# AN ANALYSIS OF THE GIZZARD CONTENTS OF 50 NORTH ISLAND BROWN KIWIS, *APTERYX AUSTRALIS MANTELLI*, AND NOTES ON FEEDING OBSERVATIONS

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SUMMARY: The kiwis analysed contained a wide range of invertebrate food species, most of which are associated with the bush margin. Individual gizzards contained high numbers of cicada nymphs and other species that are numerous, available throughout the year, or gregarious, and their presence is believed to reflect their availability rather than the bird's ability to select. Earthworm chaetae were present in 94%, and coleoptera (30% as adults, 70% as larvae) in 90% of 50 gizzards examined. A list of all invertebrates recorded in this, and earlier studies, is appended. Vegetable matter was found, often as incidental ingesta, in 93% of the samples and seed intake appeared to be inversely related to grit ingestion with hinau berries in particular playing a part in grinding food. Observations of captive birds indicates a likely intake of 330 Kcal of food each night, and their willingness to catch aquatic prey suggests that underwater foraging provides the principal use for their nasal valves. Both captive and feral kiwis demonstrate a reliance on olfaction for locating foods.

## INTRODUCTION

Avian competence in foraging and feeding typically relies on flight and keen sight. The flightless kiwis (Apterygidae), probably the most enigmatic and aberrant of all birds, are also nocturnal but, unlike owls, have poor vision. Notwithstanding any limitations these, and other, abnormalities may impose, kiwis adapt to a variety of habitats. Primarily creatures of dense indigenous forests, they, at times, utilize adjacent swamp and sub-alpine zones and, since European colonization, have locally (and successfully) colonized regenerating scrub-lands, exotic *Pinus* plantations and farm pasture. This versatility indicates a capacity to exploit many food sources and utilization of a broadly based diet. Conversely, anatomical and physiological characteristics of the kiwi should (perhaps) limit its ability to take some invertebrates common within its feeding zone.

Studies of the kiwi's brain and sensory organs in embryos (Parker, 1891; Krabbe, 1957) and adults (Owen, 1871; Strong, 1911; Craigie, 1930; Durward, 1935; Cobb, 1960; Portmann, 1961; Bang and Cobb, 1968) indicate poor vision is compensated for by a keen sense of smell. The eyes and optic lobes are small and poorly developed while the mammalian-type olfactory structures are enlarged and elaborate. Furthermore, to ensure greater functional olfactory sensitivity, the external nares are located at the tip of the long, slender bill. Although numerous observations indicate that kiwis use smell (Buller, 1888; Benham, 1906; Strong, 1911; B. Rowe, pers. comm.; C. Roderick, pers. comm.) and, probably, also sound (Reid and Williams, 1975) to locate food, there is no evidence that sight is important for feeding. Indeed, their clumsy avoidance of obstacles suggests that kiwis have poor visual acuity or focussing, and it seems doubtful that their laterally-placed eyes have adequate forward convergence to provide the binocular vision so important for judging distances and positions of small items in the otherwise two-dimensional environment of night.

The limited role of vision is apparent from the performance of a female North Island brown kiwi (*Apteryx australis mantelli*) with congenital blindness that was taken from the wild as an adult of unknown age in 1960. She is now in her 22nd year of captivity and has maintained excellent health throughout. She is, however, very small, being only 60-70% of the weight of other *A.a. mantelli* females in a similar 'well-fleshed' condition (Reid, 1972), and her stunted size may result, either directly or indirectly, from her total blindness impairing foraging competence during her growing period, as chicks also feed unaccompanied during daylight when limited vision may be of some assistance.

Wenzel's (1968) experiments, on the other hand, have demonstrated conclusively that kiwis are capable of locating buried foods by smell alone. They are,

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thus, well suited to take invertebrates inhabiting ground-litter and surface soils. While numerous probe holes to depths of 10-15 cm testify to the importance of these food sources in suitably soft or friable conditions, ground fauna may become scarce seasonally; or even unavailable, because of an impenetrable terrain during droughts.

The kiwi's furtive nocturnality prevents direct observations on the relative efforts given to exploiting different feeding niches. It is not known whether, or to what extent, they prey on invertebrates occurring on plants. Being of similar size to domestic poultry, kiwis should, perhaps, be capable of taking fauna living less than 45-60 cm above ground level. Their dependence on smell, and probably also sound, however, has disadvantages as neither sense establishes immediately the precise position of the prey. This, presumably, restricts prey in this zone to those animals that either remain immobile for considerable periods, or are sluggish in movement. Furthermore, the shape and dimensions of a bill suited for extracting from the soil do not facilitate the quick seizure or easy swallowing of rapidly moving creatures.

