

Breeding biology of North Island kokako (*Callaeas cinerea wilsoni*) at Mapara Wildlife Management Reserve, King Country, New Zealand

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Abstract Breeding of North Island kokako (*Callaeas cinerea wilsoni*) was studied at Mapara, King Country, New Zealand, from 1990 until 2000. Sixty-seven adult and 167 nestling kokako were colour-banded, and radio-transmitters were attached to 49 to identify individuals and to help locate nests. Pair bonds were stable: 7% of pairs split each year for reasons other than mate death. More than 200 nests were located, which permitted observations of breeding-season length, nesting behaviour, clutch and brood size, incubation and nestling periods, and nest success. The nesting season began in late Oct but varied greatly in duration, lasting from 7 weeks in 1993/94 to 21 weeks in 1994/95. We attributed this variation to changes in abundance of key food fruits. Females made up to 5 breeding attempts and fledged as many as 6 chicks in a season. Male-male pairs also built nests, though the apportioning of effort differed from that of conventional pairs. Mean clutch and brood sizes were 2.31 and 1.96, respectively. The incubation period was 18 days and fledging took a further 34-42 days. Sixty-one percent of nesting attempts successfully fledged young when mammalian pests were controlled, as against 8% when there was no predator control. Predation of eggs and chicks by ship rats (*Rattus rattus*) and brush-tailed possums (*Trichosurus vulpecula*) was the main cause of nest failure, whereas deaths of nesting adult females mostly caused by stoats (*Mustela erminea*). Kokako are well adapted to cope with avian predation, but their future conservation depends on management of key small mammalian pests.

Flux, I.; Bradfield, P.; Innes, J. 2006. Breeding biology of North Island kokako (*Callaeas cinerea wilsoni*) at Mapara Wildlife Management Reserve, King Country, New Zealand. *Notornis* 53(2): 199-207.

Keywords North Island kokako; *Callaeas cinerea wilsoni*; Callaeatidae; breeding biology; King Country; New Zealand

INTRODUCTION

The North Island kokako (*Callaeas cinerea wilsoni*) is a member of a New Zealand endemic family, the Callaeatidae or New Zealand wattlebirds. The kokako is the only wattlebird remaining on the New Zealand mainland, but it has suffered a dramatic reduction in range (Lavers 1978; Innes & Flux 1999). Kokako are currently classed as endangered (BirdLife International 2000; Hitchmough 2002) and occur mainly in small, disjunct areas of lowland forest in the central and northern North Island. An adaptive management programme examined the causes of population decline through manipulations of introduced pest

mammal populations at 3 North Island sites. Predation of eggs and nestlings by possums (*Trichosurus vulpecula*) and ship rats (*Rattus rattus*) was identified as the major agent of decline (Innes *et al.* 1999). These threats are now being managed in keeping with the kokako recovery plan (Innes & Flux 1999), and most kokako populations are now recovering.

Before 1989, a total of only 33 kokako nest attempts had been described (Innes & Hay, 1995) despite considerable effort to locate nests. The lack of sightings by earlier observers probably resulted in part from non-managed kokako populations being strongly male-biased. The

population at Mapara Wildlife Management Reserve (1400 ha, near Te Kuiti), for example, consisted of 16 pairs during 1992, only 5 (31%) of which are thought to have involved a female (Innes *et al.* 1999; IF, unpubl. data). In addition, in the presence of high pest densities, many kokako nests would have been preyed upon or disturbed within days of egg laying, rendering it unlikely for an infrequent observer to detect a nest.

Predator management at Mapara during 1989–1997 increased adult densities and nesting success, and allowed the identification and monitoring of a large sample of kokako nests. At Mapara, we have been able to locate over 200 nests, of which we were able to access and study 189 between 1992 and 2000. This has greatly increased our knowledge of kokako nesting biology. This paper adds to the information presented by Innes & Hay (1995). We expect that the detailed information about kokako breeding presented here will assist species managers to efficiently focus kokako conservation efforts and to monitor populations.

STUDY AREA AND METHODS

Study area

The Mapara Wildlife Management Reserve is in steep hill country covered in a lowland forest of mixed broadleaf and scattered podocarps, 260–600 m above sea level. It is isolated from other forests by surrounding pasture and young plantation forests. Extensive control of introduced mammalian browsers and predators was undertaken between 1989 and 1997. This greatly increased kokako breeding success and allowed new pairs to establish (Innes *et al.* 1999). The vegetation and topography are described in detail by Leathwick *et al.* (1983), though the vegetation composition, structure, and density, has changed considerably since then with the control of goats and possums (Corson 1997).

