

Energetics of free-living kakapo (*Strigops habroptilus*)

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Abstract The doubly-labelled water technique was used to measure energy expenditure in 20 free-living kakapo (*Strigops habroptilus*) on Codfish and Little Barrier Islands. Daily energy expenditure (DEE) averaged 799 kJ/d, equivalent to 1.4 x BMR (basal metabolic rate), the lowest value recorded for any adult wild bird. DEE was higher in males than females, and was greater on Codfish Island than on Little Barrier Island. Supplementary food taken from hoppers by kakapo supplied about half of their DEE; a few individuals apparently obtained virtually all their energy needs from supplementary food. Use of food from hoppers did not affect energy expenditure directly, but apparently did so via long-term elevation of body mass. Supplementary feeding, particularly of energy-dense items such as nuts and seeds, greatly depressed body-water turnover rates. Some implications of the often high level of supplementary food taken by kakapo are discussed. Adjusting the supplementary feeding programme to meet more precisely the needs of individual birds would probably improve the overall nutrition of the surviving kakapo population.

Bryant, D.M. 2006. Energetics of free-living kakapo (*Strigops habroptilus*). *Notornis* 53(1): 126-137.

Keywords Kakapo; *Strigops habroptilus*; kea; *Nestor notabilis*; Psittaciformes, energetics; flightlessness, diet; conservation; supplementary feeding

INTRODUCTION

The kakapo (*Strigops habroptilus*) is a giant (1.5 - 4.0 kg), flightless, lek-breeding parrot endemic to New Zealand. The heaviest of all parrots, kakapo are further unusual in being nocturnal and feeding on a diverse range of plant foods including such non-nutritive items as fern fronds and leaves. Once widespread on the North and South Islands of New Zealand, there are now (2005) only 86 kakapo, all of which were either transferred to, or were hatched on, islands that lack predatory mammals except rats (*Rattus* spp.) (Elliott *et al.* 2001; Powlesland *et al.* 2006).

This study, conducted in 1996 when the kakapo population was dispersed on three islands (Codfish, Little Barrier and Maud; Lloyd & Powlesland 1994), sought to improve understanding of the nutritional requirements of kakapo. A prevailing hypothesis was that kakapo bred only in response to mast fruiting of podocarps, particularly rimu (*Dacrydium cupressinum*); to test this a supplementary feeding regime had been introduced (James *et al.* 1991; Powlesland & Lloyd 1994). This study's aim was to measure the energy expenditure of non-breeding wild kakapo, particularly in relation to sex, supplementary feeding regimes and habitat. Because the species displays a unique suite of features, extrapolation from congeners or species with similar habits was not possible.

There were three objectives.

1. To measure energy expenditure and hence, under an assumption of energy balance, the energy requirements of non-breeding kakapo, using the doubly-labelled water (DLW) technique (Bryant 1989). This would allow the energetic contribution of the supplementary food provided to kakapo to be quantified;
2. To allow adjustment of supplementary food to match the differing energetic requirements of individual birds. Energetic measurements might also offer an explanation for the apparent differences in response to supplementary food between the kakapo populations on Little Barrier Island, where breeding appears to have been induced by food supplements (James *et al.* 1991; Powlesland & Lloyd 1994), and on Codfish Island where there has been no apparent relationship between supplementary food and breeding.
3. Direct energetic measurements could serve, in due course, to parameterise time-activity-laboratory (TAL) models of energy expenditure throughout the year. These could, in turn, help to identify energetic bottlenecks during the annual cycle (Bryant & Tatner 1988).

An understanding of the energy expenditure of free-living kakapo could also make three important contributions of fundamental interest to evolutionary and functional ecology: provide evidence concerning the relationship between basal and active metabolism (Daan *et al.* 1990); extend an emerging pattern of low field metabolism amongst many Australasian endotherms; and, contribute to the debate about the evolutionary causes and consequences of flightlessness in insular animals (McNab 1994).

Received 19 August 2005; accepted 20 October 2005 • Editor M. Williams

STUDY AREA AND METHODS

Field studies were carried out on Codfish (46° 46' S, 167° 43' E) and Little Barrier Islands (36° 12' S, 175° 05' E). Both islands are predominantly covered by native forest, but Codfish is temperate and markedly seasonal while Little Barrier is sub-tropical with less seasonal variation in temperature.

The kakapo populations on these islands were established in the late 1980s by introducing birds from the relict Stewart Island population and the sole surviving Fiordland kakapo (Lloyd & Powlesland 1994; Elliott *et al.* 2001). Stewart Island kakapo have a high degree of genetic similarity (Miller *et al.* 2003; Robertson 2006). This has the advantage that, apart from the single surviving Fiordland individual, any differences in energy expenditure that emerge between sites or individuals are unlikely to be due to genetic differences.

Measurements of energy expenditure

Fieldwork was conducted in the period 7 - 22 July 1996. An identical field procedure was used on all individuals in the study. All kakapo studied carried 36.5g radio-transmitters which allowed them to be located up to 2 km away. After capture at daytime roosts, doubly-labelled water was injected into the peritoneal cavity of each bird. Oral introduction was not feasible because kakapo resist manipulation of their bills, and therefore might not have swallowed all the water.

A mixture of 20 AP H₂¹⁸O and 99.9 AP D₂O was injected at a dosage of 5 cm³/kg live mass; this represented about 1% of body water (Tatner & Bryant 1989). Since kakapo may eat a diet high in plant fluids, it was possible that water turnover might have been unusually high, leading to rapid deuterium depletion. Against this, eating supplementary food with low water content would most likely reduce water turnover. This uncertainty led to the choice of isotope dose concentrations identified as optimal from earlier studies (Tatner & Bryant 1989), with no allowance being made for the kakapo's diet.

Isotope injection was followed by equilibration of tracers with the body water. During this equilibration period, birds were kept in semi-darkness, either in large bags or, when available, a pet-crate lined with forest litter. Equilibration time was also chosen by comparison with other studies. Most studies of equilibration in small endotherms have revealed full isotope mixing in less than an hour. In large animals, such as humans, up to 4 h is required. Based on such comparative data, an equilibration period of 2 h was chosen. This was considered to be the minimum time necessary and thereby the best compromise between the requirements of the DLW study and the welfare of kakapo.

In practice, some birds equilibrated for slightly longer, and this variation was subsequently used to confirm that equilibration was indeed complete (see results). Nevertheless, the period in captivity was less than 3 h in virtually all cases. Blood was withdrawn from the brachial

vein and flame-sealed in micro-capillaries (10 x 5 µl). Four days (about 96 h) later, birds were recaptured and a second set of blood samples was obtained. A suitable interval between release and re-capture was derived from equations in Tatner & Bryant (1989) with the aim of achieving ideal final enrichment levels; a four day interval was chosen. Birds were then re-released where they had been captured. In two cases the activity of birds was monitored at night when they are normally active. These 'follows' lasted about 2 h.

