THE NESTING OF THE NORTH ISLAND KOKAKO (*Callaeas cinerea wilsoni*) - REVIEW OF ACCOUNTS FROM 1880 TO 1989

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ABSTRACT

We review 16 published and 17 previously unpublished accounts of the nesting of North Island Kokako (*Callaeas cinerea wilsoni*) recorded between 1880 - 1989. Nests were on average 8.5 m above ground, in many different tree species, but usually with dense overhead cover. Kokako laid eggs from October to February. The modal clutch had three eggs or young, four nests had two. Only the female built the nest, incubated, and brooded young, though the male fed the female at or near the nest throughout the nesting period. Incubation took about 18 days and fledging about 31 days. We suggest that several aspects of Kokako nesting evolved in response to diurnal avian predation, and that these behaviours give ineffective protection against nocturnal, arboreal, introduced mammal predators.

KEY WORDS: Kokako, *Callaeas cinerea*, nesting, behaviour, predation

INTRODUCTION

The North Island Kokako (*Callaeas cinerea wilsoni*) (henceforth called 'Kokako') is a declining endemic New Zealand passerine, now confined to scattered populations in the northern half of the North Island (Lavers 1978, Hay 1984, Rasch 1992). Kokako individuals or pairs maintain largely exclusive, year-round territories by loud singing from tall trees (R. Hay unpublished). Most pair bonds and territories are maintained from year to year but many are not (J. Innes *et al.* unpublished). Kokako are omnivores, feeding on flowers, fruit, foliage and insects in proportions which vary by territory, season and year (Powlesland 1987, Best & Bellingham 1991). They are long-lived, perhaps to 25 years, although their breeding success in mainland New Zealand forests is poor (0.1 young fledged per female per annum) in the absence of pest control (R. Hay unpublished). Juveniles are known to have dispersed up to 5 km from their natal site to set up a territory (J. Innes *et al.* unpublished). It is the last remaining species of the endemic wattlebird family Callaeidae on the mainland and is the subject of an active recovery programme to improve its conservation status from 'endangered' (Rasch 1992).

Historically the species was regarded as a reclusive nester. For example, nests were 'diligently pursued' by J. and R. St Paul and H. R. McKenzie in the Hunua range from 1943 to 1973 and only eight were found, of which

four were in use (St Paul & McKenzie 1974). Only five nests were found in three breeding seasons by the Forest Bird Research Group at Rotoehu, Mapara, and Pureora in the central North Island (R.Hay unpublished).

In this paper we review published and unpublished information about 33 Kokako nests described from 1880 to 1989, thus extending the more limited reviews by McKenzie (1951), St Paul & McKenzie (1974), and Hay (unpublished). We also intend to provide a general account of Kokako nesting biology.

SOURCES OF DATA

Our sources of data include previously published material (16 nest records) plus 17 unpublished accounts collated by us since 1980. We included only first hand accounts which gave data on the date the nest was found and its geographical location, and excluded accounts which referred only to courtship (eg Lovegrove & Towle 1974) or fledged broods (eg Hatch 1979). We have as far as possible avoided repeating the anecdotal descriptions which constitute most of the original accounts, so many detailed field observations can still be found there. We have emphasized accounts where quantitative data were taken on female attentiveness and adult visit rates, but collated all nest accounts by stage of the breeding cycle so that other authors can quickly locate accounts of, say, incubation. We recalculated all incubation and fledging times from given data rather than just accept the figures of the original authors.

Throughout this paper, statements are sourced to accounts of particular nests by reference (in parenthesis after the statement) to the summary of nests given in Table 1. The accounts vary from a single observation of an incomplete nest (Nest 28) to virtually continuous observation of a nest from building stage to nestlings (Nest 15). No nests were observed from building to successful fledging, and in only one instance (Nest 29) was a banded chick subsequently followed to adulthood. Most accounts are brief and refer to only part of the nesting cycle. Appendix 1 shows which nests refer to each stage of nesting.

New nesting accounts

Data from two substantial accounts of Kokako nests are published here for the first time. The first (Nest 16) is from an unpublished Wildlife Service file note (undated) written by Jack Johnson, who made observations at a nest near the Tapu-Coroglen Road (Coromandel, ref. NZMS 260 T11 407653). Johnson's 16-page account describes the location, structure, and invertebrate fauna of the nest, and the behaviour of adults and nestlings during 15-26 March 1978, the 12 days before the chicks fledged. Chick vocalisations were recorded and analysed by Hughes (1981).

The second account is of a nest (Nest 29) located in the Pikiariki Ecological Area (Pureora, ref. NZMS 260 T17 362964) by Maria Hansby on 31 January 1983, 10 days before the chicks hatched. Maria Hansby and Brent Calder observed the nest on 6 of the 10 days before hatching (average 3.7 hours observation per day), and on 25 of the 33 days from 8 February (hatching) to 12 March (fledging; average 7.75 hours observation per day).

TABLE 1 – Features of 33 Kokako nests described from 1880 to 1989, arranged in chronological order by discovery date.

