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SHORT COMMUNICATION

# INCUBATION TEMPERATURES OF GREAT SPOTTED KIWI, *APTERYX HAASTII*

**Summary:** Incubation temperatures of the great spotted kiwi were studied by telemetry methods at the Otorohanga Zoological Society in October 1989. The male maintained the core temperature of the egg at about 28-31.8°C. When he emerged to feed at night, the female started to incubate. She did not have a brood patch, but could heat the egg to 28-28.5°C, sufficient for embryo growth.

Some of the reasons why female great spotted kiwi might help with incubation are discussed. In cold, mountain environments, the energetic costs of incubation could be so high that males alone cannot meet them. The hypothesis predicts that there are also places in the North Island where female brown kiwi *(Apteryx australis mantelli)* should share in incubation.

**Keywords:** *Apteryx haastii;* great spotted kiwi; ratite; incubation; incubation temperature.

## Introduction

Recent field studies show that incubation in kiwi *(Apteryx* spp. Shaw and Nodder) is not always performed entirely by males. Female brown kiwi *(A. australis)* help with incubation on Stewart Island (Sturmer and Grant, 1988), and at Okarito on the west coast of the South Island (R. Colbourne, *pers. comm.).* Great spotted kiwi in sub-alpine and lowland forests of Northwest Nelson also share incubation duties (McLennan and McCann, 1989). Female help has not, however, been recorded in the North Island (McLennan, 1988; Potter, 1989; Jolly, 1989), except in one unusual circumstance where a pair of brown kiwi had an egg in each of two different nests (McLennan, 1988).

In the great spotted kiwi, males incubate throughout the day and during the early evening. Incubating males shed the feathers on their lower belly and develop a large, naked, brood patch, presumably to increase the transfer of heat from their body to the egg. Females incubate for three to eight hours each night when males emerge to forage, but do not seem to develop a brood patch (McLennan and McCann, *unpubl.).* We have examined three females at varying stages of incubation, and all have retained the usual, although somewhat sparse, covering of feathers on their lower belly. This raises the question, then, of whether they can warm the egg sufficiently for the embryo to develop. We answered this by measuring egg temperatures.

## Methods

Our methods were similar to those used by Rowe (1978) for brown kiwi, in that we installed telemetering equipment in a dummy egg. We used a standard, two-stage radio transmitter, equipped with a sensor and modulator, which caused the pulse rate to change with temperature. A decoder plugged into the headphone jack of the tracking receiver converted the signals into a digital readout, enabling temperature to be monitored continuously. The sensor had an accuracy of ± 0.25°C, with a resolution of 0.1 °C, and the transmitter had a range of several hundred metres.

We made our measurements at the Otorohanga kiwi house near Hamilton, where a captive pair of great spotted kiwi lived in a quarter-hectare enclosure containing a mixture of native and introduced plants. The pair laid in early September 1989, in a burrow approximately 60 cm long which they had dug into the side of a steep bank. They incubated their egg for 35 days until the curator transferred it to an artificial incubator, at which point we substituted our dummy egg.

The dummy egg was a great spotted kiwi egg whose contents had been replaced with paraffin wax. This material has a specific heat similar to that of albumen (Varney and Ellis, 1974). The dummy contained a transmitter embedded at embryo depth in the centre of the egg, and another just beneath the shell, but this one failed during the experiment.

The birds accepted the dummy immediately. We monitored the temperature of the egg during the following two nights, and intermittently during the intervening day. We stationed ourselves in their enclosure at night so that we could record when the birds entered and left the nest.

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# Results

### Incubation temperatures

The temperatures in the core of the egg varied throughout a 24 hour period, irrespective of whether the male or female was incubating (Fig. 1). As expected, the egg lost heat more quickly as the air cooled, so maximum incubation temperatures were lower at night (26∞∞C to 28∞∞C) than during the day (30∞∞C to 31.8∞∞C). The temperature of the egg, though, was always higher than the temperature of the air. Ambient temperatures on 16 October ranged from 4.5∞∞C to 17.5∞∞C, while those on October 17 varied from 6∞∞C to 18∞∞C.