It has long been known that kiwis also ingest plant material. Buller (1888) recorded both seeds and invertebrates in the stomachs of two *A.a. mantelli* from Pirongia. While more detailed analyses of the stomach contents from a further four North Island birds endorse his findings (Gurr, 1952; Bull, 1959; Watt, 1971; Simpson, 1971) and suggest a wide utilization of vegetable matter, the dietary value of some plant items is questionable.

The various foraging patterns and, at times, surprising acceptances of unfamiliar or 'artificial' foods (spaghetti and jellymeat ahead of earthworms by some kiwis in captivity) present conflicting evidence about food preferences. The analysis of 50 North Island brown kiwi gizzards was undertaken to (hopefully) evaluate more precisely, the relative contributions of earthworms, other invertebrates and vegetable matter to the natural diet and, from knowledge of the prey's ecology, to gain understanding of this kiwi's feeding habits and food sources.

## MATERIAL AND METHODS

Kiwis are totally protected by legislation and this study was confined to gizzards from birds found dead or critically injured in localities frequented by man.

The cadaver (27 males, 23 females) included 41 adults, five juveniles weighing 900-1575 g and estimated to be aged 5-9 months, and four chicks weighing 320-460 g and believed to be less than 7-8 weeks old. Twenty-three specimens came from Northland, 19 from Taranaki and the remaining eight from other districts.

The time of death of eight birds is not known. Of the others, 11 were reported as having died during summer (December-February), seven during autumn (March-May), 13 during winter (June-August) and 11 during spring (September-November).

Twenty-three of these birds presumably were killed at night while out foraging and 16 died in their nests as a consequence of daytime mishaps. The former includes 12 struck by vehicles, eight poisoned and three caught in traps, and the daytime losses include two birds crushed by earth-moving machinery and 14 taken by pig dogs. The causes of death of the other 11 birds are not known.

To enable food analysis to be carried out, the pro-ventriculus and gizzard were removed, their contents washed out and the worm chaetae, seeds and invertebrates then examined separately. The gut below the gizzard was tied off and retained for a study of parasites but not investigated for food remnants. After seven birds had been examined, the feasibility of seed identification became apparent, and this was carried out for 43 birds. Young kiwis fend for themselves at an early age and a separate analysis of their gizzards was not necessary.

## GIZZARD CONTENTS

The gizzard measures approximately 75 x 55 mm and has an estimated maximum capacity of 40-45 cc. Only one gizzard was judged to be fully distended. It contained 49 g of material including 14.2 g grit, earthworm chaetae and the remains of 92 insects. Several birds, whose death was not instantaneous, contained very small gizzard samples. Gizzards from birds killed at night, as expected, generally contained more food than those killed by day, but the average quantity of grit was similar. Excluding earthworms, the former contained an average of 27.3 invertebrates and 5.5 g grit and the latter averaged 14.1 invertebrates plus 5.1 g grit.

Summaries of the gizzard contents are given in Tables 1 (invertebrates) and 2 (plant material), and identifications of all material from this and previous studies are presented in Appendices 1 (insects), 2 (other invertebrates) and 3 (seeds).

## DISCUSSION

The relative contributions of various items to the diet cannot be determined from gut analyses alone. Gizzard fragmentation of soft-bodied creatures is rapid and observations on one captive kiwi showed a high food intake results in a quick passage through the gut—when actively feeding, the interval between

TABLE 1. *Occurrence of invertebrates in the gizzards of 50 North Island brown kiwis.*

