Breeding biology of the New Zealand kaka (*Nestor meridionalis*) (Psittacidae, Nestorinae)

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Abstract The kaka (*Nestor meridionalis*) is an endemic parrot of New Zealand, and is nationally endangered. Conservation of the species is primarily dependent on intensive control of introduced mammalian nest predators, particularly stoats (*Mustela erminea*) and brushtail possums (*Trichosurus vulpecula*). Breeding was studied in 4 sites: Waipapa (1996-2002) and Whirinaki (1998-2002) in the North Island, and Rotoiti (1997-2002) and Eglinton (1998-2002) in the South Island. In total, 145 nests were found. The proportion of radio-tagged females that bred at a site in a given year varied from 0-100%, with most breeding occurring in years of mast-fruiting or seeding by key food tree species. Kaka nested mainly in trunk cavities of live canopy or emergent trees. Egg-laying occurred from Oct to Mar, but differed between years within sites by up to a month, and was usually 2 months later at the most southern site (Eglinton) than elsewhere. Mean egg length was 41.5 mm, mean maximum breadth was 31.5 mm, and fresh egg mass was 22.6 g or 5.65% of female body weight. Clutches consisted of 1-8 eggs, most being of 3, 4 or 5 eggs (mode = 5), and mean clutch size did not differ significantly between the sites. The female alone carried out incubation, with her mate feeding her 8-12 times a day. Overall, hatching success varied from 39-66% between sites, but it also varied between breeding seasons at each site, in part due to the level of control of introduced predatory mammals. Kaka nestlings were covered in white down at hatching, and left

the nest when *c.* 70 days old. Even when 11-20 days old, they were left unattended at night for 20-70% of time and by day for 50-85% of time. Twice females were filmed aggressively attempting to evict stoats that had killed broods in their nest cavities. Breeding productivity (proportion of eggs that produced fledglings) in the 4 study sites varied from 19% at Whirinaki (no control of predatory mammals) to 53% at Eglinton (intense control of predatory mammals). The implications of the breeding biology of the kaka are discussed in relation to conservation management of the species.

INTRODUCTION

The kaka (*Nestor meridionalis*) is a large (350 - 690 g; T.C. Greene *unpubl. data*) and sexually dimorphic (Moorhouse *et al.* 1999), endemic New Zealand parrot. Based on anatomical, morphological and ethological characteristics, Smith (1975) included kaka and kea (*Nestor notabilis*) in the tribe Nestorini, and suggested that they along with the Strigopini (kakapo, *Strigops habroptilus*), Cacatuini (cockatoos, mainly from Australia) and Platycerini ('broad-tailed' parrots, mainly from Australia) were closely allied having derived from a common ancestor. Using DNA techniques, De Kloet & de Kloet (2005) recognised a similar phylogeny, with *Nestor* and *Strigops* genera comprising an ancient New Zealand lineage that diverged from all other parrots with the break-up of Gondwana *c.* 85 million years ago. The next group to diverge were the Australian Cacatuini at *c.* 55 million years ago. Two subspecies of kaka are currently recognised, *N. m. meridionalis* in the South Is, and *N. m. septentrionalis* in the North Is (Turbott 1990, Higgins 1999) despite there being no genetic, or consistent morphological differences in the skeletal structure (Holdaway *et al.* 2001, Sainsbury *et al.* 2006).

Formerly, kaka were widespread and common in native forests throughout mainland New Zealand and on some offshore islands. They were so abundant in pre-European times that when flocking to seasonal foods, such as the nectar of flowering northern rata (*Metrosideros robusta*), they were killed in their thousands (Buller 1877, Fulton 1908). Today North Is kaka are either absent or rare in most regions, with population strongholds restricted to the larger remnant tracts of podocarp/hardwood forest (especially Pureora and Whirinaki) in the central North Is (Bull *et al.* 1985), and some predator-free islands, such as Great Barrier, Little Barrier and Kapiti Is. The South Is kaka is widespread, although in declining numbers, through the larger tracts of beech *Nothofagus* spp. and podocarp/hardwood forest of the South Is. It also occurs on Stewart and Codfish Is. This dramatic decline in range (Robertson *et al.* 2007) has been attributed mainly to historical clearance of native forest (Heather

& Robertson 2005) and the continuing impacts of various introduced mammalian competitors and predators (Wilson *et al.* 1998, Veltman 2000, Moorhouse *et al.* 2003, Greene *et al.* 2004). Even in areas of the North and South Is where kaka are still relatively common, they often exhibit a strong sex ratio bias towards male birds (Greene & Fraser 1998, Greene *et al.* 2004). While intensive and sustained pest control has dramatically improved the density and sex ratio of kaka populations in a few areas where mammalian pest control has been carried out, throughout the rest of its range the kaka is declining (Greene *et al.* 2004). As a result, both subspecies are classified as 'nationally endangered' (Hitchmough *et al.* 2007), with an estimated total population of 1000-5000 mature individuals. In the last 100 years there has been a decline of ≥ 60% in the total kaka population and habitat area due to existing threats (Molloy *et al.* 2002). Kaka are also listed by the International Union for Conservation of Nature and Natural Resources (IUCN) as 'endangered' because its population has declined by ≥ 50% over the last 3 generations, and a population decline of the same magnitude is predicted to continue over the next 3 generations (IUCN 2006).

Prior to 1990 information available on kaka breeding biology was limited (Higgins 1999) and was largely based on nests found by chance at a variety of locations that were monitored infrequently (Oliver 1955, Jackson 1963, Forshaw 1989, Heather & Robertson 2005). Since that time, however, more intensive studies have been carried out. Moorhouse (1991) reported clutch size, hatching success and fledging success for 35 nests found on Kapiti Is during the 1988 and 1989 breeding seasons. Wilson *et al.* (1998) reported the productivity from 20 nests in Big Bush, near Nelson, during 11 breeding seasons (1985/86 to 1995/96). To identify the factors responsible for the kaka's continued national decline and to develop management techniques which could reverse the trend, a research plan was developed for 1996-2000 (Moorhouse & Greene 1998). It was suspected that predation of eggs, nestlings and adult female kaka in nests by introduced mammalian predators, particularly
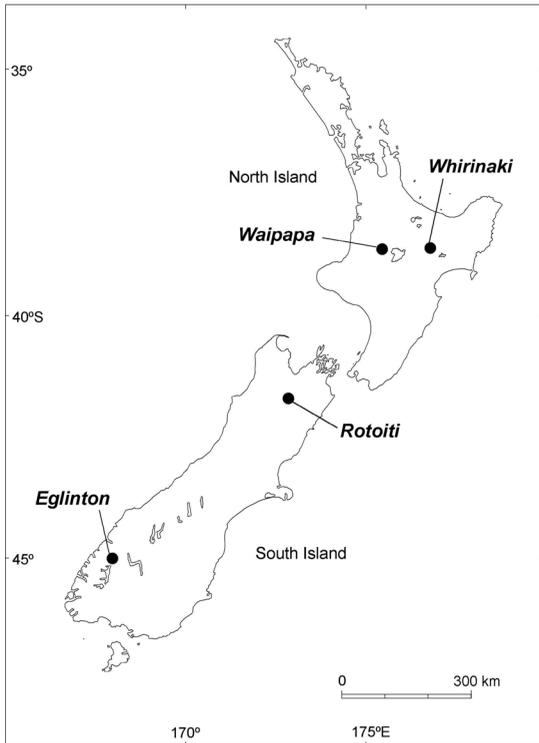
Fig. 1. Map of New Zealand showing locations of kaka (*Nestor meridionalis*) study sites.

stoats (*Mustela erminea*) and brushtail possums (*Trichosurus vulpecula*), was largely responsible for the continuing population decline (Wilson *et al.* 1998). As a result, kaka breeding was monitored in 4 study sites, 2 in the North Is and 2 in the South Is, to assess the impact of introduced mammalian predators on adult kaka survival and breeding success (Moorhouse *et al.* 2003). In the course of this research, 145 nests were found. This paper summarises information derived from these nests, and suggests changes to the current management of kaka populations.

