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BREEDING OF NORTH ISLAND BROWN KIWI, *APTERYX AUSTRALIS MANTELLI*, IN HAWKE'S BAY, NEW ZEALAND

Summary: Three pairs of kiwis were fitted with radio transmitters and followed for two years in a forest remnant in Hawke's Bay. Laying began in late June or July, when both sexes reached peak weight, and usually finished in November. Twelve of 14 nests were in burrows, 470-900 mm long. Females laid 2-5 eggs each season, 21-60 days apart; clutches which failed in the first few weeks of incubation were replaced. Completed clutches comprised two eggs. A second clutch laid after the first had successfully hatched was recorded only once. Males did all of the incubating and emerged every night to feed, except when chicks were hatching. Their feeding bouts averaged 4.9 h, about half the feeding time of non-incubating kiwis. The weights of both sexes declined during the breeding season - females by about 20% and males by about 13%. Only 6 of 21 eggs laid in the two years hatched. One chick died while hatching, and two died soon afterwards. Three fledged 16-20 days after hatching, giving a productivity of 0.5 chicks/pair/year. The breeding behaviour and mating system of kiwis in Hawke's Bay are discussed.

Keywords: Apteryx australis mantelli; North Island brown kiwi; ratite; breeding season; nest sites; clutch size; productivity; incubation behaviour; weight changes; mating system.

Introduction

It is common knowledge that kiwis lay huge eggs which the male alone incubates. Less well known is that the egg contains more energy than any other of similar size (Reid, 1971b), that incubation takes 75-80 days, or that the young hatch fully covered in feathers rather than down (Reid and Williams, 1975).

Surprisingly, these few facts are almost all that is known about breeding of brown kiwis in the wild. Details of nest sites, mating systems, breeding seasons, and reproductive rates are either sketchy or lacking. Early naturalists such as Buller (1888) and Layard (1863) gave descriptions of nests, clutches and breeding times, since supplemented by other chance observations (eg. Turbott and Wightman, 1955). These indicate that brown kiwis lay in any month of the year, but mainly between July and February (Reid and Williams, 1975). Colbourne and Kleinpaste (1984) noted that calling by brown kiwis in Waitangi State Forest, Northland, increased in late winter, and suspected that this signified the onset of breeding. Falla (1979) observed a female accompanying two males and suggested that they might be polyandrous, as are some other ratites (Lack, 1968).

Some aspects of the reproductive physiology and behaviour of brown kiwis have been studied in captivity (eg. Robson, 1958; Clayton, 1972; Calder, 1979). Much, but perhaps not all of this information, applies to wild kiwis. Reid (1981) states, for example, that free-living females lay 1-2 eggs a year, whereas captives may lay 4-6. In addition, the eggs of captive

females are generally smaller than those of wild kiwis (Reid, 1981).

This study describes the breeding behaviour and success of three pairs of kiwis which were radio-tagged and followed for two years in a bush remnant in Hawke's Bay.

Study Area

The study was undertaken between March 1984 and April 1986 at Haliburtons, a 770 ha patch of privately owned forest in steep hill country, near the confluence of the Mohaka and Te Hoe Rivers in inland Hawke's Bay (39°06'S., 176°48' E.). The forest was formerly part of a large tract extending from the west bank of the Mohaka River to the southern Ureweras. Clearing in 1980 left it a forest 'island', bordered mainly by pine *(Pinus radiata)*. About half the remnant was covered in tall forest, dominated by tawa *(Beilschmiedia tawa)*, beech *(Nothofagus* spp.)and podocarps, chiefly rimu *(Dacrydium cupressinum)* and matai *(Prumnopitys taxifolia)*. The other half was young forest, dominated mainly by kanuka *(Kunzea ericoides)*, kamahi *(Weinmannia racemosa)*, rewarewa *(Knightia excelsa)* and tanekaha *(Phyllocladus . trichomanoides)*. Both forests were heavily browsed by possums *(Trichosurus vulpecula)* and red deer *(Cervus elaphus)*. Feral cats *(Felis catus)* were often seen in the study area, and a ferret *(Mustela putorius)* was observed twice in pasture on the edge of it. During the study, Haliburtons contained eight adult kiwis (three pairs and two unmated females). They lived mainly in

the mature forest, but sometimes fed in the neighbouring kanuka forest and young pine plantations (McLennan *et al.,* 1987).