Estimates of carbon dioxide production obtained from the DLW studies were used to derive rates of energy expenditure. For this it was assumed that 26.44 kJ were liberated for each litre of CO₂ produced. This presumes a respiratory quotient (RQ) of 0.75. The choice of respiratory quotient in DLW studies is often difficult to justify, especially where diet composition is poorly known or variable, and both were the case in this study. A RQ of 0.80, which is also commonly adopted in animal studies, would imply 25.11 kJ/l of CO₂, leading to a reduction of 5% in estimated energy expenditure. Energy expenditures of kakapo presented here should be recognised as incorporating an assumption of this kind.

Measurements of energy expenditure were made on four categories of individuals. Sample sizes were constrained by the time available and the rarity of the species, so emphasis was placed on making comparisons relevant to the conservation programme which also offered an opportunity to detect sufficiently large energetic differences. Hence male and female expenditures were compared on Codfish Island (both sexes were supplementary-fed), while energy expenditure in relation to environmental and habitat factors was examined by comparing fed males on Little Barrier and Codfish. The effect of supplementary feeding on energy expenditure was compared between two groups of males (fed and unfed) on Codfish Island alone. All the males involved in this study subsequently performed normal lek-courtship behaviour (Merton *et al.* 1984) and several of the females nested a few months after the sampling was completed.

Energy expenditure of kea (*Nestor notabilis*) was measured using DLW, during 7 - 10 August 1996, at the Mount Robert ski field (41° 50' S, 172° 48' E). The aim of this was to provide data from a flying parrot to compare with the flightless kakapo. The kea had access to food provided by day visitors which, to some extent, approximated the supplementary food provided to kakapo. Protocols were identical to those used for kakapo except that only two days (48 h) were allowed between the initial and final blood samples, appropriate to the more rapid isotope turnover expected in this smaller, more active, species.

Supplementary feeding

The supplementary feeding programme was established several years before this study and involved training kakapo to take food, comprised of honey-water, vegetables, fruits and nuts, with added vitamins and minerals, from hoppers

Table 1 Energy densities of food items provided for kakapo at supplementary feeding stations on Codfish and Little Barrier Islands. All energy values are for fresh foods, apart from (dried) chickpeas.

Food Item	Energy density (kJ/100g)
Honey water	Unknown - assumed zero
Apple	150
Kumara	481
Sprouts	172
Carrots	92
Chickpeas	1515
Sunflower seeds	2155
Safflower seeds	1406
Pumpkin seeds	1406 (assumed same as above)
Almonds	2386
Walnuts	2227
Brazil nuts	2528

(James *et al.* 1991; Powlesland & Lloyd 1994). Dependence on supplementary food was known to differ between individuals. Therefore, the amount of supplementary food consumed from hoppers within each bird's home range was recorded. This involved weighing the amount of supplementary food eaten by kakapo over two three-day periods which overlapped the four-day period of doubly-labelled water measurements. In some cases, more than one kakapo might have been using a hopper; this would have led to an over-estimate of an individual's dependence on supplements.

Twelve food-types were provided as supplements during the study. These comprised honey-water (sugar concentration variable and unknown), apple, kumara (sweet potato), sprouts, carrots, chickpeas, sunflower seeds, safflower seeds, pumpkin seeds, almonds, walnuts and brazil nuts. All food types were taken by one or more kakapo (or possibly other animals, such as kiore (*Rattus exulans*)). The energy densities of these food items were obtained from WHO (1979) and Bender (1993) (Table 1).

To estimate the contribution of these food items to the diet it was assumed that assimilation efficiency was 70% in all cases, since there was no experimental information on the assimilation efficiency of kakapo. The value chosen lies in the middle of the range indicated as appropriate for wild birds (Ricklefs 1974). Hence the metabolised energy derived from supplementary feeding, on a 2 x 3 day basis, was: (Energy density, kJ/100g x 0.70)/100 x (fresh mass taken, g), summed across all 11 food items (honey-water was taken as zero energy density). This was then expressed as a mean daily rate to permit direct comparisons with daily energy expenditure (DEE).

Environmental conditions

Data were collected on other factors which could be measured under field conditions and which might have an impact on energy expenditure. Ambient temperature within 10 cm of the ground was measured at sea level and

on the summits of both islands. Wind and solar radiation were not measured since they were unlikely to have had much effect on a ground living, nocturnal species in dense forest. Occasionally, kakapo roost in dense foliage in trees in which case they would be more exposed to wind and sun. Possible effects of tree roosting on energy expenditure were examined by comparing birds with different roosting behaviours.

The weather on Codfish Island was mainly sunny and cold with light winds. Temperatures ranged from -1.7 °C to 10 °C at sea level and from +1 °C to +7 °C at ground level near the summit. On Little Barrier Island, the weather was mild but cloudy with rain and only occasional sunshine. Temperatures ranged from 9 °C to 16 °C at sea level. Summit temperatures, recorded during the day, all lay within this range. Temperatures at the kea study site on Mount Robert ski field ranged from -6.2 °C to 0.8 °C (G. Elliott pers. comm.).

The 'active period' was assessed by determining each bird's first and final movements each night, as indicated by radio-tracking on Codfish Island. The relationship of this to sunset and sunrise was used to determine the active period on Little Barrier Island for construction of a model energy budget for comparison with direct measurements from DLW. These results will be reported elsewhere. All individuals were studied during their protracted moult, however, quantitative moult data were not available. The health status of all individuals was investigated, specifically regarding gut and blood parasites and pathogens. No birds involved in this study were found to have any significant health problem (G. Elliott pers. comm.). Results are presented as mean \pm *sd*, unless stated otherwise.

RESULTS

Evaluation of methods

Choice of injection sites and volumes and the interval between first and second samples could not be determined by a pilot study. Therefore, it was necessary to assess

Table 2 Body mass and doubly-labelled water measurements (\pm sd) for male and female kakapo and male kea, July-August 1996.

Variable	Kakapo (σ^7)	Kakapo (σ^9)	Kea (σ^7)
Body mass	2499 \pm 477	1875 \pm 233	1000 \pm 85
CO ₂	0.54 \pm 0.16	0.54 \pm 0.18	1.34 \pm 0
*BMR _{A&P}	1.42 \pm 0.41	1.31 \pm 0.44	2.75 \pm 0.06
*BMR _{McN}	1.86 \pm 0.56	1.84 \pm 0.62	1.88 \pm 0
DEE	852 \pm 266	641 \pm 219	848 \pm 70
WTO	66.4 \pm 55.9	75.5 \pm 92.9	115
N	15	5	2

Units: Body mass in grams; CO₂ cm³ CO₂ g/h; *BMR multiples of BMR calculated from Aschoff & Pohl (A&P) and McNab (McN) respectively (see text); DEE kJ/d; WTO cm³ water kg/d; N = sample size. Only one value of WTO was available for kea due to uncertainty about injection volume.

Table 3 Mean daily intake (fresh mass) of, and mean daily energy derived from, supplementary food by kakapo during the period of doubly-labelled water measurements. Results from 15 feeding stations on Codfish and Little Barrier Islands.