Nest No.	Date Found	Location	Nest Site	Height (m)	Laying Month	Clutch Size	Reference
1	Early Apr 1880	Tokatea Ranges (Coromandel) Castlehill	in an *Astelia* in a rata tree	9	Feb	3	Reischek 1886
2	3 Jan 1886	Waitakere Ranges	in crown of very thick miro (*Prumnopitys ferruginea*)	?	Nov	3	Reischek 1886
3	22 Nov 1887	Clevedon	?	?	Nov	3	McKenzie 1951
4	15 Jan 1890	Whangarei	?	?	Nov	2	Buller 1892
5	12 Oct 1906	Mangamaia Valley (S Raukumara)	in large fork of leaning "tawhera" (*Ixerba brexioides*)	6	Oct	_	M'Lean 1912
6	28 Nov 1943	Mt London, Hunua Ra.	toro (*Myrsine salicina*)	5	_	?	McKenzie 1951
7	26 Dec 1943	Hunua Ranges	toro	11	Nov	?	McKenzie 1951
8	3 Nov 1950	Hunua Ranges	tawa	12	_	_	McKenzie 1951
9	2 Dec 1950	Moumoukai, Hunua	in tawa on "firm spreading side branch"	8	Nov	3	McKenzie 1951
10	2 Dec 1952	Hunua Ranges	on *Astelia* in tawa	?	Nov	3	McKenzie 1953
11	16 Nov 1953	Hunua Ranges	toro	?	_	_	St Paul & McKenzie 1974
12	18 Feb 1961	Hakarimata Range, Raglan	?	?	Jan	?	MacDonald 1966
13	Mar 1961	Hakarimata Range, Raglan	in kiekie (*Freycinetia baueriana*) clump	12	Jan	?	MacDonald 1966
14	1 Jan 1962	Hunua Ranges	in rata mass on raukawa (*Pseudopanax edgerleyi*)	8	Jan	≥2	St Paul 1963
15	23 Jan 1966	S side of Mt Pirongia	among rata vine in *Olearia ranii*	5	Feb	2	Hamilton Jun. Nat's 1975
16	2 Feb 1978	Tapu/Coroglen Rd' Coromandel	in pigeonwood by supplejack	4.5	Feb	3	J. Johnson unpublished
17	27 Nov 1978	Mapara	in hinau (*Elaeocarpus dentatus*) under rata vine clump	9	Dec	?	R. Hay unpublished
18	30 Dec 1978	Tapu/Coroglen Road Coromandel	in dense clump of suppplejack in pigeonwoood	4	Dec	2	C. Veitch unpublished
19	Nov 1979	Puketi	*Olearia ranii*	2.5	Nov	?	Anderson 1979
20	16 Nov 1979	Mapara	in pigeonwood with lawyer & supplejack overhead	6	Nov	1	R. Hay unpublished

TABLE 1 – Cont'd

Nest No.	Date Found	Location	Nest Site	Height (m)	Laying Month	Cltuch Size	Reference
21	Dec 1980	Mapara	in *Astelia* on rewarewa (*Knightia excelsa*)	20	Dec	?	R. Hay unpublished
22	23 Jan 1981	Pureora	mahoe	3	Dec	3	R. Hay unpublished
23	4 Mar 1981	Pureora	low dense canopy of broadleaf	5	Feb	?	R. Hay unpublished
24	1981/82	Pureora	mahoe	10	-	?	T. Lovegrove/M. Hansby unpublished
25	1 Jan 1982	Kaharoa	in *Cyathea cunninghamii* crown	9	Jan	1	A Saunders unpublished
26	12 Feb 1982	Pureora	mahoe with rata vine	5	Feb	?	J. Innes/I. Millar unpublished
27	4 Mar 1982	Kaharoa	in fork of tawa	9	Feb	3	A. Saunders unpublished
28	7 Jan 1983	Pureora (Bismark)	in small tawa with lawyer	7	–	–	M.Hansby/B.Calder J. Innes unpublished
29	31 Jan 1983	Pureora (Bismark)	in mahoe with lawyer	7	Jan	2	M.Hansby/B.Calder J. Innes unpublished
30	Sep 1983	Puketi	in *Collospermum* on towai (*Weinmannia silvicola*)	12	Sep	?	A. Davis/M. Bellingham unpublished
31	4 Dec 1986	Mt Bruce (captive)	fuchsia (*Fuchsia excorticata*)	1.5	Dec	3	S. Anderson/S. Sawyer unpublished
32	17 Mar 1988	Mapara	in crown of tawa	23	Feb	≥1	P. Montgomery/D. King unpublished
33	14 Feb 1989	Rotoehu	*Cyathea cunninghamii* crown	11	Feb	1	J. Innes unpublished

Note 1: the location of nest 2 is misspelled in Reischek 1886 as 'Waitakarei Ranges'.
Note 2: a typographical error in St Paul & McKenzie (1974) incorrectly reports nest 9 as found on "2 December 1956".