METHODS
Study sites
Data on kaka breeding biology were obtained from 4 sites (Fig. 1), 2 in the North Is and 2 in the South Is. The Waipapa Ecological Area (WEA) (4013 ha) of Pureora Forest Park, is one of the finest areas of dense podocarp forest remaining in the North Is, and has significant wildlife values. The tall forest cover consists of emergent podocarps (Podocarpaceae), particularly rimu (*Dacrydium cupressinum*), kahikatea (*Dacrycarpus dacrydioides*) and matai (*Prumnopitys taxifolia*), over a mainly tawa (*Beilschmiedia tawa*) canopy (Leathwick 1987). Kaka

research was conducted within an 1100 ha area of the WEA, where possum and ship rat (*Rattus rattus*) populations were controlled to low densities using poison baits (for details see Moorhouse *et al.* 2003). Some control of mustelid populations probably occurred through secondary poisoning (Murphy *et al.* 1998).

The 2nd North Is study site was in Whirinaki Forest Park (Fig. 1). The forest consists mainly of tall stands of podocarp and hardwood species, such as emergent rimu, with scattered kahikatea, matai and miro (*Prumnopitys ferruginea*) over a mainly tawa canopy. On some exposed ridges and slopes, the podocarp-hardwood forest was replaced by a mixture of rimu, miro, red beech (*Nothofagus fusca*) and Hall's totara (*Podocarpus hallii*) (Morton *et al.* 1984). Kaka research was carried out in an area of about 5000 ha. There was no systematic predator control at Whirinaki during our research, although recreational possum hunting did occur.

Like the study site in the WEA, the Rotoiti Nature Recovery Project study site (RNRP) (Fig. 1) was the site of an on-going ecosystem restoration project designed to benefit kaka as well as other species (Butler 1998). Situated on the western side of the St Arnaud Range, and bordered partly by farmland and Lake Rotoiti, the site encompassed 825 ha and was covered in beech forest. The lower slopes are dominated by red beech and silver beech (*N. menziesii*), with mountain beech (*N. solandri* var *cliffortoides*) and kanuka (*Kunzea ericoides*) at sites with poor drainage, and upper slopes by silver beech and mountain beech grading to pure mountain beech at the tree line (Butler 1998). Possum, ship rat and stoat populations were controlled to low densities using toxic baits and traps (Moorhouse *et al.* 2003). Some control of mustelid populations probably occurred through secondary poisoning (Murphy *et al.* 1998).

The 2nd South Is study site was in the Eglinton Valley (Fig. 1), in Fiordland National Park, and was the site of a stoat and possum control programme to protect a remnant population of mohua (*Mohoua ochrocephala*), an endemic passerine. It is a valley shaped by past glaciation, having steep sides and a flat floor 0.5-1.0 km wide. There are open, grassy areas near the Eglinton River, but otherwise the valley is forested up to 1000 m a.s.l. Forest composition varies, ranging from pure stands of silver beech along the forest margin to stands of red beech further into the forest. Mountain beech occasionally occurs in the canopy at low altitudes, and becomes more common with increased altitude (O'Donnell 1996). The 13,000 ha study site contained a 40-km long stoat trap-line along the length of the valley, which has been in continuous operation since from Jan 1998. Possums were controlled with 1080™ baits placed in bait stations along the valley

since 1994 (Moorhouse *et al.* 2003).

Masting tree species formed an important component of the canopy in all of our study sites. Masting is a feature of some New Zealand trees and tussocks (*Chionochloa* spp.) whereby they produce a super-abundance of fruit or seed at irregular (1-7 years) intervals, but little or no seed or fruit in the intervening years (Norton & Kelly 1988, Kelly 1994). Masting species in the 2 North Is study sites were the podocarps rimu, matai, and kahikatea, while in the 2 South Is study sites they were the *Nothofagus* species, mountain beech, silver beech and red beech. The seeds and fruit of masting species form a major component of the diet of breeding kaka (Wilson *et al.* 1998).

Capture, marking and monitoring of adult kaka

Adult female kaka were captured and radio-tagged so that their nests could be located. They were caught in canopy-height mist-net rigs (Dilks *et al.* 1995). Kaka were attracted into mist-nets using play-back of calls of the local kaka dialect. In addition, some females were caught in mist-nets erected a few metres from their nests. As adult kaka are sexually dimorphic, particularly in culmen length (Moorhouse *et al.* 1999), the gender of each bird was readily apparent.

The tarsi of kaka are quite short (*c.* 35 mm) and so to enable individual identification using colour bands, 2 6-mm high powder-coat painted metal bands were fitted to 1 leg, and a 12 mm high uniquely numbered metal band to the other (left leg for females and right leg for males). In addition, on some nestlings, the 12 mm metal band had also been painted to indicate the year each was banded. Transmitters were fitted to all captured female kaka and some males. Two-stage Sirtrack® transmitters were attached to the birds using a back-mounted harness design (Karl & Clout 1987). The transmitter and harness together weighed 24-29 g. To extend battery life, the pulse rate was set to 20 pulses per minute, and the transmitter incorporated a duty cycle of 12 hours on/12 hours off, giving a potential field-life of 64 months.

We attempted to locate each radio-tagged kaka once a week to monitor survival and breeding. This involved approaching them on foot using a radio-receiver and a hand-held yagi antenna until the individual was sighted, or was known to be directly above but unsighted in a tree. Once located, most kaka nests (cavities in trunks or large branches) were checked twice a week to determine whether they were occupied and active. Occupancy checks involved determining whether the female's transmitter signal indicated that she was in the cavity, or by observing her entry or exit from the cavity (only females enter nest cavities to care for eggs and nestlings). Less frequent physical

inspection of nest contents were timed to provide information on clutch size, hatching success, chick survival and numbers of fledglings produced where possible. Some nests were monitored day and night using time-lapse infra-red (IR) video equipment (Brown *et al.* 1998), and video footage was viewed on a VHS video recorder to note timing and duration of nest activity.

In most cases, the dates of egg-laying for clutches were not known accurately. The month that each clutch was laid was estimated from behaviour of the female (once incubating she spends most of her time in the nest cavity, coming out for a few minutes every 1 – 2 hours to be fed by her mate), or from the age of chicks (Moorhouse & Greene 1995).

Statistical analyses

The computer package SigmaStat® was used for Student's *t*-tests, one way ANOVA, and Mann-Whitney U tests to compare various data sets. Where either the *t*-test or 1-way analysis of variance was inappropriate because the data were not normally distributed, the Mann-Whitney U test was used to test for significance. All data were expressed as means ± sd.

To test whether site had an effect on nesting success (hatching success, nestling-rearing success, breeding (egg to fledging) success), data were analysed using logistic generalised linear mixed models with one fixed effect (site) and two nested random effects (breeding season and nests). The analyses were carried out using the function glmer in the package lme4 in the statistical package R (R Development Core Team 2008). The same function and statistical package were used to test the effect of treatment (pest control) on nesting success, with one fixed effect (treatment) and three nested random effects (sites, breeding seasons and nests).

