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The endangered kiwi: a review

James SALES

Bosman street 39, Stellenbosch 7600, South Africa; e-mail: James_Sales_1@hotmail.com

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A b s t r a c t . Interest in ratites has necessitated a review of available information on the unique endangered kiwi (*Apteryx* spp.). Five different species of kiwis, endemic to the three islands of New Zealand, are recognized by the Department of Conservation, New Zealand, according to genetic and biological differences: the North Island Brown Kiwi (*Apteryx mantelli*), Okarito Brown Kiwi/Rowi (*A. rowi*), Tokoeka (*A. australis*), Great Spotted Kiwi/Roroa (*A. haastii*), and Little Spotted Kiwi (*A owenii*). As predators were found to be the main reason for declining kiwi numbers, predator control is a main objective of management techniques to prevent kiwis becoming extinct in New Zealand. Further considerations include captive breeding and release, and establishment of kiwi sanctuaries. Body size and bill measurements are different between species and genders within species. Kiwis have the lowest basal rates of metabolism compared with all avian standards. A relative low body temperature (38 ºC), burrowing, a highly developed sense of smell, paired ovaries in females, and a low growth rate, separate kiwis from other avian species. Kiwis have long-term partnerships. Females lay an egg that is approximately 400 % above the allometrically expected value, with an incubation period of 75–85 days. Kiwis mainly feed on soil invertebrate, with the main constituent being earthworms, and are prone to parasites and diseases found in other avian species. It can be concluded that kiwis present a biological rarity, with several features more characteristic of small mammals than birds.

Key words: kiwi, taxonomy, conservation, reproduction, nutrition

Introduction

Kiwis (Order Struthioniformes, family Apterygidae) are endemic to the three major islands of New Zealand. Contrary to expectation, phylogenetic analysis shows that kiwis are more closely related to Australian (emus) and African (ostriches) ratites than to moas. The latter are an extinct group of 11 ratite species that lived during the Pleistocene era in New Zealand (C o o p e r et al. 1992).

Apart from their highly distinctive taxonomic status and conservation significance, kiwis are incorporated in the New Zealand culture. They are the unofficial national emblem of New Zealand, and recognized by Maoris as natural treasures to be treated as sacred. Kiwi is the name by whom all New Zealanders are known (H e r b e r t & D a u g h e r t y 2002).

Interest in ratites in recent years has increased. Mostly because of the potential of ostriches, emus and rheas to produce skins, meat and feathers under farming conditions, but also due to the conservation efforts to save the cassowary and kiwi from extinction. Despite been well familiar with the name 'kiwi', and the occurrence of kiwis in several zoological parks outside New Zealand, the kiwi seems a mystery to most people, even inside its country of origin. As at February 2003, there were 145 North Island Brown Kiwis held in captivity, of which 39 outside of New Zealand. The largest holdings outside New Zealand are at San Diego Zoo, USA (8 birds) and Frankfurt Zoo, Germany (11 birds). Average life expectancy for females and males in captivity is 12 and 18 years, respectively, with a maximum longevity of 33 and 28 years, respectively (Kiwi Captive Management Advisory Committee 2004).

Literature and research reported on kiwis are fragmented, and most often published in regional journals. In an attempt to introduce the kiwi and its unique characteristics to a wider audience, a review has been compiled on research conducted. This is aimed to serve as a source of references in the attempts currently started to prevent these species from becoming extinct, and should be especially of use for institutes outside of New Zealand that are keeping kiwis in their collections.

Taxonomy

Because of a number of extraordinary biological features that could impact their intraspecific phylogeography, phyleogeographic subdivision has always been implicit in the taxonomy of the kiwi (Baker et al. 1995). North and South Island New Zealand populations of kiwis were recognized in 1850 as separate species *(Apteryx mantelli* and *A. australis,* respectively) on the basis of morphological characters, such as length of facial bristles, size of body parts, plumage color, wing quills, and tarsus scutellation (Bartlett 1850). However, subsequent research with additional specimens suggested that the only valid character separating them was the stiffer feather tips of the North Island species. Thus, in 1899, Rothschild relegated the North and South Island Brown Kiwis to subspecies *(A. australis mantelli* and *A. a. australis,* respectively), and also recognized the Stewart Island population as *A. a. lawryi*. For more than a century the taxonomy within the enigmatic kiwi family has been debated, with no fewer than nine species (six Brown and three Grey, or Spotted Kiwi) having been named and described (Table 1, Herbert & Daugherty 2002, Burbidge et al. 2003). Conservation management of kiwis has been based on the taxonomy of Mathews (1931). According to the latter all Brown Kiwis are *A. australis*, with three subspecies: *A. a. australis* from the South Island, *A. a. mantelli* from the North Island, and *A. a. lawryi* from Stewart Island. The Great Spotted Kiwi is named *A. haastii*, and the Little Spotted Kiwi put in a new genus *Stictapteryx*, divided into three subspecies: *S. owenii owenii*, *S. o. occidentalis* and *S. o. iredalei*. However, most authors have placed all species in the genus *Apteryx*, omitting *Stictapteryx*, and all subspecies of the Little Spotted Kiwi in the single species *A. owenii* (Herbert & Daugherty 2002).

Genetic and other biological data have recently been presented showing that at least three discrete lineages of Brown Kiwis exist in New Zealand as a result of divergence in allopatry. They likely have accumulated enough biological differences to cause them to become reproductively incompatible (Table 2, Baker et al. 1995, Burbidge et al.

Table 1. Species of kiwis described in the nineteenth century (adapted from Herbert & Daugherty 2002).