Types	Amount
Total fruit and vegetables	25.7 g
Total nuts and seeds	25.2 g
Total food	50.9 g
Total, incl. honey-water	61.5 g
Energy via fruit and vegetables	117.5 \pm 206.0 kJ
Energy via nuts and seeds	554.9 \pm 341.1 kJ
Total energy of food	672.4 \pm 505.0 kJ

whether the expected responses occurred; specifically, whether initial isotope concentrations were as predicted from equations derived by Tatner & Bryant (1989) and whether isotope turnover was sufficiently complete to ensure accuracy of the technique (Nagy 1980). In practice, initial isotope concentrations were broadly as expected, confirming that intra-peritoneal injection was appropriate, and that no compartmentalisation of isotopes had occurred. In no case was too little or too much of either isotope turned over, and so appropriate concentrations remained to yield reliable results.

A third requirement was that the 2 h equilibration period was sufficient for complete equilibration. When variation in isotope concentrations over the span of intervals between injection and first sampling was used to examine this aspect, no trend was detected. This analysis necessarily excluded two samples where a lower and higher concentration was induced (respectively, because some DLW was lost during injection and body mass data were not available prior to injection). This analysis confirmed that equilibration was effectively complete, as comparisons with the intervals for similar-sized and larger endothermic species had earlier indicated.

By injecting known mass-specific isotope doses (5 cm³/kg), inferences could be drawn about body composition from variation in initial isotope concentrations. Since water content and lean mass in animals are invariably closely related (Robbins 1983), variation between individuals most likely reflects variation in lipid stores. Initial isotope concentrations were not, however, related to body mass in kakapo, implying a proportionately similar lipid mass in individuals of differing

mass. Direct assessments of body water content using deuterium dilution (Schoeller *et al.* 1980), supported this view, with no change in estimated percentage body water in relation to body mass.

For this assessment, initial isotope dilutions were obtained from the blood samples taken after 2 h equilibration. These observations led to adoption of a mean body water estimate of 47% based on deuterium dilution of all kakapo for which reliable data on injected isotope volumes were available. This relatively low value can be compared with 56% body water for a 2 kg endotherm predicted from the equation of Robbins (1983). The difference is likely to reflect the high levels of lipids stored by kakapo (Livezey 1992).

Natural abundance of isotopes

Background isotope concentrations in kakapo blood were 2005.84 ppm for ¹⁸O and 150.98 ppm for D₂ on Codfish Island, and 1944.61 ppm ¹⁸O and 151.84 ppm D₂ on Little Barrier Island. These are typical natural isotope abundances for the circumstances in which they were found. The background concentrations for each island were used in calculations of isotope turnover appropriate to the islands from which birds came. Background isotope concentrations from kea near Nelson were 1993.54 ppm for ¹⁸O and 144.70 ppm for D₂.

Body mass

Twenty kakapo were measured using the doubly-labelled water technique (Table 2).

Birds changed in mass between the first and second captures by an average of -70 \pm 60 g (-3%),

Table 4 Energy expenditure and water turnover of individual kakapo measured using the doubly-labelled water technique.

Bird	Name	CO ₂	DEE	*BMR _{ASP}	WTO
ka1	Waynebo	0.38	647	1.02	108
ka2	Sandra	0.33	334	0.77	124
ka3	Suzanne	0.78	878	1.87	86
ka4	Alice	0.44	527	1.07	53
ka5	Sara	0.67	807	1.63	58
ka6	Basil	0.70	1151	1.85	14
ka7	Nog	0.60	639	1.41	160
ka8	Ben	0.62	1191	1.72	16
ka9	Whiskas	0.72	921	1.79	144
ka10	Lee	0.73	932	1.81	26
ka11	Lionel	0.60	1100	1.63	31
ka12	Bonus	0.50	643	1.23	156
ka13	Sess	0.29	366	0.72	128
ka14	Margaret Marie	0.47	661	1.19	57
ka15	Felix	0.77	1204	2.01	44
ka16	Ken	-	background	-	-
ka17	Richard Henry	0.63	909	1.62	40
ka18	Dobbie	0.26	433	0.69	61
ka19	Luke	0.42	762	1.13	33
ka20	Arab	0.51	1038	1.44	30
ka21	Barnard	0.43	844	1.19	8
ka22	Heather	-	background	-	-

Units: CO₂ Carbon dioxide production (cdp) cm³ CO₂/g/h; DEE Daily energy expenditure kJ/d; *BMR_{ASP} Multiples of basal metabolic rate derived from the equation of Aschoff & Pohl (1970) (resting phase, non-passerine); WTO Water Turnover cm³ H₂O/kg/d. Birds ka1 - ka16 were from Codfish Island and ka17 - ka22 from Little Barrier Island. All individuals except those with **bold names** ate supplementary food.

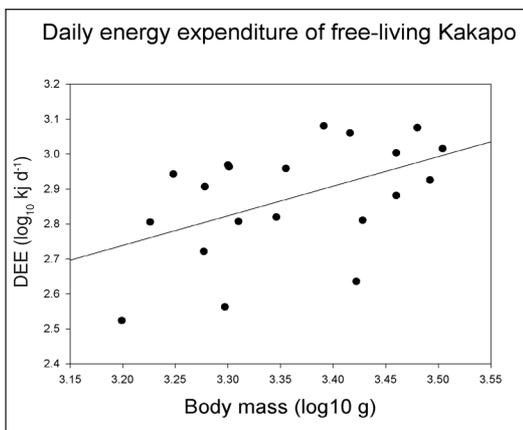


Figure 1 Daily energy expenditure of kakapo in relation to body mass. The equation (Eq.1) of the fitted line is $\text{Log } y = \text{log } a + b \text{ log } x$: where $y = \text{log DEE}$, $a = -0.06$, $b = 0.87$, $x = \text{log Body mass}$ ($r = 0.50$, $n = 20$, $P = 0.025$).

(range: -140 g to +130 g). This was equivalent to an average mass loss of 17.5 g/d (<1% mass). Body mass was measured by placing individual birds in a cloth bag which was then weighed with a spring balance accurate to 0.1 kg. In the early stages of the study it was often assumed that the bag alone weighed exactly

0.2 kg. This approach does not permit firm conclusions about small body mass changes to be drawn for all individuals, although it is likely that minor mass losses occurred in most individuals over the four day measurement period.

Supplementary feeding

All kakapo supplied with supplementary food made use of this during the DLW measurements. The amounts and energy values of food consumed in the first three day period did not differ from that in the second three day period. This may suggest that use of feeding stations was not affected by initial captures or handlings. The bulk of the energy derived from supplementary food came from nuts and seeds, with fruit and vegetables contributing a relatively minor component (17%) (Table 3).