Capture and banding

Kokako pairs occupied territories throughout the year. Recorded kokako song was played to lure birds into mist-nets rigged in the forest canopy within previously identified territories. All captured kokako were fitted with a unique combination of leg-bands: 1 of metal and up to 3 of coloured plastic. Kokako were measured to investigate techniques for sex differentiation, and 49 were fitted with radio-transmitters to assist in the location of nests. We fitted radio-transmitters to known-female kokako, or to the smaller member of a pair, as females tend to be smaller (Flux & Innes 2001). Nestlings were colour banded at *c.* 15 days. From 1992 to 1996, nearly all chicks were banded; from 1996 we banded as many as

possible, but the population had become too large for us to locate all the nests. In total, 234 kokako were banded.

Monitoring of pairs and their breeding

A different sample of kokako pairs was monitored each year (mean = 18 ± 5 pairs year⁻¹). They were checked weekly from 1 Nov until all breeding had finished, and details of their behaviour and any interactions were recorded. Females with transmitters could be followed directly to locate nests. Where transmitters were not fitted, we mostly followed the males; occasionally males would lead observers directly to nests, but more frequently they led us to the female, who could then be followed to the nest. Nests were located at various stages, usually during building or incubation, but a few were not located until chicks had already hatched. Each week observers recorded details of pair activity at nests without approaching the nest closely. Nests were considered to be active if kokako visited them.

So as not to bias another theme of our research – the investigation of agents of kokako decline – we minimised the number of times we climbed to nests. Most nests were only climbed up to once, either to band chicks when they were *c.* 15 days old, or to ascertain the fate of a failed nest. Nest details were recorded on a standard form, and included topography, location, vegetation supporting the nest, estimated percentage vegetation cover above and around the nest, position of the nest in the tree (including height and distance to the canopy directly above), and nest construction.

Between 1992 and 1995 we watched a selection of nests each year for periods of up to 4 h at a time, in order to record relative parental contribution at different stages of nesting. Observers watched from the furthest point at which they could view the nest while remaining as concealed as possible. Observers left the nest area if their presence seemed to influence the kokako behaviour. We recorded the frequency of visits by either parent, their activity, time on and off the nest, and in some instances the nature of food being carried.

Clutch size and egg measurements

A few nests were visited more frequently to record clutch size and egg measurements. We visited 26 nests by visiting after the female had been incubating for 1–2 weeks to determine clutch size. Egg length and breadth were measured using Vernier callipers (± 0.1 mm). Eggs in 10 complete clutches were measured, as were eggs recovered after nest predation, disturbance or abandonment. Egg and nestling weights were measured at 2 nests using a Pesola® spring-balance (± 1 g).

RESULTS

Pair bond

Pair bonds were generally stable. Pairs generally remained together and defended joint territory throughout several years. The tenacity of pairing seemed to vary among individuals, the lowest fidelity being demonstrated by a female that paired with 4 different males in a 5-year period. During the study, 7.4% of pairings split per annum for reasons other than the death of a previous partner. When new pairings formed, they mostly occupied the previous territory of either the male or the female. Of 77 new pairings, 40 used territory already occupied by the male, 18 used territory already occupied by the female, and 19 were at territories new to both partners. These observed results are possibly skewed toward males because of the over-representation of males at the start of this study and the higher loss of females to predation.

Throughout the year, pairs are involved in some level of courtship activity. Members of pairs will frequently preen each other about the base of the bill while perching side by side. Mutual preening is often observed between partners when they are involved in a confrontation with other kokako. Males will also offer food items to their mates throughout the year, though this occurs more frequently as the breeding season approaches. In the 2-3 weeks preceding nesting, male, and sometimes female, kokako will collect and carry twigs and other nest materials for short distances. Males will often carry such items while performing an elaborate "Archangel" display (Lovegrove 1980 – running along branches near the female with head held downwards and wings extended above the head).

Breeding season

Most paired, female kokako attempted to breed at least once annually. From 130 instances in which known females were monitored through a breeding season, we recorded only 11 instances when 1 did not breed in a given year. Of these non-breeders, 6 were newly paired and had never previously bred, whereas 5 had nested during at least 1 previous season. No known-female kokako missed more than 1 breeding season in succession.

Few laying dates were known exactly, though most were known to within 7 days. Most lay dates were estimated by back calculation from hatch dates or from the estimated age of nestlings at banding. In deriving dates we allowed 18 days (see later) for incubation. Nestling age was estimated by comparing their weight to that of known-age chicks (Innes & Flux 1999). When nests failed before banding, we estimated the lay date as the

midpoint between when birds were last seen without a nest or building a nest, and when incubation was first observed. The earliest date recorded for the start of incubation of a 1st clutch at Mapara was 31 Oct. Mean annual laying dates for the 1st clutch ranged between 17 Nov and 4 Dec, with the mean of all years being 25 Nov (Table 1).

Practice nests

Some kokako may build practice nests. We recorded 3 probable practice nests, from different known breeding pairs. Nests were completed and then apparently abandoned and the birds went on to construct new nests in which they laid. However, it was impossible to tell whether these were practice nests or whether nests were abandoned after predator visits: it is possible that predators disturbed these females before they laid or cleanly removed an egg soon after laying, causing the bird to desert.