Species	Common name	Source
Apteryx australis	Brown Kiwi	Shaw & Nodder (1813)
Apteryx owenii	Little Spotted Kiwi	Gould (1847)
Apteryx mantelli	Northern Island Brown Kiwi	Bartlett (1850)
Apteryx haastii	Great Spotted Kiwi	Potts (1871)
Apteryx mollis	Brown Kiwi	Potts (1872)
Apteryx fusca	Brown Kiwi	Potts (1872)
Apteryx bulleri	Northern Island Brown Kiwi	Sharpe (1888)
Apteryx maxima	Stewart Island Brown Kiwi	Buller (1891)
Apteryx lawryi	Stewart Island Brown Kiwi	Rothschild (1893)
Apteryx occidentalis	Spotted Kiwi	Rothschild (1893)

Table 2. Characteristics for morphology and allozyme variation of regional populations of kiwis (from Baker et al. 1995, Burbidge et al. 2003).

Character	Brown Kiwi					Little and Great Spotted
	North Island	Okarito Rowi	Tokoeka			
			Haast	Fiordland	Steward Island	
Morphology						
Plumage colour	Brown/grey/ black/rufous	Grey and white	Rufous	Dark grey	Dark brown	Spotted fawn
Feather tips	Stiff	Soft	Soft	Soft	Soft	Soft
Large tarsal scutes	17	7	4	5	6	6
Facial bristles	Long	Short	Short	Short	Short	Short
Allozymes and mtDNA						
Ak-1	A > 0.9; C absent	A = 0.95; B = 0.05	B = 0.17; C = 0.83	A = 1.0	A = 1.0	A > 0.98
Hb-2	A = 1.0	A = 1.0	B = 1.0	B = 1.0	B = 1.0	B = 1.0
Ldh-2	A > 0.8; B and C rare	A = 0.4; C = 0.6	A = 1.0	A = 1.0	A = 1.0	A = 1.0
Cytochrome *b*	2 – 11	12 and 13	14	15 and 16	17 – 22	1 and 23

2003). Therefore, B u r b i d g e et al. (2003) recommended that the taxon *A. mantelli* should be reinstated to describe the North Island Brown Kiwi, and *A. australis* should remain as the Tokoeka on the southern South Island. A new species *A. rowi* should be erected to describe the Brown Kiwi at Okarito. Tokoeka should be split into at least three conservation management units (Haast, Fiordland and Stewart Island). Currently the Department of Conservation in New Zealand defined kiwis as follow: North Island Brown Kiwi (*A. mantelli*), Okarito Brown Kiwi/Rowi (*A. rowi*), Southern Tokoeka (*A. australis*), Haast Tokoeka (*A. australis* Haast), Great Spotted Kiwi/Roroa (*A. haastii*), and Little Spotted Kiwi (*A. owenii*) (R o b e r t s o n & C o l b o u r n e 2003, Kiwi Captive Management Advisory Committee 2004). The latter is the taxonomical nomenclature that will be used in the subsequently text of this review to describe different species of kiwis.

Conservation status

All species of kiwi are threatened in New Zealand: Okarito Brown Kiwis and Haast Tokoekas are classified as 'nationally critical', North Island Brown Kiwis as 'seriously declining', Great Spotted Kiwis and Southern Tokoekas as 'gradually declining', and Little Spotted Kiwis as 'range restricted' (H i t c h m o u g h 2002). Distribution and population estimates of kiwis in New Zealand are presented in Table 3.

Table 3. Distribution and population estimates of kiwis in New Zealand (Data for 2006 projected, without management) (R o b e r t s o n 2003).

Kiwi	Location	1996	2006
North Island Brown	North Island	35000	20000
Okarito Brown	Okarito, South Island	150	100
Haast Tokoeka	Near Haast, South Island	225	125
Southern Tokoeka	Stewart Island/Rakiura and Fiordland, South Island	27000	24000
Little Spotted	Kapiti Island and several smaller offshore islands	1100	1200
Great Spotted	Northern South Island	22000	12000

It was not until 1991, with the launch of the Kiwi Recovery Programme, that significant coordinated conservation management action was taken to prevent kiwis from becoming extinct (B u t l e r & M c L e n n a n 1991, R o b e r t s o n & C o l b o u r n e 2003). Management comprises a variety of mainly experimental approaches. This include predator control (B a s s e et al. 1999, P i e r c e & W e s t b r o o k e 2003), raising juvenile kiwi in captivity to return to the wild upon reaching a size of 800 to 1200 g (a size at which they are believed to be capable of resisting stoats) (G r a n t 2001, Kiwi Captive Management Advisory Committee 2004, M c L e n n a n et al. 2004), establishment of 'kiwi sanctuaries' (R o b e r t s o n 2004), and support advocacy for kiwi conservation (J a m e s 2001).

The main cause of declines in the kiwi populations in New Zealand is thought to be predation (T a b o r s k y 1988, M c L e n n a n & P o t t e r 1992). Kiwis evolved in the absence of mammalian predators, but co-exist today with as many as seven obligate or facultative carnivores (cats, dogs, ferrets, pigs, possums, stoats, weasels) introduced by Polynesians and Europeans to New Zealand. Young kiwis have no behaviours or defenses that protect them against introduced mammals. In a survey of all available information on the impact of predators on free-living kiwi adults, eggs, and chicks (M c L e n n a n et al. 1996), it was found that predators killed at least 8% of chicks, 45% of juveniles, and possibly as many as 60% of all young kiwis. Whereas ferrets and dogs were the main predators of adult kiwis, eggs were destroyed mostly by possums and mustelids. Stoats and cats were largely responsible for mortalities in young kiwis.

