

Incubation behaviour and egg physiology of kiwi (*Apteryx* spp.) in natural habitats

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Abstract: Incubation behaviour varies among the different taxa of kiwi. For North Island brown kiwi (*Apteryx mantelli*) and little spotted kiwi (*A. owenii*), only the male incubates the eggs, except for in the first week. Meanwhile, for Okarito brown kiwi (*A. mantelli*) and the tokoeka (*A. australis*), incubation is shared by both sexes. In addition, amongst southern tokoeka, family group members can assist with incubation to the extent that breeding males may take no part in incubation at all. This study shows that kiwi turn their eggs regularly, an observation that contradicts earlier findings. There is a mean incubation temperature of 36.5°C at the top of the egg but the bottom may be 10°C lower in North Island brown kiwi and 5–8°C lower in Okarito brown kiwi eggs. Experiments inducing water loss from fertile and infertile eggs show that the presence of an embryo does not influence rate of water loss. North Island brown kiwi, Okarito brown kiwi and tokoeka regularly have more than one clutch in a season, and some North Island brown kiwi females lay up to seven eggs each year.

Keywords: *Apteryx*; egg physiology; incubation; kiwi; parental care.

Introduction

Amongst birds, kiwi lay one of the largest eggs in relation to their body weight (Calder *et al.*, 1978). These enormous eggs have attracted much interest and much has been written about incubation by kiwi, particularly the North Island brown kiwi (*Apteryx mantelli*) which is widely held in captivity (Robson, 1947; Reid and Rowe, 1978). However, in captivity food is readily available to incubating kiwi, which could influence the amount of time incubating birds need to spend away from the nest and size and number of clutches, thereby giving a different breeding pattern to that in the wild. Captive kiwi also lay smaller eggs than those in the wild (Reid, 1981). Because of the secretive nature of incubating kiwi, little is known of behaviour at the nest. By using a dummy egg in the nest of a captive North Island brown kiwi, Rowe (1978) found that the temperature at the top of the egg varied from 37.1°C during the day to 35.5°C at night, with a gradient of about 10°C from the top of the egg to the bottom. He reported that kiwi were one of very few birds, along with the Megapodes, that do not turn their eggs. Rowe reasoned that kiwi would have difficulty rolling the egg over because of their long, thin bill and confined nest burrow.

Data on clutch size, laying dates and nest attendance of wild North Island brown kiwi are reported by McLennan (1988) and Potter (1989). Jolly (1989) observed that male little spotted kiwi (*A. owenii*) incubated the egg on all but one of 168 checks from 18 nests on Kapiti Island. Relatively little information is available on incubation behaviour of the other kiwi species. However, Eason (1988), McLennan and McCann (1989, 1991), Sturmer and Grant (1988) and Colbourne (1991) reported that both male and female great spotted kiwi (*A. haastii*), tokoeka (*A. australis*), and Okarito brown kiwi (*A. mantelli*) incubate. On Stewart Island, family groups of up to seven southern tokoeka share territories (Colbourne, 1991) and helpers of both sexes assist with incubation and with brooding chicks. Generally, breeding males of all kiwi and breeding females of tokoeka from Stewart Island, Fiordland, Haast, and brown kiwi at Okarito develop well defined brood patches, as do some non-breeding male and female 'helpers' of southern tokoeka that assist with incubation. Although female great spotted kiwi also sit on eggs, they do not seem to develop brood patches (McLennan and McCann, 1991).

Of all bird eggs, those of kiwi have the lowest percentage of water at the time of laying (Vleck *et al.*, 1984). Kiwi also have one of longest incubation periods

at 74-84 days (Calder *et al.*, 1978). Obviously there must be water conservation strategies in place, either in the construction of the egg or during incubation, as birds eggs lose 10-23% of the initial mass of the egg during incubation and outside these limits hatchability rapidly decreases (Ar and Rahn, 1980). Because water retention is important in the kiwi egg, the questions arise as to whether incubation behaviour of kiwi can potentially influence water-loss from the developing egg and whether the embryo can influence water loss to some extent.

This paper reports data on incubation by kiwi in the wild. This information may be useful in improving our management of wild kiwi populations and also captive breeding performance; in particular, the raising of chicks from wild-laid eggs.

Study sites

The study sites were chosen to provide as great a north-south separation as possible to maximise the likelihood of detecting effects of climate on breeding behaviour. Kiwi are winter-spring breeders so differences in climate during this colder period is particularly important.