Field energy expenditure of kakapo

Carbon dioxide production of kakapo averaged 0.54 ± 0.16 cm³/g/h ($n = 20$) (Table 2). Mean DEE was 799 ± 256 kJ/d; higher for the heavier males (852 ± 266 , $n = 15$) than for the females (641 ± 219 , $n = 5$). Mass specific metabolic rates (CO₂ cm³/g/h), or expenditure expressed as a multiple of basal metabolic rate (BMR; calculated from Aschoff & Pohl (1970)), did not differ between the sexes (see below). Across all individuals,

Table 5 Daily energy expenditures (kJ/d) of male and female kakapo under different conditions on Codfish and Little Barrier Islands. Standard deviations are given in the text for figures in bold. These refer to direct measurements of DEE, whereas all others are extrapolated values (see text). All extrapolated values have been rounded to the nearest 10.

Type	Codfish Island	Codfish Island	Little Barrier	Little Barrier
	Males	Females	Males	Females
Fed	1116	641	797	460
Non-fed	643	370	460	260

energy expenditure was positively related to body mass (Fig.1). The exponent relating log mass and log daily energy expenditure was $b = 0.87$. This exponent did not differ significantly from either 0.75 or 1.0. Because energy expenditure was not related to measured mass changes, observed expenditures were likely to be representative of kakapo in energy balance. Body mass changes of this magnitude do not, anyway, much affect the reliability of estimates of energy expenditure (Nagy 1980).

Contributions of supplements to kakapo diets

Energy uptake by supplementary-fed kakapo averaged 672.4 ± 505.0 kJ/d (Table 3). Since it was assumed that assimilation efficiency was 70% for all food types, DME (daily metabolised energy) averaged 471 kJ/d, which is $55 \pm 36\%$ of energy expended. At the individual level, supplements contributed from 6 -140% of estimated daily energy expenditure. There was an anomaly at the upper end of the range since assimilated energy exceeded expended energy in one case and yet the bird involved (Arab) did not gain mass. The most likely explanation is that other kakapo, or animals, also took food from the hopper(s) concerned. In the only other case in which intake exceeded expenditure the bird involved gained mass (+5%, Luke), indicating that the excess energy income may have been realistic.

The apparent importance of supplementary food was greater on Little Barrier Island (94%) than on Codfish Island (36%). Even when two exceptionally high values (>100%) from Little Barrier Island were omitted (i.e. leaving the mean DME as 74% of expenditure, $n = 3$), the difference between the two sites remained significant ($P < 0.01$). Comparison of supplementary-fed males on Codfish and Little Barrier Islands confirmed the difference, the latter having obtained about twice as much energy from supplementary food as the former ($P < 0.01$).

Comparisons of energy expenditure between treatment groups

Three comparisons were made between four treatment groups, each group comprising five individuals; supplementary fed males ('fed males') on both Codfish and Little Barrier Islands, supplementary fed females ('fed females') on Codfish Island, and non-fed males on Codfish Island.

For the fed males, CO_2 production (cdp) and DEE were significantly higher on Codfish Island ($F_{\text{cdp}} = 11.1$, $df = 1,8$, $P = 0.01$; $F_{\text{dee}} = 7.9$, $df = 1,8$, $P = 0.02$) with mass specific and daily energy expenditures averaging 52% and 40% respectively more at the southern site (Table 4). Mean DEE of fed males on Codfish Island was 1116 ± 110 kJ/d and 797 ± 227 kJ/d on Little Barrier Island. Mean DEE for fed females on Codfish Island was 641 ± 219 kJ/d and, if the same relativity between male and female measurements also applied on Little Barrier Island, fed females on Little Barrier Island may have had an average DEE of around 460 kJ/d.

Supplementary feeding did not affect mass specific metabolism significantly ($P = 0.06$, see below), although DEE did differ between feeding treatment groups ($F = 22.0$, $df = 1,8$, $P = 0.001$) (Table 4). Mean DEE of non-fed males on Codfish Island was 643 ± 196 kJ/d, 42% lower than fed males. This difference between treatment groups may arise from the greater mass of fed birds (fed σ^2 2600 ± 401 g; non-fed σ^2 2076 ± 365 g; $P = 0.06$) in combination with their modestly elevated mass specific metabolic rates. Supplementary diets, being higher in protein, could also have generated a higher heat increment of feeding and this might also have elevated DEE.

Mass specific metabolism of males did not differ from that of females ($P > 0.1$), although DEE did ($F = 18.7$, $df = 1,8$, $P = 0.002$), following from the significantly greater mass of males ($F = 12.2$, $df = 1,8$, $P = 0.008$). If, for illustrative purposes, the available data on DEE are extrapolated using simple ratios to categories for which no raw data were obtained, the anticipated mean energy expenditure of fed and non-fed males and females at both study sites can be obtained (Table 5). This exercise would yield more accurate results if extrapolations were made directly from body mass data for each 'missing' sex/site/feed category, but these were not available at the time of this study. This caution particularly applies to the extrapolated value for non-fed females on Little Barrier Island. Additional raw data are required to construct a robust multi-factorial statistical model of kakapo field energy expenditure.

Factors influencing energy expenditure of kakapo

An ANOVA with body mass entered as a covariate was used to compare DEE of fed and unfed kakapo. This allowed the full sample to be combined for analysis. Fed

kakapo did not differ in their energy expenditures from unfed individuals ($P = 0.15$), supporting the conclusion from the single factor analysis across treatment groups. Comparisons of the two study sites, again controlling for body mass, confirmed the significant effect of 'site' on energy expenditure identified above: DEE was significantly lower on Little Barrier. Sex did not have a significant effect on DEE after controlling for body mass, again consistent with the single factor analysis.

An additional analysis was possible, based on observations of roosting behaviour amongst the individuals studied. An ANOVA, with body mass entered as a covariate ($P = 0.016$) and roosting site as a factor, showed that birds roosting above ground level may have had a marginally higher DEE ($P = 0.06$) than those roosting on the ground. This was consistent with CO_2 production being significantly higher in tree-roosting kakapo ($F = 4.79$, $df = 1,18$, $P = 0.04$). For these analyses it was assumed that the final roost site was used throughout the foregoing period of DLW measurement, although this was not confirmed by observation. Nevertheless, this assumption is likely to hold in most cases because the majority of birds were faithful to their roost type between first and second captures.

Water turnover

Water turnover (WTO) was estimated from loss of the deuterium label between the initial and final sample. Mean WTO was 69 g/kg/d and strikingly higher in the non-fed (natural diet) group (fed males 26 ± 12 g/kg/d; non-fed males 139 ± 21 g/kg/d; $F = 107.3$, $df = 1,8$, $P < 0.0001$) and significantly lower in fed females compared to fed males ($F = 11.7$, $df = 1,8$, $P = 0.01$) (Table 5). No other factors, apart from sex (see above) affected WTO. In particular, WTO was not related to mass change, suggesting that variation in mass loss was not just a product of birds differing in their rates of water loss.