Five areas, chosen to include significant populations of Okarito Brown Kiwis and Haast Tokoekas, the most endangered taxa of kiwi, and sample populations of North Island Brown Kiwis, the species suffering the greatest rate of decline, were established as 'kiwi sanctuaries' in 2000 as part of the New Zealand Biodiversity Strategy (Robertson 2004). Numbers of the Little Spotted Kiwi were increasing in 1996, following several successful transfers to predator-free offshore islands (Colbourne & Robertson 1997). Kiwis are cryptic birds, and the most reliable monitoring regimes to evaluate the impact of conservation efforts currently involve radio tracking, using trained dogs to sample age structure (Robertson et al. 1999), and call count responses (Pierce & Westbrooke 2003).

Description of the animal

Size of adult free-living kiwis is presented in Table 4. These data accentuate the well-known fact that females are larger in size than males. Bill measurements seem to show an almost

Table 4. Body weight and dimensions (mean) of free-living adult kiwis (number measured in brackets).

	Body weight (kg)	Body length (mm)	Tarsus length (mm)	Source
North Island Brown				
Male	2.04 (34)	729 (4)	88 (4)	Miles et al. (1997), McLennan et al. (2004)
Female	2.66 (22)	866 (2)	98 (2)	Miles et al. (1997), McLennan et al. (2004)
Little Spotted				
Male	1.14 (51)	–	74 (56)	Jolly & Daugherty (2002)
Female	1.35 (41)	–	80 (46)	Jolly & Daugherty (2002)
Great Spotted				
Male	2.31 (39)	812 (25)	–	McLennan & McCann (2002)
Female	3.19 (29)	933 (15)	–	McLennan & McCann (2002)

Table 5. Bill length (mm) measurements (number measured in brackets) (from Robertson & Colbourne 2003).

Kiwi	Location	Male	Female
North Island Brown	Central Northland	99.5 (96)	135.6 (104)
	Waikaremoana	92.2 (16)	117.0 (12)
Okarito Brown	Okarito	94.8 (48)	125.5 (51)
Haast Tokoeka	Haast	92.8 (12)	119.9 (8)
Southern Tokoeka	Stewart Island	104.4 (3)	141.8 (22)
Little Spotted	Kapiti	68.1 (131)	83.7 (111)
Great Spotted	Hurunui	93.4 (8)	118.3 (14)
	Kahurangi Point	93.0 (6)	114.0 (5)
	Saxon Hut	98.3 (22)	122.6 (23)

complete separation between adult males and females (Table 5, Grant 2001). In the North Island Brown Kiwi the bill of the female grew faster in females (0.11 mm/day) than in males (0.08 mm/day) in the period from 201 to 300 days after hatching. In females bill growth continued for 1300 to 1400 days after hatching, whereas it stopped in males at an age of around 950 to 1000 days (McLennan et al. 2004).

Kiwi feathers, with a proportion of 4.7 to 6.8 % of body weight in chicks and adult kiwis, are long and flexible, lacking the usual interlocking mechanism (Reid 1972, Reid & Williams 1975). The chick hatches with the same kind of plumage than the adult. According to Pycraft (1901) the down feathers of the nestling are not driven out by the teleoptiles. The animal lacks an external tail, and its wings are reduced to vestiges that are hidden under its plumage (Calder 1978).

Anatomy

Several studies had described the musculature anatomy (Owen 1841, 1842, 1849, 1979, Parker 1891, Beddard 1899, Pycraft 1901, McGowan 1979, 1982, Vanden Berge 1982), skeleton (Owen 1841, 1879, Mivart 1877, Beddard 1899, Pycraft 1901), digestive system (Owen 1841, 1879, Beddard 1899), respiratory system (Owen 1841, 1879, Huxley 1882), internal and reproductive organs, brain (Owen 1841, 1879), trachea (Forbes 1881), blood vessels (Owen 1841, Glenny 1942) and middle ear (Saiff 1982) of the kiwi in great detail. A thorough summary of the above studies is outside the scope of the present manuscript. In general the anatomy of the kiwi followed the same patterns than in other ratites and primitive orders of birds.

Parker (1891, 1892) described the development of skeleton and brain in North Island Brown and Little Spotted Kiwis, based on preserved embryos, loose bones, and skeletons. Although differences in skeleton, such as dimensions of the pelvic girdle, sternum and hind limb, had been demonstrated between species and sexes in the latter study, unfortunately no absolute age could been assigned to stages of development. Through the technique of radiographing a North Island Brown Kiwi has been aged according to skeleton development as presented in Table 6. However, after five years of age the technique becomes invalid due to the further lack of change in the skeleton (Beale 1991).

McGowan (1979) described in detail the hind leg musculature of the North Island Brown Kiwi, based upon dissections of two frozen specimen, with an indication of the possible function of each muscle by assessing its size, action, and fiber-arrangement, together with tentative data on the relative abundance of twitch and tonus fibers. The wing muscular of the North Island Brown Kiwi is closely similar to that of other ratites, but markedly different to that of the carinates. They lack propatagial muscles, and neither the *Muscularis pectoralis* nor the *M. supracoracoideus* is well developed (McGowan 1982).

Kiwis have small and poorly developed eyes and optic lobes, whereas the mammalian-type olfactory structures are enlarged and complex (Reid et al. 1982). The ratio of the diameter of the olfactory bulb to the diameter of the cerebral hemisphere is 34 %, compared to 15 % for the domestic fowl (Bang & Cobb 1968). Studies of the brain and sensory organs in embryos (Parker 1891, Krabbe 1957) and adults (Strong 1911, Craigie 1930, Durward 1932, Bang & Cobb 1968) suggest that a highly developed sense of smell compensate for absence of good vision in the kiwi. External nares located at the tip of the long, slender bill ensure greater functional olfactory sensitivity (Reid et al. 1982). On the basis of refractive terms (Walls 1942) and behavioral

Table 6. Maturation of skeleton of the North Island Brown Kiwi as determined by radiology (from B e a l e 1991).

Age	Ankle	Knee	Skull
Hatched	Tarsal bones well defined. No ankle sesmoid visible.	No patella visible.	Cranial sutures open and readily visible.
1 year	Tarsal bones unchanged. Ankle joint sesamoid appearing.	Patella appearing.	No change.
2 years	Tarsal bones unchanged. Ankle joint sesamoid well developed.	Patella well defined.	No change.
3 years	No change.	Little change.	No change.
4 years	Tarsal bones start to fuse with adjacent bones.	Patella start to fuse with upper tibia.	Sutures still visible.
4.5 years	Fusion almost complete with tarsal bones no longer definable. Ankle joint has mature form.	Fusion complete. Knee joint has mature form.	No change.
5 years	Fusion complete.	No change.	Sutures closed. Skull has mature form.
6–10 years	No change.	No change.	No change.

observations (D a v i s & G r e e n w e l l 1976, R e i d et al. 1982) it was believe that kiwis are myopic, thus incident light rays focus before the retina. However, by retinoscopy and photorefraction it was found with both restrained captive North Island Brown Kiwis (S i v a k & H o w l a n d 1987) and free-living birds (H o w l a n d et al. 1992) that kiwis are hyperopic (farsighted).

M e t a b o l i s m

Kiwis have the lowest basal rates of metabolism compared with all avian standards (C a l d e r & D a w s o n 1978, M c N a b 1996). Even by the lowest standard commonly used, the nonpasserine curve of A s c h o f f & P o h l (1970), captive North Island Brown Kiwis (3.02 to 3.14 kg body weight, n = 2 animals and 42 measurements) have a weight-specific basal rate that is 61 % (0.261 to 0.288 cm^3 O_2 g/h) of predicted rates. For Little Spotted Kiwis (1.19 to 1.56 kg body weight, n = 2 animals and 26 measurements) and Great Spotted Kiwis (2.53 kg body weight, n = 2 animals and 25 measurements) values were 81 % (0.478 to 0.551 cm^3 O_2 g/h) and 78 % (0.375 cm^3 O_2 g/h) of predicted rates, respectively. Differences in basal rates between different species might be associated with phylogeny or with geographic distribution (M c N a b 1996). Low basal rates found in kiwis are in agreement with the hypothesis that flying ancestors of kiwis (H o u d e 1986, C o o p e r et al. 1992) flew to New Zealand after it had separated from the Australia-Antarctican remnant of Gondwanaland. Energy conservation, due to limited sources available on New Zealand, was most likely the motivation for the development of flightlessness hereafter (M c N a b 1994).

Ranges for body temperature, heart rate and respiration rate for 23 juvenile North Island Brown Kiwis during physical restraint were reported as 36.6 to 40.3 ºC, 70 to 240 bpm, and 12 to 60 bpm, respectively (J a k o b - H o f f 2001). F a r n e r et al. (1956) reported daytime (resting) body temperatures of 36.4 to 37.2 ºC for North Island Brown Kiwis, and 38.3 to 39.9 ºC at night (active period). This is 2 to 4 ºC lower than would be expected in similar sized neognathous birds, but within the normal range for most mammals (C l a r k

& McKenzie 1982). North Island Brown Kiwis have a zone of thermoneutrality that extended at least from 30 down to 10 ºC, Little Spotted Kiwi from 29 to 6 ºC, and Great Spotted Kiwi from 30 to 5 ºC. Estimates of minimal thermal conductance being no greater than 65 to 69% of the values expected from body weight. This facilitates energy conservation at cool to cold ambient temperature and, without doubt, is derived from the distinctive, highly overlapping feather structure of the kiwi (McNab 1996).

Behaviour

Although the North Island Brown Kiwi typically is regarded as an entirely nocturnal inhabitant of the native forests of New Zealand, recent evidence suggests that they are capable of living in a diverse range of habitats, such as exotic pine forests (Colbourne & Kleinpaste 1983, 1984, Taborsky & Taborsky 1991, 1992), regenerating forest, overgrown pasture (Potter 1989), lowland tussock grassland and even in sanddunes. This suggests substantial flexibility in this species regarding use of habitat. It seems that availability of food and shelter sites are the main determinants of habitat types, regardless of whether they are natural or anthropogenic territory (Taborsky & Taborsky 1995).

Kiwis are highly territorial, with evidence been presented that free-living North Island Brown Kiwi males were more defensive than females (Taborsky & Taborsky 1992). Responses to foreign kiwi odours suggest that kiwis could use olfactory signals to mark territories (Jenkins & Potter 2001). It is unknown why males sheltered in burrows significantly more often than did females, nor why adult kiwis, which have apparently evolved in the absence of mammalian predators, should bother to burrow at all (McLennan et al. 1987).

Female and male kiwis have clearly distinguishable calls (Grant 2001, Robertson & Colbourne 2003). Whereas vocalization seems similar between North Island Brown Kiwis, Okarito Brown Kiwis, Southern Tokoekas, Haast Tokoekas, and Great Spotted Kiwis, calls from Little Spotted Kiwis are different (Robertson & Colbourne 2003). Birds are most vocal in winter and spring.

Reproduction

Different populations of kiwis differ remarkably in their social and mating patterns (Table 7). Most kiwis have long-term partnerships and very high partner fidelity. Territory defense and degree of polygamy depend primarily on parental demands, and not on the distribution of resources and mates (Taborsky & Taborsky 1999). In contrast to previous belief, deviations from a solely paternal incubation have been reported (Table 7, Sturmer & Grant 1988, Potter 1989). Breeding display, consisting of bill-to-bill grunting, has been reported in captive North Island Brown and Great Spotted Kiwis, and free-living Little Spotted Kiwis (Jolly 1989). Great Spotted and North Island Brown Kiwis indulge in wild chasing and leaping, together with loud screeches and snorting preliminary to copulation (Reid & Williams 1975). The male and female of a pair usually feed separately at night, but spend about 20% of days together. First possible reproduction in captivity is 3 years 9 months for females and 2 years 3 months for males, with peak reproduction at 5 to 26 and 7 to 28 years, respectively (Kiwi Captive Management Advisory Committee 2004).

Free-living North Island Brown Kiwi females lay one to two eggs during a breeding season in burrows of 45 to 125 cm long (Potter et al. 1996), whereas captives may lay

Table 7. Breeding and social behavior characteristics of regional populations of kiwis (from Burbidge et al. 2003).

Character	Brown Kiwi					Little Spotted	Great Spotted
	North Island	Okarito Rowi	Tokoeka				
			Haast	Fiordland	Steward Island		
Breeding							
Incubator	Male	Male and female	Male and female	Male and female	Male and female	Male	Male and female
Incubation time	75 – 85 days	65 – 75 days	65 – 75 days	65 – 75 days	65 – 75 days	65 – 75 days	~ 70 days
Clutch size	1 to 2	1	1	1	1	1	1
Number of clutches	1 to 3	1 to 2	1 to 2	1 to 2	1 to 2	1 to 2	1 to 2
Egg colour	White	Pale green	White	White	Pale green	White	Pale green
Laying season	May – Feb	July – Dec	July – Dec	June – Dec	July – Nov	Sept – Jan	July - Dec
Social							
Family groups	No	Yes	Probably	Yes	Yes	No	No
Tolerate intruding juveniles	Yes	No; kill other juveniles	Unknown	Unknown	No; kill other juveniles	No	Unknown

four to six (Reid 1981), even up to eight (Cockrem et al. 1992). Eggs of captive North Island Brown females were found to be generally smaller (360 g) than those of free-living kiwis (431 g). This was related to a possible influence of diet (Reid 1981). Interval between eggs laid in a clutch was most commonly 21 to 30 days in captive North Island Brown Kiwis kept either indoors or outdoors, and 31 to 40 days in captive Little Spotted Kiwis (Cockrem et al. 1992).

Kiwis have a seasonal pattern of egg laying with a peak from mid winter to mid spring (McLeannan 1988, Cockrem et al. 1992). It was mentioned that kiwis lay eggs in all months of the year in captivity, with the removal of eggs to incubators likely to stimulate replacement laying (Jolly 1989). However, a distinct egg laying pattern similar to that of free-living birds were recorded for North Island Brown, Great Spotted and Little Spotted captive kiwis when eggs were either naturally incubated or remove to artificial incubation (Cockrem et al. 1992). Mean plasma testosterone levels in North Island Brown Kiwi males were low (less than 0.18 ng/ml) during February to April, rose in May to a broad peak lasting four months (maximum levels 1.90 ng/ml), whereafter it declined. The above is in accordance to the breeding season in New Zealand. Mean estradiol levels in males followed a similar pattern, with the exception of peak levels (1750 pg/ml) reached in April. In females estradiol levels stayed low during the non breeding season, increased over the three months before egg laying, and started to decline in the two weeks before laying. Mean testosterone levels were low (less than 0.10 ng/ml) throughout the year in female kiwis, and progesterone concentrations did not change significantly during the year in either male or female kiwis (Potter & Cockrem 1992).

In contrast to most other avian species, female kiwis have paired ovaries, both functional (Kinsky 1971). Egg production is an extremely expensive task for kiwi females (Calder et al. 1978), affording an extra energy expenditure equivalent to about 100 % of basal metabolic rate during the period of egg production, which lasts for about 34 days (Taborsky 1994). The common view that brood care is the main demanding parental duty in birds probably does not apply to kiwi, seen the major production cost in the production of female gametes, which apparently bears on the mating system (Taborsky & Taborsky 1993). Female North Island Brown Kiwis lost about 9 % of peak body weight for each egg they laid, with a corresponding figure of 17 % for males that incubated full-term (Potter et al. 1996).

North Island Brown Kiwis lay an egg (416 g) that is approximately 400 % above the allometrically expected value for a bird with a body weight of 2.2 kg (Prinzinger & Dietz 2002). Yolk content presents of up to 65 % of fresh egg mass, compared to around 32 % in domestic fowl eggs (Calder et al. 1978). Egg weights of 330 to 519 g for North Island Brown Kiwi females with a body weight of 2.09 to 3.27 kg, and 275 to 368 g for Little Spotted females (1.04 to 1.25 kg body weight), have been reported (Reid 1971). Values of 121 to 139 mm and 76 to 81 mm were found for length and width, respectively, of eggs from free-living North Island Brown Kiwis (McLennan 1988). Dimensions for eggs from free-living Little Spotted Kiwi were 106.5 to 112.3 mm in length, 67.2 to 71.9 mm in width, with an eggshell thickness of 0.44 mm (Jolly 1989). In North Island Brown Kiwis the incubation time is approximately 75 to 85 days, compared to an expected time of 42 to 44 days for an egg of this size. The increase of embryonic oxygen consumption rate reaches a plateau phase (0.113 ml O_2/g/h) between day 22 and five before hatching. Mean total oxygen uptake per egg (43.01 L O_2), corresponding to an energy turnover rate of 2.04 kJ/g during embryonic development, is well within the expected value for all birds (2.00 ± 0.8 kJ/g)

(Prinzinger & Dietz 2002). This illustrates that the kiwi is as efficient as other avian embryos (Calder 1979). The kiwi embryo utilizes approximately 17% (847 kJ) of the energy originally stored in the egg (4942 kJ), with 48% of the egg's initial yolk mass found as spare yolk in the hatchling (34% of chick weight). The latter can serve as the chick's sole source of energy and substrate for tissue production for up to at least 17 days after hatching (Calder 1979, Prinzinger & Dietz 2002). Triacylglycerol (83.2%) and phospholipids (8.4%) form the majority of the total lipid contents of the kiwi egg (Body & Reid 1983). The fatty acid and amino acid composition of kiwi eggs are presented in Tables 8 and 9.

Incubation behaviour varies among the different species of kiwis. Whereas for North Island Brown and Little Spotted Kiwis only the male incubates the eggs, except for in the first week, Okarito Brown Kiwis and the Tokoekas share incubation between genders. Group members in the Southern Tokoeka family can assist with incubation to the extent that breeding males may take no part in incubation at all (Table 7). Incubating males of all species and females of North Island Brown Kiwis, Okarito Brown Kiwis and Tokoekas shed the feathers on their lower belly and develop a large, naked, brood patch., presumably to increase the transfer of heat from their body to the egg (Colbourne 2002). In the Great Spotted Kiwi, males incubate throughout the day and during the early evening. Females incubate for three to eight hours each night when males emerge to forage, but do not seem to develop a brood patch (McLennan & McCann 1991). In contrast to previous believe (Rowe 1978), Colbourne (2002) found that North Island Brown Kiwis turn their eggs regularly. In nature incubation of all species of kiwi studied did not begin until one to seven days after laying. Incubation temperatures are presented in Table 10.

Table 8. Fatty acid composition of triacylglycerol and phospholipids constituents of infertile North Island Brown Kiwi eggs (weight % of total fatty acids, n = 2, egg weight = 375 g, lipid content = 82 g) (Body & Reid 1983).

Fatty acid	Diet	Egg	
		Triacylglycerol	Phospholipids
14:0	2.0	0.4	tr
15:0	0.5	0.2	tr
16:0	20.2	26.2	16.6
17:0	1.1	0.9	0.9
18:0	23.1	3.1	22.8
19:0 – 22:0	tr	0.4	0.6
14:1	0.7	tr	tr
15:1	0.5	tr	tr
16:1	2.9	4.3	1.1
17:1	0.4	0.9	0.2
18:1	30.6	52.1	17.8
18:2	13.4	10.3	8.2
18:3 – 20:1	3.1	1.3	0.7
20:2	-	-	tr
20:3	-	-	1.1
20:4	1.5	tr	19.1
20:5	-	-	2.5
22:4	-	-	0.3
22:5	-	-	1.9
22:6	-	-	6.3

Tr, trace, indicate less than 0.1.

Table 9. Amino acid composition of infertile North Island Brown Kiwi eggs (g amino acid/100 g amino acids, n = 2, egg weight = 375 g, protein content = 40.9 g) (Body & Reid 1983).

Amino acid	Kiwi	Domestic fowl
Alanine	4.97	8.48
Arginine	5.65	5.74
Aspartic acid	8.87	8.04
Cystine	2.17	1.25
Glutamic acid	13.13	10.77
Glycine	3.22	6.50
Histidine	2.52	2.39
Isoleucine	5.20	5.24
Leucine	8.23	8.08
Lysine	7.85	6.25
Methionine	3.73	3.52
Phenylalanine	5.52	5.10
Proline	4.70	5.68
Serine	8.13	8.26
Threonine	5.79	5.42
Tyrosine	4.50	3.58
Valine	5.82	5.70

Table 10. Natural incubation characteristics reported for kiwi eggs.

Kiwi	Temperature (°C)		Water loss (%)	Source
	Top	Bottom		
Free-living				
North Island Brown	36.5	27.0	12.5	Colbourne (2002)
Okarito Brown	36.5	28.5-32.0	-	Colbourne (2002)
Captive				
North Island Brown	37.1	26.0	-	Rowe (1978)

Kiwis do not hatch in the typical way of avian species in that, on hatching, the chick is able to rotate within the egg and, with the use of its egg tooth, pips a liberating circle of punctures. Instead, a single puncture is made in the air-cell end, where the shell is thinner than in the rest of the egg. The hatching chick may pause for as long as two days before finally flexing and rupturing the shell, which usually fractures along the line of the air-cell (Rowe 1978). Hatching weight of captive North Island kiwis is reported as approximately 75 % of fresh egg weight, with a decrease in body weight till day eight post-hatching. Body weight starts to increase 12 days after hatching (Prinzinger & Dietz 2002).

Hatching success of kiwis has found to be low (Table 11). However, using knowledge of the incubation requirements of other ratites, and an adaptive management framework, hatching rate has been improved through artificial incubation (Bassett et al. 2003).

Kiwi eggs, with a massive yolk for culture, very long incubation period, disproportionately thin shell that is easily hair-line cracked, and exposure to bacteria and fungi in a damp underground burrow, could represent a good opportunity for invading microbes (Calder 1979). This suggestion is supported by a substantial incidence of late embryonic death and decay during natural incubation in free-living North Island Brown

Kiwis (McLennan et al. 1996). However, egg white of North Island Brown Kiwis contains a high concentration (2.3% vs 1.5% for domestic fowl) of ovoinhibitor, a broad spectrum fungal proteinase with implied antimicrobial defense action (Osuga & Feeny 1968). Also high contents of lysozyme *g* (3.75 compared to that in Emden goose taken as 1.00), that attacks peptiglycans from gram-negative bacteria (Prager et al. 1974). Potter & Bassett (2001) ascribed late embryo deaths in naturally incubated eggs to nest desertion. Embryo mortality in partially artificially incubated eggs collected from the wild was found to remain constant across age classes.

Table 11. Hatchability of kiwi eggs.

Kiwi	Number of eggs	Hatched (%)	Source
Free-living			
North Island Brown	83	31	McLennan et al. (1996)
	21	29	McLennan (1988)
	26	23	Potter et al. (1996)
Great Spotted	19	37	McLennan et al. (1996)
Captive			
North Island Brown, Little Spotted, Great Spotted	158	23	Cockrem et al. (1992)

North Island Brown Kiwi, Okarito Brown Kiwi, Southern Tokoeka, and Little Spotted Kiwi chicks in the wild leave the nest at one week of age. North Island Brown Kiwi chicks return daily for up to six weeks and leave the parental territory at six to nine weeks. Okarito Brown Kiwi chicks remain in the parental territory for six months to several years, and Southern Tokoeka for up to seven years. Great Spotted Kiwi chicks return daily for two to four weeks, and leave the parental territory in four to 12 months (Robertson & Colbourne 2003). The Department of Conservation, New Zealand, distinguishes age stages of kiwis as presented in Table 12.

Table 12. Age categories defined for kiwis (Robertson & Colbourne 2003).

Kiwi	Chick	Juvenile	Sub-adult	Adult
North Island Brown, Great Spotted	0 to 10-50 days, In nest or return every day.	10-50 to 180 days, Independent from nest.	80 days to 4.5 years.	Over 4.5 years.
Okarito Brown, Southern Tokoeka Little Spotted	< 60 days. In nest.	60-180 days. Independent birds of < 500g.	80 days to 4.5 years. Independent birds of > 500g.	Over 4.5 years. Fully-grown birds of > 1 kg.

Nutrition

Kiwis have exceptionally slow growth rates for birds, and are still growing at ages of 3 to 5 years, while their weight may not stabilise until 4 to 6 years old (Robertson 2004). The growth of wild North Island Brown Kiwis until 1500 days after hatching were described with second-order polynomial regressions by McLennan et al. (2004):

Male (n = 34) - $y = 339 + 3.872x - 0.002x^2$
Female (n = 22) - $y = 294 + 4.613x - 0.002x^2$
where y = weight (g) and x = age (days).

Absolute growth rates declined from 6.3 g/d at day 30 to around 0.9 g/d at 500 days after hatching. Ongoing research on the management of captive kiwis at Massey University, New Zealand, illustrates that growth rates are faster than in the wild, but final adult size may be smaller (H. Robertson – personal communication).

The gizzard of the adult North Island Brown Kiwi measures approximately 75 x 55 mm and has an estimated maximum capacity of 40 to 45 cc (Reid et al. 1982). According to Owen (1841) the oval-rounded muscular stomach of the kiwi resembles more the membranous stomach of carnivorous birds than that of a sub-compressed shape gizzard. The kiwi's nocturnal and secretive behaviour makes it virtually impossible to identify food taken by surveillance (Reid et al. 1982, Colbourne & Powlesland 1988). Knowledge of kiwi diets in the wild has depended largely on examination of gizzard contents from accidentally killed kiwis. In a total of 146 faeces samples from Southern Tokoekas examined, 15 invertebrate groups were recognised as prey (Colbourne & Powlesland 1988). The occurrence of annelids in faeces was greater than 70% for most of monthly samples, and averaged 80% overall. Reid et al. (1982) found annelids in 94% of 50 gizzards of North Island Brown Kiwis, and Colbourne et al. (1990) recorded them in 75% of 61 faeces samples from Little Spotted Kiwis. The above is in accordance to the long established and popular belief, assumed from bill shape and probe holes (Buller 1888), that New Zealand's rich earthworm fauna provides the kiwi's staple diet. This is supported by the generally better initial acceptance of, and sustained preference for, earthworms over other items by newly-captured North Island Brown Kiwis (Lint 1966, Clayton 1972, Davis & Greenwell 1976). The four invertebrate groups excluding Annelida which contributed most soft tissue dry matter to the sample in the study of Colbourne & Powlesland (1988) were Lepidoptera (36%), Coleoptera (21%), Arachnida (19%) and Hemiptera (10%).

Vegetable matter, including miro, hinau (*Elaeocarpus dentatus*) (Buller 1888), and leaves of *Gleichenia dicarpa*, *Leptospermum scoparium*, *Halocarpus biforme*, a *Coprosma* sp., the liverwort *Bazzania* sp. and unidentified mosses (Colbourne & Powlesland 1988), have been reported in the gizzards of kiwis (Gurr 1952, Bull 1959, Watt, 1971, Reid et al. 1982). Analyses of the subcutaneous fats from a free-living North Island Brown Kiwi (Shorland & Gass 1961) showed that linoleic (C18: 2) and linolenic (C18: 3) fatty acids, which generally are associated with a vegetarian diet, together represented nearly 6 % of the fatty acids in the kiwi. The widespread ingestion of grit indicates further the importance of foods other than soft-bodied species to kiwis (Reid et al. 1982).

A pair of mucusal 'diving' valves, characteristic of aquatic birds, is found at the proximal end of the terrestrial kiwi's nasal passages (Bang 1971), which presumably functioned to reduce dust inhalation when birds are sniffing for food. As kiwis probably evolved in humid rain forests with generally damp humus and soils, and as pneumoconiosis seems more prevalent among kiwis living in drier habitats (Smith et al. 1973), Reid et al. (1982) suggested that these valves may facilitate feeding from water.

Reid et al. (1982) concluded that, due to, the diverse feeding habits of North Island Brown Kiwis, and intake of components that are accessible, a 'typical' diet probably does not exist. Furthermore, rapid gizzard fragmentation of soft-bodied worms and insects and quick passage through the gut complicated the determination of relative contributions of various items to the diet from gut analyses alone. His estimation of the relative contributions of different items to an 'average' diet is 40 to 45% earthworms, 40 to 45% other invertebrates, and 10 to 15% plant material. In the latter seeds and fruits are at least twice as important as greens. Items taken are small, or, because of high water or indigestible content, low in available energy content.

Whereas Reid et al. (1982) suggested that North Island Brown Kiwis may be random feeders and that numbers of prey ingested reflect supply rather than choice, Little Spotted Kiwis are selective feeders, choosing large (body length > 8 mm) slow-moving invertebrates from the upper layers of soil (Colbourne et al. 1990). According to McLennan

Table 13. Parasites found in kiwis.

Species	Kiwi	Source
Feather lice		
Apterygon mirum	North Island Brown	Clay (1961), Tandan (1972)
Apterygon dumosum	Southern Tokoeka	Tandan (1972)
	Little Spotted	Tandan (1972)
Apterygon hintoni	Great Spotted	Clay (1966), Tandan (1972)
Apterygon okarito	Okarito Brown	Palma & Price (2004)
Rallicola gadowi	Southern Tokoeka	Clay (1972)
Rallicola gracilentus	Great Spotted	Clay (1972)
Rallicola pilgrimi	Little Spotted	Clay (1972)
Rallicola rodericki	North Island Brown	Palma (1991)
Feather mites		
Kiwialges palametrichus	North Island Brown	Gaud & Laurence (1981), Bishop (1984)
	Southern Tokoeka	Gaud & Atyeo (1970), Bishop (1984)
	Little Spotted	Gaud & Atyeo (1970), Bishop (1984)
	Great Spotted	Gaud & Atyeo (1970), Bishop (1984)
Kiwialges phalagotrichus	North Island Brown	Bishop (1984)
	Southern Tokoeka	Gaud & Atyeo (1970), Bishop (1984)
	Little Spotted	Gaud & Atyeo (1970), Bishop (1984)
	Great Spotted	Bishop (1984)
Kiwialges cryptosikyus	Southern Tokoeka	Gaud & Atyeo (1970), Bishop (1984)
	Great Spotted	Bishop (1984)
Kiwialges haastii	Great Spotted	Bishop (1984)
Ticks		
Haemaphysalis longicornis	North Island Brown	Heath (1977)
Ixodes anatis	North Island Brown	Dumbleton (1953)
Fleas		
Parapsyllus nestoris nestoris	Southern Tokoeka	Smit (1979)
Haematozoa		
Babesia kiwiensis	North Island Brown	Peirce et al. (2003)
Hepatozoon kiwii	North Island Brown	Peirce et a.l (2003)
Nematodas		
Cyrnea apterycis	North Island Brown	Harris (1975)
		Clark & McKenzie (1982)
Heterakis apterycis	North Island Brown	Clark & McKenzie (1982)
Toxocara cati	North Island Brown	Clark & McKenzie (1982)
Porrocaecum ensicaudatum	North Island Brown	Clark (1983)
Cupillaria sp.	North Island Brown	Clark (1983)
Tetrameres sp.	North Island Brown	Clark (1983)
Protozoa		
Eimeria sp	North Island Brown	Thompson & Wright (1978)
Fungi		
Cryptococcus neformans var. *gattii*	North Island Brown	Hill et al. (1995)

(1988) incubating North Island Brown Kiwi males at Hawke's Bay spent about half the feeding time of non-incubating kiwis, with feeding bouts averaged 4.9 h in the former.

Evidence indicates that kiwis use smell (Buller 1888, Benham 1906, Strong 1911, Wenzel 1968, 1971) and, probably, also sound (Reid & Williams 1975), to locate food, with no proof that sight is important for feeding (Reid et al. 1982).

Diseases

Ingestion of foreign bodies, egg-related peritonitis, yolk sac retention and infection, septicaemia, pneumonia, bronchitis, cryptococcosis, aspergillosis, coccidiosis, visceral gout, dermatitis, avian tuberculosis, steatitis, goitre, necrotic enteritis and lipidosis have been recorded as causes of mortality in captive kiwis (Boardman 1998, Jakob-Hoff 2001).

Several pathogens found in kiwis are presented in Table 13. In New Zealand *Ixodes anatis* is the most commonly found tick species on North Island Brown Kiwi and is known as the kiwi tick (Peirce et al. 2003).

Conclusions

Kiwis, the smallest of the extant ratites, are still a mystery, even in their country of origin, New Zealand. Due to an extremely fast rate of becoming extinct interest in these birds was stimulated at the beginning of the 1990's. Currently research mainly concentrated on conservation efforts inside New Zealand.

The kiwi represents a biological oddity. It is thus surprising that not more studies are devoted to this avian species. Most facts about kiwis are based on generalized, often contradictory, observations, such as the egg laying pattern of birds in captivity.

Although hatching of kiwis in captivity has been noted since 1945, captive breeding, with the aim of releasing juvenile birds into the wild, is still in its infancy. Careful consideration of factors such as genetics, behaviour and feeding, have to be taken into account in such practices. This urged for further in depth studies on biology and behaviour of wild populations. Very little is known about the digestive physiology of the kiwi. Attention has to be focus on the tolerance of the digestive mechanism of the kiwi to nutrients supplied by captive diets, which are mostly formulated based on requirements of domesticated species. A further point of concern would be the possible effect of nutritional imprinting caused by captive diets on nutritional adaptation of birds to the nutrient content of food available in the natural environment.

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