Rarewarewa is a 60 ha volcanic cone covered in native forest and surrounded by farmland and other small patches of forest. It is situated 20 km north west of Whangarei (Fig. 1). At Rarewarewa the population of North Island brown kiwi has one of the highest densities (about 1 pair per 3 ha) anywhere in the North Island. Generally, summers are warm and winters are mild with few frosts.

Kapiti Island (1965 ha) lies 5 km offshore from the lower North Island and has a population of about 1000 little spotted kiwi. Most of the island supports regenerating native forest. Being surrounded by sea Kapiti Island has few days of frost in the winter and has mild summers.

The Okarito site in Westland, South Island, which supports the Okarito brown kiwi consists of 9800 ha of lowland podocarp and hardwood forest immediately south and east of the Okarito township. Here, winters there are cold with hard frosts and summers are mild and wet. The Okarito brown kiwi population of about 160 individuals was in decline during this study. There was no recruitment to the population from the 12 breeding attempts monitored and chicks rarely survive more than one month, largely because of predation by stoats (*Mustela erminea*). Okarito and North Island brown kiwi are currently classified as the same species (Baker *et al.*, 1995).

Mason Bay on the western coast of Stewart Island lies in the path of the prevailing moist westerly winds which bring cold temperatures in winter and generally cool conditions in summer. Frosts are common in

winter but snow is rare. Vegetation consists of pingao (*Desmoschoenus spiralis*) and marram-grass (*Ammophila arenaria*) on sand dunes, coastal scrub, red tussock (*Chlionochloa rubra*) and old farm pasture. Although southern tokoeka territories are about 5 ha per pair, densities of kiwi at Mason Bay can be some of the highest in New Zealand because often more than one extra family group member also occupy each territory.

Methods

Kiwi were caught before the breeding season using trained dogs or netted at night when they were off nests. They were radio-tagged (Sirtrack, double pulse transmitters, 25g, strapped to tarsus with soft plastic hospital identification tags) so that nests could be later found and monitored. Nesting was monitored at least fortnightly over three years in the case of Okarito (1992-95) and North Island brown kiwi (1994-97). Eight visits were made to Mason Bay, Stewart Island, of two to three weeks duration (1988-1998) to monitor nests of southern tokoeka. Three visits of a week each (1994) were made to monitor little spotted kiwi on Kapiti Island.

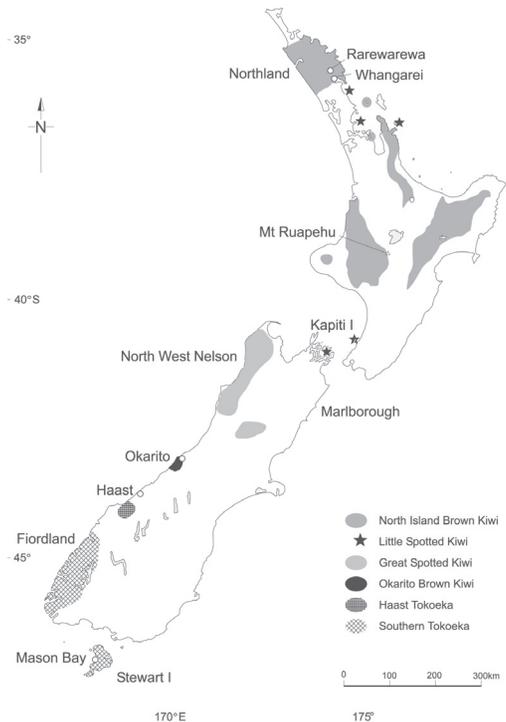


Figure 1. Map of New Zealand showing distribution of kiwi, study sites and locations mentioned in text.

Nest attendance of three pairs of North Island brown kiwi from Rarewarewa, Northland, was monitored by data-loggers (for periods of up to a week at a time). The data-logger recorded the presence of the specific transmitter that each male and female was wearing. A further eight pairs were directly observed at their nests (95 observations) over three breeding seasons and nest attendance was indirectly observed by determining bearings and changes in strength of transmitter signals that indicate mobility (215 observations). One pair of nesting Okarito brown kiwi was monitored for three days with a data-logger and another pair for five months with a video camera and recorder. One nest of a little spotted kiwi on Kapiti Island was monitored by data-logger for 19 days over a thirty day period and a pair of Stewart Island tokoeka was observed with a video camera from a hide outside the nest entrance. Three nests of Stewart Island tokoeka were monitored by data-loggers for a period of five to seven days and 23 more nests were observed at least once during visits to Mason Bay.