RESULTS
Breeding effort

In the WEA, most tagged females (73-94%) attempted to breed only when there was mast fruiting of podocarps (rimu, matai and kahikatea in 1997/98, kahikatea in 1998/99, rimu, kahikatea and matai in (2001/02)) (Table 1). Similarly, at Whirinaki, when there was mast fruiting of podocarps (kahikatea in 1998/99, rimu in 2001/02) most tagged females bred (69-89%). In the non-masting breeding season of 2000/01 at both the WEA and Whirinaki, a small proportion (5-29%) of females bred. Overall, at the 2 North Is podocarp forest sites, a significantly higher proportion of females bred in masting years than non-masting years (x^2 = 85.2 with Yate's correction, d.f. = 1, $P < 0.0001$). At Rotoiti and the Eglinton Valley, where kaka inhabited beech forests, all females bred when mast seeding by red beech and

Table 1. Proportion of radio-tagged female kaka (*Nestor meridionalis*) breeding and the occurrence of masting breeding season[1] at each of 4 study sites, New Zealand.

Breeding season	Waipapa			Whirinaki			Rotoiti			Eglinton		
	N[1]	% breeding[2]	Masting[3]	N	% breeding	Masting	N	% breeding	Masting	N	% breeding	Masting
1996/97	2	100	unknown	-	-		-	-		-	-	-
1997/98	11	73	yes	-	-		4	100	Yes	-	-	-
1998/99	18	94	yes	9	89	yes	5	100	Yes	10	100	yes
1999/00	21	0	no	14	0	no	5	100	Yes	13	100	yes
2000/01	20	5	no	17	29	no	5	0	No	13	0	no
2001/02	20	85	yes	16	69	yes	15	100	Yes	7	0	no

[1]Number of radio-tagged females present per breeding season
[2]Proportion of radio-tagged females that bred
[3]Whether mast fruiting (super-abundant fruit or seed production) by podocarp (Podocarpaceae) or beech (*Nothofagus* spp.) trees occurred (authors unpubl. obs)

silver beech occurred (Table 1).

Females that failed at their first breeding attempts at Waipapa and Whirinaki occasionally produced a replacement clutch. At Whirinaki in the mast-fruiting seasons of 1998/99 and 2001/02, 50% of 4 unsuccessful females re-nested and 67% of 6 females re-nested respectively, but none of 4 females re-nested in the 2000/01 breeding season when mast fruiting did not occur. One female at Whirinaki produced 2 replacement nests in the 2001/02 season, but no female that successfully reared young to fledging in any season at Whirinaki attempted to raise a 2nd brood.

In the WEA, during the 1997/98 and 1998/99 mast-fruiting seasons, neither of the 2 unsuccessful females in either season re-nested. In the 2001/02 mast-fruiting season, 4 females re-nested once (1 after a failed nesting, and 3 after successful nestings), 2 re-nested twice (1 reared a brood followed by 2 failed attempts, and the other reared a brood, failed at her 2nd nesting, and was successful at her 3rd nesting), and 1 female re-nested thrice (reared 2 broods between which she had 2 failed nestings).

At Rotoiti in the 1999/00 breeding season, when there was an unusually abundant crop of beech seeds (Fig. 2), 2 females fledged 2 broods each. Female L-33560 bred with male L-33558 initially and they reared 4 fledglings. Twenty-two days after the last of these nestlings left the nest, L-33560 was seen copulating with an unbanded male, while her previous mate was still caring for the fledglings. Three fledglings resulted from L-33560's 2nd nesting, 7 in total for the season. Female L-33569 reared 3 fledglings from her 1st nesting. Ten days after the last of those nestlings fledged, she was found inside a new cavity, probably preparing it prior to egg-laying. Two fledglings were reared from this 2nd breeding attempt of L-33569, 5 in total for the season. Although 2 banded males were both seen at L-33569's nest trees, only 1 (L-33553) seemed to feed her during incubation at each nest. Similarly, in the 2001/02 season, female L-30485 fledged 1 brood of 2 chicks on 8 Feb 2002, and started laying in a new nest about 5 Mar 2002 but was killed by a stoat.

At Eglinton in the 1998/99 breeding season, 8 females were monitored and neither of 2 females that had failed breeding attempts re-nested. However, 1 female that successfully fledged a brood laid a 2nd clutch and successfully reared fledglings from it. In 1999/00, of 2 females that had failed breeding attempts, 1 laid a replacement clutch, and none of the successful females (n = 9) laid 2nd clutches.

Nest cavity characteristics

Most nest cavities at both Waipapa and Whirinaki were in matai or rimu trees, with the others mainly in totara, miro, hinau (*Elaeocarpus dentatus*) and

Fig. 2. Viable beech seed production (log^{10} of seeds per m^2) by red beech (*Nothofagus fusca*), silver beech (*N. menziesii*) and mountain beech (*N. solandri* var. *cliffortioides*) in the Rotoiti Nature Recovery Project study site, Nelson Lakes National Park, during the summers of 1997/98 to 2001/02. Seeds were collected in 20 0.28 m^2 funnel-shaped seed traps, sorted to species, and tested for viability. Results provided by M. Maitland, Nelson Lakes Area Office, Department of Conservion.
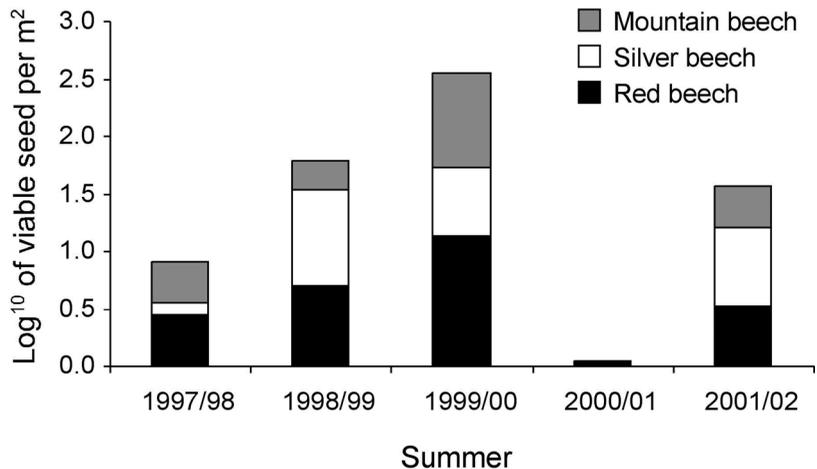
dead trees of unknown species (Table 2). Most nest trees at Waipapa, Whirinaki, Rotoiti and Eglinton were living, and more than 90% of nests were in trunk cavities (Table 2). Mean nest tree height was significantly higher at Whirinaki than at Waipapa (*t* test, *t* = 6.40, df = 87, *P* < 0.001). However, all the other factors relating to kaka nest cavities (Table 2), except for nest chamber diameter (*t* test, *t* = 5.08, df = 72, *P* < 0.001), were not significantly different. While the mean nest entrance dimensions (height and width) at Waipapa and Whirinaki were similar, they varied considerably (Table 2). A few were just large enough for a kaka to squeeze through, while others were about 10 times wider. Similarly, cavity depth was also quite variable, from being level with the entrance to up to 6 m below in 1 case.

Comparing the cavity characteristics of kaka nests at the Rotoiti and Eglinton study sites, both beech-dominated forests, mean nest tree height (*t*-test, *t* = 3.88, df = 69, *P* < 0.001), mean nest entrance height (*t*-test, *t* = 2.92, df = 65, *P* < 0.01), and nest tree mean diameter at breast height (DBH) (*t*-test, *t* = 3.01, df = 55, *P* < 0.01) were all significantly greater at Eglinton (Table 2). While the 2 mean cavity entrance dimensions were not significantly different, mean cavity depth of the Rotoiti nests was significantly greater than that of the Eglinton nests (*t*-test, *t* = 2.68, df = 60, *P* < 0.05).