Methods

Capture

Kiwis were caught using trained dogs, then radio-tagged as described by McLennan *et al.* (1987). All adults carried radio transmitters for at least 16 weeks, and most for over 50 weeks. At least one member of each pair carried a functioning transmitter between May 1984 and April 1986. Tagged birds were located on most days between May 1984 and March 1985, then at least once a week until April 1986.

Inspection of nests

Males were suspected of nesting if they returned to the same site on several consecutive days, or if vegetation was found stacked at the entrance of a burrow. I revisited such sites at night, after the occupant had emerged. Eggs were sometimes visible, but usually I had to feel for them. Although this must have left some scent, the birds always returned within a few hours.

Active nests were visited at least once a week, mainly in daylight, to check if a bird was on the nest and to identify it. Night visits were more frequent towards the end of incubation to determine hatching dates.

Weights of kiwis

Radio-tagged kiwis were removed from daytime shelters and weighed in most months from December 1984 to December 1985 inclusive, so that seasonal changes in weight could be related to known reproductive effort. Some females were weighed weekly or fortnightly during the laying period. Males were not removed from nests in case they deserted, so they were not weighed during incubation.

Observations at nests

The behaviour of males emerging from nests was observed using night-viewing equipment. Nests were watched when eggs were hatching, and when chicks were present. The times when incubating males left and returned to nests were determined by watching, by listening for variations in the transmitter signals which indicated that the birds were moving or stationary, and by using electronic timers set at the entrances of nests.

Results

Mating system

The kiwis at Haliburtons were monogamous. The members of each pair shared the same territory throughout the year, and stayed together for both breeding seasons. Two unpaired adult females entered the territories of bonded pairs briefly (McLennan *et al.,* 1987) but were never recorded near nests.

Breeding season

The three pairs laid 21 eggs between them in two years. Laying started in June or July and usually finished in November (Fig. 1). If first clutches failed in the first few weeks of incubation they were replaced, usually in August or September. One pair bred twice in the 1985/86 season. The chicks from the first clutch left the nest in October 1985 and the second clutch was laid in early January and February 1986.
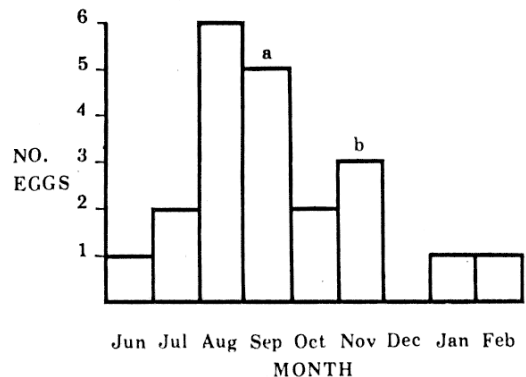

Figure 1: *Time of laying by three pairs of kiwis in inland Hawke's Bay, 1984-86. a) One egg in the September total may have been laid in the first week of October. b) One egg in the November total may have been laid in the first five days of December. First clutches and early replacements were laid from June to September, late replacements from October to November, and second clutches in January and February.*

Nest sites

Fourteen nests were found. Twelve were in burrows, one under a thick layer of fallen *Dicksonia* fronds, and one in a cavity under a tree stump covered by dense water fern, *Histiopteris incisa*. Burrows were selected as nest sites significantly more often than they

Table 1: *Comparison of sites selected by kiwis for nesting and for sheltering by day. Data from paired adults only.*

		% of occasions in			
	n	Burrow	Natural cavity	Hollow log	Under vegetation
Nest site	14	86	7	0	7
Shelter site	348	37	28	9	26

were used as daytime shelters (Table 1; $X^2 = 10.0$ (corrected for continuity) p<0.05).