A 'dummy egg' containing radio-transmitters that recorded temperature (accurate to $+0.25^{\circ}\text{C}$) was constructed to determine egg temperatures during different phases of incubation. This egg consisted of a North Island brown kiwi shell (125.3 mm long; 82.4 mm wide) containing five transmitters with their sensors placed 1 mm under the shell and spaced equally around the maximum diameter. A sixth transmitter was positioned in the core. Molten paraffin wax was used to fill the egg. This wax has similar specific heat properties to egg albumen (Varney and Ellis, 1974). Varney and Ellis calculated that by using wax their dummy egg conducted heat 18% faster than a real egg of similar size. The completed egg weighed 480 g, the same as the fresh weight of the original kiwi egg. The egg was put into a North Island brown kiwi nest when the male was away feeding, the original egg having been removed and placed in an incubator or in another kiwi's nest. Temperature readings were recorded on a data-logger every ten minutes for each transmitter. Information was collected from a nest with a two week old egg (data-logger run continuously over five days) and from a nest with two eggs at least six weeks old (run continuously over seven days). The same dummy egg was later substituted for a wild egg (121.0 mm long; 79.7 mm wide) in an Okarito brown kiwi nest and data collected over three days.

Four eggs from two adjacent North Island brown kiwi nests were weighed at night (three weeks apart, four measurements each egg) when the male was away from the nest using 'Mettler-Toledo' scales accurate to $\pm 0.1\text{g}$ to determine rate of mass (water) loss.

To test whether the embryo had a direct influence on water regulation, three North Island brown kiwi eggs of similar external dimensions were placed side

by side in an artificial incubator (Brinsea hatchmaster) for a month with a temperature of 35.8°C set at the top of the eggs. The first egg was 45 days into incubation, with an already well-developed air sac. The second was fertile and two weeks old, and the third an infertile egg also about two weeks old. All eggs were turned once a day and weighed at the same time to find out how much water had been lost through the shell. On the eighth day water was removed from one of the two water trays of the incubator and then replaced on the ninth day to see if there was a reaction. Another North Island brown kiwi egg was incubated in a separate incubator with different external humidities over a two-week period to determine changes in the rates of water loss. The humidity in the incubator was changed by adding water in one tray, water to two trays, and by operating with no added water. Relative humidity was recorded at the top of the egg at 36.1°C .

All kiwi that hatched from eggs taken from the wild and artificially incubated during this study were released back into the wild when they were old enough to defend themselves from predators.

Results

Incubation pattern

North Island brown kiwi

Of 95 nest observations made during the day, the male was alone in the nest 88 times, the female alone three times and both were present four times. In 215 night-time checks for transmitter signal motion only males were at the nest or, if off the nest, the nest remained unattended.

Figure 2a shows the nest attendance of a pair of North Island brown kiwi at Rarewarewa that was monitored by a data-logger. On 24 June 1994 the female laid her first egg of the season and spent the rest of that day in the nest alone. The next day (25 June) both birds were off the nest, sleeping together 70 m from the nest. Although the female was observed in the nest at different periods in the days following the first egg being laid, it did not appear that she was incubating. She may have been turning the egg, as a pencil mark on it was seen to be in different positions when the nest was checked at night. On 26 June the data-logger was set up at the nest. The female was alone in the nest until dusk when she left, and the male visited the nest for four hours soon after midnight and then spent the next day sleeping with the female away from the nest. He began sitting on the egg just after 2 am on 28 June. This pair had two eggs in the first clutch. The second egg was laid on 18 July (20 days after the first). The male did not sit on it for at least a day. He remained sitting tightly on the first egg and had pushed this second egg towards the entrance of the nest cavity.