| | A | | B[1] | | C[2] | D | E | F[3] | G | Occurrence in 50 Gizzards | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Number of Specimens | | Positive Gizzards | | Total Inverts in B | % of Gizzard Inverts. A/C | Max. No. in a Gizzard | Total Inverts in E | Max. % of Gizzard Inverts E/F | Northland 23 | Taranaki 19 | Elsewhere 8 |
| | No. | % | No. | % | | | | | | | | |
| Annelida: | — | — | 47 | 94 | — | — | — | — | — | 20 | 19 | 8 |
| Chilopoda: | 9 | 0.9 | 9 | 18 | 181 | 5.0 | 1 | 6 | 17 | 3 | 4 | 2 |
| Diplopoda: | 19 | 1.8 | 15 | 30 | 294 | 6.5 | 4 | 51 | 8 | 4 | 9 | 2 |
| Orthoptera: | 24 | 2.3 | 10 | 20 | 306 | 7.8 | 6 | 16 | 37 | 3 | 6 | 1 |
| Dermaptera: | 1 | 0.1 | 1 | 2 | — | — | 1 | 59 | 2 | 0 | 0 | 1 |
| Hemiptera: *Amphisalta* sp. | 248 | 24.0 | 26 | 52 | 719 | 34.5 | 65 | 65 | 100 | 12 | 11 | 3 |
| Lepidoptera: mainly *Oxycanus* | 36 | 3.5 | 8 | 16 | 254 | 14.2 | 24 | 92 | 26 | 4 | 2 | 2 |
| Diptera: Tipulidae, larvae & pupae | 75 | 7.3 | 12 | 24 | 341 | 22.0 | 40 | 59 | 68 | 3 | 4 | 5 |
| Hymenoptera: Formicidae | 2 | 0.2 | 2 | 4 | 30 | 6.7 | 1 | 13 | 8 | 1 | 1 | 0 |
| Coleoptera: gen. sp. indet. | 3 | 0.3 | 2 | 4 | 33 | 9.1 | 2 | 16 | 12 | 1 | 1 | 0 |
| Cicindellidae (larvae) | 3 | 0.3 | 3 | 6 | 100 | 3.0 | 1 | 23 | 4 | 2 | 1 | 0 |
| Carabidae | 20 | 1.9 | 14 | 28 | 351 | 5.7 | 3 | 92 | 3 | 7 | 5 | 2 |
| Elateridae (larvae) | 54 | 5.2 | 21 | 42 | 418 | 12.9 | 10 | 59 | 17 | 9 | 10 | 2 |
| Lucanidae | 3 | 0.3 | 2 | 4 | 59 | 5.1 | 2 | 9 | 22 | 1 | 0 | 1 |
| Scarabidae: gen. sp. indet. | 18 | 1.7 | 4 | 8 | 69 | 26.0 | 12 | 16 | 75 | 3 | 0 | 1 |
| Scarabidae: Costelytra (larvae) | 192 | 18.6 | 22 | 44 | 590 | 32.5 | 41 | 51 | 80 | 10 | 8 | 4 |
| Scarabidae: Melolonthinae (larvae) | 135 | 13.1 | 15 | 30 | 336 | 40.2 | 43 | 50 | 86 | 8 | 6 | 1 |
| Scarabidae: *Odontria* sp. | 55 | 5.3 | 26 | 52 | 563 | 9.8 | 10 | 18 | 55 | 10 | 12 | 4 |
| Scarabidae: *Heteronychus arator* | 92 | 8.9 | 12 | 24 | 267 | 34.5 | 37 | 40 | 92 | 11 | 0 | 1 |
| Araneae | 22 | 2.1 | 15 | 30 | 315 | 7.0 | 3 | 29 | 10 | 6 | 7 | 2 |
| Crustacaea | 1 | 0.1 | 1 | 2 | — | — | 1 | 4 | 25 | 0 | 1 | 0 |
| Isopoda | 2 | 0.2 | 2 | 4 | 30 | 6.7 | 1 | 14 | 7 | 0 | 1 | 1 |
| Mollusca | 18 | 1.7 | 5 | 10 | 115 | 15.6 | 5 | 26 | 19 | 2 | 2 | 1 |

[1] Number of gizzards in which particular animal (or family etc.) occurred.
[2] Total number of all invertebrates in all gizzards in which the particular animal occurred.
[3] Total number of all invertebrates occurring in the gizzard in which the maximum number of the particular animal occurred.

TABLE 2. *Occurrence of plant material in the gizzards of 43 North Island brown kiwis*

| Locality | Northland | Taranaki | Elsewhere | % of |
|---|---|---|---|---|
| Number of Gizzards in Sample | 20 | 17 | 6 | Gizzards |
| With plant material | 19 | 16 | 5 | 93 |
| With monocot. leaves | 10 | 10 | 5 | 58 |
| With dicot. leaves | 9 | 7 | 3 | 44 |
| With monocot. and dicot. leaves | 6 | 4 | 3 | 30 |
| Total with leaves | 14 | 12 | 5 | 72 |
| With fern frond | 2 | 3 | — | 12 |
| With moss | 1 | 2 | — | 7 |
| With seeds | 13 | 13 | 5 | 72 |
| With Hinau Seeds* | 8 | 10 | 3 | 49 |
| With seeds and leaves | 11 | 11 | 2 | 56 |
| With bark and twigs | 10 | 7 | 2 | 44 |

* *Elaeocarpus dentatus*

ingestion and defecation was 70-85 minutes. Gizzard contents, thus, represent mainly those foods ingested during the preceding few hours or less (i.e. perhaps not more than 0.05% of the annual consumption) when the availability of many items is seasonal and, perhaps, also influenced by time of day. Furthermore, they may contain disproportionate quantities of hard-bodied or less digestible remains and also include items swallowed incidentally (small invertebrates, twigs or leaves adhering to earthworms etc.), or eaten previously by the prey species. Other items, although having food value, may be taken primarily to improve mechanical digestion and thus be selectively retained in the gizzard for extended periods.