Some burrows appeared to be excavated solely for breeding. They were significantly shorter than burrows used as daytime shelters ($\bar{x} \pm SE = 650 \pm 50$ mm (n = 12) and 1010 ± 60 mm (n = 76) respectively, t = 4.8, d.f = 47, P <0.001), but similar in diameter (100-200 mm). The female laid her egg in the entrance to one nest with a very narrow opening, presumably because in her gravid state she could not squeeze through to the chamber. The male subsequently moved the egg about 300 mm to the end of the burrow. One nest was so shallow that the incubation male was exposed to the sun for several hours on fine days. In four out of 12 burrows the eggs were clearly visible from the entrance; in eight others they were hidden by a bend in the tunnel. Terrain and aspect did not seem to influence the selection of nest sites, nor did cover; five of 14 nests were on hillsides with little undergrowth.

Nesting burrows were excavated months and possibly years before they were used, long enough for moss and small ferns to re-establish at the burrow entrance and for all traces of excavated soil to disappear. In the fortnight before laying, the birds covered the floor of the chamber with a thin layer of vegetation, and sometimes placed leaves and twigs over the burrow entrance. More material was taken into the nest chamber by females when they laid their first egg, and by males during incubation.

Whenever a clutch failed, the birds moved to another burrow to re-lay. If replacement clutches also failed soon after laying, the birds shifted again, so some pairs used 3-4 nests in a breeding season. The pair which laid a second clutch in 1986 moved to a new burrow to do so, despite being successful in their first site. None of the 8 nesting burrows used in 1984 were re-used in 1985.

Laying
Six completed clutches contained two eggs. Incubation sometimes started with the first egg, so was not a reliable indication of a completed clutch. Eight nests were deserted or failed within four weeks of the first egg being laid. All of these were assumed to be incomplete clutches because those that did survive for longer invariably had a second egg added.

Paired females laid two to five eggs each breeding season, 21 to 66 ± 10 days apart (Table 2). The laying dates of some eggs were not determined precisely enough to calculate intervals. Laying intervals seem highly variable, and may shorten as the breeding season progresses.

Seven eggs ranged from 121 to 139 mm in length, and 76 to 81 mm in width. Average dimensions were 129 ± 2 mm x 78 ± 1 mm. The fresh weights of three eggs were 458, 430 and 425 g, about 70 g heavier on average than those laid in captivity (Reid, 1981).

Incubation
Females usually stayed in the nest burrow for one or two days after laying their first egg, but not after laying their second. The onset of incubation changed as the breeding season progressed and varied between males. For first clutches, one male started incubating immediately after the female left, and another started 10-14 days later. The third male incubated intermittently (about one day in six) for 20-30 days before settling into a steady routine. In replacement layings, all males started incubating immediately after the first egg was laid.

Females were not found in nests again during the day (156 inspections) until chicks hatched. There was an exception in August 1984, when a pair had an egg in two different nests. The female occasionally incubated the more recent one while her mate incubated the other. His egg was rotten and could be smelt from several metres away, but he persisted with it for several weeks. He eventually moved to the second nest 19 days after the egg was laid, and the female then ceased incubating.

Incubating males emerged every night to feed (100% of 66 inspections), except when chicks were hatching. Times of emergence ranged from 26 minutes to 5.5 hours after sunset (n = 50, $\bar{x} \pm SE = 102 \pm 10$ min.), and did not change systematically as incubation progressed (Table 3). Non-incubating males and females emerged significantly earlier in the evening (n

Table 2: *Time and pattern of laying by three kiwis in Hawke's Bay during 1984/85 and 85/86. N.C. = not calculated.*

Female	Egg number	1984 Laying date	Interval (days)	1985 Laying date	Interval (days)
				Breeding season	
	1	?, found 06-09-84		24 to 27-08-85	
			min. 21		N.C.
	2	27-09-84		? before 18-10-85	
1			26		N.C.
	3	23-10-84		01-11-85	
			21		
	4	13-11-84			
	1	08-08-84		12 to 18-06-86	
			max. 26		66±10
2	2	? before 04-09-84		13 to 27-08-86	
					28±11
	3			12 to 21-09-86	
	1	21-06-84		09-07-85	
			53		35±2
	2	13-08-84		11 to 15-08-85	
			48 ± 2		N.C.
3	3	28-09 to 01-10-85		? before 31-10-85	
			N.C.		N.C.
	4	? before 05-12-84		? late Dec. 86	
					N.C.
	5			?, late Jan. 86	

Table 3: *Time of emergence of incubating males in relation to the stage of incubation. E = first four weeks of incubation, M = 5-8 weeks inclusive, L = > 8 weeks. Data from three males combined.*

	No. of occasions male emerged		
	E	M	L
< 100 min. after sunset	8	6	13
> 100 min. after sunset	4	7	12

= 11, $\overline{x}$ ± SE = 38 ± 8 min., t = 5.1, p<0.0001) than incubating males.