Comparing nest tree characteristics (condition, height and DBH) from all 4 sites, it was evident that kaka nested mainly in the trunks of live canopy and emergent trees with a minimum trunk diameter at breast height of *c*. 600 mm. While the dimensions of the entrance (width) and the cavity (depth, diameter) were quite variable, the minimum dimensions were about 50 and 300 mm respectively.

Re-use of nest sites

Of 10 sites at Whirinaki used in the 1998/99 breeding season, none was re-used in the 2000/01 or 2001/02 seasons. Similarly, of 5 sites used in 2000/01, only 1 was re-used in the 2001/02 season. Of 4 females that bred in 2 consecutive breeding seasons, 1 used the same site both seasons even though she had been unsuccessful initially. Two of 6 females that bred twice in a season re-used the same sites that they had used unsuccessfully initially, even though their nesting failures were due to clutches being preyed upon. At Eglinton, of 13 nest cavities used in the 1989/99 breeding season, just 2 (15%) were re-used in the 1999/00 breeding season, both by females that had used them during the previous season, the other 11 females occupied new cavities each season. At Waipapa, none of 3 sites used in the 1996/97 season were re-used in the subsequent 3 breeding seasons. Similarly, of 9 nests used in the 1997/98 breeding season, just 2 (22%) were re-used the following breeding season. In contrast, of 20 nests used in the 1998/99 breeding season at Waipapa, 12 (60%) were re-used in the 2001/02 season when most females bred. No comparative information was available from the Rotoiti study site.

Nest preparation

Kaka rely on natural cavities for nest sites. The main modification that a female made to a cavity prior to egg-laying was to its base. The nest was developed from dry, rotten wood within the cavity, the female energetically grubbed into the litter to a depth of 50–100 mm, and supplemented this material with live or dead wood chewed from the cavity walls. Any large woody pieces were broken up by biting and chewing to form a well-aerated dry tilth on which she developed a nest-bowl about 300 mm in diameter and 20 mm deep.

Table 2. Kaka (*Nestor meridionalis*) nest cavity characteristics at each of 4 study sites, New Zealand.

	Waipapa	Whirinaki	Rotoiti	Eglinton
Tree species				
Matai	39 (61.9)	21 (61.8)	-	-
Rimu	8 (12.7)	7 (20.6)	-	-
Totara	5 (7.9)	2 (5.9)	-	-
Miro	2 (3.2)	2 (5.9)	-	-
Hinau	3 (4.8)	-	-	-
Kahikatea	1 (1.6)	-	-	-
Red beech	-	1 (2.9)	42 (95.4)	25 (92.6)
Silver beech	-	-	2 (4.6)	-
Unknown	5 (7.9)	1 (2.9)	-	2 (7.4)
All tree species combined	63 (100)	34 (100)	44 (100)	27 (100)
Tree condition score[a] (%)	4 (37.5%)	4 (52.9%)	3 (45.4%)	4 (96.4%)
n	56	34	44	27
Cavity type score[b] (%)	1 (91.5%)	1 (97.0%)	1 (100%)	1 (100%)
n	59	33	45	27
Mean nest tree height (m)	28.8	39.4	22.1	27.0
s.d., range, *n*	8.0, 9-50, 57	7.2, 21-54, 32	3.9, 14-30, 44	5.8, 20-40, 27
Mean nest entrance height (m)	11.7	13.4	8.3	12.5
s.d., range, *n*	5.0, 3.3-24.7, 56	5.0, 4.5-25.5, 34	3.5, 3.7-18.7, 47	5.7, 3.3-21.0, 18
Mean DBH[c] of nest tree (cm)	132.2	125.3	95.1	127.9
s.d., range, *n*	48.9, 61-375, 53	41.5, 60-266, 34	15.8, 54-133, 44	38.4, 62-195, 13
Mean entrance height (mm)	590	512	456	448
s.d., range, *n*	558.1, 70-2600, 54	605.5, 120-3000, 39	38.0, 70-1550, 51	327.2, 105-1440, 16
Mean entrance width (mm)	115.2	126.0	86.6	90.0
s.d., range, *n*	98.0, 52-650, 55	64.0, 40-360, 39	2.2, 55-790, 51	45.2, 60-250, 16
Mean cavity depth (mm)	837.9	722.7	813.8	519.4
s.d., range, *n*	1005.2, 0-6300, 56	632.7, 0-2100, 33	60.4, 0-2300, 46	437.7, 100-1630, 16
Mean chamber diameter (mm)	473.2	912.2	-	573.1
s.d., range, *n*	176, 230-1240, 46	436, 400-2050, 28	-	128, 320-760, 16

[a] Tree condition: 1 – dead, 2 – some dieback, 3 – odd dead branch, 4 – without dead branches
[b] Cavity type: 1 – trunk, 2 – spout, 3 – branch, 4 – other
[c] DBH: diameter at breast height (approx. 1 m)

Table 3. Number of clutches laid per month by kaka (*Nestor meridionalis*) in 4 study sites, New Zealand. Missing breeding seasons are those when no breeding occurred (see Table 1).

Breeding season	Oct	Nov	Dec	Jan	Feb	Mar	Total
Waipapa							
1996/97	-	-	2	1	-	-	3
1997/98	-	-	4	2	3	-	9
1998/99	-	13	5	-	1	-	19
2000/01	-	-	1	-	-	-	1
2001/02	-	12	9	2	1	3	27
Total	-	25	21	5	5	3	59
Whirinaki							
1998/99	-	3	1	3	2	-	9
2000/01	-	1	4	-	-	-	5
2001/02	1	3	7	1	1	3	16
Total	1	7	12	4	3	3	30
Rotoiti							
1997/98	1	3	-	-	-	-	4
1998/99	-	2	3	-	-	-	5
1999/00	-	1	2	1	1	3	8
2001/02	1	9	1	1	2	2	16
Total	2	15	6	2	3	5	33
Eglinton							
1998/99	-	-	2	6	1	1	10
1999/00	-	-	-	2	10	1	13
Total	-	-	2	8	11	2	23

Prior to egg-laying, a male at Rotoiti was observed over 2 days to enter his mate's nest cavity 7 times while she was inside. Each time the male was in the cavity for 1-2 minutes. This was the only time at any of the study sites that a male kaka was seen going into an occupied cavity, including during the incubation and nestling-rearing periods.

Copulation

Kaka were seen copulating on several occasions in each of the study sites, and this took place on sturdy branches under thick canopy foliage within 100 m of nest sites. Prior to mounting, the male walked up to the female several times, gently pushing her with his beak and forehead or a foot, and then moved away. If she stood her ground and assumed her copulatory posture (head lowered, back flattened and wings slightly flexed), the male mounted and, with flapping wings to retain his balance, assumed his copulatory position, cloaca to cloaca. The male maintained a rhythmic and slow but vigorous wing-flapping, along with a yawing movement of his body, for up to 15 minutes. During copulation the female had her head and tail slightly raised, and the male 'knocked' his beak against hers during each yawing movement. Thus males remained mounted throughout copulation, but probably made cloacal contact only briefly during each yawing movement. Females often made a soft, high-pitched squeaking noise throughout copulation. After dismounting, the male remained perched and still by the female for several minutes before flying off. We have no data from which to determine mean duration or frequency of copulation. No kaka were seen approaching mating pairs.