This account contains very detailed data on female attentiveness, male and female visit rates in the latter half of incubation and during the nestling period, plus many other observations of adult and subadult behaviour before and after the successful nesting.

BREEDING BIOLOGY

Breeding season

The month in which eggs were laid was deduced for 28 nests from descriptions of the nest contents and assuming incubation to take 18 days and fledging 31 days (see later). Laying was from October to February (late spring to summer). These data are consistent with new subadult Kokako having been observed only from December onwards (J. Innes, unpublished). Nests from December onwards may have been renests. Kokako renested after failure at Mapara in 1980-81 (after the failure of Nest 21) and at Pureora in 1981 (Nests 22, 23). The Mapara pair lost a clutch to predators in December 1980 but must have laid again by early February 1981 since they fledged two juveniles shortly before 18 March 1981. The Pureora pair lost chicks to predators on 28 January 1981, but had laid again by 4 March. In both instances the interval between initial failure and re-laying was 4-5 weeks.

Nest building, structure, and location

There are five accounts describing nest building. Females alone built nests. Only one account (Nest 14) mentioned that the male may have assisted with actual nest-building, with two accounts (Nests 14, 30) mentioning both adults collecting nest material. At Nest 14 "The male assisted with the building of the nest but was not seen at any time to sit on it." The observer at Nest 30 reported that only one adult actually constructed the nest. The three remaining accounts (Nests 10, 17, 29) reported that only one adult carried or placed nest material. The female building at Nest 10 made eight visits with nest material between 06:03 and 06:42 on 2 December 1952. At Nest 17 one adult carried "mud and sticks" 80 m back to the nest site, in one observation making five return visits in 20 minutes. Total duration of nest-building is known only from a captive pair breeding at Mt Bruce (Nest 31), where it took 5 days, and the female was first incubating 5 days later. This is similar to observations of wild birds. Time from early building to incubation was at most 7 days (Nest 14) to 9 days (Nest 15). At Nest 29, the female was seen carrying nest material for 6 days (11-16 January 1983) and was probably incubating (only the male was observed in 25 min. contact) on 20 January, 4 days later.

The mean nest height above ground (excluding pairs in captivity) was 8.5 m (N = 27; range = 2.5-23 m, Table 1). Nests were in a wide range of tree species, characteristically in the subcanopy or understory, on a firm base, and screened by very dense foliage of the host tree and lianes (supplejack *Ripogonum scandens*, lawyer *Rubus cissoides*, rata vine *Metrosideros* spp.) or epiphytes (*Astelia*, *Collospermum* spp.) (Nests 1, 9, 10, 13-18, 20, 21, 26, 29, 30). Two nests (11, 28) were not on firm bases, which later apparently caused them to be abandoned.

Most accounts do not describe nest location in terms of ridge/gully physiography or aspect; however, these apparently vary. Nest 5 was in a small gully, Nests 15 and 16 were on ridges, Nests 24, 26, 28 and 29 were on flat terrain, and Nests 32 and 33 were 10-12 m off the crest of a ridge, the former with an easterly aspect.

Detailed accounts of nest structure were published by M'Lean (1912) (Nest 5), McKenzie (1951) (Nest 9), and Hamilton Junior Naturalists' Club (1975) (Nest 15), and four others are unpublished. The twigs which formed the nest bases were up to 10 mm diameter and 58 cm long, although they averaged 3-5 mm diameter and 25-40 cm long. Species used were tawa *Beilschmiedia tawa*, mahoe *Melicytus ramiflorus*, putaputaweta *Carpodetus serratus*, pigeonwood *Hedycarya arborea*, wineberry *Aristotelia serrata*, kamahi *Weinmannia racemosa*, Pittosporum sp., and supplejack (Nests 9, 29). Occasional protruding twigs sometimes gave a nest a rough and irregular appearance (Nests 1, 5, 26). Onto this base were woven moss, lichen, and rotten wood with long stems of epiphytic orchid *Earina mucronata*, filmy fern *Hymenophyllum* spp., rata vine or clubmoss *Lycopodium* spp. This aggregate structure was 25-30 cm diameter and, including the twig base, 16-20 cm deep. The bowls were usually, but not always, lined with treefern scales and were 12-16 cm in diameter and 6 cm deep (Nests 5, 9, 16, 26, 29, 33). If chicks survived to fledging, they finally trampled the nest structure until it was little more than a flat platform (Nests 9, 29).

Only one nest (16) was examined for nest invertebrate fauna. Dr J.C. Watt (then of Entomology Division, Department of Scientific and Industrial Research) found several fungus and detritus feeders but no parasites (J. Johnson, unpublished).

On two occasions pairs did not complete building nests. Nest 8, found in November, consisted of a flat platform of sticks with a flat mass of moss on it which lacked a nest bowl. A month later, an active nest (9) by the same pair was discovered. Nest 28, found in early January, was being built in a slender tawa stabilised mainly by living bushlawyer. However, it slumped sideways before completion, and the pair rebuilt 50 m away (Nest 29).