The active periods of incubating males averaged 4.9 ± 0.4 (SE) hours (range = 2.0 - 8.2 h, n = 16), which amounted to about one third of the night in August, and half the night in December. This was significantly shorter than the active period of non-incubating kiwis (7.4 ± 0.6 h, n = 7, t = 3.5, p <0.005). On one of 156 occasions, an incubating male remained off a nest for at least 20 hours, roosting during the day in a shelter about 200 m away. He resumed normal incubation the following night.

Two of the three males covered the nest entrance with pieces of vegetation before they moved off; these were gathered from the ground or pulled off living shrubs. They were usually carried in the bill and placed over the entrance, but were sometimes tossed in the general direction from a distance of about 500 mm. The third male covered his nest entrance intermittently in the first three weeks of incubation, but not thereafter. Males sometimes turned and pulled vegetation over the entrance after re-entering nests, as did some females when them entered to lay.

During incubation, eggs were positioned side by side in the chamber and half-buried in vegetation. On 17 of 20 occasions, eggs were not covered while the male was absent. In one clutch, one egg was fully covered with feathers and the other was exposed on the three times it was inspected. This was probably accidental,

rather than a deliberate ploy to manipulate cooling rates and synchronise hatching.

The incubation periods of two eggs were 85 days and 92 ± 4 days. In another nest, the first egg was laid on 7 August and the second was discovered on 5 September. Only one egg hatched, on 21 November, after a minimum incubation period of 77 days and a maximum of 106 days, depending on which egg failed. The interval between hatching of first and second eggs was recorded for two replacement clutches as 13 ± 1 and 5± 2 days. Incubation started with the first egg in the first of these clutches, but the other clutch was not discovered until after the second egg was laid.

Changes in body weight during laying and incubation

Both sexes reached their peak weights for the year in late winter, at the onset of breeding (Fig. 2). Females lost an average of 530 g (19% of peak weight, n = 4) between the start and finish of laying, about 180 g for each egg laid. The weights of males declined 7.5% -23% during incubation (n = 4).

I did not weigh any non-breeding kiwis, but these weight changes probably resulted from breeding rather than from a seasonal decrease in food. One male who incubated for only 16 days between June and December 1984 lost 60 g, whereas two that incubated for at least 77 days lost an average of 210 g. Similarly, a female which laid two eggs lost half as much (350 g) as those that laid three (680 g), or four (620 g).

Hatching and behaviour of young chicks

I watched one next continuously when the first of a two-egg clutch was hatching. The male stayed in the nest for over 40 hours (two days and one night), finally emerging 5 hours after sunset on the second evening.

Females visited nests soon after eggs hatched. One roosted in the entrance of a nest burrow for four consecutive days while her mate brooded the chick. Another was seen at night at the entrance of a nest two days after a chick hatched. The male emerged when she arrived and both left together.

Males brooding young chicks emerged at variable times to feed each night, and returned before daylight. Females did not remain with chicks when males were foraging, and I never saw parents feed chicks.

Three chicks emerged from the burrow for the first time when 4, 6 and 7 days old. Initially they fed entirely within a few metres of the nest, often returning to it through the night. When 10 days old they moved quickly and nimbly, and fed further away. Apparently adults did not accompany young chicks;

on eight occasions I watched a chick foraging when I knew its parents were at least 70 m away. In another brood of two, the oldest chick emerged and foraged while the adult male stayed in the nest with the younger one. However, the adult female was not radio-tagged, so she may have been nearby.

The age of fledging, when they left the nest for good, was recorded for two chicks as 20 and 17± 1 days. One radio-tagged chick was found 80 m from the nest one day after fledging, and about 200 m away three days later. On both occasions the chick was roosting alone under dense vegetation. Two other chicks were not seen again after fledging.