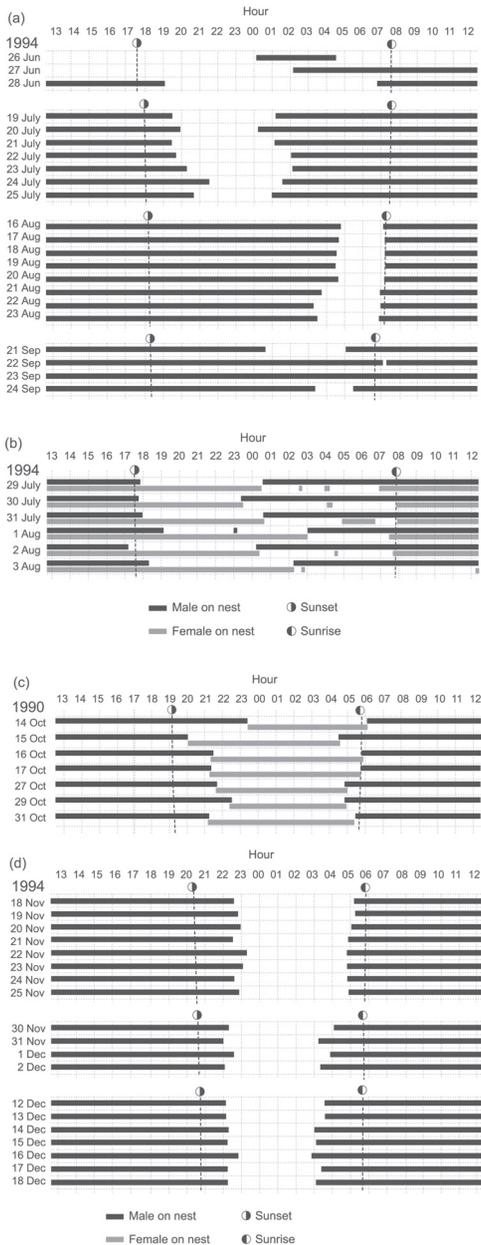


Figure 2. (a) Night-time nest attendance: Male North Island brown kiwi: Rarewarewa Northland, June-September 1994. First egg laid 24 June and hatched 22 September. (b) Night-time nest attendance: Okarito brown kiwi, July-August 1994. Egg laid 2 July and hatched 1 September. (c) Night-time nest attendance: Southern tokoeka, Mason Bay, October 1990. Date egg laid and hatched unknown. (d) Night-time nest attendance: little spotted kiwi, Kapiti Island, November-December 1994. Egg laid 13 November, egg smashed by storm 22 December.

Even though the female did not visit the nest for most of the incubation period following the first few days after laying, she did remain in the vicinity. When the male left the nest to feed, both birds were seen feeding together on many occasions. When the male left the nest during the first half of incubation, he completely covered the nest entrance with leaves, but by the time the first egg was 60 days old he often failed to do so and the nest entrance became more obvious. The first egg was also often covered by leaves in the first week when the male left the nest, and throughout the entire incubation both eggs were partially embedded in the nesting material. Figure 2a shows a definite change in activity from early incubation to late incubation. In the first month the male came off the nest one or two hours after nightfall. Sixty days later he did not come off the nest until two to three hours before daybreak.

Both eggs hatched, the first after 91 days, the second after 75 days. On 22 September, when the first egg hatched, the male left the nest for a total of only five minutes in 48 hours. That departure occurred 45 minutes after sunrise. On hatching chicks are wet, with little insulation, and until their feathers dry and erupt from their sheaths they are likely to be vulnerable to chilling. The warmth of the male is probably essential at this time. During this period, after the first chick hatched, the female began visiting the nest again. On one occasion she entered the nest for at least a minute, having apparently never been within five metres of the nest entrance since laying the second egg 10 weeks previously. The second chick hatched on 30 September. When each chick was about five days old, they began to emerge from the nest, but returned each morning. The first chick finally left the nest three weeks after hatching and left the parent's territory 55 days later. The second chick left the nest two weeks after hatching. On leaving they sheltered away from the adults.

The female laid in a new nest 67 days after the second egg hatched and then laid another egg 18–20 days later. Both eggs hatched and the pair successfully fledged all four chicks within that breeding season. In the next two breeding seasons (1995 and 1996) the pair had two clutches each year, which not unusual in this Northland population (H. Robertson and P. Miller, Department of Conservation, N.Z., *pers. comm.*). All six nests of this pair were in different sites. The first nest monitored (Fig. 2a) had old eggshell fragments indicating it had been used for breeding within the previous two years. Of twenty North Island brown kiwi nests from which eggs were taken for artificial incubation, fourteen had been used in previous seasons, as they contained old eggshell fragments.

Other kiwi were studied in the same area at the same time. The pattern of nest attendance of two neighbouring males of the first pair was very similar to

that of the first male. Thirty-five checks on each of the nests during early incubation and later before the eggs hatched showed these males left the nest at almost the same time. This synchrony may have been triggered by vocal cues. Within a minute or two of leaving the nest males regularly gave a series of loud calls. When most males were incubating, the forest was often silent for the first four hours of darkness (1 call/hr; 10 hours listening). During the three months before the breeding season the call rate heard at the same site was 8 calls/hour (24 hours listening, Kiwi Recovery Programme monitoring data). Call rates only approached this level within the two to three hours before sunrise. The following year, in a remnant of forest only 1 km away, the nest attendance pattern in the last four weeks of incubation was reversed, with five incubating males coming off the nest early in the night and returning before midnight. Call rates were high (up to 10 calls per hour) during the first hour of darkness.