Because of these provisos, discussion on the contribution of various items to the diet includes details on captive kiwis and also other findings that allow inferences or interpretations.

*Earthworms*

Both Gurr (1952) and Watt (1971) questioned the long established and popular belief (assumed from bill-shape and probe holes; Buller, 1888, 1896) that New Zealand's rich earthworm fauna (180-190 species; Lee, 1959) provides the kiwi's staple diet, and and other items merely supplement the ration when worms are scarce or inaccessible. However, this belief is supported by the generally better initial acceptance of, and sustained preference for, earthworms over other items by newly-captured birds (Lint, 1966; Clayton, 1972; Davis and Greenwell, 1976), and our analyses indicate the importance of annelids to wild birds as unidentified earthworms or their chaetae were present in 47 (94%) of the gizzards.

Captive kiwis are known to take worms ranging in size 0.3-6.5 g, and the diet of brown kiwis on Little Barrier Island includes three species (Roach, 1954) that vary greatly in size and are characteristic of different habitats, i.e. the 0.7-1.0 g *Megascolides maoricus* of forest top soil and leaf mould, the 1.0-1.5 g *Allolobophora caliginosa* characteristic of pasture and cultivated soils, and the giant 50-160 g *Spenceriella gigantea* of forest sub-soils. The latter reaches a length of 60-140 cm and, from the dismembered fragments around kiwi probe holes, would seem to be extracted piecemeal with, possibly, the severed portion remaining firmly in the ground.

The large numbers of kiwis held by some New Zealand institutions have forced these into providing substitute diets and worms are seldom available in quantity. At the Otorohanga Zoological Society's facilities, captive kiwis maintain consistent weight and breed regularly on a meat and cereal ration that provides approximately 1380 Kjoules (330 Kcal.) gross energy per bird each night (Reid & Rowe, 1978). Analyses of the organic composition of earthworms (Laverack, 1963; McInroy, 1971; Hansen and Czochanska, 1975) show that a kiwi would require at least 500 1 g earthworms averaging 10 cm x 0.35 cm diameter to furnish equivalent energy to the artificial diet (Reid, 1970). To survive on earthworms of this size during the summer months, a kiwi would need to locate and extract them (often from deep sites in dry soils) at an average rate of one per minute during the entire period of darkness. As approximately one-third of the New Zealand earthworm species weigh 0.5 g, or less, and only one-third consistently exceed 3.0 g, more versatile feeding habits have obvious advantages and birds have been seen foraging the hard, baked, clay pasture lands of

North Auckland during mid-summer when annelids are difficult to obtain.

*Other Invertebrates*

It may be inferred from Table 1 that, after annelid worms, cicada nymphs (*Amphisalta*), and melolonthids (*Odontria*) and their larvae are preferred foods but these insects are abundant, available throughout the year and gregarious. The total list of ingested species (Appendix 1, 2) shows a wide range of items and it may well be that brown kiwis are random feeders and that numbers of prey ingested reflect supply rather than choice. For example, the occurrence of blackbeetle (*Heteronychus arator*) in gizzard samples agreed with its known distribution in 1974. It was present in 11 of 23 Northland birds (as the only invertebrate in two gizzards and the principal item in a third), but in none from Taranaki. Furthermore, both blackbeetle and grassgrub (*Costelytra*) occurred mainly in birds that died during the autumn and their ingestion coincides with their normal seasonal peak availability in pasture (Essen, 1974; Fenemore, 1974).

Conclusive evidence of above-ground feeding is lacking. A few species that represent only a very minor portion of the ingesta (some spiders and wetas etc.) may favour elevated sites on vegetation, but also occur at ground level. There is a small component, e.g. Lucanidae which can be associated with wood, and both Buller (1888) and Watt (1971) reported others. Buller found ten huhu grubs (*Prionoplus* larvae) in one bird but none were recovered in the present sample.

With the exception of earthworms, most food items were between 10-30 mm in length, and apart from there being a preponderance of ground-dwelling species, or stages, among the prey (of the 590 coleoptera found, 69.5% were larvae), we are unable to confirm that feeding is selective. Kiwis often forage almost continuously throughout the night in order to get sufficient food and, as the diversity of items in some gizzards show (e.g. 31 invertebrates representing 18 species, excluding worms, in one bird; Gurr, 1952), this leaves little scope for selection.