Eggs

Egg-laying was recorded by time-lapse video equipment at Waipapa and Whirinaki on 8 occasions. The moment of egg-laying was preceded by pelvic movements, hunching of the back, and fanning and depression of the tail. Soon after egg-laying, the female circled around, and using her beak, moved the new egg under her body with the rest of the clutch.

The complete laying sequence was video-taped in a single nest of a 4-egg clutch at Waipapa in Nov and Dec 1998. The interval between the laying of the first (19:09 h on 21st) and second eggs (14:10 h on 25th) was 3.8 days; the 2nd and 3rd eggs (19:20 h on 28th) was 3.2 days; and the 3rd and 4th eggs (12:12 h on 2nd) was 3.7 days. On 2 occasions at Whirinaki, video cameras were inserted into nests during egg-laying. In Nov 2001, the laying of eggs 5 (19:14 h on 22nd) and 6 (17:58 h on 25th) of a 6-egg clutch were evident, giving a laying interval of 2.9 days. Similarly, in Dec 2001, the laying of eggs 3 (12:12 h on 4th) and 4 (08:30 h on 8th) of a 4-egg clutch occurred at an interval of 3.8 days. The mean egg-laying interval of these 5 instances was 3.5 ± 0.41 days (range = 2.9-3.8).

Kaka eggs were white, slightly oval, and their surface tended to be slightly rough. Twelve eggs were retrieved from 7 nests at Whirinaki following abandonment or part clutches that remained unhatched for more than a week after the rest had hatched. Mean length was 41.5 mm ± 1.25 (range = 40.2-44.4), and maximum breadth 31.5 mm ± 0.83 (range = 30.1-33.0).

Fresh egg mass of kaka eggs was estimated following Hoyt (1979): mass (g) = (length x breadth^2) x K. K = 5.449 x 10^{-4} was used, being that determined for the kakapo (Eason *et al*. 2006), the closest relative of the kaka for which the constant

Table 4. Frequency of clutch sizes of kaka (*Nestor meridionalis*) in 4 study sites, New Zealand.

Breeding season	Clutch size								Total	Mode	Mean	SD
	1	2	3	4	5	6	7	8				
Waipapa												
1997/98	-	-	3	2	-	-	-	-	5	3	3.4	0.5
1998/99	-	-	3	1	2	1	-	-	7	3	4.1	1.2
2000/01	-	-	3	2	-	-	-	-	5	3	3.4	0.5
2001/02	1	3	2	3	7	-	1	-	17	5	3.9	1.6
Total	1	3	11	8	9	1	1	-	34	3	3.8	1.3
Whirinaki												
1998/99	-	-	-	1	-	-	-	-	1	-	-	-
2000/01	-	-	1	-	2	-	-	-	3	5	4.3	1.2
2001/02	-	1	2	2	5	1	-	2	13	5	4.8	1.8
Total	-	1	3	3	7	1	-	2	17	5	4.7	1.6
North Is total	1	4	14	11	16	2	1	2	51	5	4.1	1.4
Rotoiti												
1999/00	-	-	-	-	2	-	-	1	3	5	6.0	1.7
2001/02	-	1	-	1	3	-	-	-	5	5	4.2	1.3
Total	-	1	-	1	5	-	-	1	8	5	4.9	1.6
Eglinton												
1998/99	-	-	3	5	2	1	-	-	11	4	4.1	0.9
1999/00	-	-	-	7	6	-	-	-	13	4	4.5	0.5
Total	-	-	3	12	8	1	-	-	24	4	4.3	0.7
South Is total	-	1	3	13	13	1	-	1	32	4/5	4.4	1.1
TOTAL	1	5	17	24	29	3	1	3	83	5	4.2	1.3

had been determined. Thus, an average sized kaka egg was estimated to weigh about 22.4 g, or 5.61% of mean female body weight at 400 g (Moorhouse *et al*. 1999).

The start of egg-laying at each study site varied by up to a month (Table 3). At Waipapa, Whirinaki and Rotoiti, breeding usually began in Oct or Nov, but was 2 months later at Eglinton. In seasons when most radio-tagged females nested at Waipapa and Whirinaki (1998/99, 2001/02) (Table 1), egg-laying occurred about a month earlier than in seasons when only a small proportion of females nested. This trend was not observed at the Rotoiti and Eglinton study sites (Table 3).

Clutch size
Most clutches consisted of 3, 4 or 5 eggs (mode = 5) (Table 4). Mean clutch sizes did not differ significantly between the 2 North Is sites (Mann-Whitney U test, $P = 0.067$), the 2 South Is sites (Mann-Whitney U test, $P = 0.169$), nor between the combined North Is and combined South Is sites (Mann-Whitney U test, $P = 0.217$).

Incubation
During incubation, only females entered nest cavities and incubated eggs. When incubating, females apparently spent most of their time asleep, with brief sessions of egg turning, preening or

Table 5. Incubation behaviour of 1 female kaka (*Nestor meridionalis*) at Waipapa during the 1998/99 breeding season, and 3 at Whirinaki during the 2001/02 breeding season from the day after the last egg was laid until the day before the first egg hatched. Female identity is band number. Figures in brackets are s.d.

Female identity	Mean number of absences			Mean time (mins) per absence			
	night[-1]	day[-1]	24 hrs[-1]	night[-1]	day[-1]	24 hrs[-1]	range
L-33585[1]	4.6 (1.60)	8.3 (3.34)	12.9 (3.21)	5.7 (9.27)	5.1 (3.10)	5.3 (5.30)	0.4 - 62
L-35239[2]	1.8 (0.98)	11.8 (3.57)	13.6 (3.75)	5.8 (4.07)	3.8 (2.58)	4.1 (2.89)	1 - 15
L-35236[3]	2.4 (1.18)	12.1 (2.57)	14.5 (2.85)	3.5 (3.92)	4.4 (2.95)	4.2 (3.14)	1 - 17
L-35228[4]	4.4 (2.22)	12.2 (2.74)	16.6 (3.25)	4.1 (2.51)	6.2 (4.61)	5.6 (4.26)	1 - 34

[1] observed incubating 3/12/98 to 18/12/98 (Waipapa, n = 16 nights / days)
[2] observed incubating 26/11/01 to 10/12/01 (Whirinaki, n = 11 nights / days)
[3] observed incubating 9/12/01 to 25/12/01 (Whirinaki, n = 17 nights / days)
[4] observed incubating 20/12/01 to 1/01/02 (Whirinaki, n = 13 nights / days)

nibbling nest material. Males occasionally landed at the entrance and looked inside. Generally, males with incubating mates approached to within about 20 m of the nest trees and called. Females invariably emerged and flew with their mates *c.* 50 m from the nest, where they were fed regurgitated food. Females invariably returned to the nest after only a brief absence (Table 5). Often more than 1 male was seen perched nearby and occasionally investigating cavity entrances when females were preparing nests or incubating, especially at sites where there was a skewed sex ratio, pest control was non-existent or had just commenced (T.C. Greene, *pers. obs.*).

Due to the difficulty of checking kaka nest contents and determining chick hatching times from time-lapse video tapes, we have little data on the duration of the incubation period (interval between the laying and hatching of the last egg; Rowley 1990). For videoed nests, the incubation period was 23.0 days for 1 nest at Waipapa during the 1998/99 season, and 20.5 days for 1 nest at Whirinaki during the 2001/02 breeding season.