On a few occasions, the adults re-arranged either the nest material or the position of the egg itself before settling onto it, resulting in an occasional delay of up to 25 minutes between their entry into the nest and a rise in the temperature of the egg (see, for example, 2130 h on 16 October).

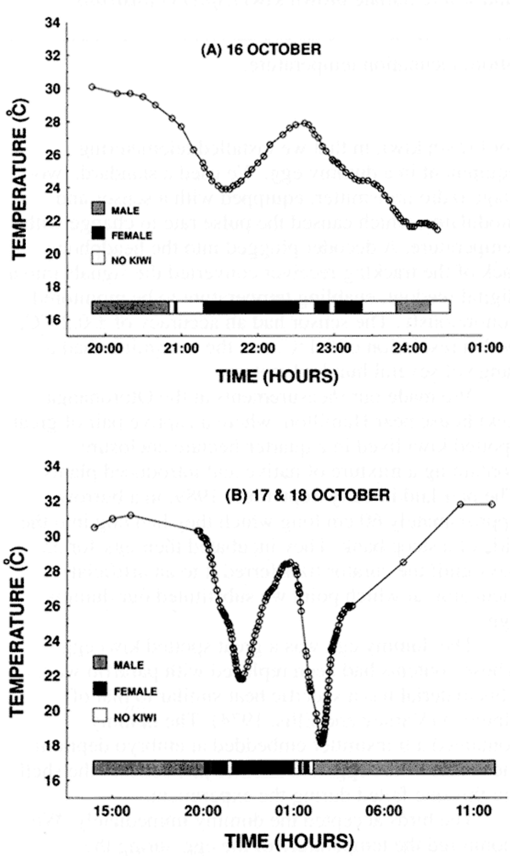


Figure 1: *Core temperatures of the dummy egg on (A) 16, and (B) 17 and 18 October. 1989. The bar shows the arrival and departure times of the adults in the nest. At no time were both birds in the nest together. Open circles show spot recordings of the continuous readout. The line was fitted by eye.*

### Incubation by the female

On both nights, the female entered the nest after her mate emerged to feed. She did not stay in there continuously, as is usual in the wild, but instead made a series of visits to the nest varying in duration from a few minutes to 3.4 hours. The egg temperatures rose by as much as 6.7∞∞C during her longer visits, showing that she was incubating while in the nest (Fig. 1). When unattended, the egg cooled at a rate of 2∞∞C to 8.4∞∞C per hour, depending mainly on the thermal difference between itself and the air (Fig. 1). Clearly then, the female could heat the egg to temperatures well above those of the surrounding air, although she had no brood patch.

# Discussion

### Incubation temperatures and incubation behaviour

Incubation temperatures of great spotted kiwi are similar to those of brown kiwi (Rowe, 1978). In both species, the daytime equilibrium temperatures at embryo depth hover around 31∞∞C. The eggs are cooler at night, with the actual temperature depending mainly on the attendance patterns of the adult(s).

Rowe (1978) found a l0∞∞C difference between the top and bottom of brown kiwi eggs, with the temperature on the upper surface approaching that of the male's brood patch (about 37∞∞C). There should be less of a thermal gradient in the eggs of great spotted kiwi, even though they are similar in size to those of brown kiwi. This is because great spotted kiwi cradle the egg on their toes, and heat it from both sides, whereas brown kiwi simply squat on their eggs and heat them only from the top.

The degree to which the two species line their nests with vegetation also differs, probably as a consequence of their methods of incubation. Brown kiwi often bury their eggs to the midline in vegetation, presumably to reduce heat loss to the surrounding air (McLennan, 1988). In great spotted kiwi, the egg is laid on a mat of vegetation, but is otherwise entirely exposed. There is not the same need for them to insulate the egg, because the female takes over when the male leaves to feed, and the egg probably needs to be free of vegetation so that they can shuffle it onto their toes.