Clutch size and eggs

Modal clutch size was three eggs or young (N = 9); four nests had two (Table 1). No egg measurements are given in any of the accounts. Twelve Kokako eggs measured by Gill (1993) were 34.2-42.1 mm long and 25.7-29.2 mm wide. Reischek (1892) described "grey eggs, marked with brown spots;" Hamilton Junior Naturalists' Club (1975, Nest 15) wrote of ..."two eggs in the nest, one stone grey with fawn spots and one fawn with brown splotches."

Laying and incubation

The laying interval is not known from any account. At a Hunua nest (10), three eggs were laid between the morning of 6 December and the evening of 11 December 1952.

Only the female incubates. Three accounts (Nests 15, 16, 31) permit estimates of the incubation period, which were 14-18 days, 20 days, and 17 days respectively. No details of the observations leading to the 20-day

estimate for the 1978 Coromandel nest appear in Johnson's file report. It simply says: "Mr Rei Hammond [sic] informs me that there were three Kokako eggs laid on the 2nd February 1978. Two eggs hatched on the 22nd February 1978. One egg was infertile." The first egg in Nest 31 (captive pair at Mt Bruce National Wildlife Centre) was seen on 12 December, and the female started incubating the following day. Three eggs were seen for the first time on 20 December when the sitting female was off the nest, but the laying dates of the second two are unknown. A broken eggshell, indicating that at least one chick had hatched, was found on 30 December (S. Anderson, in litt.). Observations presented by R. St. Paul (Nest 14, 1963) permit an incubation estimate of 17-25 days rather than 'approximately 25 days' which he concluded. The laying date was not precisely known, and the chicks may have hatched on any day between 25 and 30 January 1962. An incubation period averaging 18 days seems most likely in view of these four accounts.

Both Anderson and Johnson refer to one chick of the clutch being smaller; the smaller chick of Nest 31 at Mt Bruce was found dead on 5 January 1986. These accounts, and the observation at Mt Bruce that the female started sitting the day after the first egg was laid, suggest that Kokako may not wait until the clutch is complete to begin incubation.

Adult behaviour before incubation

Pre-incubation behaviour is described in detail from only one nest (29) with a colour-banded male at Pikiariki Ecological Area, Pureora. Key features of the observations were that Kokako in breeding mode were difficult to follow in comparison to non-breeding pairs or all pairs outside the breeding season. Movements (especially the female's) recurred in a certain subsection of the territory. The male performed a courtship display in which the wings and tail were held spread out for several seconds, accompanied by a 'chirr' sound. When the nests were being built, observers sometimes followed a single bird and sometimes the pair. The female picked up twigs, moss, and other nesting material which was either dropped or carried to the nest. These observations were infrequent; this suggests either that observation inhibited nest-building or that building was a sporadic activity which happened to occur outside the observation periods.

Adult behaviour during incubation

During the last seven days of incubation of Nest 29, the female spent 80-92% of time incubating the eggs (Figure 1). Her mean time of continuous sitting was 67 minutes (range 36-100, N = 13), and mean time off (to feed and preen) was 8 minutes (range 2-16, N = 20) (Figure 2). The male visited the nest to feed the female (Figure 3), always approaching furtively and pausing before moving directly to the nest. The mean interval between his visits to the nest was 36 minutes (range 11-76, N = 11). His visits were brief, but their duration was not accurately measured. Most were less than 10 seconds, and all were less than 30 seconds. However, only 59% (N = 34) of visits by the male to the female were at the nest. Often the male would give soft "took" calls or a single "mew" nearby, and the female would leave to join him. The mean interval between male-female contacts both at and off the nest was 35 minutes (range 11-76, N = 23). The proportion of off-nest