Breeding success

Of 21 eggs laid in the two years, only 6 (29%) hatched (Table 4). Nine eggs (43%) were deserted at various stages of incubation, three apparently because they had cracked or chipped and begun to decay. I probably caused one incubating male to desert when I changed its transmitter. Most of the remaining desertions were by one young male (Pair 1 in Table 4): he was about 18 months old when caught in February 1984, and probably bred for the first time the following spring. His mate laid four eggs in 1984 but he deserted each one, 2-11 days after it had been laid. I uplifted the last and incubated it artificially, but it was infertile. The following year, with the same mate, his two egg-clutch failed in the fifth week of incubation.

Only one egg in an attended nest was definitely eaten by a predator. Three other eggs were also eaten, but they had already been deserted some days or weeks beforehand. On each occasion, the predator chewed an 80-120 mm wide hole in the top or side of the egg; the size of the holes, and hairs found' adhering to the shell of one egg indicated that possums were the culprits. In another nest, a clutch of two was smashed and trampled into the lining, possibly by the incubating male. On two occasions, one egg of a clutch of two disappeared without trace.

One of the six chicks died when hatching. Two died before they fledged, after catching a leg in a cleft stick near their nest; one ripped open its belly when struggling to free itself, the other was suspended over a small bank. Fledging success during the study was 19%, giving an average production per pair of 0.5 chicks per year.

Table 4: *Breeding success of three pairs of kiwis in Hawke's Bay*.

	1984/85			1985/86		
PAIR	Clutch No.	No. eggs	Fate	Clutch No.	No. eggs	Fate
	1	1	Deserted within two weeks of laying	1	2	Smashed, deserted after 5 weeks
1	2	1	"	2	1	Eaten by mammal within 1 week
	3	1	"			
	4	1	"			
2	1	2	One hatched, other lost during incubation	1	1	?, Not known
				2	2	Deserted in 10th week of incubation, 1 egg cracked & rotten
	1	1	Deserted in 4th week of incubation. Cracked & rotten	1	1	Deserted within 2 weeks of laying (intact)
3	2	1	Deserted in 3rd week of incubation	2	2	Both hatched
	3	2	Both hatched	3	2	One chick died when hatching. Other egg disappeared 1-7 days later

DISCUSSION

Breeding behaviour of wild and captive kiwis

Wild kiwis in Hawke's Bay have a shorter, more defined breeding season and spend more time feeding during incubation than do captive kiwis (Robson, 1958; Goudswaard, 1985). The latter difference probably means that eggs of wild kiwis take longer to hatch.

The females at Haliburtons did not differ from captives in the number of eggs laid each year, nor in the rate at which they laid them (Kinsky, 1971; Goudswaard, 1985). However, wild females began each breeding season about 500 g heavier than captives, possibly because they required more stored reserves to manufacture their eggs. Rowe's measurements (cited by Calder, 1978) suggest that captive females gather most of the materials they require as the egg is being formed, because their total increase in weight between successive layings almost exactly equals the weight of the egg subsequently produced. By comparison, the females at Haliburtons (e.g. F1 and F2 in Fig. 2) recovered little or no weight between successive layings, except in the beginning of the breeding season. The losses over the season averaged about 180 g for each egg laid, perhaps indicating that they were obtaining about 40% of the material for each egg from stored reserves. If lipids were transferred from stored reserves into yolk, the energy demands of wild females during laying would not increase by 180%, as Calder's (1978) studies on captives suggest.

The behaviour and development of newly hatched chicks is probably similar in the wild and in captivity, with one exception. The chicks at Haliburtons were entirely nocturnal, whereas captives are often active during daylight (Robson, 1958; Reid and Williams, 1975). Chicks which emerge during daylight may be hungry, but we do not know if captive chicks grow more slowly than wild ones.