Although the first female monitored did not appear to incubate her egg, another female, alone in the nest, was definitely incubating an egg five days after laying. That egg was warm when removed for artificial incubation.

Most nesting kiwi appeared tolerant when observed directly with a small torch. However, one male was very wary and repeatedly deserted his nest, resulting in his mate laying a total of at least seven eggs in that season followed by a further two at the start of the next season before we ceased monitoring the pair. The male deserted if anyone approached to within 10 metres of his nest.

Okarito brown kiwi

Nests from two different pairs were monitored. A video camera at the first (Fig. 2b) revealed that both sexes incubated. Both birds developed well-defined brood patches, and both spent up to 75% of their time in the nest. All but one of 15 nest inspections during the day showed the male to be on the egg. He left the nest shortly after dark. The female remained in the nest for the first half of the night and left to feed when the male returned, usually at or just after midnight. On three occasions the female fed for about two hours after sunrise before returning to the nest. This same nest was used for three consecutive years and was also used frequently during the rest of the year as a shelter burrow. The nest was a large cavity in a rotted tree stump and during incubation the nest entrance was never covered with leaf material and the birds could be seen clearly from some distance away. The eggs of Okarito pairs were never partially buried in the nesting material like those of the North Island birds, but always sat fully exposed on the nest floor surface. This pair had one egg per clutch but when that egg hatched the second egg of the season was laid within a month. In

one instance the second egg was laid a week before the first egg hatched. Over four consecutive years, the pair hatched five of seven eggs (J. Reid, Department of Conservation, Takaka, N.Z., *pers. comm.*). One egg was preyed on by a possum (*Trichosurus vulpecula*) and the other was abandoned after possible nest disturbance by a possum.

A dummy egg was substituted in the other Okarito brown kiwi nest and monitored with a data-logger (Fig. 3b). Both sexes incubated, but the nest-attendance pattern was quite different from that pair monitored by the camera. The female left the nest at sunset and returned about midnight to incubate for the remainder of the night until the male returned. Occasionally he returned to the nest up to an hour and a half after daybreak. When an egg was hatching, changeovers at the nest occurred more frequently at night, at times every five minutes (J. Reid, *pers. comm.*).

Southern tokoeka

Twenty-seven nests were found over ten years. Males were observed during the day in 27 nests; females in eight; and helpers in nine. At night, 15 nests checked showed a lone female present in 14 and a lone helper present once. It was likely that helpers also entered the nest at night more frequently than encountered on these checks. A data-logger revealed two helpers entering the nest four times during one night and remaining inside between five and fifteen minutes each time. All nests had only one egg except on one occasion when an egg was laid less than a week before the first egg hatched. Four of the 'alpha' females laid a second egg within a month of the first egg hatching. Five times an 'alpha' female was gravid when handled, twice during the same season ($n = 75$ handles), but female helpers ($n = 41$ handles) were never found gravid. At least six of ten second nests were deserted, possibly because of fleas (*Parapsyllus nestoris nestoris*) that occurred in the nesting cavities during the summer (at densities of at least a thousand fleas per nest). The southern tokoeka monitored always used a new nest each season.

In one nest monitored in 1990 (Fig. 2c) only the adult pair incubated, despite another adult female sharing that territory. However, three years later the same three kiwi were observed incubating one egg.

A family group of two males and a female was observed at a nest during the week before and after the female laid her egg. When heavily gravid she spent the two days before laying amongst fern and rushes in a hollow filled with one to two centimetres of water. The day after the egg was laid the 'alpha' male was in the nest with the egg but not sitting on it. The next day the female and 'alpha' male were in the nest. The following day the other male (their chick from three years before) was incubating the egg and the next day the 'alpha'