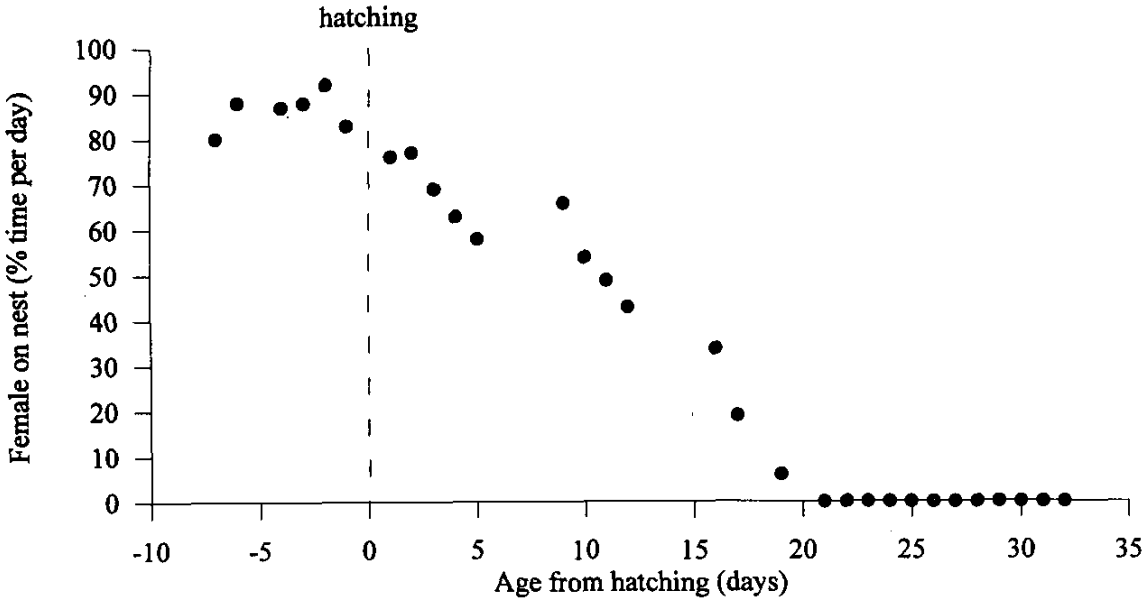

FIGURE 1 – Proportion of nesting female's time spent on the nest from late incubation to fledging, Pureora, 1983 (Nest 29).

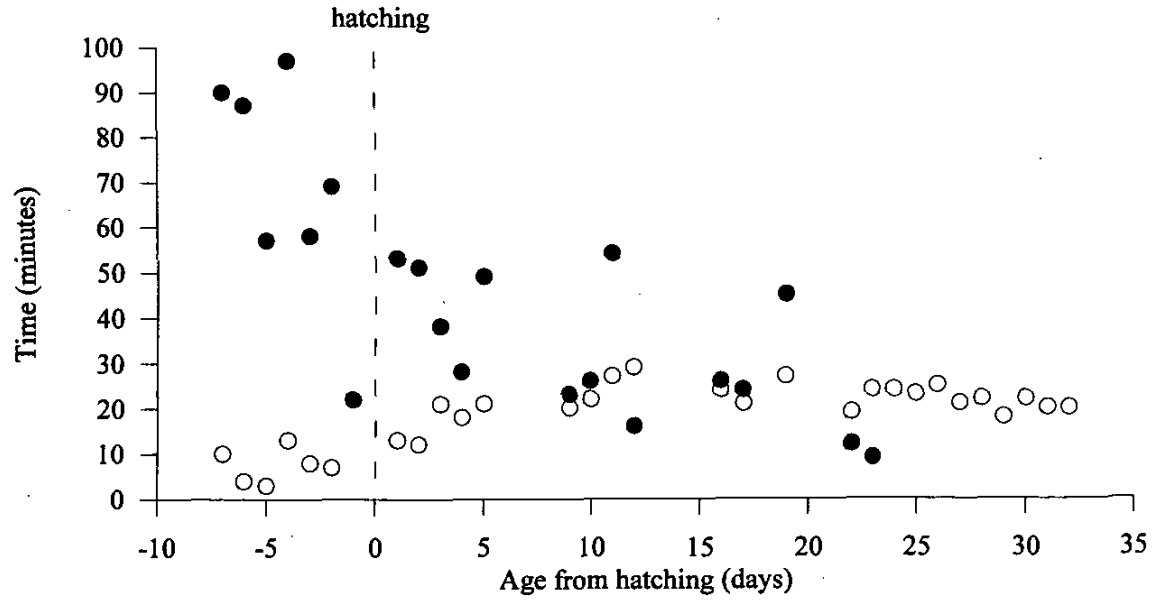

FIGURE 2 – Mean duration of female's time on nest (solid circles) and away from nest (hollow circles) from late incubation to fledging, Pureora, 1983 (Nest 29).