Predation and anti-predator behaviour

Some 17 of New Zealand's 46 endemic species of land and freshwater birds have become endangered or extinct since the arrival of humans and mammalian predators (Mills and Williams, 1978). Long-lived species with slow rates of reproduction ('K selected') and specialised habitat requirements have generally fared badly, whereas generalists with high turnover rates ('r selected') have on the whole survived (Moors, 1983). Brown kiwis are a local exception. Despite being both K-selected and flightless, they flourish in some parts of the mainland, especially Fiordland, Taranaki and Northland (Bull *et al.,* 1985). Their persistance is even more remarkable given that their
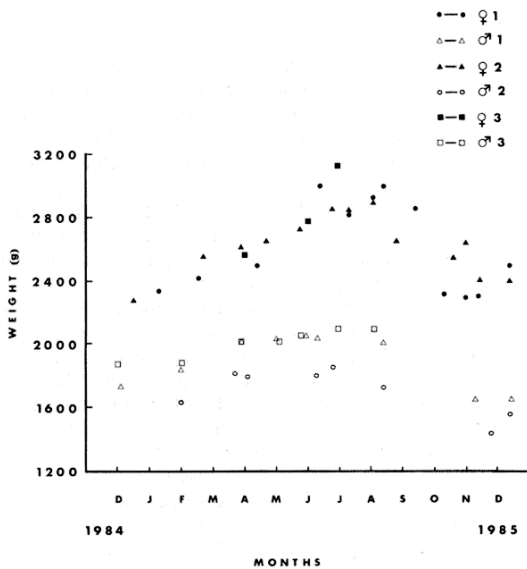
Figure 2: *Seasonal changes in weight of kiwis in Hawke's Bay from December 1984 to December 1985 inclusive.*

eggs are vulnerable to predators for at least 75 days during incubation, and newly hatched chicks are left unattended while adults forage.

Their resiliance is probably attributable in part to the size and aggressiveness of the adults. At two to three kilograms, they exceed the size of prey commonly taken by feral cats (Fitzgerald and Karl, 1979). They can kick hard, and do so to defend themselves and their nests. In this study, there was a suggestion that deserted eggs were eaten more frequently than attended ones, perhaps implying that males repelled predators. (Alternatively, old eggs may have been easier to find.) Only 5% of attended eggs were eaten in the two years, extremely few for a mainland species. Moors (1983), for example, found that mammalian predators ate 40% of the eggs of robins, *Petroica australis,* in Kowhai Bush near Kaikoura; McLennan and MacMillan (1985) reported similar losses for greenfinches, *Carduelis chloris,* in Hawke's Bay.

Egg losses may be higher in parts of East Cape, Westland, and Fiordland where brown kiwis overlap with the endemic weka, *Gallirallus australis* (Bull *et al.,* 1985). In a five-year study of little spotted kiwi *(A. owenii)* on Kapiti Island, Jolly (1985) found that

wekas ate up to 66% of the kiwi eggs laid each season. Nests were usually raided at night, when incubating males were away foraging.

Until recently, wekas and brown kiwis co-existed throughout most of New Zealand, and have probably done so for about 25 million years (Fleming, 1962). Four behavioural traits of brown kiwis appear to have an anti-predator function, perhaps in response to wekas: 1) they prefer burrows for nesting (compared to more exposed daytime shelters); 2) they select burrows that have had little or no previous use; 3) the males forfeit foraging time to incubate; and 4) they cover the burrow entrance with vegetation. Traits 1), 3) and 4) may also (or entirely) serve to reduce the rate at which eggs cool.

A preference for short breeding burrows is a paradox, especially when adults excavate longer ones for roosting. Eggs in short burrows probably suffer more predation, although experiments with seeded eggs are needed to test this. There may be compensatory advantages for incubating males, eggs or young to be close to the surface, but it is difficult to imagine what these may be.

The eggs of kiwis represent an extreme in avian evolution, both in their large size and high energy content (Reid, 1971a,b). Lack (1968) believed the main advantages of a large egg were that it enabled the chick to hatch with a large reserve of food or at a later stage of development. However, as Lack pointed out, large eggs often take longer to incubate, so are more vulnerable to predation. Calder (1979) thought this was unlikely to apply to the kiwi because "New Zealand had no predators that would enter a kiwi burrow. It He went on to suggest this as the main reason why the eggs did not scale down to normal allometric size as smaller descendants appeared from the moa-kiwi lineage. Predation by wekas need not, however, favour a reduction in egg size. Helpless chicks would require the male to spend more time away from the nest collecting food, and thus could be just as difficult to defend against wekas as a large egg.