Selected or not, some invertebrates formed a significant part of the food. Whether considered as a percentage of the total invertebrates ingested (24% excluding earthworms), or on the basis of the number of gizzards that contained them (52%), or as a percentage of the invertebrates in these 'positive' gizzards (34.5%), cicada larvae were the most important items (Table 1). They were the most numerous invertebrates in 12 of 50 gizzards. One bird contained 65, another 59 nymphs, and Bull (1959) found 70 nymphs in the stomach he analysed. The preponderance of mature nymphs in our sample suggests shallow feeding, since nymphs move nearer the surface prior to emergence.

The presence of grassgrub beetles and larvae and *Heteronychus arator* imagoes, alone, or in various combinations, in 80% of the gizzards analysed during this study support the findings of Watt (1971) that the bush-dwelling kiwi is adapting successfully to new environments. Watt found that three species (*Teleogryllus commodus, Thyreocephalus chloropterus* and *Heteronychus arator*), believed to be exclusive to pasture or cultivated land, comprised 45% of the combined total of 147 insects present in the stomachs of two birds accidentally killed near Kaitaia, Northland.

*Vegetable Matter*

This was present in 40 of 43 gizzards (Table 2). In several birds, the quantity and nature of the vegetation (minute bark and twig fragments, solitary small, fibrous leaves of *Cyathodes, Leptospermum* etc.) were indicative of incidental ingestion, but the quantity of softer leafy material (unidentified broadleaf and grass species) in three gizzards suggests limited browsing, or grazing, while the number and variety of seeds in 24 gizzards suggest that some berries and fruits are actively selected (Appendix 3).

The quantity of plant material in these 40 gizzards may not, however, reflect the extent of its consumption. During post-mortem examinations of a further 13 birds found dead, a cursory inspection of the gizzards showed no obvious animal remains in one which was filled with finely macerated (but unidentifiable) leaves, while the bulk of the contents in three consisted of fibrous grass-like material and grit—and several observations show that vegetable matter (particularly fruits) is often selected ahead of other items.

At Mt Bruce Native Bird Reserve, a brown kiwi rejected its standard ration and for several nights fed almost exclusively on fallen, ripe Kahikatea (*Podocarpus dacrydiodes*) fruit. At Russell, another bird largely ignored garden invertebrates as it nightly walked the rows of strawberries and plucked ripe fruit through a protective wire mesh (T. G. Lovegrove, pers. comm.). At Napier, a bird was seen snipping and swallowing considerable quantities of grass near its untouched feed bowl.

A bird described by Watt (1971) also contained more vegetable than animal matter. Predominant were the large, juicy (and possibly toxic) seeds of cape honey flower (*Melianthus major*), a native to

TABLE 3. *Relationship between the number of hinau seeds and the quantity of grit in the gizzards of 40 North Island brown kiwis.*

| Number of Seeds in Gizzard | 0 | 1-5 | 6-15 | >15 |
|---|---|---|---|---|
| Number of Gizzards | 19 | 10 | 5 | 6 |
| Hinau Seeds; Average Number | 0 | 3.4 | 10.0 | 30.3 |
| Grit; Ave. Number of pieces | 87 | 50 | 33 | 2 |
| Grit; Ave. Weight (g) | 8.8 | 5.8 | 2.9 | 0.2 |
| Grit; Max. Number per Gizzard | 225 | 134 | 75 | 6 |
| Grit; Max. Weight per Gizzard (g) | 20.2 | 12.5 | 6.4 | 0.6 |
| Gizzards without grit | 0 | 0 | 1 | 4 |

South Africa that locally has spread from homestead gardens to adjacent pastures (Simpson, 1973).

The widespread occurrence of seeds from some plants in gizzard samples may exaggerate their importance as foods and, perhaps, indicate a dual function. The nutritive (Williams, 1982) 0.9-1.1 g olive-like drupe of hinau (*Elaeocarpus dentatus*), which falls in March-May, is frequently ingested. Fresh drupes, or drupes plus seeds, were present in 10 gizzards, and seeds alone in 11 gizzards. The latter included five of the nine gizzards from birds that died during spring when fresh drupes would not have been available for several months. It would appear that old, clean, hard seeds are taken in place of grit, and that seeds may be selectively retained as grinding aids over long periods, for all 3-10 hinau seeds in five gizzards were abraded smooth. Gizzards without hinau seeds tended to have the greatest quantity of grit, and the volume decreased as the number of seeds increased (Table 3).

Although the widespread ingestion of grit (in 88% of the sample, an average content of 54 pieces over 1 $mm^3$ and averaging 5.3 g per gizzard) indicates further the importance, to kiwis, of foods other than soft-bodied species, their gizzard musculature (32.5 g in a 2.35 kg brown kiwi compared with 70.5 g in a 2.30 kg takahe (*Notornis mantelli*), a flightless vegetarian) is such that the eating of coarser vegetation, high in fibre and low in available energy, may result from shortages of alternative foods, as it is doubtful that a kiwi could maintain condition on a diet of predominantly rough pasture alone.

Indirect evidence, indicative of the importance of plant foods for feral kiwis, is inconclusive. Of nine unrelated eggs recovered from the wild, only one exceptionally small 365 g egg (average egg, 431 g; Reid, 1981), laid by a bird found in pasture land, contained bright yellow, xanthophyll-pigmented yolk characteristic of greens in the diet (Romanoff and Romanoff, 1949). The other yolks were a pale, dull clay-yellow colour.

On the other hand, analyses of the sub-cutaneous fats from a North Island brown kiwi (Shorland and Gass, 1961) and a takahe (Hartman and Shorland, 1968) showed linoleic (C18:2) and linolenic (C18:3) fatty acids, which generally are associated with a vegetarian diet, together represented nearly 16% of the fatty acids in the kiwi, but only 6.2% in the takahe. The ratio of C18:2 to C18:3 in both birds, and in earthworms (Hansen and Czochanska, 1975)—and the ratio of combined linoleic/linolenic to C20 unsaturated fatty acids in the kiwi and in earthworms—supports the belief that seeds and fruits contribute significantly more of the kiwis foods than green vegetation and, also, that earthworms (or aquatic animals? Shorland and Gass, 1961) are principal items in the diet.

*Aquatic Foods*

The pair of mucusal 'diving' valves, characteristic of aquatic birds, at the proximal end of the terrestrial kiwi's nasal passages (Bang, 1971) were assumed to have the protective function of reducing dust inhalation when birds are sniffing for food. As kiwis presumably evolved in humid rain forests with generally damp humus and soils, and as pneumoconiosis seems more prevalent among kiwis living in drier habitats resulting from recent European land use (Smith, Poole and Martinovich, 1973) these valves may facilitate feeding from water. Direct evidence of this is limited, but parts of one freshwater crayfish were recovered during the present study and also from a faecal sample of *Apteryx haasti*.

In captivity, a South Island brown kiwi (*A.a. australis*) from Okarito showed considerable skill in feeding on some freshwater animals. Immediately after capture, the bird was kept in an indoor pen for 18 days. Its nightly ration consisted of 250 g of earthworms and other invertebrates in soil, and 5-12 live freshwater crayfish in a container of water. Live fish, *Gobiomorphus sp.* and *Galaxias fasciatus*, were sometimes provided. On some nights, the bird

favoured worms, but on others, it fed first on the crayfish, and on most nights it ate several crayfish ranging in size 2.5-7.5 cm. Larger specimens were lifted clear of the water and dismembered by a flicking motion. Only half the fish were caught and these, including some 10 cm long, were swallowed whole after being stunned. When the bird was searching the container, its bill was in water for up to three minutes at a time and air was seen to escape from the submerged nostrils (C. D. Roderick, pers. comm.).

## CONCLUSIONS

Kiwis are territorial but, because none of the birds examined had been under observation, the habitat can only be inferred from the food remnants recovered. Many were reported as living in scrubland and regenerating bush, and this is endorsed by a study of the invertebrates ingested. The presence of some insects probably indicates pasture feeding, but most of the food consisted of species commonly associated with bush margins.

It seems highly probable that the probing capacity of the bill is fully utilized, and the ingesta also includes animals that would not normally occur deep in the ground. No evidence of extensive above-ground feeding was found and this is consistent with observations made on captive birds in which the meals of meat slivers were divided into several portions and placed at different elevations. The kiwis confined their intake to the 45-50% of their usual ration placed on, or within 10-15 cm of the ground. Although the birds, presumably, were hungry, these results require confirmation as the methods of elevating the food possibly created unfamiliar conditions for kiwis already conditioned to a standard routine at a fixed feeding station.

The diverse feeding habits of kiwis are such that a 'typical' diet probably does not exist. In some localities, worms appear to be the principal food items, in other habitats insects are the more important, and plant material provides a lesser portion throughout. An estimate of the relative contributions of these components to an 'average' diet is earthworms 40-45%, other invertebrates 40-45%, and plant material 10-15% with seeds and fruits being, perhaps, at least twice as important as greens.

Kiwis eat what is accessible and Carroll's (1963) analysis of the gizzard contents from 86 flightless North Island weka (*Gallirallus australis*) permits a similar interpretation, as animal matter formed a lower proportion of the diet during winter when a number of the food species listed would not be available. Although these wekas came mainly from Gisborne agricultural lands (horticultural to rough pasture) having an average annual rainfall of 800-1200 mm and the kiwis used in this study came predominantly from wetter bush and scrub localities (average annual rainfall, 1600-2400 mm), earthworms and coleoptera (beetles) were the most common invertebrate foods of both species. Earthworms were present in 76% of the weka gizzards. Coleoptera occurred in 90% of the kiwis and in 86% of the wekas, but while adult beetles were present in 78% of kiwi and 76% of weka gizzards, their larvae were found in 72% of the kiwi, but only 15% of the weka gizzards. The low intake of beetle larvae was matched by the absence of cicada larvae in the weka samples. It seems highly probable that, in a shared habitat, these two species would compete for many invertebrates, with the kiwi more adept at digging out larvae and the nimble weka more successful at catching adults.

Regardless of seasonal, or other, variations in food supply, most items taken are either small, or, because of high water or indigestible content, low in available energy. A large number are thus required and the need for prolonged foraging may explain the uncharacteristic but, apparently, quite common twilight and even day-time activities of the larger Stewart Island brown kiwi (*A.a. lawryi*). Compared with the North Island brown kiwi, the Stewart Island subspecies is 20-40% heavier and lives in mean ambient temperatures 3-6°C colder. Enlarged size and reduced temperatures both increase energy requirements and the short nights on Stewart Island in summer (5-6 hours) may be inadequate to obtain sufficient food.

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## APPENDIX 1

*Insects identified from gizzards of 56 North Island brown kiwis. Source: a = Buller, 1888; b = Gurr, 1952; c = Bull, 1959; d = Watt, 1971; e = this study.*

| | Max. No. in one gizzard | Source |
|---|---|---|
| ORTHOPTERA: | | |
| *Blataria* sp. (cockroaches) | 1 | e |
| *Dienacrida* sp. (wetas) | 3 | a |
| *Hemiandrus* sp. (ground wetas) | 4 | e |
| *Hemideina crassidens* (tree wetas) | 3 | e |
| *Onosandrus*? sp. | 1 | c |
| *Teleogryllus commodus* (field cricket) | 24 | d |
| DERMAPTERA: | | |
| Gen. sp. indet. (earwigs) | 1 | e |
| HEMIPTERA: | | |
| Gen. sp. indet. (cicadas) | 70 | c |
| *Amphisalta* sp. (cicadas) | 65 | e |
| LEPIDOPTERA: | | |
| Gen. sp. indet. (moths) | 2 | b |
| Agrotidae | 6 | c |
| Hepialidae | 4 | c |
| Melanchridae | 1 | e |
| Noctuidae (army worms) | 2 | e |
| *Oxycanus* sp. (Porina larvae) | 24 | e |

APPENDIX 1 CONTINUED

| | Max. No. in one gizzard | Source |
|---|---|---|
| HYMENOPTERA: | | |
| Formicidae Gen. sp. indet. (ants) | 1 | e |
| *Amblyopone australis* (ants) | 1 | e |
| DIPTERA: | | |
| Tipulidae (cranefly larvae and pupae) | 40 | e |
| COLEOPTERA: | | |
| Carabidae: gen. sp. indet. (ground beetles) | 5 | b |
| *Agonum sulcitarse* | 2 | d |
| *Ctenognathis bidens* | 1 | d |
| *Cyclothorax insularis* | 1 | e |
| *Holcaspis dentifera* | 2 | d |
| *H. mucronata* | 2 | e |
| *H.* sp. | 2 | e |
| *Mecodema* sp. | 1 | e |
| *M. crenaticolle* | 3 | e |
| *Megadromas* sp. | 1 | e |
| *Zabronothus* sp. | 1 | e |
| Cerambycidae: *Coptomma* sp. (longhorn beetles) | ? | a |
| *Prionoplus* (huhu grubs) | 10 | a |
| Cicindellidae: *Neocicindella* sp. (tiger beetle larvae) | 1 | e |
| Curculionidae: gen. sp. indet. | 1 | e |
| Elateridae: gen. sp. indet. (click beetle larvae) | 10 | e |
| Lucanidae: gen. sp. indet. (stag beetle) | 6 | c |
| *Lissotes oconnori* | 1 | e |
| *L. planus* | 1 | d |
| *L. stewarti* | 2 | e |
| Scarabidae: gen. sp. indet. | 1 | b |
| *Costelytra* sp. | 32 | c |
| *Costelytra* sp. (cockchafer larvae) | 41 | e |
| *C. longicornus* | 37 | d |
| *C. suturalis* | 1 | e |
| *Xylostignus brookesi* | 2 | e |
| *Heteronychus arator* (black beetle) | 37 | e |
| Melolonthid larvae (grass grubs) | 43 | e |
| *Odontria* sp. (grass grub beetles) | 10 | e |
| *O. borealis* | 4 | d |
| *O. magnum* | 1 | e |
| *O. piciceps* | 3 | e |
| *O. sylvatica* | 4 | d |
| *O. xanthosticta* | 5 | d |
| *Onthophagus posticus* | 1 | e |
| Staphylinidae: *Cafius* sp. | 2 | e |
| *Thyreocephalus chloropterus* | 6 | d |
| Tenebrionidae: gen. sp. indet. | 2 | c |
| *Uloma tenebrioides* | 1 | d |