Female incubation attentiveness was determined from time-lapse video footage for 1 female at Waipapa in the 1998/99 breeding season, and 3 females at Whirinaki in the 2001/02 breeding season. During a 24-hour period, females left the nest a mean of 13-17 times, 8-12 of those during daylight hours (Table 5). During Dec-Jan, females incubated, on average, for 73-109 minutes between absences from the nest. Females were absent for a mean of 4-6 minutes per absence, with a range of 1-62 minutes. Females L-33585 and L-35239 spent a greater mean time off the nest at night than during the day; the reverse was the case for the other 2 females (Table 5). For each Whirinaki female, the mean time absent

at night was significantly different from that by day: L-35239, Mann-Whitney U test, $P = 0.017$; L-35236, Mann-Whitney U test, $P = 0.002$; L-35228, Mann-Whitney U test, $P < 0.001$. Overall, the 3 Whirinaki females during incubation spent a mean of just 3.9%, 4.2% and 6.5% of each 24-hour period out of their nest cavities.

Hatching success
Average hatching success at sites varied from 38.7% (Whirinaki) to 66.0% (Eglinton), but was as low as 34% at Waipapa and Whirinaki in 2001/02, and as high as 88% at Waipapa in 1997/98 (Table 6A-D). Of 17 clutches (80 eggs) monitored at Whirinaki, 3 (18 eggs) were eaten by predators. Of the remaining 62 eggs, 31 hatched (50.0%), 6 were infertile or contained early dead embryos (9.7%), 2 broke during incubation (3.2%), 2 remained unhatched for unknown reasons (3.2%), 7 were abandoned (11.3%), and the other 14 (22.6%) remained unhatched for at least a fortnight after the last nestling hatched, but disappeared during nestling-rearing. Twenty-two of 53 eggs at Whirinaki remained unhatched at the end of incubation, thus hatching failure (infertility/ embryo death) was 41.5%. Neither site nor treatment (pest control) had a significant effect on hatching success ($x^2 = 2.671$, d.f. = 3, $P = 0.445$; $x^2 = 0.967$, d.f. = 1, $P = 0.325$, respectively).

Nestling rearing
Females alone entered nest cavities during nestling-rearing and cared for the brood. The time of hatching for each egg of 2 clutches (4 eggs and 5 eggs) was determined. Assuming the eggs hatched in the order laid, the time interval between the hatching of the 1st and 2nd eggs for the 2 clutches

Table 6A-E. Productivity and mortality of kaka (*Nestor meridionalis*) eggs, nestlings, and fledglings at 4 study sites (Waipapa, Whirinaki, Rotoiti and Eglinton) during each breeding season, and in total. Results in the first 7 lines of tables A to E are only from nests for which clutch-size was known. Subsequent results were derived from all nests whether clutch size was known or not.

A. Waipapa	1997/98	1998/99	2000/01	2001/02	Total
Number of nests	5	7	2	17	31
Eggs laid	17	29	7	67	120
Eggs hatched (nestlings <20 days)	15 (88.2%)	15 (51.7%)	6 (85.7%)	23 (34.3%)	59 (49.2%)
Nestlings fledged	7 (46.7%)	13 (86.7%)	3 (50.0%)	8 (34.8%)	31 (52.5%)
% of eggs fledged	41.2%	44.8%	42.9%	11.9%	25.8%
Mean number of fledglings per breeding pair per breeding season (± sd, range)	1.2 (± 1.3, 0-3) (n=11*)	2.2 (± 1.2, 0-4) (n=19)	0.1 (± 0.5, 0-2) (n=20)	1.6 (± 1.3, 0-5) (n=27)	1.3 (± 1.4, 0-5) (n=77)
Number of radio-tagged fledglings	7	7	2	17	33
Tagged fledglings surviving after 4 months	6 (85.7%)	4 (57.1%)	1 (50%)	11 (64.7%)	22 (66.7%)

*Number of radio-tagged females monitored in a given season. Does not include the 1999/00 season when none of the 23 radio-tagged female kaka bred.

B. Whirinaki	1998/99	2000/01	2001/02	Total
Number of nests	1	3	13	17
Eggs laid	4	13	63	80
Eggs hatched	1 (25.0%)	8 (61.5%)	22 (34.9%)	31 (38.7%)
Nestlings fledged	0 (0.0%)	3 (37.5%)	12 (54.5%)	15 (48.4%)
% of eggs fledged	0.0%	23.1%	19.0%	18.7%
Mean number of fledglings per breeding pair per breeding season (± sd, range)	1.4 (± 1.8, 0-4) (n=9*)	0.2 (± 0.5, 0-2) (n=17)	0.8 (± 1.3, 0-4) (n=16)	0.7 (± 1.3, 0-4) (n=42)
Number of radio-tagged fledglings	5	3	10	18
Tagged fledglings surviving after 4 months	3 (60.0%)	0 (0.0%)	5 (50.0%)	8 (44.4%)

*Number of radio-tagged females monitored in a given season. Does not include the 1999/00 season when none of the 14 radio-tagged female kaka bred.

C. Rotoiti	1999/00	2001/02	Total
Number of nests	3	5	8
Eggs laid	18	21	39
Eggs hatched	10 (55.6%)	9 (42.9%)	19 (48.7%)
Nestlings fledged	8 (80.0%)	3 (33.3%)	11 (57.9%)
% of eggs fledged	44.4%	14.3%	28.2%
Mean number of fledglings per breeding pair per breeding season (± sd, range)	3.5 (± 3.1, 0-7) (n=4*)	1.7 (± 1.6, 0-4) (n=6)	2.4 (± 2.4, 0-7) (n=10)
Number of radio-tagged fledglings	11	15	11
Tagged fledglings surviving after 4 months	7 (63.6%)	-	7 (63.6%)

*Number of radio-tagged females monitored in a given season. Does not include the 2000/01 season when none of 5 radio-tagged female kaka bred.

Table 6A-E. Continued.

D. Eglinton	1998/99	1999/00	Total
Number of nests	10	14	24
Eggs laid	45	58	103
Eggs hatched	33 (73.3%)	35 (60.3%)	68 (66.0%)
Nestlings fledged	26 (78.8%)	29 (82.9%)	55 (80.9%)
% of eggs fledged	57.8%	50%	53.4%
Mean number of fledglings per breeding pair per breeding season (± sd, range)	2.6 (± 2.1, 0-7) (n=10*)	2.2 (± 1.6, 0-4) (n=13)	2.4 (± 1.8, 0-7) (n=23)
Number of radio-tagged fledglings	2	10	12
Tagged fledglings surviving after 4 months	2 (100.0%)	10 (100.0%)	12 (100.0%)

*Number of radio-tagged females monitored in a given season. Does not include the 2000/01 and 2001/02 seasons when none of 13 and 7 radio-tagged female kaka bred respectively.

E. Totals	Waipapa	Whirinaki	Rotoiti	Eglinton
Number of nests	31	17	8	24
Eggs laid	120	80	39	103
Eggs hatched	59 (49.2%)	31 (38.7%)	19 (48.7%)	68 (66.0%)
Nestlings fledged	31 (52.5%)	15 (48.4%)	11 (57.9%)	55 (80.9%)
% of eggs fledged	25.8%	18.7%	28.2%	53.4%
Mean number of fledglings per breeding pair per breeding season (± sd, range)	1.3 (± 1.4, 0-5) (n=77*)	0.7 (± 1.3, 0-4) (n=42)	2.4 (± 2.4, 0-7) (n=10)	2.4 (± 1.8, 0-7) (n=23)
Number of radio-tagged fledglings	33	18	11	12
Tagged fledglings surviving after 4 months	22 (66.7%)	8 (44.4%)	7 (63.6%)	12 (100.0%)

*Number of radio-tagged females monitored at each study site during the study.

was 0.3 and 0.4 days, 2nd and 3rd eggs was 1.2 and 0.3 days, 3rd and 4th eggs was 1.3 and 3.3 days, and the 4th and 5th eggs of the 2nd clutch was 1.0 day. Overall, the mean hatching interval was 1.1 ± 1.0 days (range = 0.3-3.3).