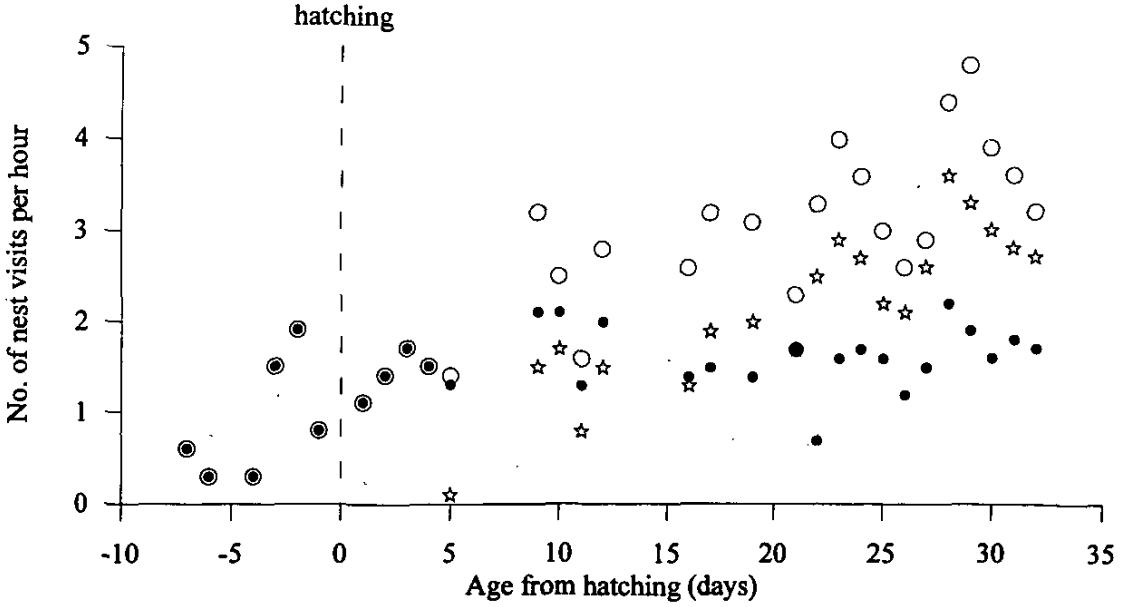

FIGURE 3 – Mean number of visits to the nest per hour by the male (solid circles), female (stars), and total (ie, male or female or both together - hollow circles) from late incubation to fledging, Pureora, 1983 (Nest 29). For 'total' data, male and female visiting together was counted as one visit, not two.

contacts in which the male fed the female is unknown. Both on and off the nest, the female flapped her wings slowly behind her back when being fed by the male.

When approaching the nest, the female was hurried and less furtive than the male, often flying in without hesitation. However, she was always very quiet when leaving the nest. On one occasion the female sang full song in duet with the male while she was on the nest. On 12 January two large pieces of Kokako eggshell from a naturally hatched egg were found 6 m from the nest, presumably where they were dropped by one of the pair.

Adult behaviour in the nestling period

At Nest 29, the female brooded the young less and fed the chicks more as the nestlings grew, while the male continued to feed her and the chicks at the nest at a steady rate until the chicks fledged after 32 days, on 12 March 1983.

Female attentiveness declined steadily from 76% on 8 February, the day after the chicks probably hatched, to zero on 28 February and thereafter (Figure 1). The mean length of time between her nest visits increased from about 10 minutes on 10 February to about 25 minutes on 18 February, and remained at 20-25 minutes until the chicks fledged (Figure 2). Conversely, the mean time she spent on the nest declined steadily through the same period, until after 2 March she did not sit on the nest at all (Figure 2) except to roost there each night. Her first chick-feeding visit to be followed by leaving the nest rather than remaining to brood was 5 days after hatching. Thereafter, the mean rate at which she visited to feed chicks increased rapidly and peaked 5 days before the chicks fledged, although the visiting rate of

the male remained constant throughout at, on average, a visit each 37 minutes (i.e., 1.6 visits per hour; range 0.67-2.22, N = 24) (Figure 3). The length of time spent away from the nest by the female during the nestling period tended to be greater after 15:00 (mean = 24.1 minutes) than between 11:00 and 15:00 (mean = 20.0 minutes), and that before 11:00 was intermediate (mean = 21.2 minutes) but the difference was not quite significant (2-way ANOVA, observation days x time of day, p = 0.06, F = 3.04, d.f. = 2). The mean times spent on the nest by the female in these time intervals (before 11:00, mean = 25.0 minutes; 11:00-15:00, mean = 37.6 minutes; after 15:00, mean = 59.2 minutes) were not significantly different (2-way ANOVA, p = 0.08, F = 3.08, d.f. = 2).

After 16 February, feeding visits were by either one parent or both. From 16 February to 12 March, on average 25% (range 7-54%) of daily feeding visits were by both parents together. The total number of feedings of the chicks per hour was therefore greater than shown in Figure 3, which treats a visit by both parents together as one visit, not two. Singing by one or both adults continued throughout the nesting period.

Accounts of other nests

Other less detailed accounts of Kokako nesting (Nests 9, 14, 15, 16, 17, 20-23, 32) are consistent with that from the Pureora nest (29). Data from two other nests also suggest a gradual decline in female attentiveness and nest visit rates. This could be used to roughly determine the stage of nesting. Nest visits recorded at Nest 16 on 17 March (9 days before fledging) averaged 3.75 visits per hour (mean visit duration = 16 minutes, range = 1-35, n = 35); on 21 March (5 days before fledging) there were 4.1 visits per hour (mean visit duration = 14.7 minutes, range = 1-46, n = 58). Visits by two adults together were 54% and 33% of visits for the two days respectively. At Nest 17 during 7.5 hours of observation on the day following hatching (27 November 1978) the female spent 80% of time brooding the chick. Eight days later (5 December 1979) this had dropped to 70%, then to 66% after two more days. This trend continued until the chick was taken by a predator.

A measure of female attentiveness (which declines steadily; Figure 1) could be used to roughly determine the right time to climb to a nest to band chicks, if the hatching date is unknown. If chicks are to be banded 15 days after hatching, this would be when the female spent 25% of her time brooding.

The pair at Nest 32 continued to sing in the early morning in the nestling period, although for less time than usual. Both adults were observed in a territory-boundary interaction with neighbours. After the pair lost the nestling to a predator they became "more casual in the way they moved about their territory."