Effects of supplementary feeding on energy expenditure and water turnover of individual kakapo

Energy expenditure was not related to the amount of food taken from feeding stations. Energy expenditure, expressed as a multiple of BMR to control for body mass (see above), was not related to supplementary food intake amongst the 15 birds using hoppers ($r = 0.012$, $df = 13$, $P = 0.95$, daily energy intake). Similar results were obtained for energy expenditure v. the mass of food taken daily ($r = -0.06$), or its fruit and vegetable ($r = -0.12$) and nut and seed components ($r = 0.10$). In contrast, water turnover was negatively dependent on the amount and nature of certain food supplements taken. Across the full sample of kakapo, including those wholly reliant on natural diets, the most significant correlation identified was for water turnover in relation to the mass of nuts taken (Figure 2; $r = -0.76$, $P = 0.0001$, $n = 20$). Correlations between

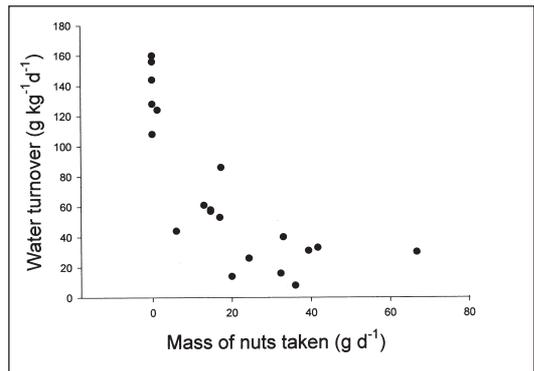


Figure 2 Water turnover by free-living kakapo in relation to the mass of nuts and seeds taken from hoppers. Water turnover was derived from deuterium turnover rates over a period of four days. Food data refer to a period of six days which overlapped the WTO measurement period.

WTO and food intake became progressively weaker as lower energy-density foods containing more water were considered (WTO v. total food intake, $r = -0.52$, $P = 0.02$, $n = 20$; WTO v. total vegetable intake, $r = -0.36$, NS, $n = 20$). The individuals with the highest WTO were those with a completely natural diet. The same ranking of correlation coefficients was found within the supplementary-fed group, ranging from WTO v. nuts, $r = -0.59$, $P = 0.02$, $n = 15$, to WTO v. vegetable intake, $r = -0.23$, $P = 0.41$).

Energy expenditure and water turnover of kea

Only two of five kea injected with DLW were recaptured. CO_2 production of $1.34 \text{ cm}^3/\text{g/h}$ was exactly the same in both individuals, while DEE was $848 \pm 70 \text{ kJ/d}$. Water turnover in one individual was 115 g/kg/d (Table 2).

Comparisons of energy expenditure and WTO with allometric predictions

Comparisons are made with predictions of BMR from Aschoff & Pohl (1970; non-passerine, resting phase) and with direct measures or estimates of BMR from McNab (1995). Energy expenditure of kakapo was $1.39 \pm 0.41 \times \text{BMR}_{\text{A\&P}}$ and $1.85 \pm 0.56 \times \text{BMR}_{\text{McN}}$ (Table 2). Equivalent ratios for kea were $2.75 \times \text{BMR}_{\text{A\&P}}$ and $1.88 \times \text{BMR}_{\text{McN}}$.

WTO was predicted from the non-passerine allometric equation of Williams *et al.* (1993). The observed WTO of non-fed kakapo ($139 \pm 21 \text{ g/kg/d}$) was close to the predicted value (mass 2343 g, WTO = 143 g/kg/d), whereas supplementary fed kakapo ($45 \pm 30 \text{ g/kg/d}$) and kea (115 g/kg/d) had lower WTOs, being respectively 31% and 62% of predicted values (kea: mass 1000 g, WTO = 186 g/kg/d).

Daily energy expenditure of kakapo and kea can be compared with predictions from allometric equations for non-passerine birds in general (DEE or FMR (field metabolic rate) = $8.47 \text{ mass}^{0.704} \text{ kJ/d}$; Williams *et al.* 1993). The predicted DEE of kakapo was 1996 kJ/d whereas the observed value

was approx. 60% lower at 799 kJ/d. Kea are predicted to use 1096 kJ/d but the field measurement (848 kJ/d) was 77% of this.

DISCUSSION

Potential biases in measurements of energy expenditure amongst kakapo

Three factors may have biased the estimates of energy expenditure in kakapo compared with an unmanaged population.

Firstly, all birds carried radio-transmitters, which added mass and hence transport costs and could also have reduced insulation. Both these factors would tend to increase expenditure by comparison with untagged individuals. Radio-transmitters have been estimated to increase expenditure in birds by up to 52% (Gessaman & Nagy 1988). Excessively high values of this kind are very unlikely to apply here, however, because the transmitters were relatively small (only 1-2% of body mass). Kenward (1987) proposed 5% of mass as a normal upper limit for transmitter size in birds, although even relatively small birds will readily carry larger loads. Furthermore, in kakapo, the transmitters do not have to be carried in flight, which will much reduce their impact on energy expenditure. However, Godfrey *et al.* (2003) reported a 8.6% increase in DEE in a flightless rail, takahe (*Porphyrio hochstetteri*), as a consequence of carrying radio-transmitters equal to 1.4 - 2.3% of body mass; they suggested feather disruption by transmitter and harness increased thermoregulatory costs.

The proportion of the surface area covered by the transmitters was small, approximately 1% (assuming 18 cm² for upper surface area of a transmitter while surface area of kakapo was 1770 cm²; calculated after Calder & King (1974)). As a result, any thermal window would also be equivalently small. However, tags were 'warm' on removal and thus were acting as a heat window, as Godfrey *et al.* (2003) found for takahe.

Secondly, food provision may have reduced the need to forage widely, and this could have reduced daily activity costs. However, because no difference in mass specific metabolism was detected between unfed and fed birds on Codfish Island, any such effect must have had only a small direct influence on energy expenditure. The lack of effect was confirmed when energy expenditure of individuals was compared with their dependency on food from feeding stations. Fed birds were rather heavier which increased DEE, albeit also non-significantly. Observations of two individuals indicated that movements of DLW-loaded birds were regular throughout the night. Furthermore, location fixes differed between successive checks during the DLW measurements for some birds, so they clearly moved between days as well as within nights. Fed birds, therefore, maintained an apparently normal foraging pattern. It does not necessarily follow, however, that food supplementation did not reduce energy expended on foraging. For example, if reduced foraging costs were compensated by higher exploratory or

other costs (related to mating or territory occupation, etc.), total daily costs would have remained relatively constant, as was observed.

Thirdly, handling may have had a direct or indirect affect on energy expenditure. Direct effects could arise from a stress response to handling; indirect effects from changes in behaviour after release which might also have affected energy expenditure. Since measurements were made over four days, and both of the birds closely followed by radio-telemetry were known to be active on their first night after capture, the impact of any changes in resting metabolic rates, whether positive or negative, or any necessarily small changes in post-release behaviour, would only have had a small effect in the context of the full sample period. Against this, handled birds mostly lost body mass, a possible indication of a related elevation in metabolism, a reduction in food intake, or an imbalance in water intake and loss.