Female activities and absences from nests during nestling-rearing were determined for 5 nests at Whirinaki in the 2000/01 and 2001/02 breeding seasons (Table 7). During the 1st 10 days after hatching, kaka nestlings were covered in white down, and their eyes were closed. When not being brooded, they huddled closely together, raising their heads only when stimulated by the female. Large fragments of shells from hatched eggs were often treated as though unhatched, the female repeatedly drawing them under her when covering her brood. One female was regularly seen to chew on fragments of shell, as though to ingest material rather than just to fragment the shell. Eventually shells ended up at the edge of the nest cavity and covered by faeces and nest material.

While the nestlings were less than 10 days old, the number of absences by females from nests at night (2-3) and day (12-13) (Table 7) was similar to that during incubation (Table 5). However, even at this young age, nestlings were left unattended for a mean range of 7-25 minutes compared to 4-6 minutes during incubation. Overall, the percentage of time absent from the nest increased from 4-7% during incubation to 9-27% (Table 7). Throughout the nestling-rearing period, nestlings were not fed at night even though females were often absent from the nest for extended periods.

Between 11 and 20 days, nestlings developed a dense covering of grey down, had partially open eyes, developed the ability to sit up on their haunches, moved about readily, including to the edge of the nest floor to defecate, and responded quickly to the female entering the cavity by stretching up to be fed. While females attempted to brood nestlings of this age class, if there was more than 2, parts of some nestlings were not covered by

Table 7. Nestling-rearing attentiveness (mean number of absences by night and day from the nest, mean number of minutes per absence, percentage of night and day absent) by 5 female kaka (*Nestor meridionalis*) to their broods at 10-day intervals at Whirinaki during the 2001/02 breeding season. If the day of hatching was not known, nestling age was estimated on the assumption that the first nestling fledged at 70 days of age. [1]Female identity is her band number. [2]Number of days of data during the 10-day period.

Nestling age days)	Mean number of absences			Mean time (mins) per absence			% of time absent		
	night[-1]	day[-1]	24 hrs[-1]	night[-1]	day[-1]	24 hrs[-1]	night[-1]	day[-1]	24 hrs[-1]
L-35239[1], 4 nestlings fledged, hatched days 1, 2, 4 & 7, 11/12/01 to 25/02/02									
1-10 (8)[2]	3.0	13.4	16.4	25	7	8	8	10	9
11-20 (10)	4.9	16.3	21.2	70	47	48	47	81	69
21-30 (8)	4.8	15.0	19.8	86	49	54	51	78	67
31-40 (10)	2.3	8.0	10.3	139	110	112	45	97	77
41-50 (9)	6.3	15.4	21.8	33	44	40	32	77	59
51-60 (7)	3.7	16.3	20.0	146	53	59	60	90	78
61-70 (10)	3.5	18.3	21.8	150	42	54	75	86	81
71-80 (5)	2.4	19.6	22.0	257	34	52	86	74	79
L-35236, 2 nestlings fledged, hatched days 1, 1, 2 & 3, 1 died day 20, 1 died day 54, 26/12/01 to 4/03/02									
1-10 (8)	2.8	11.9	14.6	13	28	25	8	37	27
11-20 (10)	2.3	9.0	11.3	124	82	88	42	75	63
21-30 (9)	2.2	9.9	12.1	126	86	92	55	84	74
31-40 (8)	4.8	12.5	17.3	49	40	42	41	54	49
41-50 (6)	4.2	12.3	16.5	87	39	50	57	57	57
51-60 (8)	3.9	12.1	16.0	148	34	60	84	48	63
61-70 (5)	2.2	11.8	14.0	309	32	69	92	45	65
L-36663, 1 nestling fledged, assumed 1 nestling fledged on day 70, other died on day 17, 15/01/02 to 8/03/02									
11-20 (3)	5.7	12.3	18.0	23	35	31	23	48	38
21-30 (8)	5.6	18.5	24.1	28	28	27	24	58	44
31-40 (10)	4.5	18.6	23.1	63	27	33	42	58	52
41-50 (10)	4.2	17.8	22.0	119	32	44	62	66	65
51-60 (10)	4.1	16.7	20.8	131	30	46	76	59	66
61-70 (10)	4.3	13.9	18.2	144	43	63	83	67	75
L-33025, 2 nestlings fledged, assume first fledged on day 70, and second on day 71, 10/01/01 to 4/03/1									
11-20 (3)	4.0	9.7	13.7	80	93	86	69	86	79
21-30 (8)	3.8	14.8	18.5	119	53	65	76	86	82
31-40 (10)	5.0	15.2	20.2	97	55	61	75	87	82
41-50 (10)	4.4	15.1	19.5	125	54	66	84	88	87
51-60 (7)	1.6	6.1	7.7	298	119	144	96	95	96
61-70 (8)	2.8	6.4	9.1	231	142	159	95	98	97

Table 7. Continued.

Unbanded female, 3 nestlings fledged, assume first nestling fledged on day 70, and other 2 on days 78 & 87, 11/ 04/02 to 23/05/02									
41-50 (6)	3.5	10.2	13.7	244	62	102	96	97	96
51-60 (10)	2.6	9.1	11.7	348	74	125	96	96	96
61-70 (9)	4.6	9.3	13.9	185	65	99	92	96	94
71-80 (6)	3.8	10.0	13.8	236	61	101	95	97	96

the female. By day 20 little brooding was carried out; when in their nest cavities females mainly fed or preened nestlings, grubbed into the nest cup, and occasionally stripped bits of wood off the cavity walls. This latter activity seemed to be to add clean material over that matted by the nestlings' faeces and weight. When nestlings were 11-20 days old (Table 7), the mean number of absences at night ranged between 2-6 of 23-124 minutes duration. By day, there was a mean of 9-16 absences of 35-93 minutes duration. Even at this young age, nestlings were left unattended for 23-69% of night, and 48-86% of day (Table 7).

Between ages 21 and 30 days, nestlings' eyes opened fully, development of remiges began to extend beyond their down, and nestlings became active about the base of the nest cavity, rather than mainly remaining huddled together. When feeding such broods, some females clung to the side of the cavity, only moving on to the cavity floor once feeding had been completed. It was noticeable that when females had completed feeding their nestlings, or even if they did not feed any, nestlings never solicited food from their mothers. After feeding nestlings, females usually preened nestlings or stripped wood from cavity walls. The mean number of absences, mean time per absence, and percentage of time absent from the nest by females when nestlings were 21-30 days old changed little from that of the previous 10-day period (Table 7).

Nestlings aged 31-40 days old developed a partial covering of contour plumage, but their remiges and rectrices were still growing. Three females with broods of this age class were absent for a mean range of 17.3-23.1 occasions per 24-hour period, but a 4th was absent for a mean of only 10.3 times (Table 7). The mean time per absence varied from 33 to 112 minutes, and the proportion of time ranged from 49 to 82%.

When 41-50 days of age, kaka nestlings were almost completely covered by contour plumage, especially towards the end of this age class. Such nestlings spent much time chewing on cavity walls and attempting to climb up to the entrance if they were in deep cavities. Most females with broods of this age class were absent from their nests for a mean range of 16.5-22.0 occasions per 24-hour period, of which nearly a quarter occurred at night (Table 7). For 4 of the 5 females, the absences at night were much longer than those by day, and overall averaged 57 minutes. While 3 females were absent for *c*. 60% of time, for the other 2 it was *c*. 90%. The latter 2 females spent very little time in their nest cavities other than to feed nestlings.