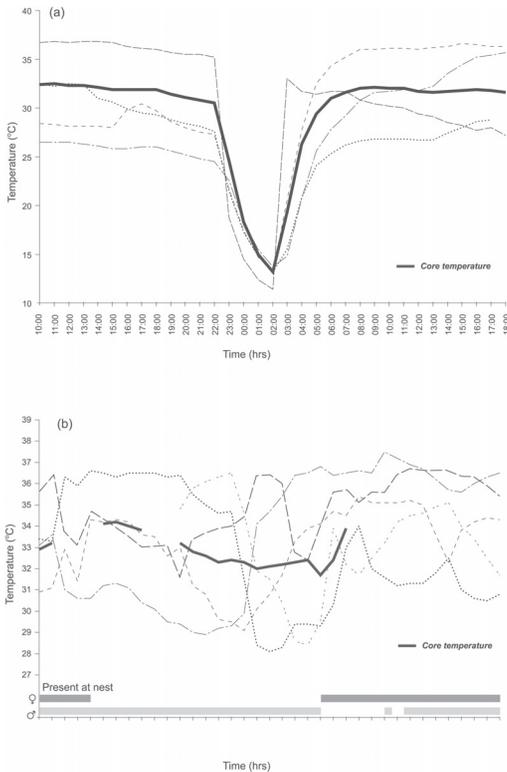


Figure 3. (a) Transmitter temperatures in dummy egg in North Island brown kiwi nest, showing temperatures, nest attendance and egg turning. Note data from one of the transmitters beneath the shell is absent due to transmitter failure. For most of the sequence, this transmitter was on the side of the egg, not top or bottom (but may have been at the top between 3:00 and 5:00). (b) Transmitter temperatures in dummy egg in Okarito brown kiwi nest, showing temperatures, continuous nest attendance and egg turning. Note data from one of the transmitters beneath the shell is absent due to its failure during certain orientations of the egg. In the sequence, this transmitter was on the side of the egg, not top or bottom, when the signal failed.

male was incubating. Both sexes developed brood patches and some of the older helpers did as well. Another trio was noted in which two females had fully developed brood patches but the male had none (cf. Colbourne 1991).

Little spotted kiwi

One pair of little spotted kiwi on Kapiti Island monitored by a data-logger showed the same pattern of male-only incubation as North Island brown kiwi. They had a one-egg clutch. The female did not enter the nest from three days after laying. The data-logger was set-up five

days from laying and ran in three periods over thirty days of incubation until the egg and nest were destroyed by a cyclone (Fig. 2d).

Incubation temperatures

North Island brown kiwi

Figure 3a shows a 32-hour sequence of data representative of that observed on the other days the egg was monitored. Outside that period at least two transmitters did not register on the data-logger because of the direction the aerials lay in relation to the receiver. The sequence shows the transmitter temperature at the top of the egg, just beneath the brood patch, at a mean of 36.5°C (when incubated) but reaching 37°C. The opposite transmitter, in contact with the bottom of the nest, reached only 27°C. This gave a 10°C gradient through the egg when the outside air temperature was 8°C. The surface and core temperatures of the egg dropped rapidly once the male left the nest, with the core dropping to 13.0°C, not much warmer than the surface temperatures. After the male returned to the egg the temperatures rose quickly, but the orientation of the egg changed soon after. The temperature of the warmest transmitter, previously at the top of the egg, dropped to below 30°C while the transmitter near the bottom of the nest increased to 37°C, which indicated that the egg had been turned about 120°. This confirmed what was observed with three freshly laid eggs where pencil marks on the shell showed the eggs were turned at least 170°, 150° and 60° in one day. During the 24 hours following the period shown in Fig. 3a the dummy egg completed a 180° turn. Turning rates varied from at least one 180° turn then back again within six hours to not being turned for a complete 24 hour period. When eggs were inspected during the last weeks of incubation they were all found in the same position, with the large air sac uppermost. The eggs were still being turned at that stage, but because of their asymmetric weight distribution they naturally tended to return to the position with most of the weight at the bottom (with an egg as large as the kiwi's the top half could be up to 90 grams lighter than the bottom half).

At the nest of a North Island brown kiwi, it took about 10 days after the first egg was laid for the male to show any signs of brood patch development. During the first week of incubation, the temperatures at the top of the dummy egg were at least 0.5°C lower than those in the same egg under the same male a month into incubation, by which time his brood patch was well developed. This lower initial incubation temperature may partially contribute to the longer incubation period of the first egg in a clutch. The average time between laying the first and second egg was 20 days (range 18–23 days, $n=5$ nests), whereas the average time between hatching was 13 days (range 3–30 days, $n=9$ nests). In

a two-egg clutch only a small area of brood patch is in contact with each egg at any one time. On a cold day, when eggs were removed from a sitting male, the eggs only felt 'hot' over an area with a diameter of 50 mm, the rest of the eggs felt only warm. No difference was recorded in temperature at the top of the egg during day or night incubation.

Okarito brown kiwi

Figure 3b shows a 36-hour sequence of data representative of that observed on the other days the egg was monitored. For most of the sequence the temperature at the top of the egg was 36.5°C. At 0700 hr the temperature reached a maximum at 37.5°C. This occurred when the female returned from foraging and possibly her body temperature was higher than usual after running to the nest. The temperature soon returned to about 36.5°C. Unlike the North Island brown kiwi, incubation is continuous. The female added more heat than the male. She brought the core temperature up to 34.2° from his mean of 32.2°. The difference in temperature between top and bottom of the egg was reduced from his 8°C gradient to only 4.5°C. This may be expected as female kiwi are about 20% larger than males, and are likely to cover a greater surface area of the egg. Figure 3b shows one major 180° turn of the egg at 1900 hr. This occurred on each of the three days the egg was monitored.