Nestling food and disposal of chick faeces

Food for nestlings was carried by adults in the bill and upper throat, the latter sometimes bulging. Adults often regurgitated food for nestlings. Foods seen to be fed to chicks were scale insects (*Ctenochiton viridis*), berries and/or chewed leaf, the latter "imparted with much saliva", given to one chick or

divided between two or three (Nests 9, 16). Foods identified from droppings were ripe fruits of supplejack and pigeonwood, green fruits of raurekau (*Coprosma grandifolia*), leaves of unknown species, and invertebrates (cicada, weevil, bagmoth, spider). Adults at Nest 29 fed themselves mainly on scale insects, and to a lesser extent on leaves and fruit of five-finger, bush lawyer, wineberry, supplejack, and putaputaweta; presumably these foods were also fed to chicks.

At Nest 16 the female cleaned the nest extensively each day, often pushing the chicks to the perimeter to do so. Both adults either consumed faecal sacs or dropped them away from the nest. At Nest 9 adults 'ate droppings which fell in the nest but did not trouble with those which lodged on the outside'. Hay (unpublished) observed that adults ate nestling faecal sacs for the first 2-3 weeks, then chicks ejected faeces over the nest edge.

Tolerance of humans

Several accounts (Nests 9, 10, 16) refer to the considerable tolerance of human activity by Kokako at their nests. McKenzie (1951, Nest 9) relates how Fraser Murray climbed to the nest and sitting female and 'gently stroked its tail', and in his unpublished report Jack Johnson found Kokako apparently undisturbed by vegetation removal (by television personnel), photographic flashlights, loud hammering, and the general presence of people (Nest 16).

Nestling development and behaviour

The development of chicks from 2-3 days after hatching to fledging is described in detail only by McKenzie (1951; Nest 9). When found, they were unable to lift their heads, their eyes were not open, the egg-tooth was prominent and the skin was bare except for linear tracts of natal down. Five days later, they lifted their heads readily, their eyes were half-open, primary and secondary wing feathers were ca 14 mm sprouted, and there were naked patches among down on the side of the bodies. After 12 days, their plumage was bluish-grey like the adults but some brownish down showed in the feathers; their legs were strong and the chicks stretched often but the tail and wings were still small. After 22 days the chicks were making short journeys from the nest to adjacent branches, and they fledged 25 days after being located. The day of hatching is difficult to pick, since the female initially broods the new chicks as attentively as she incubated the eggs (Figure 1). At Nest 29 the male suddenly spent 1 minute at the nest the day after chicks probably hatched, instead of the usual 5-20 seconds. From about 10 days after hatching, chicks frequently stretch legs and wings and become more visible to observers (Nests 9, 16, 29, 32). Fledging is gradual, with chicks moving increasing distances from the nest although still being fed there. Finally, one or both adults lead all the chicks away with soft "took" calls, repeated often. At the time of fledging chicks are clumsy and often misjudge moves, and so fall onto or near the ground, eventually scrambling back up into the trees (Nests 9, 16, 29).

Wattles in nestling kokako are pinkish lavender, edged with pale blue, and are small, concave and rounder than adults' (Nests 9, 29).

Chicks fledge with lavender wattles which change to the blue colour characteristic of adults; the time this takes is unknown.

When they fledged from their Pureora nest, young at Nest 29 had pink, concave (dimpled) wattles and conspicuous down on thighs and head. They were very quiet until fed, at which time adults gave "tooks" or "chirrs" and chicks uttered 'wheezes'and "oos". At Nest 16 also chicks were quiet in the nest until fed, when they began begging and vocalising. The chicks' begging calls were described as "not unlike the whining noises made by juvenile mice." Hughes (1981) presented sonograms of 10-day-old chicks' food-begging calls recorded at this nest. He noted that the female parent often responded with "soft song" before regurgitating food for the chicks, and observed a six-week-old fledgling also making begging calls before being fed. At Nest 9, chicks about 10 days old gave "a small croaking noise" when parents approached with food; at about 17 days they "made a hissing noise like a miniature of the hissing of an angry goose."

Time to fledging

The four reliable observations of time to fledging indicate a mean of 31 days (range 27-34 days, Nests 9, 16, 29, 31). This, combined with an incubation period estimate of 18 days (see above), gives a total of 49 days from incubation to fledging.

DISCUSSION

Taken together, the accounts provide a coherent overview of Kokako nesting despite the time-span of more than a century between the earliest (1880) and latest (1989) nests reviewed here. Kokako produce small clutches and apparently breed only once per year, but invest considerable energy in their young which may remain in their parents' territory for up to a year (Reischek 1892; J. Innes, unpublished). In many ways the breeding of Kokako is similar to that of the Saddleback (*Philesturnus carunculatus*), the only other extant member of the family Callaeidae. In both species, the nest is built by the female alone over several days; only the female incubates and broods, although the male feeds the female at or near the nest throughout; nests have a twig base with grasses and other material and are often lined with tree-fern scales. Saddleback eggs have "pinkish grey base with mauve, reddish-brown, dark brown and black spots and blotches, especially at the larger end" (Lovegrove 1980), like Kokako eggs, although there is considerable variation in both species. Fledged saddleback juveniles also remain in their parents' territory for some months (Jenkins 1976; Lovegrove 1980). However, Saddlebacks are hole-nesters and hole-roosters whereas Kokako nest in open cup nests and probably also roost in the open.

Predation was the most frequent cause of failure of the Kokako nests reviewed here, ending 10 of the 33 attempts, and six of the nine successful nests were protected against predators in some way. None of the predators was identified with certainty, but introduced small mammals were suspected in all cases. Predation alone may be sufficient to explain the ongoing decline of Kokako populations on the mainland, as suggested by McKenzie (1951) for the Hunua population. Features of Kokako nesting which may render

them vulnerable to predators include a long nesting duration (7 weeks) and the late nesting season (October to March), which coincides with seasonal increases in populations of ship rat (Innes 1990), feral cat (*Felis catus*; Fitzgerald 1990), and stoat (King 1990). Predators may be attracted by frequent visits by both parents to the nest to feed young, by begging calls of chicks when they are fed, and by the deposition of faeces around the nest rim. Also, newly fledged chicks are clumsy and often end up on or near the forest floor, where they are vulnerable to feral cats and mustelids. No accounts reported adult female kokako killed on the nest, which suggests either that adults can escape nest predators or that predators deliberately target eggs and chicks.

The almost universal placement of nests under dense overhead cover is a characteristic feature of Kokako nesting. Kokako are likely to have evolved strong behavioural responses to avian predators, since the pre-human New Zealand avifauna included five diurnal (Haast's Eagle *Harpagornis moorei*, New Zealand Falcon *Falco novaeseelandiae*, a Goshawk *Circus eylesi*, Australasian Harrier *Circus approximans* and a Crow *Palaeocorax moriorum*) and three nocturnal predators (Owlet-nightjar *Megaegotheles novaezealandiae*, Laughing Owl *Sceloglaux albifacies*, and Morepork *Ninox novaeseelandiae*) (Holdaway 1989; Worthy & Holdaway 1993). Indeed, Kokako react quickly to passing harriers, moving to dense cover and staying very still (J. Innes, pers. obs.). A nesting Kokako was observed to drive a Morepork away from the nest vicinity by flying at it (Nest 29)

Food supply and predation are the major influences on reproductive success in passerines (Ricklefs 1969; Martin, 1987, 1992, 1995). Evolved nesting adaptations by Kokako that reduce predation risk from avian predators or maximise fecundity in the face of predation are therefore expected. With Kokako, such adaptations may be behavioural (eg nest location among dense vegetation, a cryptic nest structure incorporating live vegetation, furtive approaches to the nest by adults, and renesting after failure) or physiological (moderately cryptically patterned eggs) (Collias & Collias, 1984). Predation may also be reduced by birds guarding their young or by actively defending the nest with distraction displays or attack (Martin 1992). No anti-predator distraction displays were reported by any observer of the Kokako nests reviewed here, but Kokako can apparently deter Moreporks by attacking them. Adults were never observed to attack harriers, from which they would themselves be at risk of predation, as would have been the case with most of the pre-human avian predator species.

However, with the exception of attack and renesting after failure, the adaptations suggested above would be unlikely to be effective against arboreal, nocturnal, mammalian predators such as rats, stoats or brush-tailed possums. Genetic naivity about mammalian predators, tameness, limited dispersal ability, generally small populations, small clutch sizes and low productivity are all features of Kokako which increase its risk of extinction on the New Zealand mainland (McDowall 1969; Gibb & Flux 1973; Moors 1983; Holdaway, 1989; Bell 1990; Lovegrove 1992). Mainland kokako survival may depend on how quickly individuals can learn to recognize and avoid introduced mammalian predators.

Several aspects of Kokako nesting biology remain little known. At present there are only four estimates of incubation time and of time to fledging. Larger samples of both are needed, as well as accounts of the laying interval, about which little is known. Also, studies on food availability, food provisioning and energetics and studies of food competition with introduced browsing mammals (Leathwick *et al.*, 1983) would make a valuable contribution to the current debate on the causes of Kokako population decline. Predation is apparently an important determinant of nesting success. Measures of the actual predation rate and manipulative predator control experiments are necessary to evaluate its importance and the relative roles of different predator species.

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APPENDIX 1 – Stages of breeding referred to in each of the 33 accounts of Kokako nesting. The nest numbers are from Table 1.

Nest building: 14, 15, 17, 25, 30
Nest location & structure: 3, 5, 8-11, 16, 18-24, 26-29, 31-33
Laying: 15, 31
Incubation, eggs: 3, 6, 10, 14-16, 23-27, 29, 31, 33
Nestlings: 1-4, 7, 9, 12, 13, 15, 16, 19, 20, 22, 25, 27, 29, 31, 32

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