It seems most likely that initial handling did affect subsequent behaviour to a limited extent, as has been found in a number of studies using doubly labelled water (Uttley *et al.* 1994), but that in this case the effect was apparently trivial, and did not influence estimates of energy expenditure because there was no relationship between mass change and DEE. This would be consistent with mass changes being largely due to a slight excess of water loss over intake.

Alternatively, if mass change is considered to have been due wholly to fat catabolism, this would yield energy equivalent to about a third of mean daily energy expenditure. This is not a precise exercise, however, since birds were only reliably weighed to the nearest 100g. Furthermore, the composition of mass losses are very unlikely to be wholly fat, so the maximum impact of any putative depletion of fat stores on observed DEE would be comparatively small.

Overall, several points suggested that an elevated rate of DEE might result from our study procedures and others a reduction. In addition, the standard assumptions apply and these allow that relatively minor inaccuracies might occur in the course of DLW measurements (Nagy 1980; Tatner & Bryant 1989). No serious bias was likely unless one factor dominated all others, and evidence for this was lacking.

Basal metabolic rates of New Zealand parrots

No data on the basal metabolic rates of parrots were available from this study. The metabolism of a wide range of parrots (Psittaciformes) at rest has, however, been studied. Amongst the five species occurring in New Zealand, four were studied by McNab (1995). These all had basal metabolic rates substantially higher than predicted from the Aschoff & Pohl (1970) 'non-passerine' allometric regression equation. Although no measurements were made on kakapo, McNab (1994, 1995) surmised that it would have a low basal metabolic rate because of a correlation established across parrots and other species which suggested that a low pectoral muscle mass would be linked to a low metabolic rate. McNab (1994, 1995) did not specify whether the pectoralis correlation was likely to imply a causative effect. Since skeletal

muscle at rest has a relatively low tissue metabolism, this is not likely. It seems more likely, following Daan *et al.* (1990), that heart mass, and possibly other organs with high rates of tissue metabolism, would be relatively small in the flightless kakapo. McNab (1995) suggested a BMR of $0.39 \text{ cm}^3 \text{ O}_2/\text{g/h}$ for kakapo (BMR_{McN}).

The predicted BMR for kakapo contrasts with that measured for kea at $0.95 \text{ cm}^3 \text{ O}_2/\text{g/h}$, and based on multiple daytime measurements of two males. Since both kea had been kept in captivity, they may not mirror the pattern in wild kea, because other studies have indicated changes in BMR of captives compared to free-living individuals (Weathers *et al.* 1983). Nevertheless, because no other data were available these results were used in comparisons between field metabolic rate and BMR. The measured BMR of kea was 2.4 times that estimated for kakapo (McNab 1995).

Daily energy expenditure

Energy expenditure of non-breeding kakapo ranged between 334 to 1204 kJ/d: the highest value being over three times the lowest (Table 5). While at the level of individual measurements there is generally more error inherent in the DLW technique than applies to mean DEE values, where it is usually <5%, the wide range of values found amongst free-living kakapo is nevertheless striking. This most likely reflects differences in body size, differences in the circumstances and activity of birds during their measurement periods, as well as inherent differences in individual metabolic rates. Previous studies using DLW suggest that differences of this kind between individuals would persist across repeated measures made under similar circumstances.

The kakapo is characterised by its exceptionally low field metabolic rate. Expressed as a multiple of BMR_{McN} it was 1.85, and as a multiple of Aschoff & Pohl (1970) ($\text{BMR}_{\text{A\&P}}$), it was 1.39. These are the lowest values obtained to date from any adult wild bird using the DLW technique. Because the lowest values were at or below BMR_{McN} , which are not sustainable, it is possible that the true BMR of kakapo is even lower than McNab's (1995) estimate. If this was the case, then the mean multiple of species-specific BMR would be higher. This might not apply, however, because multiples of BMR values used here were calculated from a mean BMR estimate, and individuals with the lowest DEEs might also have had a BMR below this mean value.

One possible explanation for the exceptionally low multiple of BMR is that kakapo might have saved energy by lowering their core body temperatures while roosting during the day. Available data do not support this however. A single cloacal temperature, measured immediately after the bird's capture at 1100 h, was 37.7 °C, which does not indicate a marked daytime depression of core body temperature. This is also consistent with observations of B. Lloyd (40.5°C, $n = 5$, quoted in McNab & Salisbury 1995).

The low level of energy expenditure recorded will partly reflect the season in which the measurements were made. With no breeding activity evident, and moult typically being a period without substantial elevation of DEE (Brown & Bryant 1996), energy costs were unlikely to be at their highest levels for the year. The principal cause of the kakapo's low metabolic rate most likely is its flightless habit, combined with an energetically economical lifestyle. This will be intimately bound up with body structure, so that it is not obvious whether selection has operated on morphology with the observed energetic consequences, or on energy expenditure itself, as suggested by McNab (1994).

Even compared to the only other flightless bird for which there are comparable data, the ostrich (*Struthio camelus*), energetic costs were low. Williams *et al.* (1993) showed that ostriches averaged $2.71 \times \text{BMR}_w$ (after Withers 1983) or $2.18 \times \text{BMR}_{\text{A\&P}}$ (Aschoff & Pohl 1970), both around or above the highest individual rates recorded from kakapo. The kakapo is one of the few wild animals to display energy expenditures which compare closely with the low levels found in 'western man' (Prentice *et al.* 1985; Livingstone *et al.* 1991). The shared characteristics of a sedentary lifestyle, low energy expenditure, current dependence on a diet of higher quality than the ancestral diet, and a relatively high body mass index (i.e. frequent 'obesity') may not be coincidental.

Comparisons of kakapo and kea

DEE of kakapo may be compared with the two results from kea, themselves virtually identical. The kea is characterised by a relatively high BMR but low DEE for its mass. A low DEE of this order is seen amongst some other Australasian birds (Bryant in prep.). McNab (1995) found BMR of kea was 146% of that expected from Aschoff & Pohl (1970), while DEE was only 77% of the value for field metabolism predicted from Williams *et al.* (1993). Expressed as a multiple of basal rates, kea field expenditure was $2.75 \times \text{BMR}_{\text{A\&P}}$ or $1.88 \times \text{BMR}_{\text{McN}}$.

The similarity in the multipliers for kakapo and kea based on McNab's (1995) measurements is notable, and most likely indicates that BMR is a consequence of factors regulating DEE, rather than *vice versa* (Daan *et al.* 1990). Equally, the divergence of multiples of BMR calculated after Aschoff & Pohl (1970), which here serves as a convenient standard against which field metabolism can be measured, confirms the low energy expenditure amongst kakapo, even by comparison with the relatively economic lifestyle of kea (kakapo $1.39 \times \text{BMR}_{\text{A\&P}}$; kea $2.75 \times \text{BMR}_{\text{A\&P}}$). Clearly, by any comparison, the kakapo has strikingly low energy expenditure, which is consistent with a reduced requirement for food.

Water turnover was normal in kakapo that had an exclusively natural diet. Yet it was greatly reduced in kakapo that had access to supplementary food and somewhat reduced in kea, which had access to human-provided food

at the ski-field. This is to be expected given the contrast between the natural diets of these species, in which vegetative material predominates, and the supplementary food they obtain from humans, which are generally low in water and high in energy content.

Supplementary feeding

The low DEE of kakapo has substantial implications for the supplementary feeding programme that is now such a conspicuous part of kakapo conservation management. Clearly, the lower the normal energy demands of an animal the smaller the supplement necessary to meet demands, in part or in full. There is an obvious risk that supplements might be delivered at such a level that would make birds largely or wholly artificially fed, rather than just supplementing their natural diet. This would risk oversupplying birds with energy, possibly leading to obesity, or maybe an under-supply of minor nutrients, causing deficiency symptoms and consequences.

If nutrient intake regulates the timing of breeding for example, either directly or indirectly, then additional feeding could advance breeding or elevate clutch size in a mal-adaptive way (Nilsson 1994). The observation that energy use from hoppers ranged from only 6% to complete substitution, suggests that supplementation could indeed lead to significant nutritional problems for heavily dependent individuals. To view this in context, however, five further points should be considered. First, present estimates of energy taken at hoppers may be inaccurate, because more than one kakapo (or other animal) may have used some hoppers, or food may have been removed but not eaten. Second, the assumptions made about energy density and assimilation efficiency could have been incorrect. Third, the study period may not have been representative of all times of year. Fourth, capture and handling may have increased or decreased supplementary food consumption. Fifth, even small daily supplements, provided they involve an excess of total intake (from all sources) over losses, may lead to cumulative mass gains. Cumulative mass gains, if sustained, could lead to obesity. However, none of these points affects the substance of the conclusion that supplementary food often provided the bulk of the energy intake of kakapo.

The wider implications of supplementary feeding are not yet clear (G. Elliott pers. comm.). On Codfish Island, where use of supplements averages 36% of DME, reliance on natural food sources remains relatively high and presumably the risks of adverse effects are correspondingly low, if not wholly absent. This pattern may relate to the suitability of vegetative cover on Codfish Island, resembling the habitat on Stewart Island from which the birds originally came. In contrast, dependence on supplements on Little Barrier Island appeared to be greater. Notwithstanding the uncertainty about degree of dependence of individuals on supplementary food, its consumption, at least by males, seems to have been generally high on Little Barrier Island. If this is representative over the longer term, and

also applies to females (which were not studied on Little Barrier Island), then it implies an underlying problem. It could suggest a lesser availability of suitable food plants on Little Barrier Island which is a very different floristic environment from the one the birds came from. A scarcity of natural foods, therefore, may have caused a greater reliance on supplementary food to develop, at least during winter months.

Supplementary feeding depressed rates of water turnover amongst kakapo. This appeared to occur primarily as a result of eating energy-dense foods, such as nuts and seeds. The consequences of an unnaturally low water turnover are not clear. It might mean that birds are less able to deal with water shortage during drought, but under these circumstances they would seem likely to resort to moist natural foods or drink naturally available water, unless both drought and a shortage of suitable natural foods coincided. More problematic might be deficiencies of micro-nutrients normally obtained from plant fluids or plant tissues in general, or specifically from certain food species.

Over-reliance on supplementary food might also prevent the ingestion of sufficient quantities of the phyto-chemical cues that could initiate breeding, resulting in a decline in productivity. As a precautionary measure, the amount of dry, high energy food should be reduced, and possibly replaced by foods with greater water content at certain times of year, such as the pre-breeding, laying and moulting periods. In contrast, during chick rearing, any potential hazards of supplementary food to adults (but maybe not their young) would seem much reduced, especially when weighed against the advantages of providing birds with extra nutrition at this time.

CONCLUSIONS

To the unusual suite of characteristics displayed by kakapo can be added an exceptionally low field energy expenditure, averaging only 1.39 times BMR as predicted from Aschoff & Pohl's (1970) equation. Males are more demanding of energy than females, although this is mainly or wholly due to their larger body mass. Daily energy expenditure (kJ/d) can be predicted from body mass (g) for both sexes using the equation: $DEE = 0.87 \text{ Mass}^{0.87}$ (Equation 1).

Energy expenditure of kakapo is likely to be affected by activity level and the thermal environment. A response of this kind was inferred from a lower expenditure of kakapo on Little Barrier Island. Whether it was the more benign thermal environment or lower activity levels allowed by the nature of the habitat, however, is not clear. One other factor may be important in its effect on energy expenditure: choice of roost site. Roosting above ground level was more costly energetically.

Supplementary feeding apparently had an effect on energy expenditure, but largely as a result of a long-term increase in body mass which was itself most likely due to consumption of supplementary food. Water turnover was depressed in supplementary fed birds, particularly when taking high-energy, low water content foods. Water

turnover was also lower in the sample of fed-females compared to fed-males on Codfish Island. This suggests that females were generally more reliant on supplementary food than males, or consumed a higher proportion of dry food, but there was no direct evidence to support these propositions. Alternatively females may normally include a higher proportion of dry natural foods in their diet, such as bark or seeds, than males.

A supplementary feeding programme would be expected to provide a specified but limited proportion of the dietary needs of an animal. Since the kakapo has such low energy expenditure, it is possible that their diet is supplemented at a higher level than originally anticipated. Furthermore, there are potential risks associated with a high dependency on supplements, and some of these are discussed above. An alternative view is that food supplements, far from being either damaging or neutral, were instrumental in allowing breeding, particularly on Little Barrier Island. The present results, which show both a high intake of artificial foods combined with a low energy expenditure on Little Barrier Island, could

be interpreted as indicating circumstances required for reproduction exist on Little Barrier Island. First breeding on Little Barrier Island occurred shortly after the provision of supplementary food (Powlesland & Lloyd 1994; Elliott *et al.* 2006).

Data are now available which will allow more precise matching of supplements to energy requirements. In all cases, energy intake by kakapo, and hence the energy content of supplements presented, will need to exceed the fraction of expenditure to be subsidised by 1/DE (digestive efficiency or assimilation efficiency). The unusual nature of the digestive tract of kakapo makes it desirable that the DE of a range of foodstuffs should, at some point, be measured directly. A simple rule for roughly estimating energy expenditure of wild kakapo, at least during the non-breeding season, is that expenditure equals 300 kJ/kg/d. A more precise estimate may be derived using the allometric Equation 1 above. With additional data, equations could be developed which more exactly matched kakapo expenditure and requirements to mass, sex, season, habitat and other circumstances.