Egg water loss

Four wild North Island brown kiwi eggs, weighed from two nests in adjacent territories, had similar rates of water loss over a one to two month period despite one egg being infertile or suffering early embryo death (Table 1). If these rates were representative of the entire incubation period (DL1 = 91 days; DL2 = 75

days) then each of these two eggs would have lost respectively 12.3% and 12.7% egg mass by the time of hatching.

Rates of water loss from the three artificially incubated eggs are shown in Fig. 4. Until the moment the shell of the oldest egg was fractured, there was no apparent difference in the rate of mass loss of any of the eggs. When water from one of the two incubator trays was removed (day eight) all three eggs immediately lost weight at a similar rate. The rate increased again when water was added the following day. Both fertile eggs hatched successfully.

The rate of mass loss of the single egg artificially incubated over two weeks with different humidities is shown in Table 2. Increasing the area of water in the incubation trays has a strong relationship by decreasing the mass loss of the egg.

Discussion

Shared incubation and family grouping

White and Kinney (1974) regarded shared incubation as primitive behaviour amongst birds. On this basis the male-only incubation of North Island brown kiwi could be considered to be of more recent origin than the shared incubation of Okarito brown kiwi or Tokoeka. Baker *et al.* (1995) also believed North Island brown kiwi to be a recent offshoot, based on mitochondrial DNA and blood protein variation.

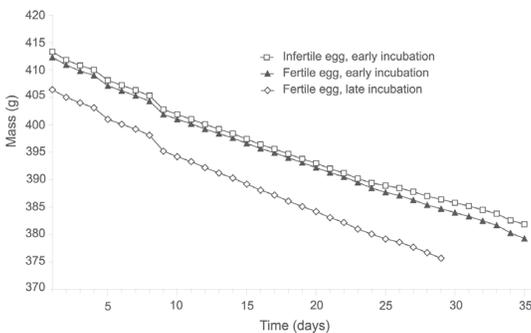


Figure 4. Mass loss of three equal sized eggs (two fertile and one infertile) in artificial incubator. All three eggs responded with increased rate of mass loss when water was removed from incubator on day eight.

Table 1. Average percentage mass loss per day of three fertile wild North Island brown kiwi eggs and one infertile egg (CN1*), Rarewarewa, Northland.

Egg	fresh-weight (g)	days monitored	mass loss/day (g)	%loss/day
DL1	409.4	62	0.55	0.135
DL2	409.0	34	0.69	0.169
CN1*	375.0	57	0.60	0.160
CN2	453.6	41	0.77	0.170

Table 2. Mass loss (grams per day) of North Island brown kiwi egg in artificial incubator with varying humidity.

Day	trays of water	humidity	mass loss/day (g)
1-3	0	0.62	1.22
4-6	1	0.73	0.81
7-10	2	0.8	0.7
11-14	0	0.62	1.26

Although the female little spotted kiwi monitored on Kapiti and those recorded by Jolly (1989) rarely if ever shared the nest with the male, Potts (1872) noted female little spotted kiwi from the west coast of the South Island in the nest with the male for some months and sharing incubation. Oliver (1955) described two forms of little spotted kiwi: the smaller *Apteryx owenii* from Marlborough and Nelson and the larger now extinct *A. occidentalis* from the west coast of the South Island. If Potts was correct, the previously widespread little spotted kiwi (found in the top of the North Island to the bottom of the South Island) had more than one type of incubation behaviour. These different incubation behaviours may have come about through differences in climate, notably temperature. Being warmer in the north it is therefore possible to leave the egg unattended, with the male only needed for incubation. Being cooler in the south the egg would need constant incubation and females and others would be required to share duties. However, in other situations kiwi incubation patterns seem to be inflexible. North Island brown kiwi living on the slopes of Mt Ruapehu, where average temperatures during the breeding season are colder than those at Okarito or Mason Bay, maintain the same male-only incubation pattern recorded in North Island brown kiwi from Northland (J. Miles, Department of Conservation, Gisborne, N.Z., *pers. comm.*).

There is the possibility of family grouping at Okarito. On one occasion a pair (not that monitored) was seen sharing a burrow with a subadult female (J. Reid, *pers. comm.*). The lack of family groupings observed may be because young are not surviving, and the population density is very low. The first chick that hatched in the nest monitored by the video camera remained with its parents daily, for nine weeks, while they incubated the second clutch, but was then eaten by a stoat.