For nestlings of age classes 51-60 and 61-70 days, their contour plumage was essentially complete, but some primaries and all rectrices were still developing. When not asleep, they were interacting with each other, sometimes quite noisily, preening, attempting to climb to the nest entrance, or at the entrance. There was little change in the behaviour of females (number of absences, mean time per absence, and proportion of time absent) during these 2 age classes, but there were differences between individuals (Table 7). Two females visited their nests by day for just 1-2 minutes to feed their nestlings, and at night they made 1-4 brief visits to preen nestlings and/or strip bits of wood off the cavity walls. The other 3 females spent 19-37% of time with their broods, mainly preening and stripping wood, but occasionally they slept among the nestlings.

Predation of broods, and interactions of breeding female kaka with stoats

The predation of 3 broods was recorded on video tape. At Whirinaki a brood of 5 nestlings from about 5-days of age were uncharacteristically left unattended for much time each night. By day 11 just the eldest 2 chicks survived. That night the female kaka left the cavity at 20:54 h on dusk, and 2 hours later a brushtail possum entered the cavity and ate the 2 nestlings before departing 78 minutes later. The female kaka returned the next morning at 08:34 h, remained for 3 minutes and then left.

At Rotoiti on 9 Mar 2002, a brood of 3 12-day old nestlings was killed by a stoat while the female was absent from the cavity during the day. Having killed each nestling with a bite to the back of the head, and being unable to drag each up to the cavity entrance, the stoat dug a hole in the nest material and dragged each nestling into

it. On returning to her nest a few minutes later, the kaka walked around on the nest floor and peered into the hole where the stoat and chicks were hidden. Over the next 2 h 52 min, the kaka repeatedly clambered between the nest entrance and the floor of the cavity, peering into the hole, and occasionally moving about on the floor. On 8 occasions the kaka and stoat interacted, usually involving the stoat with just its head out of the hole and the kaka clinging to the cavity wall or standing on the nest floor. On most occasions, the kaka aggressively lunged at the stoat, regaining its balance by a flicking action of both wings.

On 19 Apr 2002 at Rotoiti, a stoat killed a lone *c.* 14-day old chick while the female was absent during the day. Again, unable to lift the chick up to the entrance of the cavity, the stoat dug a hole in the nest material. While feeding on the chick before dragging it into the hole, the female kaka returned. The female attacked the stoat without hesitation and fought with it on the floor of the cavity for 10 seconds before the stoat fled. The kaka remained in the cavity and 20 minutes later when the stoat re-appeared in a new hole in the nest material, she again reacted aggressively. A few minutes later she left the cavity, returning 67 minutes later to walk about on the nest floor and peer into the stoat hole.

Nestling-rearing success
While nestling survival from hatching to fledging was similar for Waipapa (52.5%), Whirinaki (48.4%) and Rotoiti (57.9%), it did vary considerably between breeding seasons at each study site (Table 6A-C). Nestling-rearing success was much greater at Eglinton (80.9%) than at the other study sites, and varied little between the 2 seasons for which data are available (Table 6D). While site had a nearly significant effect on nestling-rearing success (x^2 = 7.585, d.f. = 3, P = 0.055), treatment had a significant effect (x^2 = 4.562, d.f. = 1, P = 0.033). Overall, the percentage of eggs that resulted in fledglings varied from 18.7% at Whirinaki to 53.4% at Eglinton (Table 6E). Both site and treatment had a nearly significant effect on breeding productivity (x^2 = 6.833, d.f. = 3, P = 0.077; x^2 = 3.611, d.f. = 1, P = 0.057, respectively).

The productivity of radio-tagged females varied considerably from season to season, and between sites (Table 6A-E). At Waipapa in 1998/99 and at Rotoiti in 1999/00, when mast seeding or fruiting occurred, mean productivity was 2.2 and 3.5 fledglings per female respectively. In contrast, in the 2000/01 breeding season, when only a small proportion of females bred at Waipapa and Whirinaki (Table 1), productivity per female was just 0.1 and 0.2 fledglings, respectively (Table 6A-B). Overall, productivity per female was greatest at

Rotoiti (2.4) and Eglinton (2.4) where pest control was carried out, lower at Waipapa (1.3) where pest control was also carried out, and least at Whirinaki (0.7) where no pest control was carried out.

Even though few females bred during breeding seasons when masting of podocarp trees did not occur at the 2 North Is study sites, the difference in mean nesting success (number of fledglings per nest) did not differ significantly from that at the same study sites in masting seasons (no masting: mean = 0.67 ± 0.82, n = 6; masting: mean = 1.44 ± 1.33, n = 81) (Mann-Whitney U test, P = 0.18). In contrast, the nesting success at Waipapa, Rotoiti and Eglinton study sites (mean = 1.83 ± 1.39, n = 105), where pest control was carried out at each, was significantly greater than at Whirinaki, where no pest control occurred (mean = 0.93 ± 1.36, n = 29) (Mann-Whitney U test, P = 0.003).

Fledgling behaviour and survival
Because video cameras were usually attached to the upper internal walls of nest cavities, the nest entrance was not "in view" and so the actual act of fledging was rarely caught on tape. On the few occasions recorded, nestlings mostly left of their own accord, but on 1 occasion a nestling at the entrance was jostled out by a sibling trying to reach the entrance from behind.

The number of days from hatching to fledging for 2 broods (4 and 2 nestlings) at Whirinaki was calculated on the assumption that they fledged in the order of hatching; 64.8, 70.3, 72.1 and 69.5 days, and 68.2 and 67.9 days, respectively (mean = 68.8 ± 2.5). The interval between the fledging of successive nestlings in a brood of 4 was 6.3, 3.8 and 1.1 days, a brood of 3 was 7.0 and 9.7 days, and a brood of 2 appeared to fledge within a few minutes of each other.

Initially kaka fledglings were poor fliers, some ending up on the ground and remaining there for 3-4 days until strong enough to either climb into the canopy or fly away. Fledglings on the ground usually attempted to hide under low vegetation or logs. Others perched in under-storey shrubs and trees, or in the canopy. Initially, fledglings were quite sedentary, and when radio-tagged fledglings on the ground were approached to check their survival they remained motionless to avoid detection. However, on 2 occasions single fledglings at Whirinaki near the ground were located by their noisy calling and flapping as they attempted to climb into the canopy.

Survival of radio-tagged fledglings for the first 4 months was poor at Whirinaki (44% of 18), moderate at Waipapa (67% of 33) and Rotoiti (64% of 11), and high at Eglinton (100% of 12). Survival of fledglings varied between breeding seasons at Waipapa and Whirinaki (Table 6A-B).

Retention of pair bonds

Just 1 pair of kaka at Whirinaki involved both birds being radio-tagged. They bred together in the 1997/98 season, rearing 2 fledglings, and had 2 unsuccessful nests in the 1998/99 season. Along with other Whirinaki kaka, the pair did not breed in the 1999/00 season, and reared 2 fledglings in the 2000/01 season. At Rotoiti, each of 4 partnerships, all members of which were banded, remained paired during the 1997/98 and 1998/99 seasons, and 2 of the pairs bred again in the 1999/00 season.

DISCUSSION

Breeding effort

Kaka are episodic breeders regardless of habitat (Greene *et al.* 2004). Kaka did not breed annually in any of our study sites, and in some years only a small proportion of radio-tagged females bred. At the Eglinton Valley 3 years have elapsed without breeding by kaka on 2 occasions since 1999 (P. J. