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Gastrointestinal tract of the brown kiwi (*Apteryx mantelli*)

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Abstract

The caeca of the brown kiwi *Apteryx mantelli* increased in length isometrically with body mass, but wall mass and thus mucosal thickness increased allometrically. Kiwi caeca are sacculate, with greater thickness of mucosa in the proximal portions. The caecal mucosa is similar to the small intestinal mucosa, with well-developed mucosal folds, villi, and crypts of Lieberkühn or intestinal glands. The solid matter in caecal digesta contained disproportionately large quantities of material that was not retained by a 75 μm sieve. The per cent of incombustible material (total ash) within the caeca digesta did not differ significantly from those within adjacent small intestinal or rectal segments. The fine particles within the caeca were not composed of fine crystalline uric acid; chemical analyses showed only low levels of uric acid in caecal digesta. These findings indicate that the caeca of this flightless insectivorous ratite are a site for the sequestration and fermentative digestion of fine particulate material, such as plant fibre, fragmented chitin or uric acid crystals.

Introduction

Avian caeca have diverse functional capabilities that may vary in importance with the diet and nutritional strategy of the species (Clench & Mathias, 1995). Thus, the organ may have a predominantly fermentative function in herbivores such as the capercaille *Tetrao urogallus* and willow grouse *Lagopus lagopus* that are known to harbour caecal cellulolytic organisms (Suomalainen & Arhimo, 1945), a water-conserving function in the rock ptarmigan *Lagopus mutus* (Gasaway, White & Holleman, 1976), a nitrogen-recycling capability in chickens (Moretensen & Tindell, 1981), a role in defence against pathogens (Glick, Chang & Jaap, 1956; Barnes, 1977) and a site for the synthesis of vitamins by microbial symbionts (Couch *et al*., 1950). Attempts to correlate the mucosal histology (Naik, 1962) and the gross morphology (Clench & Mathias, 1995, 1999) of the caecum with these functions (Duke, 1989; Angel, 1996; DeGolier, Mahoney & Duke, 1999; Jozefiak, Rutkowski & Martin, 2004) have met with limited success. Thus, although herbivore caeca are generally larger and carnivore caeca smaller (Clench & Mathias, 1995), caecal size also varies between insectivores and piscivores (McLelland, 1989) and within piscivorous, insectivorous and herbivorous species. If the caecum is able to selectively retain finer, potentially more nutritious, particles (Duke, 1986), it is likely that the organ will become prominent in species that require the mass of retained digesta to be minimized, such as in marsupial arboreal folivores (Hume, 1999).

In the light of the above, it is likely that caecal form is influenced by a number of factors, including phylogeny, dietary niche, availability of water (Clench & Mathias, 1995) and volancy. Therefore, in order to gain a better understanding of the manner in which caecal function is adapted to dietary niche, it is useful to assess caecal morphology and function in phylogenetically well-delineated groups of avian species. It is possible that the caeca of insectivorous avian species may be adapted to fermentation of chitin or uric acid, the latter being produced in significant quantities with a diet that is rich in protein and nucleic acids. However, little information is available regarding such adaptation for any insectivorous species.

Ratites are an ancient lineage (Tuinen, van Sibley & Hedges, 2000) whose caecal size has likely developed without the restrictions imposed by flight, thereby allowing morphological adaptation to be more readily attributed to the effects of diet and ecological niche. Ratite caeca may be particularly well suited for water and fermentative nitrogen conservation as the ureters in this group open directly into the coprodeum, a position that may facilitate the reflux of 'urine' into the large intestine (Oliviera *et al*., 2004).

The gross morphology of the gastrointestinal tract (hereinafter termed 'gut') has been described in a number of large herbivorous ratite species (Angel, 1996). Caecal length comprises around 6–8% of total gut length in the ostrich (Angel, 1996; Ullrey & Allen, 1996), an arid-zone grazer/browser, around 21% of total gut length in the rhea, a pampas grazer (Pereira, Martella & Navarro, 2003), and around 2% in the emu, an opportunistic feeder that prefers

fruits, seeds, flowers, insects and young foliages, but is able to survive on poor-quality foliage (Davies, 1978). The lack of caecal development in the latter species may result from the presence of a sacculated distal small intestine where there is fermentative digestion (Herd & Dawson, 1984), which may compromise caecal filling by antiperistaltic colonic contractions (Duke, 1989).

The caeca of the brown kiwi *Apteryx mantelli,* a temperate rainforest insectivore, have been noted to be relatively large (Mitchell, 1901; Maumus, 1902), but neither the anatomy of the digestive tract, the histology of the mucosa nor the nature of the contained digesta have been described. The current work was undertaken to assess caecal adaptation in this endangered species by the use of accidentally killed specimens obtained opportunistically.

Materials and methods

Samples

Seventy-three kiwi carcasses (or parts thereof) were supplied for this study from the Tongariro-Taupo, Northland and East Coast-Hawke's Bay conservancies of the Department of Conservation. All specimens came from the North Island, New Zealand (latitude 35–40°; longitude 172–178°) during the period 1996–2002, and were immediately frozen on recovery. No chicks were included; thus allometry coefficients that were derived were not ontogenetic.

The cause of death of the birds was varied and included road traffic accidents, inadvertent trapping (and subsequently euthanasia), drowning, hypothermia and predation by dogs, pigs, cats, stoats and ferrets.

Morphometric measurements

Thirty-six carcasses were judged suitable for morphometric measurement, although some were incomplete owing to damage of particular segments of the intestinal tract. Reduced major axis (RMA) analyses were restricted to 28 carcasses that were complete. Particle size analyses were restricted to 13 carcasses that were freshest and had complete sets of digesta for all gut sections. (*Note*: In the kiln treatment one sample was inadvertently lost, reducing the sample size to 12.) Carcasses that had been exposed to formalin were not used, as this is known to cause changes in the relative proportions of components of the digestive tract (Lentle, Stafford & Henderson, 1997) and to influence particle size distribution by causing aggregation (Hume, Jazwinski & Flannery, 1993).

The viscera were removed from each thawed carcass via a ventral midline abdominal incision. The digestive tract was divided proximally at the mid-thoracic oesophagus and distally at the point of entry of the rectum into the cloaca. All mesenteric attachments to the gut were then freed, and measurement of the gut components was carried out on a flat moist stainless steel surface to prevent any inadvertent stretching.

The overall length of each segment of the gastrointestinal tract was measured with a flexible tape measure (± 1 mm). The following dimensions were recorded: the long axis of the proventriculus from the junction with the oesophagus to the junction with the gizzard; the long axis of the gizzard; the length of the small intestine from the junction with the gizzard to the entry of the caecal ostia; the lengths of the two caeca from their junction with the small intestine to their tips; and the length of the rectum/colon from the point of entry of the caecal ostia to the cloaca.

The diameter of the various gut components was determined with vernier calipers (± 0.05 mm) at the following points: the gizzard at its maximum diameter; the small intestine at its commencement, at the junction of the first and second quarter, at its midpoint, at the junction of the third and fourth quarter and at its termination; the caecum at the junction of the first and second quarter, at its midpoint and at the junction of the third and fourth quarter; and the rectum at its midpoint.

After these measurements were taken, the intestinal tract was divided into its component segments; the digesta were expressed from each segment, weighed and then frozen pending further analysis. The wet mass of tissue in each segment (± 0.1 g) was determined with the proventriculus and the gizzard combined together. Caecal morphology was examined using a dissecting microscope with indirect illumination. Segments *c.* 5 mm in length were taken from the proximal end and the midpoint of the best-preserved caeca and placed in 10% formalin for subsequent histological examination.

Allometric analysis (White & Gould, 1965; Gould, 1966; Reiss, 1989) was used to investigate the relationships between the lengths of all gut components with total gut length, following the method of Lentle *et al.* (1998).

Particle size analyses

After thawing, samples of digesta were suspended in 30 mL TRIS buffered saline at pH 10 (1.21 g of trihydroxymethylamine plus 4.4 g of NaCl, made up to 500 mL with deionized water) and agitated with a Rocker model 25 (Labnet International S2025-D-220 #771) at 100 oscillations per minute for 10 min in order to suspend solid matter and hydrolyse any adherent mucus. The mixture was subsequently washed through a stack of Endocott sieves of 2000, 1000, 500, 250, 106 and 75 μm mesh size with deionized water. The contents of each sieve were washed onto hardened, ashless, Whatman 541 filter paper in a Buchner funnel. The filter papers and their contents were dried overnight at 80 °C in a forced-draft oven before weighing. The total volume of the sieve eluate was determined and a sub-sample of known volume was dried in a pre-weighed container in the forced-draft oven. This enabled the total dry matter content of fines and soluble material in the digesta sample to be calculated after subtraction of the known quantity of solids (calculated to be 0.3366 g) in the 30 mL of TRIS buffered saline that was added to ensure mucus hydrolysis. The percentage of solids in each of the

filter fractions and of the eluate was calculated as a percentage of their sum.

The percentage size distribution of particles in each gut segment was calculated as the dry mass of the digesta fraction in each sieve for each kiwi divided by the total mass of sieves for that kiwi times 100% [using fines minus the tris value (= 0.3366)].

The percentage size distribution of particles $>75\,\mu$m in each gut segment was calculated as the dry mass of the digesta fraction in each sieve $>75\,\mu$m for each kiwi divided by the total mass of sieves $>75\,\mu$m for that kiwi times 100% [using fines minus the tris value (= 0.3366)].

The percentage of incombustible material (total ash) within each particle size group was calculated as the mass of total ash for sieve 1 for kiwi 1 divided by the dry mass of sieve 1, plus the mass of total ash for sieve 2 for kiwi 1 divided by the dry mass of sieve 2, and so on for each sieve, and then repeated for each kiwi. Total ash was determined by incinerating weighed dried samples of digesta at 550 °C for 16 h in a muffle furnace.

Histology

The transverse samples of caeca were processed into paraffin wax using an automatic tissue processor (Leica TP 1050, Germany). Microtome sections were cut at 4 μm in thickness and collected onto clean glass slides. After air drying, the slides were stained with haematoxylin and eosin (H&E) using standard histological methods. The stained and mounted sections were examined and imaged by brightfield microscopy (Zeiss, Axiophot, Germany).

Chemical analysis

Samples of wet caecal digesta were alkalinized and particulate matter was centrifuged at 13 000 rpm (g-max = 11 337) for 2 min. The uric acid content of the supernatent was determined by a colorimetric assay using the uricase colorimetric peroxidase amino-phenazone (PAP) method (Yuki, Yajima & Kawasaki, 1980). This method is based on the colorimetric reaction of hydrogen peroxide formed during the decomposition of uric acid to allantoin using uricase.

Statistics

RMA and other analyses were conducted in the Systat statistical software suite (Wilkinson, 1990).

Results

Gross anatomy

The relative lengths of the components of the kiwi gastrointestinal tract are shown in Table 1 (ratite species do not possess a crop). The two caeca were similar in size, each with a somewhat spatulate conformation with a noticeably narrowed neck. *In vivo*, each lay lateral to the lumen of the distal small intestine in a near-vertical position and opened separately into the lateral aspect of the rectum (not in a conjoined manner as reported previously by Clench & Mathias, 1995).

Table 1 Dimensions of the gut components of the brown kiwi *Apteryx mantelli* based on all available samples

Parameter	*n*	Mean	SE
Total length of gut[a]	28	166.10	6.24
Proventriculus length	32	2.96	0.10
Gizzard length	36	5.69	0.20
Small intestinal length	36	122.94	4.13
Total length of caeca[b]	34	33.00	1.15
Rectal length	35	12.20	0.50
Small intestinal width	36	0.78	0.03
Caecal width	32	0.68	0.03
Wet tissue mass of gizzard and proventriculus	36	26.00	1.61
Wet tissue mass of small intestine	35	22.95	2.28
Total wet tissue mass of caeca[b]	33	6.20	0.56
Wet tissue mass of rectum	33	4.41	0.56

Length and width in cm; mass in g.
[a]Determined from the proximal end of the proventriculus to the cloaca, plus the combined length of the two caeca.
[b]Both caeca combined.

The exterior and interior surfaces of the caeca were smooth, bearing no hairs or other filtration structures (Fenna & Boag, 1974). There were no localized increases in the thickness of the proximal wall consistent with caecal tonsil formation.

Allometric analyses

With the exception of the proventriculus, which scaled with negative allometry, and the small intestine, which scaled with positive allometry, the length of the gut components scaled with total gut length in a manner that was not significantly different from isometry (Table 2). Gut width scaled negatively allometrically with the corresponding length of the gut component in the small intestine and rectum but increased isometrically with length in the caeca (Table 2).

The wet mass of small intestinal and caecal tissue scaled with positive allometry with respect to the total mass of gut tissue whereas that of the rectum scaled isometrically. The scaling of the wet mass of caecal tissue with total mass of gut tissue was not significantly different from that of the small intestine (Student's *t*-test: $n = 30$; $t = 0.904$; $P = 0.200$).

The lengths and diameters of the caeca (Table 3a) indicated a slightly ovoid morphology with maximum diameter at the midpoint. Principal components analysis of these dimensions showed that (Table 3b) as size of caeca increased, the proximal diameter and length increased but the more distal diameters were reduced.

Histology

The caecal wall had a well-developed tunica muscularis comprising a thick inner circular layer and a thin outer longitudinal layer. The outermost part of the tunica

Table 2 Results of reduced major axis (RMA) analyses of the complete digestive tract of 28 brown kiwi *Apteryx mantelli*

Parameter	Region	Independent variable	RMA slope ± SE	r^2	Student's *t*	*P*
Length	Proventriculus	Total gut length	0.791 ± 0.098	0.715	+2.130	**0.05**
Length	Gizzard	Total gut length	1.193 ± 0.210	0.197	−0.920	>0.2
Length	Small intestine	Total gut length	1.068 ± 0.026	0.985	−2.625	**0.01**
Length	Caeca	Total gut length	1.045 ± 0.067	0.893	−0.665	>0.2
Length	Rectum	Total gut length	1.047 ± 0.149	0.474	−0.314	>0.2
Width	Gizzard	Gizzard length	0.731 ± 0.138	0.793	−1.951	0.1
Width	Small intestine	Small intestine length	0.202 ± 0.035	0.525	−22.808	<**0.0005**
Width	Caeca	Caeca length	1.110 ± 0.209	0.270	+0.527	>0.2
Width	Rectum	Rectal length	0.540 ± 0.105	0.232	+4.382	<**0.0005**
Tissue mass	Gizzard/proventriculus	Total gut tissue	0.755 ± 0.044	0.916	−5.108	<**0.0005**
Tissue mass	Small intestine	Total gut tissue	1.332 ± 0.073	0.920	+4.542	<**0.0005**
Tissue mass	Caeca	Total gut tissue	1.394 ± 0.100	0.866	+3.941	<**0.0005**
Tissue mass	Rectum	Total gut tissue	1.196 ± 0.142	0.631	+1.377	>0.1

Significant *P*-values are shown in bold.

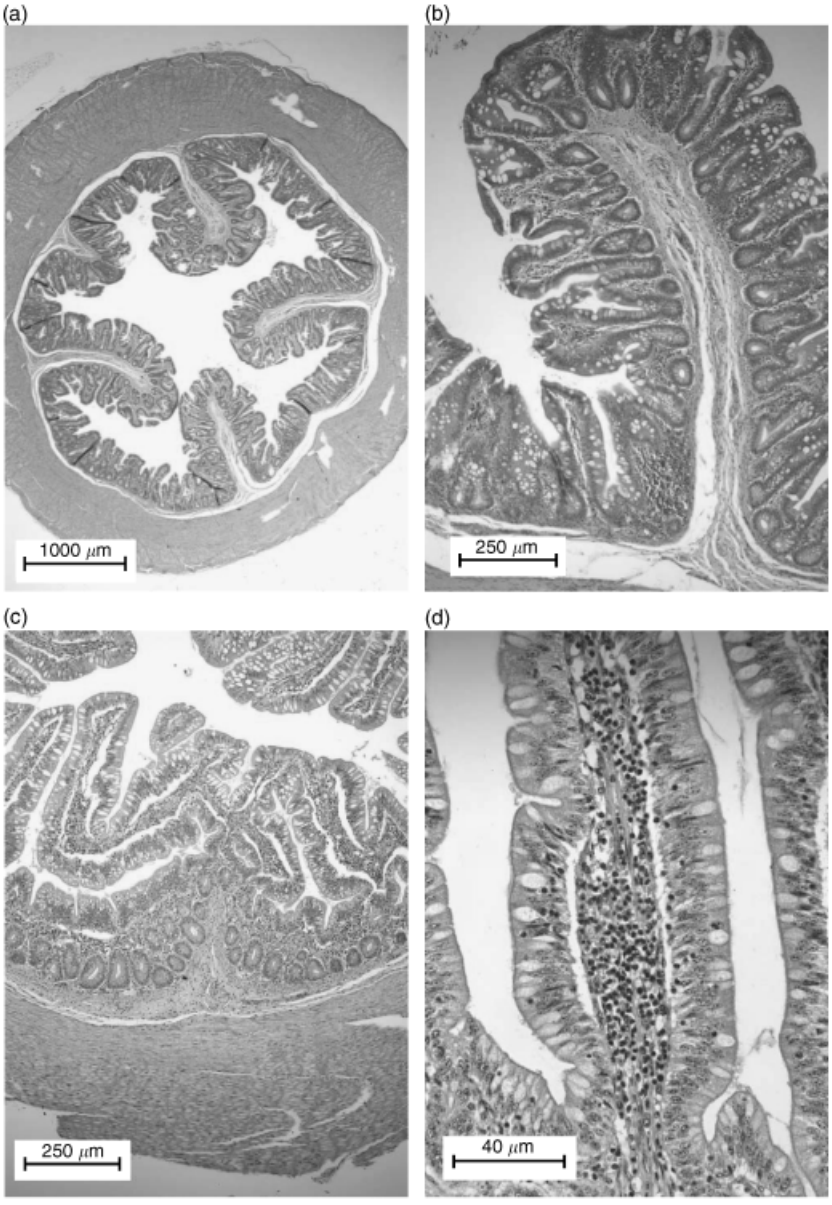

Figure 1 (a) Transverse section of proximal caecum showing long villi and well-developed muscularis mucosae and tunica muscularis. (b) Caecal villus, longitudinal section. Typical absorptive epithelium is present, with microvilli and goblet cells evident. Note the presence of lymphocytes in the epithelium and in the lamina propria. Smooth muscle derived from muscularis mucosae is seen in the core of the villus. (c) Transverse section at mid-caecum. The villi are shorter than in the proximal segment. The entire tunica mucosa is folded to form plicae. The tunica muscularis is well developed, comprising a thick inner circular layer and a thin longitudinal outer layer. The tunica serosa is typically thin. (d) Longitudinal section showing plicae. Each plica is supported by a central core of fibrous connective tissue in the tunica submucosa. The lamina propria show lymphocytic infiltration, both between crypts of Lieberkühn and in the villi.

Table 3 Brown kiwi *Apteryx mantelli* caecal dimensions (mean ± SE) and shape in post-mortem specimens

(a) *Measurement in cm*

Mean caecal width			
First quadrant	Midpoint	Third quadrant	Caecal length
0.72 ± 0.03	0.96 ± 0.07	0.79 ± 0.04	16.5 ± 0.57

(b) *Principal components analysis*

	Principal component axis	
Parameter	1	2
Mean caecal length	0.799	−0.127
Width first quadrant	0.363	−0.903
Width midpoint	0.787	0.254
Width third quadrant	0.786	0.291
Per cent variance explained	50.2	24.5

Caecal width was recorded at $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ of the total length from the ostium to the tip. $n=28$.

muscularis bore a thin serosa. The tunica mucosa was folded into numerous plicae that contained a well-developed muscularis mucosa. The luminal surface of the tunica mucosa was covered in villi that were longer proximally than distally and abutted with crypts of Lieberkühn that opened at their bases. The villous mucosa bore a typical absorptive epithelium, with microvilli and goblet cells clearly evident. There were large numbers of lymphocytes in the lamina propria both within the villi and between the crypts of Lieberkühn. In some areas the lamina propria contained small aggregates of diffuse lymphoid tissue (Fig. 1).

Particle size analysis

The relative proportions of total and incombustible particle sizes in various segments of the gut of brown kiwi are presented in Table 4. Discriminant analysis (Table 5) showed that digesta particle sizes differed significantly between all gut segments, and that successful discrimination between digesta from the various gut segments was chiefly on the basis of the relative proportions of the particles in the size range $>500\,\mu$m and particles of less than $75\,\mu$m, that is unretained fines. The former were present in highest proportions in the gizzard digesta, enabling gizzard digesta to be readily distinguished from digesta of the three remaining segments. Similarly, the particle size spectra of caecal contents were distinguishable from those of the small intestine and rectum on the basis of a greater content of unretained fines.

Discriminant analysis of the relative proportion of total ash in each particle size fraction showed less successful discrimination between gut segments (Table 6). Discrimination between the digesta from the various gut segments was based chiefly on a contrast between the proportion of total ash in the unretained fines and in the coarse factions. The relative proportion of total ash in the finest particle fraction was lowest in the gizzard (Table 4) but did not differ significantly between the small intestine, caeca and rectum (Table 6).

Table 4 Relative proportions of total and incombustible particle sizes in the guts of brown kiwi *Apteryx mantelli* (mean ± SE)

	Gizzard contents ($n=13$)			Intestine contents ($n=8$)			Caecal contents ($n=6$)			Rectal contents ($n=6$)		
Sieve size (μm)	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*	*A*	*B*	*C*
2000	72.93 ± 5.01	81.24 ± 3.72	61.08 ± 9.36	5.00 ± 1.65	6.53 ± 2.15	27.32 ± 5.35	0.73 ± 0.32	10.76 ± 6.42	27.04 ± 5.37	1.57 ± 0.56	3.47 ± 1.22	18.38 ± 11.10
1000	5.19 ± 1.41	5.87 ± 1.58	40.54 ± 7.59	5.47 ± 1.29	7.63 ± 1.85	31.46 ± 3.98	1.02 ± 0.20	7.48 ± 2.31	14.57 ± 5.11	4.16 ± 1.62	7.68 ± 2.22	15.05 ± 4.57
500	3.29 ± 0.65	3.92 ± 0.80	40.59 ± 7.07	15.37 ± 4.25	19.51 ± 3.71	46.79 ± 5.40	1.81 ± 0.62	10.77 ± 2.69	27.63 ± 5.86	5.93 ± 2.66	10.48 ± 2.92	26.87 ± 8.02
250	2.73 ± 0.48	3.29 ± 0.66	47.26 ± 5.69	12.82 ± 1.24	17.52 ± 1.10	51.98 ± 3.37	3.42 ± 1.27	13.60 ± 2.59	56.50 ± 9.68	8.15 ± 2.04	15.71 ± 1.57	36.74 ± 9.20
106	2.89 ± 0.72	3.68 ± 1.17	42.38 ± 5.44	18.99 ± 2.34	26.48 ± 3.12	55.17 ± 4.95	7.46 ± 2.70	27.89 ± 4.66	61.88 ± 6.90	14.79 ± 2.38	30.78 ± 3.90	38.16 ± 11.13
75	1.54 ± 0.39	2.01 ± 0.63	49.54 ± 7.05	16.20 ± 2.27	22.33 ± 2.72	59.06 ± 6.27	7.82 ± 2.93	29.51 ± 5.44	57.89 ± 6.20	14.94 ± 1.65	31.87 ± 3.36	49.31 ± 9.86
Fines	11.38 ± 3.09		2.82 ± 2.13	26.15 ± 6.24		37.80 ± 10.59	77.73 ± 7.18		20.56 ± 5.96	50.46 ± 7.41		24.88 ± 8.45

A, particle size distribution (dry matter g/100 g digesta); *B*, size distribution of particles ≥ 75 μm (dry matter g/100 g digesta); *C*, per cent of incombustible material within each particle size group (g total ash/g dry matter).

Table 5 Discriminant analysis of digesta particle sizes in the gut segments of 13 brown kiwi *Apteryx mantelli*

Particle fraction	Discriminant function[a]	*F*-to-remove
>2 mm	+1.522	3.41
>1 mm <2 mm	+0.636	2.05
>500 μm <1 mm	−0.172	14.38
>250 μm <500 μm	+0.281	0.74
>106 μm <250 μm	+0.281	1.19
>75 μm <106 μm	−0.085	1.12
<75 μm	+0.745	1.25

Segment	Caeca	Gizzard	Small intestine
Caeca	–		
Gizzard	23.94	–	
Small intestine	6.375	25.579	–
Rectum	8.827	26.344	4.882

Wilke's $\lambda = 0.0090$, d.f. = 7,3,29; $F = 13.048$, d.f. = 21,66, $P < 0.0005$; jack-knifed classification 82% correct.
[a]Standardized within variances.
Between-groups *F* matrix. d.f. = 7,23. All $P < 0.001$.

Table 6 Discriminant analysis of the total ash in various particle fractions and gut segments from 12 brown kiwi *Apteryx mantelli*

Particle fraction	Discriminant function[a]	*F*-to-remove
>2 mm	+0.261	0.26
>1 mm <2 mm	+0.263	1.75
>500 μm <1 mm	+0.489	5.35
>250 μm <500 μm	−0.466	0.35
>106 μm <250 μm	+0.288	0.83
>75 μm <106 μm	+0.429	0.67
<75 μm	−1.077	4.57

Segment	Caeca	Gizzard	Small intestine
Caeca	–		
Gizzard	2.618	–	
Small intestine	1.395	4.260*	–
Rectum	2.225	4.792*	2.870

Wilke's $\lambda = 0.1292$, d.f. = 7,3,27; $F = 2.970$, d.f. = 21,60, $P < 0.0005$; jack-knifed classification 52% correct.
[a]Standardized within variances.
Between-groups *F* matrix. d.f. = 7,21.

Chemical analyses

Low levels of uric acid were detected in the two samples of caecal digesta (mean = 0.030%). The fine particulate material present in the caecal digesta formed a white insoluble residue on the surface of the plug of solids formed after centrifugation.

Discussion

Allometric analyses indicated that the length of the small intestine increased with positive allometry whereas the other gut components, with the exception of the proventriculus that increased in a negatively allometric fashion, increased isometrically with total gut length. However, the relative proportion of tissue in the small intestine and in the caeca increased with positive allometry and at a similar rate, reflecting the metabolic importance of both these regions. The isometric increase in length is somewhat surprising in view of observations by McLelland (1989) that insectivorous avian species have long caeca, but McLelland (1989) did not use allometric analysis. The positive allometric increase in the mass of caecal tissue with gut size mitigates against the caeca having a role that is not quantitatively proportional to metabolic mass, such as the sequestration of enteral microorganisms in a blind-ended sack so as to reduce their rates of washout. As the histological studies show, the caecal mucosa was of typical 'small intestinal type' that is associated with digestion and absorption (Naik, 1962). The positive allometric increase in caecal tissue mass with gut mass is likely to reflect an increase in mucosal thickness.

The results of the discriminant analysis of particle size distributions suggest that fine particles 'accumulate' in the caeca of brown kiwi. This situation is similar to that in the caecum of a number of herbivorous mammals (Björnhag, 1987) where nutrient-rich, fine particles accumulate, allowing extension of residence time and fermentative digestion. Studies of a range of avian species, including insectivores, show that the caeca are capable of both peristaltic and antiperistaltic contractions, which may facilitate the entry and expulsion of particulate material (Duke, 1989). Colonic antiperistaltic contractions have been shown in a variety of species, including emus, herons, ducks, geese, hawks, galliforms, gulls, roadrunners, owls and crows (Clench & Mathias, 1995).

Peristaltic caecal contractions, in conjunction with colonic antiperistaltic contractions, may extrude the fluid component of colonic digesta, along with suspended fine particulate material (Clench & Mathias, 1995), as identified in this study. The passage of the fluid component along with suspended fine material through the narrowed proximal portion of the caeca may result in the 'selective' entry of finer particles into each lateral caecal opening. It is noteworthy that the caecal openings are separate and not fused as in other herbivorous ratites (Clench & Mathias, 1995), which may represent specialization to reduce the size of caecal ostia so as to enhance selective entry of particles. It is also noteworthy that we found no hairs or villous projections into the proximal lumen such as have been postulated to filter out larger particulate material in the caeca of other avian species (Fenna & Boag, 1974).

The results of the discriminant analysis of the relative proportions of total ash suggest that the fine particulate fraction, which occurs equally in the caeca, rectum and small intestine, does not comprise fragmented gizzard stones or the tilth from earthworms that comprise a significant proportion of the kiwi diet (Kleinpaste, 1990). Furthermore, the accumulation of fine material may be in some way selective, possibly on the basis of density in conjunction with the vertical orientation of the caeca. This could

enhance the passage of relatively buoyant material to the caecal tip and the distal sedimentation of denser, more rapidly sedimenting material.

The fine particulate matter sequestered in the caeca contains a higher proportion of combustible material than that in adjacent gut segments. *In vivo*, this may comprise plant fibre, bacterial aggregates accumulating during fermentative digestion of caecal contents, fragments of chitin produced by the action of the gizzard, or uric acid crystals from colonic and cloacal contents in the manner hypothesized for other avian species (Braun & Campbell, 1989; Clench & Mathias, 1995). We found little uric acid in the kiwi caeca. This finding fits with the reported rapid degradation of uric acid in avian caeca (Karasawa, 1999), because specimens were obtained some unknown time after death. Uric acid is excreted in a crystalline colloidal suspension of 0.5–13 μm in diameter (Braun & Campbell, 1989) that is said to allow for rapid bacterial digestion. Moreover, microbial degradation has been shown to take place rapidly *in vivo* (Karasawa, 1989).

Chitin appears to be relatively indigestible in birds. The common nighthawk *Cordeiles minor*, an insectivorous caprimulgid species that also has enlarged caeca, egests chitin in its pellets (Duke, 1989), supporting this view. Conversely, uric acid is fermented in the avian caecum, which may allow the carbon content to be salvaged as short-chain fatty acids (SCFA) (Braun & Campbell, 1989). Significant levels of uric acid have been found even in the caeca of more generalist species such as chickens (Beck & Chang, 1980). The insectivorous dietary habit of kiwi is likely to result in a significant output of uric acid. Thus the reclamation of carbon as SCFA from uric acid may contribute significantly to the kiwi's energy budget, a hypothesis that warrants further investigation.

In summary, this paper presents morphological and histological evidence that the caeca of the brown kiwi are specialized for digestive activity and that they may selectively retain fine particulate material of low density, that is with low incombustible residue.

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References

Angel, C.R. (1996). A review of ratite nutrition. *Anim. Feed Sci. Tech.* **60**, 241–246.

Barnes, E.M. (1977). Ecological aspects of the anerobic flora in the avian intestine. *Am. J. Clin. Nutr.* **30**, 1793–1798.

Beck, J.R. & Chang, T.S. (1980). Measurement of uric acid levels in chicken caecal contents. *Poultry Sci.* **59**, 1193–1196.

Björnhag, G. (1987). Comparative aspects of digestion in the hindgut of mammals. The colonic separation mechanism (CSM) (a review). *Dtsch. Tierarztl. Wochenschr.* **94**, 33–36.

Braun, E.D. & Campbell, C.E. (1989). Uric acid decomposition in the lower gastrointestinal tract. *J. Exp. Zool.* **252**, **3** (Suppl.), 70–74.

Clench, M.H. & Mathias, J.R. (1995). The avian cecum: a review. *Wilson Bull.* **107**, 93–104.

Clench, M.H. & Mathias, J.R. (1999). The avian cecum: update and motility review. *J. Exp. Zool.* **283**, 441–447.

Couch, J.R., German, H.L., Knight, D.R., Sparks, P. & Pearson, P.B. (1950). Importance of the caecum in intestinal synthesis in the mature domestic fowl. *Poultry Sci.* **29**, 52–58.

Davies, S.J.J.F. (1978). The food of emus. *Aust. J. Ecol.* **3**, 411–422.

DeGolier, T.F., Mahoney, S.A. & Duke, G.E. (1999). Relationships of avian cecal lengths to food habits, taxonomic position, and intestinal lengths. *Condor* **101**, 622–634.

Duke, G.E. (1986). Alimentary canal; anatomy regulation of feeding and motility. In *Avian physiology*: 269–288. Sturkie, P.D. (Ed.). New York: Springer Verlag.

Duke, G.E. (1989). Relationship of caecal and colonic motility to diet, habitat and caecal anatomy in several avian species. *J. Exp. Zool.* **252**, **3** (Suppl.), 38–47.

Fenna, L. & Boag, D.A. (1974). Filling and emptying of the galliform caecum. *Can. J. Zool.* **52**, 537–540.

Gasaway, W.C., White, R.G. & Holleman, D.F. (1976). Digestion of dry matter and absorption of water in the intestine and caecum of rock ptarmigan. *Condor* **78**, 77–84.

Glick, B., Chang, T.S. & Jaap, R.G. (1956). The bursa of Fabricius and antibody production. *Poultry Sci.* **35**, 224–225.

Gould, S.J. (1966). Allometry in ontogeny and physiology. *Biol. Rev.* **41**, 587–640.

Herd, R.M. & Dawson, T.J. (1984). Fiber digestion in the emu, *Dromaius novaehollandiae,* a large bird with a simple gut and high rates of passage. *Physiol. Zool.* **57**, 70–84.

Hume, I.D. (1999). *Marsupial nutrition*. Cambridge: Cambridge University Press.

Hume, I.D., Jazwinski, E. & Flannery, T.F. (1993). Morphology and function of the digestive tract in New Guinean possums. *Aust. J. Zool.* **41**, 85–100.

Jozefiak, D., Rutkowski, A. & Martin, S.A. (2004). Carbohydrate fermentation in the avian caeca, a review. *Anim. Feed Sci. Tech.* **113**, 1–15.

Karasawa, Y. (1989). Ammonia production from uric acid, urea, and amino acids and its absorption from the ceca of the cockerel. *J. Exp. Zool.* **252**, **3** (Suppl.), 75–80.

Karasawa, Y. (1999). Significant role of the nitrogen recycling system through the ceca occurs in protein-depleted chickens. *J. Exp. Zool.* **283**, 418–425.

Kleinpaste, R. (1990). Kiwis in a pine forest habitat. In *Kiwis*: 97–138. Fuller, E. (Ed.). Auckland: Seto Publishing.

Lentle, R.G., Stafford, K.J. & Henderson, I.M. (1997). The effect of formalin on rumen surface area in red deer. *Anat. Hisol. Embryol.* **26**, 127–130.

Lentle, R.G., Stafford, K.J., Potter, M.A., Springett, B.P. & Haslett, S. (1998). Factors affecting the volume and macrostructure of gastrointestinal compartments in the tammar wallaby (*Macropus eugenii* Desmarest). *Aust. J. Zool.* **46**, 529–545.

Maumus, J. (1902). Les caecums des oiseaux. *Ann. Sci. Nat. Zool. Paleo.* **15**, 1–148.

McLelland, J. (1989). Anatomy of the avian caecum. *J. Exp. Zool. Suppl.* **3**, 2–19.

Mitchell, P.C. (1901). On the intestinal tract of birds; with remarks on the valuation and nomenclature of zoological characters. *Trans. Linn. Soc. Lond. Zool.* **8**, 173–275.

Moretensen, A. & Tindell, A.R. (1981). Caecal decomposition of uric acid in captive and free ranging willow ptarmigan (*Lagopus lagopu lagopus*). *Acta Physiol. Scand.* **113**, 465–469.

Naik, D.R. (1962). *A study of the intestinal caeca of some Indian birds*. MSc thesis, Varanasi, India, Banaras Hindu University.

Oliviera, C.A., Silva, R.M., Santos, M.M. & Mahencha, G.A.B. (2004). Location of the ureteral openings in the cloacas of tinamous, some ratite birds and crocodilians: a primitive character. *J. Morphol.* **260**, 234–246.

Pereira, L.B., Martella, M.B. & Navarro, J.L. (2003). Habitat use by wild and captive-reared greater rhea *Rhea americana* in agricultural landscapes in Argentina. *Oryx* **38**, 304–310.

Reiss, M.J. (1989). *The allometry of growth and reproduction*. Cambridge: Cambridge University Press.

Suomalainen, H. & Arhimo, E. (1945). On the microbial decomposition of cellulose by wild gallinaceous birds (family Teraonidae). *Ornis. Fenn.* **22**, 21–23.

Tuinen, M., van Sibley, C.G. & Hedges, B. (2000). The early history of modern birds inferred from DNA sequences of nuclear and mitochondrial ribosomal genes. *Mol. Biol. Evol.* **17**, 451–457.

Ullrey, D.E. & Allen, M.E. (1996). Nutrition and feeding of ostriches. *Anim. Feed Sci. Tech.* **59**, 27–36.

White, J.F. & Gould, S.J. (1965). Interpretation of the coefficient in the allometric equation. *Am. Nat.* **99**, 5–18.

Wilkinson, L. (1990). *SYSTAT statistical package 1990. Version 5*. Evanston, IL: SYSTAT Inc.

Yuki, H., Yajima, T. & Kawasaki, H. (1980). A new method for determination of serum uric acid by measuring allantoid produced by the action of uricase. *Chem. Pharm. Bull.* **28**, 3375–3380.