcium: phosphorus ratio in an "estimated" diet of adult kakapo consumed during the non-breeding and breeding season of 2.2:1 and 3.8:1. The present study, as well as the results of James *et al*. (1991) indicate that the dietary Ca:P ratios are much higher compared to diets of other adult and growing animals species. The absolute concentration of Ca in the rimu fruit of 0.5 - 1 % is similar to that required by growing chickens (1 %) but the concentration of P at 0.1 - 0.2 % is lower than recommended (0.45 %) for growing chickens (NRC 1994).

Quantity of food provided

The amount of food provided to the chicks can be estimated from the data presented in the present study. The average protein deposition of the chicks can be calculated assuming an average body protein content of 19.5 % (Kamphues & Meyer 1991), an efficiency of protein deposition of 75 % and the average growth rate of the chicks (29.4 g/day). Assuming a protein digestibility of the entire rimu fruit of 60 - 70 %, the amount of entire rimu fruit (1.88 % protein/g; Table 5) required to achieve the average growth rate observed by the chicks in 2002 is 573 - 669 g/d. Four – six-week-old kakapo chicks on Codfish Island during 2002 received *c.*120 g of rimu fruit per feed, and were fed four or more times per night (DM unpubl.). Kakapo are nocturnal (Higgins 1999) making the above food intake approximately 480 g/chick which is close to the 560 - 650 g estimated from nutritional data. The average weight of an entire ripe rimu fruit is approximately 0.1 g and it therefore would require approximately 5600 - 6500 individual rimu fruit per day to feed one kakapo chick.

The present study provides the first detailed and accurate estimates of the dietary nutrient composition for growing kakapo chicks which can serve as a guide for the development of supplements and artificial rearing diets for this species. The diet of kakapo appears to have a relatively low concentration of essential nutrients when compared to other species, a characteristic which is consistent with specialised anatomical features and foraging behaviour of this parrot whereby they can discard the less digestible fraction of plants as chews. The large seasonal and periodic fluctuations in body weight observed in adult kakapo is further evidence of the consumption of a low quality diet as body fat reserves are required to be mobilised to meet energy requirements at key times when energy intake is limited.

The present study provides gross dietary nutrient compositions and further research should be aimed at determining the digestibility of individual nutrients (including energy) in the natural diet as well as the amount of food consumed in relation to the growth rate of chicks. Detailed analyses of other major food items consumed by kakapo raising chicks, such as fruit of other podocarps and, perhaps, beech and tussock seed, would increase the confidence in the nutrient requirement estimates of kakapo chicks during growth. Elucidating the mechanism by which kakapo identify and anticipate the prolific masting of certain plant species would be a major advance, and would provide a means by which the rate of kakapo recovery might be significantly increased.

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