Mating system and clutch size in kiwis
Over half of the ratite species are either polyandrous or polygamous, an exceptionally high proportion compared to other avian groups (Lack, 1968; Handford and Mares, 1985). Lack thought that kiwis laid only one or two eggs each season, making polyandry (where females lay in the nests of several males) unlikely. This study shows, however, that females may lay up to five eggs in a season.

Polygamy is less likely than polyandry among kiwis.

The eggs are so large that males could not incubate more than two or three at once, and in Hawke's Bay one female can lay this number. Polygamy may be more likely in areas such as Tangiteroria in Northland, where some females, apparently, cannot form their second egg quickly enough to lay twice in the same nest (M. Potter, pers. comm.). But even then clutches of one predominate, so polygamy, if it occurs at all, is rare.

Although both sexes can be promiscuous, monogamy is the only mating system reported for any of the three kiwi species. Monogamy is thought to result when parental care by both sexes is required to raise young to maturity (Emlen and Oring, 1977) yet clearly this does not apply with brown kiwis. Why then do female kiwis not spread their eggs among more than one male? Males may prevent them from doing this (perhaps by being very selective over which eggs they incubate) because they stand to loose far more from polyandry than the females might gain. If average egg losses are 50% or more each season, as in this study, polyandrous females would probably be no more productive than monogamous ones (assuming that females cannot lay more than five eggs in a season). Males with polyandrous mates would, however, have a greater risk of being cuckolded, and would forfeit their chances of re-lays and second clutches if they had to share the output of one female. It is also possible that females themselves may suffer additional costs by being polyandrous; for example, the energetic costs of finding, defending or competing for males could reduce their ability to manufacture eggs.

Lack (1968) argued that clutch size in cursorial birds (adapted to running) is probably determined by the amount of food available to the laying hen. The amount of food that adults can bring to young is not a consideration, since in most species, including kiwis, the young feed themselves. In kiwis, clutch size may sometimes be limited by other factors. This study has shown that females can lay three eggs over a 70-90 day period, yet clutches of this size are rare (Reid and Williams, 1975). Three-egg clutches could take a disproportionately long time to incubate and may thus be more vulnerable to predation. This would apply only if incubation started with the first egg, and if males had to spend a greater proportion of time feeding to sustain themselves during the extra 30 or so days. A more plausible explanation, that males cannot adequately cover three eggs, could be tested by adding eggs to clutches.

Kiwi numbers in Hawke's Bay

Anecdotal evidence, historical records and recent surveys suggest that kiwis are declining in Hawke's Bay, even in the largely intact forests in the ranges along the western edge of the region (McLennan, unpub.). This study indicates that the decline is not because predators eat most of their eggs or became adults do not breed. Each pair at Haliburtons fledged an average of one chick every two years despite the habitat changes induced by deer and possums and the presence of cats, pigs and mustelids.

Other likely causes of the decline include predation on newly fledged chicks, and poor adult survival, perhaps resulting from gin-trapping for possums. At Haliburtons, for example, gin-trapping has killed at least 12 kiwis in the last decade (M. Haliburton, pers. comm.) and injured three of the eight that survive there today. It is extremely unlikely that natural recruitment could offset these losses, unless chick survival was very high. Trappers operating in Urewera National Park, 20 km north-west of Haliburtons, report an average catch of only one kiwi every three to four man-years (Reid, 1986), but their figures are likely to be conservative for obvious reasons.

In small populations isolated by land clearance, intrinsic factors such as genetic deterioration and random variations in sex ratio pose additional threats to long-term survival. At Haliburtons, for example, the removal of predators and gin-traps would probably only postpone rather than avert the extinction of its kiwis. The remnant is too small to support more than 10-15 pairs, whereas some 50-500 pairs are probably required to prevent the loss of heterozygosity and vigour (Frankel and Soulé, 1981; Soulé and Simberloff, 1986).

Many other populations in Hawke's Bay and elsewhere may face extinction because they are confined to forest remnants that are too small. Regrettably, the effects of land clearance extend beyond the firebreaks and linger long after the smoke has cleared.

Acknowledgements

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