Multiple nests

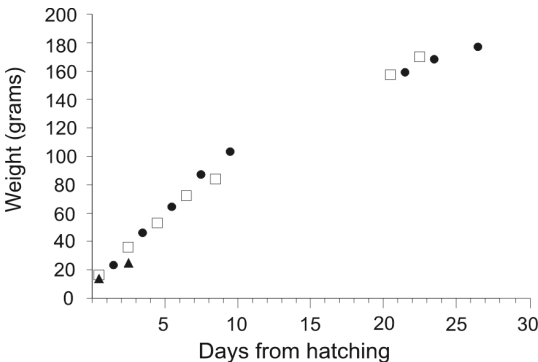
Kokako make multiple nests during some seasons. Kokako laid up to 5 clutches when successive nests failed during unmanaged years. During managed years they fledged up to 3 successive broods, totalling up to 6 fledglings, in a single season. Breeding season duration was variable but appeared to show a biennial pattern (Table 1), reflecting what we termed "good" and "bad" years. Good years appeared to correlate with heavy fruiting of important kokako food plants, notably pigeonwood (*Hedycarya arborea*) and rewarewa (*Knightsia excelsa*) (authors' unpubl. data), which may have been related to climatic variables. The duration of the nesting season (1st laid egg to last laid egg) varied from 7 weeks in 1993/94 to 21 weeks during 1994/95. The latest recorded fledging in any year (the last of 3 successful nests) was on 19 May. We had sufficient data to determine the re-nesting interval for 81 nests. When kokako re-nested after fledging or nest failure most did so within 2 weeks. Three (3.7%) re-nests overlapped, *i.e.* females built new nests up to 7 days before the fledging of their previous nest, 5 (6%) were incubating a new nest within a week, and 40 (49.4%) re-nested within 2 weeks. The remaining 33 (40.7%) re-nested after more than 2 weeks. The longest period recorded between nest failure and re-nesting was 41 days, and between fledging and re-nesting was 35 days.

Nest sites

Nest sites were evenly distributed between ridge tops (61 nests), faces (62 nests), and gullies (61 nests). This may reflect a tendency toward nesting in gullies and ridges, as faces inevitably make up the greatest area of the landscape. Where nests were on faces, kokako showed no preference for any particular aspect. Nests were in trees

Table 1 Kokako (*Callaeas cinerea wilsoni*) laying dates, number of breeding attempts, and breeding season duration at Mapara, King Country from 1991 to 2000.

Year	No. females monitored	Date 1st egg laid (week ending)	Mean laying date of 1st clutches (week ending)	Mean no. of breeding attempts female ⁻¹	Breeding duration (1st to last egg; weeks)
1991/92	3	11 Nov	-	0.7	7
1992/93	9	21 Nov	4 Dec (SD = 16, n = 6)	1.4	12
1993/94	9	18 Nov	27 Nov (SD = 15, n = 7)	1.1	7
1994/95	17	9 Nov	26 Nov (SD = 9, n = 16)	1.6	21
1995/96	18	8 Nov	24 Nov (SD = 9, n = 18)	1.3	9
1996/97	24	12 Nov	25 Nov (SD = 9, n = 23)	2.0	16
1997/98	14	11 Nov	27 Nov (SD = 15, n = 11)	1.1	7
1998/99	21	31 Nov	17 Nov (SD = 12, n = 12)	2.2	19
1999/00	15	4 Nov	21 Nov (SD = 17, n = 13)	1.1	9
Total			25 Nov (SD = 13, n = 109)		

**Fig. 1** Growth rates of 3 North Island kokako (*Callaeas cinerea wilsoni*) chicks at Mapara, King Country, New Zealand. Symbols represent chicks from different nests.

(89%, $n = 191$) or tree ferns (11%). They were either twiggy platforms built amongst branches, fronds, or tangles of vines (60%), or they were scooped into the humic mass at the base of epiphytic lilies (*Collospermum* spp. and *Astelia* spp.) (40%). Nests were located for maximum concealment from above; 89% had dense overhead cover (< 30% sky visible), 10% had moderate cover (30–69% sky), and only 1% of nests were recorded as having sparse cover (> 70% sky). At 60% of nests cover was provided, at least in part, by tangles of vines above the nest.

Nest heights ranged from 2 to 38 m (average height 13 ± 7.9 m ($n = 191$)). Kokako usually built nests toward the tops of trees: 31% of nests were built within 1 m of the canopy and 68% were within 3 m of the canopy.