APPENDIX 2

*Invertebrates (other than insects) identified from the gizzards of 54 North Island brown kiwis. Source: a = Gurr, 1952; b = Roach, 1954; c = Bull, 1959; d = this study.*

| | Max. No. in one gizzard | Source |
|---|---|---|
| ANNELIDA: | | |
| gen. sp. indet. (earthworms) | 5 | d |
| *Allolobophora caliginosa* | ? | b |
| *Megascolides maorica* | ? | b |
| CRUSTACEA: | | |
| *Paranephrops planifrons* (freshwater crayfish) | 1 | d |
| Isopoda (slaters) | 2 | a |
| CHILOPODA: | | |
| gen. sp. indet. (centipedes) | 1 | d |
| *Cormocephalus* sp. | 1 | d |
| *C. rubiceps* | 3 | a |
| *Scolopendra sp.* | 1 | d |
| *Paralamycetes validus* | 2 | a |
| *Geophilomorpha* | 1 | d |
| DIPLOPODA: | | |
| gen. sp. indet. (millipedes) | 4 | d |
| *Proceliostoma* (Pill millipedes) | 2 | d |
| ARANAE: | | |
| *Opiliones* gen. sp. indet. (harvestmen) | 2 | a |
| Araneomorphae gen. sp. indet. (web spinners) | 2 | a |
| Mygalomorphae gen. sp. indet. (trap door spiders) | 1 | a |
| Segestriidae sp. | 1 | d |
| Dipluridae sp. | 2 | d |
| Dipluridae *Porrhothele antipodiana* | 1 | c |
| MOLLUSCA: | | |
| gen. sp. indet. (snails and slugs) | ? | d |
| *Helix aspersa* | 3 | d |
| *Paryphanta busbyi* | ? | d |
| *Schizoglossa novaezeelandica* | 3 | d |
| *Rhytida dunniae* | 4? | d |

APPENDIX 3

*Seeds identified from the gizzards of 48 North Island brown kiwis. Source: a = Buller, 1888; b = Gurr, 1952; c = Simpson, 1971; d = this study.*

| | Max. No. in one gizzard | Source |
|---|---|---|
| *Podocarpus dacrydiodes* (kahikatea) | 8 | d |
| *P. ferrugineus* (miro) | 5 | d |
| *P. totara* (totara) | 4 | d |
| *Albizzia lophantha* (brush wattle) | 4 | d |
| *Carex* sp. | 1 | d |
| *Cirsium* sp. (thistle, 2 species) | 6 | d |
| *Coprosma* sp. (at least 3 species) | 80 | d |
| *Cordyline australis* (cabbage tree) | c500 | d |
| *Cyathodes acerosa* (mingi mingi) | 1 | d |

APPENDIX 3 CONTINUED

| | Max No. in one gizzard | Source |
|---|---|---|
| *Elaeocarpus dentatus* (hinau) | 63 | d |
| *E. hookerianus* (pohaka) | 7 | d |
| *Gahnia xanthocarpa* ? | many | d |
| *Geniostoma ligustrifolium* (hange hange) | 1 | b |
| *Hebe* sp. | 1 | d |
| *Leptospermum scoparium* (manuka) | 2 | d |
| *Leycesteria formosa* (himalayan honeysuckle) | 13 | d |
| *Melianthus major* (cape honey flower) | many | c |
| *Mida salicifolia* (taiko) | many | a |
| *Olea* sp. (maire) | several | a |
| *pseudopanax arboreus* (five finger) | 85 | d |
| Palm; gen. sp. indet. | 2 | d |
| *Rhopalostylis sapida* (nikau palm) | 4 | d |
| *Rubus* sp. | 1 | d |
| *R. fruticosus* (blackberry) | 1 | d |
| *Scirpus* sp. | several | c |
| *Stellaria media* (chickweed) | 2 | d |
| *Solanum* sp. | 4 | d |
| *Uncinia* sp. (hook grass) | 5 | d |
| *Urtica* sp. (nettle) | 2 | d |
| *Vitis vinifera* (grape) | 1 | d |