**Incubation by the female**

Our results show that the female heated the core of the egg to 28°C to 28.5°C, at ambient temperatures ranging from about 6°C to l0°C. These core temperatures probably exceed by about 4°C the minimum required for embryo growth in kiwi (White and Kinney, 1974).

By helping with incubation, female great spotted kiwi prevent the egg from chilling when their mate leaves the nest to feed. This in turn must enable the embryo to grow more-or-less continuously, and thereby reduce the incubation period. We do not know how long incubation takes in the great spotted kiwi, but it is probably similar to the development time of a brown kiwi egg in an artificial brooder. Such eggs hatch in about 70 days (Rowe, 1978), a little over a week earlier than those incubated under natural conditions (McLennan, 1988).

**Development of female incubation**

White and Kinney (1974) argue that single-sex incubation is a secondary development in birds, often coupled with the development of complex nests. We agree with their view generally, but suspect that kiwi are an exception. Amongst ratites, male-only incubation is typical of all species except ostriches and South Island brown and great spotted kiwi. Male-only incubation is rare in birds as a whole (Ridley, 1978) and its prevalence within the ratite group implies that the behaviour is a legacy of a common ancestor. Shared incubation seems to be a secondary development, and for great spotted kiwi, it is perhaps too recent in origin for females to have developed brood patches.

**The costs and benefits of female help**

Great spotted kiwi usually lay just one egg a year (McLennan and McCann, *unpubl.),* about a quarter to one-half the number produced by brown kiwi or little spotted kiwi *(A. owenii)* in the North Island (McLennan, 1988; Jolly, 1989; Potter, 1989). We suspect that the low reproductive rate of great spotted kiwi is the price females pay for helping with incubation. By helping, females halve their potential feeding time (McLennan and McCann, *unpubl.)* and incur the additional and significant energetic expense of keeping the egg warm (Taborsky, quoted by Aldhous, 1989). These two factors together probably force females to use stored reserves which might otherwise have been available for producing eggs.

The benefits that offset these reproductive penalties are not clear. Two of the possibilities concern predation. Incubation by females probably reduces the time eggs are vulnerable to predators (including microbes) by hastening their development. Females must also protect the egg from weka *(Gallirallus australis),* the only natural vertebrate predator of kiwi eggs capable of entering a breeding burrow. Neither of these considerations, however, seem sufficient to compensate for the loss of reproductive output. Further, there is nothing in the sub-fossil record to suggest that kiwi in the southern islands might have suffered more nest predation than those in the North Island.

We think that the most likely beneficiary of female help is the male himself. Kiwi eggs are renowned for their large size, and the costs of incubating them are high. Taborsky (quoted by Aldhous, 1989) calculated that male North Island brown kiwi expend more energy incubating eggs than females do in producing them. Taborsky goes on to suggest that male incubation and large eggs have evolved together, because females alone could not meet the combined costs of egg production and incubation.

Taborsky made his measurements at Waitangi State Forest in the Bay of Islands, where the mean air temperature in late winter and early spring exceeds 12°C. In contrast, most kiwi in the South Island breed in temperatures which are on average 5°C or less. Their incubation costs are undoubtedly higher than those of kiwi in the north, and indeed may be so high that males alone cannot meet them. By helping out at night - during the preferred feeding time - a female probably reduces her mate's energy expenditure in three ways. She saves him the cost of re-heating the egg when he returns; she keeps the embryo growing, and thereby reduces the number of days that he needs to incubate; and she probably enables him to spend more time foraging than would otherwise be possible, and thus maintain condition. In suggesting that female help is necessary for breeding in cold climates, we recognise at the same time that it does not adequately account for its existence in some populations. For example, the great spotted kiwi in coastal forest at Kahurangi Point in Northwest Nelson share incubation duties even though they breed in conditions as mild as those in many parts of the North Island (McLennan and McCann, 1989). We also recognise that our explanation predicts that female brown kiwi should help with incubation in at least two parts of the North Island: in the upper parts of the Raukumara Range, and in Tongariro National Park. Both have cold climates, with mean temperatures typical of those of great spotted kiwi habitat in much of Northwest Nelson. This prediction has yet to be tested.

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