Incubation temperatures — limitations of dummy eggs

A dummy egg cannot measure embryo temperature, and lacks internal heat circulation via blood vessels. It probably resembles temperatures in 'real eggs' for the first third of incubation only, after which the core in a real egg is likely to be warmer as the maturing embryo produces metabolic heat. The temperature of an egg that was controlled by the embryo deviated from ambient temperature by -0.5°C to $+3^{\circ}\text{C}$ when not incubated (Turner, 1985; Sotherland *et al.*, 1987). Regardless of these limitations, dummy eggs are useful for comparing the incubation heat input of brooding adult male and female birds and also for providing information, such as frequency of turning, so that natural incubation patterns can be replicated in artificial incubators.

Egg physiology and water-loss

Newly laid eggs were not incubated immediately. For all taxa of kiwi studied, incubation did not begin until one to seven days after laying. The second egg in a clutch is often pushed aside for the first few days after laying. This post-laying period, during which the egg remains cold, may have important physiological significance and may be necessary in kiwi. A gradient of acidity develops across egg membranes when an egg cools and this gradient may be the catalyst to drive various chemical processes which form the embryo (Finger, 1992).

One unusual aspect of North Island brown kiwi behaviour is the length of time eggs are left alone when brooding males leave the nest to feed. Despite eggs being covered with a few leaves (some of the time) and despite eggs usually being buried to half their depth in nesting material, recordings from dummy eggs showed that they rapidly cooled to near ambient temperatures. These temperatures were close to physiological zero (the temperature at which embryonic development ceases; White and Kinney, 1974) and yet no developmental abnormalities were recorded.

Clearly the kiwi, like most other birds, does turn its eggs. Turning is especially important during the first period of incubation (New, 1957). Deeming (1989) attributes the primary function of turning to maximising the efficiency of nutrient use by the embryo. The rotation of yolk moves the embryo into contact with fresh nutrients and away from waste products and is critical before a blood circulation system develops (Finger, 1992). Rowe (1978) may have witnessed a 24 hour period in which the kiwi decided not to turn the egg, or the egg may have been turned but returned to the same position as when put under the bird. In all of the wild North Island brown kiwi nests monitored, the nest chamber was never so tight that movement of the male was restricted. In one nest there was room for both the male and female. They were together for the first three weeks, which is quite rare with North Island brown kiwi (she was never seen incubating). One little spotted kiwi nest in a rock crevice was very tight and may have restricted movement of the egg. The egg did not hatch and the embryo was later found to be malpositioned in the shell with its bill pointed to the bottom of the egg rather than towards the air sac.

The comparison of mass loss of a fertile egg with that of an infertile egg artificially incubated under controlled humidity demonstrated that mass loss was almost entirely dependent on the environment of the eggs and not on the presence of the embryo. Despite an embryo producing CO_2 and water through respiration, the water escaped through the pores of the eggs at a rate governed by the external humidity. Potentially anything the parent does to change the humidity of the nest will

have an effect on water loss from the egg. During at least the first half of incubation, particularly with North Island brown kiwi and little spotted kiwi, nest entrances are usually covered by leaves, the incubating kiwi meticulously placing debris on exiting and entering the nest. It has often been argued that this is an adaptation to reduce predation from weka (*Gallirallus australis*) (Jolly 1989) or possibly from kea (*Nestor notabilis*). However, during the last month of incubation, this nest-covering behaviour often stops, and nest entrances are very bare, with the sitting kiwi visible from a distance. It is more likely that the blocking or unblocking of the nest entrance helps to control humidity. Okarito has a very high annual rainfall (averaging 5000 mm annually at nearby Franz Josef) and is often very humid. If the function of covering nest entrances with leaves is to create a humid environment then this is clearly not necessary at Okarito and that may be the reason kiwi there do not exhibit this behaviour. Southern tokoeka monitored sometimes covered their nest entrances, yet never left their eggs alone after the first few days. Snyder and Birchard (1982) showed in bird eggs that water loss early during incubation is more harmful than later on. Lower ambient humidity in a nest near hatching may assist water loss through the shell particularly once the embryo begins breathing within the airsac. The increased rate of gas exchange at this time may also be important as the embryo uses increasing amounts of energy for breaking through the inner membranes, breathing and preparing for hatching.

As a result of this research the hatch rate of eggs collected from the wild, as part of the Kiwi Recovery Programme's Operation Nest Egg project, has increased from 50% in 1995 to over 88% in 1998.

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