Kokako rarely used the same nest site twice. Of the 191 nests we described in detail, only 5 were in a previously used site: 2 of these were built in the same tree as a previous nest but on

different branches, 1 pair used a nest site that had been used 4 years before by a different pair, 1 pair built a new nest atop a nest they had built the previous year, and another pair laid a 2nd clutch in the same nest when their previous clutch failed to hatch.

Nest construction

We observed the building of 41 nests by breeding pairs. In conventional pairings, the female did all the building, though twice males were seen to deliver twigs to a nest.

Nests were built spasmodically and time spent building increased as egg laying became imminent. It was easy to overlook building activity in the early stages, so it was difficult to estimate how long the process took. Of 19 nests where we made 2 or more visits during the nest-building phase, 2 took at least 3 days and the others at least 5 days to complete. The longest recorded periods of building were for 2 pairs, which both took over 11 days to complete their 1st-clutch nests.

Two types of nest platforms were used: ready-made platforms provided by humus clumps formed around the roots of epiphytic plants ($n = 62$), and bird-made twig platforms ($n = 129$). The former involved minimal use of materials and in all but 3 of these nests a few twigs were found, though they served no structural function. The nest bowl was formed by digging out a cavity in humus around the epiphyte's roots, and this was lined with dry fibre and/or tree fern scales as for a conventional nest. Twig platforms were built against dead stumps (2%), on trunks of trees or tree ferns and on main branches (38%), on small branches and twigs (31%), or suspended in fine twigs and lianes (29%). Twig platforms varied greatly in size, depending on the site and the enthusiasm of the female: the maximum external

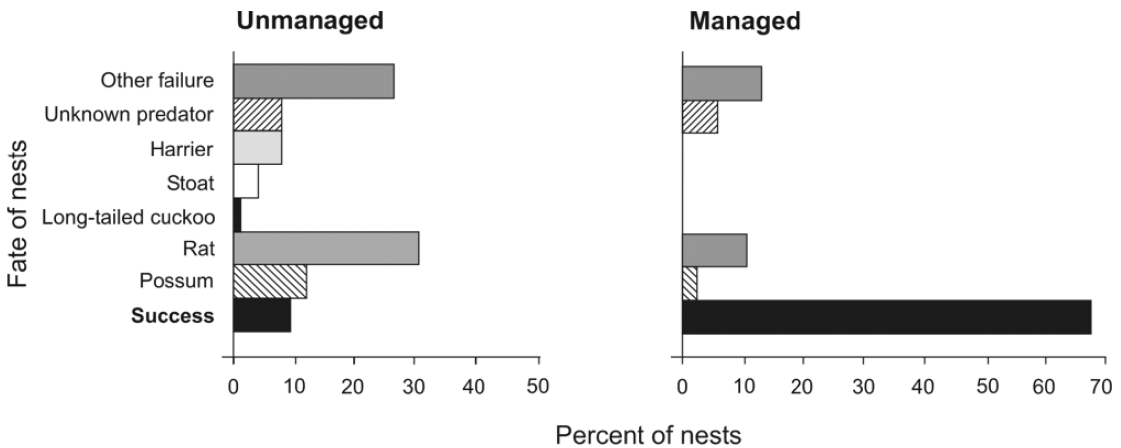


Fig. 2 Fate of North Island kokako (*Callaeas cinerea wilsoni*) nests at Mapara, King Country, New Zealand, during predator-managed and unmanaged years (managed: $n = 123$; unmanaged: $n = 75$). Fate expressed as a percentage of all nests with known outcomes.

diameter was 200 – >400 mm. They included green, leafy and dead twigs, mostly 150–300 mm long, though twigs as long as 595 mm were recorded. Filamentous mosses, lichens, supple twigs of tawa (*Beilschmiedia tawa*), rata vines (*Metrosideros* spp.), orchid stems (*Earina* spp.), and stipes of climbing ferns (*Hymenophyllum* spp.; *Pyrrosia eleagnifolius*) were commonly employed to bind the more rigid twigs together. The bowl itself was usually a complex, multi-layered structure. Inner layers included mosses, rotten wood pulp and *Collospermum* leaf bases; these layers retained large quantities of moisture and may assist in maintaining a humid environment around the eggs. Dry materials are then added to form the nest lining, including *Earina mucronata* leaves, fine grasses, and shredded plant fibre. Kokako strip fibre from dead kiekie (*Freycinetia baueriana*) or *Collospermum* leaves with their bill. Scales from *Cyathea* tree ferns completed the bowl. A long, leafy stipe of the climbing fern *Pyrrosia eleagnifolius* was added to the nest rim of >50% of nests.

Although the materials used varied little, the quantities of each differed markedly between nests, from 1 nest that used over 300 twigs and 4 L of lining material, to a simple scoop with only a trace of lining material. All females in the study built both epiphyte-platform and twig-based nests. Nest construction appeared to largely be defined by the site chosen and materials available; 1 particularly innovative female teased out an old chaffinch nest to form a ready-made nest lining.

Only 2 nests failed as a result of insecurity: 1 fell between the large branches on which it was built, and another was tipped up by the growth of

the tree fern fronds on which it was built. A further nest was built with no rim on 1 side, and 1 chick from a clutch of 2 fell from this nest when c 15 days old.

Nests of male-male pairs

Male-male pairs built at least 3 nests, 2 of which we observed during the building phase. Both birds carried and deposited nest material. One pair created only an unstructured pile of several hundred loose sticks; another pair carried twigs and then, several days later, lining materials, but the site was inaccessible so we do not know whether the nest was properly structured. A further nest built by a probable male-male pair was normally constructed, demonstrating that males can build adequate nests. This pair even sat on the completed (empty) nest for a few days after its completion, though their sessions on the nest were short (generally <10 min) and erratic.

Clutch and brood size

Final clutch size was recorded for 26 nests. Clutches consisted of 1 (15%), 2 (39%), or 3 eggs (46%) (mean = 2.31 ± 0.74). During incubation we recorded loss of eggs from some nests but we never identified the mechanism. Removal of eggs by a predator, or removal of damaged eggs by parents, were both possible. Infertile eggs and eggs with dead embryos were identified, but it was not possible to quantify such losses, as parents or predators removed unhatched eggs from some nests. Ninety-one nests were visited 10–15 days after hatching: brood sizes were 1 (24.2%), 2 (56%) and 3 (19.8%) eggs. Mean brood size was 1.96 ± 0.66 .

Egg appearance and size

Eggs were ovoid with a pinkish-grey background

of variable intensity. The eggs were variably and irregularly speckled with brown to purplish-brown streaks and spots, the greatest density of markings being at the wider end. In a clutch of 3 eggs, 1 egg was smaller and pale blue and was found to be infertile; 2 similar eggs laid at Mount Bruce National Wildlife Reserve were also infertile (P. Morton, pers. comm.). Egg length ranged from 33 to 43.75 mm (mean = 38.55 ± 2.65 , $n = 42$) and width from 22.65 to 28.35 (mean = 26.04 ± 1.20 , $n = 46$). Egg weight (± 1 g) was recorded for 4 eggs; 3 of these were 15 g and 1 was 16 g. One egg is thus *c.* 7% of mean female weight (210 \pm 12.3 g, $n = 32$).

Incubation period

One nest was checked daily, during the mid-afternoon, from when building was complete; we recorded the lay and hatch dates for the 3 eggs. The eggs were laid 1 day apart and hatched a day apart in the same order as they were laid, the first 2 eggs hatching at 17-18 days and the 3rd egg after 18-19 days of incubation. During the laying period, the female incubated irregularly, spending long periods (>1 h) off the nest. She settled into a regular incubation pattern only after laying the final egg. At 3 other nests we have incubation periods bracketed at 13-19, 15-21, and 18-20 days. Two clutches that did not hatch were incubated for 18-25 and 15-21 days before the females abandoned their nests.

Nestling period

In the only nest for which we knew both hatch and fledging date, the single nestling remained in the nest for 34 days before fledging. For 3 nests the total nesting period was 51-57 days. For another 3 nests the nesting period was at least 60 days. Thus, based on an 18-day incubation period, chicks remained in nests from 34 days to >42 days before fledging. During the last week at the nest, nestlings were often very mobile, spending much time out of the nest in surrounding vegetation and only returning to the nest when being fed or roosting.

Nestlings

At 1-day-old 3 nestlings weighed 15-16 g. They were bald and their eyes were closed. Chicks gained weight almost linearly, at *c.* 10 g day⁻¹, over the first 10 days (Fig. 1). Therefore, a useful field approximation for age of a healthy chick during its first 2 weeks is 10% of its weight. Chicks from 2- or 3- egg clutches hatched *c.* 1 day apart at the 3 nests where this was known. At 1 nest, all 3 nestlings were weighed regularly. The last-hatched nestling never gained weight and died after 3 days; the other 2 developed in parallel, but were distinguishable by weight and stage of feather development until at least day 21. At nests

where more than 1 chick was measured, weight differences of 20-40 g were normal, probably reflecting the order of hatching. Differences of > 40 g between nestlings were often associated with signs of poor condition, such as lack of vigour and dry skin, in 1 member of the brood. At 4 nests where differences of >40 g were recorded between siblings, the smaller, runt, nestlings did not fledge.

Primary feathers began to emerge on day 3. By day 6, quills were emerging on the neck and tail and sparse down was just opening on the back. By day 8, downy quills on the back, neck and tail were beginning to open; primary quills were 14 mm long and tail quills were 8 mm long. By day 18, chicks were fully feathered, but had a few downy plumes remaining. The black "mask" was the last area to be feathered and was complete at about day 20. Gill (1993) described kokako down development in detail. During development, nestling wattle colour varied between bright pink and mottled pink and blue. However, by the time of fledging the wattles were evenly pink to pale pink/lilac and, at about 9 mm diameter, were considerably smaller than those of an adult. Tails of newly fledged kokako were noticeably shorter than those of adults for at least 10 days after fledging.

Parental behaviour at nests

Kokako were almost always stealthy when approaching their nest, generally entering the nest tree from below and running up toward the nest. Kokako rarely sang in the nest tree, though this was reported at a few nests. More commonly, vocalisations near the nest were restricted to quiet contact calls.

Only females incubated (Flux & Innes 2001). Females remained on the nest for periods of 6-137 min (mean = 53, $n = 21$) during the first 3 weeks of nesting (incubation and early brooding) and left the nest for absences of 2-27 min (mean = 11, $n = 48$). Females often made a "chirr" or "mew" call a short distance from the nest as they departed. Male visits were very brief (typically 5-10 s) during which they fed the female at or near the nest throughout incubation and early brooding. Males were absent from nests for 2-82 min (mean = 32, $n = 34$) over the first 3 weeks of nesting. Males visited more frequently during the 4th and 5th weeks, feeding both the female and nestlings, with a mean return time of 18 min ($n = 40$), and females spent progressively more time off the nest. When chicks were about 7 days old, females returned to the nest on average every 17 min ($n = 31$) and then brooded for very variable periods (mean = 19 ± 15 min, $n = 24$). The high standard deviation demonstrates that brooding was erratic and differed between individuals. In part, this variation was related to time of day and weather: females apparently

brooded for longer during cold or wet weather. It was rare for females to brood nestlings older than 10 days during the day, though throughout nesting females brooded nestlings overnight. Late in the nesting cycle, parents tended to forage and return to the nest together, though average return times for males (mean = 21 min, $n = 34$) were slightly less than that for females (mean = 24 min, $n = 21$).

Parents were frequently seen to remove faecal pellets from the nest, though the diligence at this task varied markedly between individuals and decreased as nesting progressed. In 1 nest, where the parents were easily identified in recorded video footage, only the female removed faeces. Nestlings usually defaecated over the edge of the nest, but nevertheless some nests were heavily soiled and quite pungent by the time of fledging.

Predation of nests

During years of intensive mammalian pest control at the study site, 33% of kokako nests failed, 19% of which were as a result of predation. Predators were identified from nest-video footage and sign left at nests. The most significant predators were ship rat (*Rattus rattus*) (10.6% of nests, $n = 123$), Australian brush-tailed possums (*Trichosurus vulpecula*) (2.4%), and unknown predators (5.7%). Rats preyed on eggs and chicks of up to at least 10 days old. Possums ate eggs and chicks at any age, and possibly also killed incubating female kokako (Innes *et al.* 1999).

During years without pest control at Mapara, 68% of nests failed. Failures were attributed to ship rats (31% of nests, $n = 75$), possums (12%), Australasian harrier (*Circus approximans*) (8%), stoat (*Mustela erminea*) (4%), and other or unknown predators (9.3%) (Fig. 2). Innes *et al.* (1999) concluded that predation of nests was the single most important factor in the decline of kokako populations.

Nest defence

The responses of nesting kokako to a human approaching their nests varied significantly between birds. Usually females departed as the observer reached the nest and did not return until the visitor departed. However, several females sat tight and had to be lifted from the nest to allow observation of eggs or chicks. On 3 occasions, females remained on the nest while chicks were removed, banded, and returned beneath them. Some females left the nest but remained quiet and within 1-2 m of the nest while the visitor was present. Others dived, flapped, and gave alarm calls around the observer.

It appeared that there is a similarly variable response to predator visits. At 2 nests we saw

females leave the nest to chase long-tailed cuckoo (*Eudynamys taitensis*) from the nest environs. These are the only predator that we saw elicit defence behaviour from incubating females. If Australasian harriers or New Zealand falcons (*Falco novaeseelandiae*) were seen or heard, kokako sought cover among thick vegetation and remained motionless, delaying visits to their nests until the raptor left the area. Through video monitoring of nests, we know that many females leave the nest as soon as they are disturbed. However, some females will attempt to defend their nests against rats, stoats, and possums, occasionally successfully, at least where the predator was a rat. During 1 nest predation by a stoat captured on film, at least 1 adult kokako persistently dived at the stoat as it removed 2 of the 3 nestlings. The parents' behaviour might have been partly successful in deterring the stoat, as 1 nestling was left in the nest. The remaining nestling died later from the injuries it sustained, though both adults survived the attack. As with human approaches, a small number of females attempted to sit tight as predators approached. One rat had to push itself under the kokako to obtain the 1st egg, while a possum actually sat on top of an incubating kokako for almost 1 min before she escaped through the rim of the nest.

DISCUSSION

In most respects the findings of this study parallel the findings of Innes & Hay (1995), who summarised reports of 33 kokako nests that had been described between 1880 and 1989. Factors such as nest height, date of laying, and clutch size are broadly similar between the 2 studies, but these factors are likely to vary regionally depending on vegetation type, climate, and edaphic influences, so are difficult to compare directly. It is worth noting that over the past 10 years the kokako breeding season has always begun 2-4 weeks earlier in Northland and Auckland than at Mapara (N. Miller, S. Taylor pers. comm). The large sample size and our ability to monitor kokako throughout the breeding cycle without interference from predators has allowed us to add considerably to the detail presented in the earlier published accounts summarised by Innes & Hay (1995).

Perhaps the most significant new information involves reproductive output. Until 1995, kokako were thought to produce only a single clutch year⁻¹ and to invest heavily in the maintenance of fledged young (Innes & Hay 1995). However, we now know that this is only the case in "bad" breeding years (which we believe are years of low fruit availability). In such years, kokako did fledge only 1

clutch and the resulting fledglings were fed by the parents within the natal territory for at least 1-3 months, occasionally longer. When conditions were favourable, however, kokako fledged 2-3 successful clutches, females occasionally laying the next clutch before fledging her previous nest. When pairs re-nested, all fledglings from the previous nest were either ignored or actively driven from the territory. Fledglings from the last nest of a season were given the same level of parental care afforded to nestlings of single clutches. When parents re-nested, fledglings of 1st clutches were rarely sighted within natal territories more than a fortnight after fledging. Large numbers of 1st-clutch fledglings survived to breed, but there were too many confounding variables for us to assess whether their rate of survival differed from that of chicks that received post-fledging parental care.

Multiple nesting attempts have 2 important consequences in terms of the conservation of North Island kokako. Kokako fledged up to 6 young in a season when mammalian pests were managed; thus populations can recover dramatically when pest numbers are reduced. However, this same trait increases the vulnerability of adult females to predation at the nest during unmanaged years. During unmanaged years, most nests failed as a result of rat or possum predation during the 1st 2 weeks of incubation. However, during unmanaged years when fruit availability was high, females made on average 2 (range 1-5) failed breeding attempts. Consequently, they tended successive failed nests for 2-12 weeks. Females that made the greatest breeding effort during unmanaged years were vulnerable to nest predators for almost as long as an average female during managed years (*c.* 14 weeks nesting for 2 successful broods). No females were reported as being preyed on while nesting during managed years at Mapara either in this study or by Innes & Hay (1995). However, during unmanaged years at Mapara (1997 to 2000), female annual mortality increased from 0.038 to 0.15 (IF, unpubl. data), with all female losses occurring during the breeding season. Of 31 banded females in 1997, 12 were lost during the 3 subsequent years. Stoats preyed on all 3 nests at which the cause of female loss was known. Stoats were not trapped at Mapara after 1995, though it is likely that there was some secondary poisoning following rodent-poisoning operations (Murphy *et al.* 1999). Increased female kokako mortality may be attributable to a possible increase in the number of stoats after rat and possum control ceased, or to an increased tendency for stoats to attack kokako. For example, if more stoats survived in the block and bred, their

predatory activities may become locally more intense. However, kokako managers should be aware that fluctuations in stoat numbers are likely to be influenced by environmental factors as well as rat- and possum-control operations.

The occurrence of male-male pairs adds to the difficulty faced by managers in determining the status of remnant kokako populations. Pairing, courtship, and nesting activities of male-male pairs closely resembled those of conventional pairs. However, courtship food-passes in both directions or equal nest-building contributions of nesting partners or both may indicate that both individuals are male. Observers can be sure that a female is present in an unknown pair only once the incubation of eggs has been established.

The reaction of nesting kokako to predators varied widely. Innes & Hay (1995) report a morepork (*Ninox novaeseelandiae*) being chased from the vicinity of a nest by a kokako, and we twice observed similar reactions to long-tailed cuckoo. Kokako also remained motionless and delayed visits to their nests if harriers or falcons were nearby. We agree with Innes & Hay (1995) that most nests were well concealed from above, and that green leafy twigs and ferns in the nest rim also aided the camouflage. These observations suggest a response to avian predation. The observations that kokako approaching nests often do so from the ground and that the birds and their nests often smell quite strongly may well predispose them to predation from mammals with good senses of smell. The instinctive reaction of kokako to either remain motionless or attempt to drive away predators may affect adult survival when the birds are faced with an introduced mammal other than a rat. Innes & Hay (1995) suggest that survival of kokako on the mainland may depend on their ability to learn to recognise and avoid mammalian predators. Maloney & McLean (1990) have demonstrated that it is possible to teach captive birds to respond with alarm behaviours when presented with model predators, but it is much more difficult to imagine how such learning may occur in wild populations. Recognition of a body shape may not be particularly useful when confronted with predators that hunt, often at night, with stealth and speed. Some resistance on the part of a kokako may drive away a rat, but a 1st encounter with a similarly-sized stoat is likely to prove fatal. It is unlikely that there would be an opportunity for effective predator-avoidance responses to evolve when predation rates are sufficient to remove most females from the population. Predator management strategies are, fortunately, now in place for most kokako populations, and nearly all populations are increasing (Innes & Flux 1999; authors' unpubl. data). Such management

comes just in time to save some populations from extinction. Basse *et al.* (2003) presented models by which such management can be sustained in the long term as a series of management "pulses". This action, though essential, renders it even less likely that any learning about predators may occur, as kokako will be exposed to them only periodically. Management of pest mammals involves a long-term commitment. Our challenge is to develop sustainable management strategies.

ACKNOWLEDGEMENTS

Greg Sherley started the nesting study at Mapara and he played a major role in the early design of this study. Greg was an integral part of the field-team, along with Suzanne Clegg, during the mirth-filled early years as we were stumbling forward, grappling with the learning of new skills. Simon Clearwater, Denise Fastier, Cathy Rufaut, and Rachel Lander played major roles in all aspects of the field-work at Mapara; all have worked several summers at Mapara providing much appreciated continuity to the study, and assisting with the initiation and training of new assistants. Louise McGowan, John Ashton, Dianne Leversha, Tania Fechney, Dave King, Lawrence Barea, Nic Rolph, Sid Marsh, Dave Wills, Andrew Ranus, Margo Peart, Karen Riddell, Sue Waugh, Kathi Foerster, Megan Hieatt, Faith Wilson, Doug Campbell, Ray Hollingsworth, and Megan Willans have all helped in the collection of field data, as have many volunteers and friends. We thank all these people for their help, good company, and for generating the experiences and stories which we still remember and recount. Philip and Ian would also like to acknowledge our partners, Rose and Merry, for their help on several field-trips, and also for putting up with our unusual work hours, long absences, and inability to stop discussing kokako issues over many years! Thanks also to Ray Scrimgeour and the Te Kuiti/Maniopototo DOC team who have managed and conducted the hard slog of the project. They have ensured that the tracks were useable, the mammalian pests were controlled at the appropriate times and that many of the practical needs of this study were provided for.

LITERATURE CITED

- Basse, B.; Flux, I.; Innes, J. 2003. Recovery and maintenance of North Island kokako (*Callaeas cinerea wilsoni*) populations through pulsed pest control. *Biological conservation* 109: 259-270.
- BirdLife International 2000. *Threatened birds of the world*. Cambridge, U.K., Lynx Edicions and BirdLife International.
- Corson, P. 1997. Changes in Mapara Wildlife Management Reserve forests 1989–1995. Unpublished report. New Zealand Department of Conservation, Hamilton, New Zealand.
- Flux, I.; Innes, J. 2001. A field technique for gender determination in North Island kokako (*Callaeas cinerea wilsoni*). *Notornis* 48: 217-223.
- Gill, B.J. 1993. Natal down and egg size of the kokako. *Records of the Auckland Institute and Museum* 30: 87-91.
- Hitchmough, R. 2002. New Zealand threat classification system lists. *Threatened species occasional publication* 23. Wellington, New Zealand Department of Conservation, .
- Innes, J.; Flux, I. 1999. North Island kokako recovery plan. *Department of Conservation threatened species recovery plan 30*. Wellington, New Zealand Department of Conservation, NZ.
- Innes, J.; Hay, R. 1995. The nesting of North Island kokako (*Callaeas cinerea wilsoni*) – review of accounts from 1880 to 1989. *Notornis* 42: 79-93.
- Innes, J.; Hay, R.; Flux, I.; Bradfield, P.; Speed, H.; Jansen, P. 1999. Successful recovery of North Island kokako (*Callaeas cinerea wilsoni*) populations, by adaptive management. *Biological conservation* 87: 201-214.
- Lavers, R. 1978. Distribution of the North Island kokako (*Callaeas cinerea wilsoni*): a review. *Notornis* 25: 165-185.
- Leathwick J.; Hay, J.; Fitzgerald, A. 1983. The influence of browsing by introduced mammals on the decline of North Island kokako. *New Zealand journal of ecology* 6: 55-70.
- Lovegrove, T.G. 1980. The saddleback pair bond. Unpubl. MSc thesis (Zoology). University of Auckland, Auckland, New Zealand.
- Maloney, R.; McLean, I. 1990. Enemy recognition in South Island robins. *Acta XX Congressus Internationalis Ornithologici (supplement)*: 472-473.
- Murphy, E.; Robins, L.; Young, J.; Dowding, J. 1999. Secondary poisoning of stoats after an aerial 1080 poison operation in Pureora Forest, New Zealand. *New Zealand journal of ecology* 23: 175-182.