ACKNOWLEDGEMENTS

Many thanks to Graeme Elliott for steering this project from fax to field and back again. Also to all those who helped in different ways in New Zealand: Kathy, Ros Cole, Grant Harper, Rhys Buckingham, Jane, David, David, Don Merton, Paul Jansen, Ron Moorhouse, Malcolm Lightband, and to Peter Jones, Edinburgh, who gave valuable advice before my departure for New Zealand. Ron Moorehouse and Murray Williams were instrumental in ensuring publication in the kakapo issue of *Notornis*. The Department of Conservation provided both funds and facilities for the field programme. Financial support was obtained from the Natural Environment Research Council for stable isotope analysis. Jim Weir, Susan Waldron and Tony Fallick are also thanked respectively for their contributions to sample analysis and for provision of facilities in the Life Sciences Laboratory at SUERC, East Kilbride. The Carnegie Trust for the Universities of Scotland kindly gave funds to support DMB.

LITERATURE CITED

Aschoff, J.; Pohl, H. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *Journal of Ornithology* 111: 38-47.

Bender, D.A. 1993. *Introduction to nutrition and metabolism*. London, UCL Press.

Brown, C. R.; Bryant, D. M. 1996. Energy expenditure during molt in dippers (*Cinclus cinclus*): no evidence of elevated costs. *Physiological Zoology* 69: 1036-1056.

Bryant, D.M. 1989. Determination of respiration rates of free-living animals by the double-labelling technique. Pp. 85-109 In: Grubb, P. J.; Whittaker, J. B. (eds.). *Toward a more exact ecology*. BES 30th Symposium, Oxford, Blackwell.

Bryant, D. M.; Tatner, P. 1988. Energetics of the annual cycle of dippers (*Cinclus cinclus*). *Ibis* 130: 17-38.

Daan, S.; Masman, D.; Groenewold, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *American Journal of Physiology* 259 (R1CP 28): R333-R340.

Elliott, G.P.; Merton, D.V.; Jansen, P.W. 2001. Intensive management of a critically endangered species: the kakapo. *Biological Conservation* 99: 121-133.

Elliott, G.P.; Eason, D.K.; Jansen, P.W.; Merton, D.V.; Harper, G.A.; Moorhouse, R.J. 2006. Productivity of kakapo (*Strigops habroptilus*) on offshore island refuges. *Notornis* 53(1): 138-142.

Gessaman, J. A.; Nagy, K. A. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* 90: 662-668.

Godfrey, J.D.; Bryant, D.M.; Williams, M. 2003. Radio-transmitters increase free-living energy costs in the endangered takahe (*Porphyrio hochstetteri*). *Biological Conservation* 114: 35-38.

James, K. A. C.; Waghorn, G. C.; Powesland, R. G.; Lloyd, B. D. 1991. Supplementary feeding of Kakapo on Little Barrier Island. *Proceedings of the Nutritional Society of New Zealand* 16: 93-102.

Kenward, R. 1987. *Wildlife radio tagging*. London, Academic Press.

Livezey, B. C. 1992. Morphological corollaries and ecological implications of flightlessness in the kakapo (Psittaciformes: *Strigops habroptilus*). *Journal of Morphology* 213: 105-145.

Livingstone, M. B. E.; Strain, J. J.; Prentice, A. M.; Coward, W. A.; Nevin, G. B.; Barker, M. E.; Hickey, R. J.; McKenna, P. G.; Whitehead, R. G. 1991. Potential contribution of leisure activity to the energy expenditure patterns of sedentary populations. *British Journal of Nutrition* 65: 145-155.

Lloyd, B.R.; Powlesland, R.G. 1994. The decline of kakapo (*Strigops habroptilus*) and attempts at conservation by translocation. *Biological Conservation* 69: 75-85.

McNab, B. K. 1994. Energy conservation and the evolution of flightlessness in birds. *American Naturalist* 144: 628-642.

McNab, B. K. 1995. Energetics of New Zealand's temperate parrots. *New Zealand Journal of Zoology* 22: 339-349.

Merton, D.V.; Morris, R.D.; Atkinson, I.A.E. 1984. Lek behaviour in a parrot: the kakapo (*Strigops habroptilus*) of New Zealand. *Ibis* 126: 277-282.

- Miller, H.C.; Lambert, D.M.; Millar, C.D.; Robertson, B.C.; Minot, E.O. 2003. Minisatellite DNA profiling detects lineages and parentage in the endangered kakapo (*Strigops habroptilus*) despite low microsatellite DNA variation. *Conservation Genetics* 4: 265-274.
- Nagy, K. A. 1980. CO₂ production in animals: analysis of potential errors in the doubly-labelled water method. *American Journal of Physiology* 238: R466-R473.
- Nilsson, J. A. 1994. Energetic bottle-necks during breeding and the reproductive costs of being too early. *Journal of Animal Ecology* 63: 200-208.
- Powlesland, R.G.; Lloyd, B.D. 1994. Use of supplementary feeding to induce breeding in free-living kakapo (*Strigops habroptilus*) in New Zealand. *Biological Conservation* 69: 97-106.
- Powlesland, R.G.; Merton, D.V.; Cockrem, J.F. 2006. A parrot apart: the natural history of the kakapo (*Strigops habroptilus*), and the context of its conservation. *Notornis* 53 (1): 3-26.
- Prentice, A. M. *et al.* 1985. Unexpectedly low levels of energy expenditure in healthy women. *Lancet*, i: 1419-1422.
- Ricklefs, R.E. 1974. Energetics of reproduction in birds. Pp. 152-297 *In*: Paynter, R.A. (ed.) *Avian energetics*. Cambridge, Mass., Nuttall Ornithological Club.
- Robbins, C. T. 1983. *Wildlife feeding and nutrition*. New York, Academic Press.
- Robertson, B.C. 2006. The role of genetics in kakapo recovery. *Notornis* 53(1): 173-183.
- Schoeller, D. A.; van Santen, E.; Peterson, D. W.; Dietz, W.; Jaspan, J.; Klein, P. D. 1980. Total body water measurements in humans with 18O and 2H labeled water. *American Journal of Clinical Nutrition* 33: 2686-2693.
- Tatner, P.; Bryant, D. M. 1989. Doubly-labelled water technique for measuring energy expenditure. Pp. 77-112 *In*: Bridges, C. R.; Butler, P. J. (eds.) *Techniques in comparative respiratory physiology: an experimental approach*. Cambridge, Cambridge University Press.
- Uttley, J.; Tatner, P.; Monaghan, P. 1994. Measuring the daily energy expenditure of free-living arctic terns (*Sterna paradisaea*). *Auk* 111 (2): 453-459.
- Weathers, W. W.; Weathers, D. L.; van Riper, C. III. 1983. Basal metabolic rate of the Apanane: comparison of freshly caught with long term captives. *Auk* 100: 977-978.
- WHO 1979. *The health aspects of food and nutrition*. Manila, WHO.
- Williams, J. B.; Siegfried, W. R.; Milton, S. J.; Adams, N. J.; Dean, W. R. J.; Duplessis, M. A.; Jackson, S.; Nagy, K. A. 1993. Field metabolism, water requirements, and foraging behavior of wild ostriches in the Namib. *Ecology* 74 (2): 390-404.
- Withers, P. C. 1983. Energy, water, and solute balance of the ostrich (*Struthio camelus*). *Physiological Zoology* 56: 568-579.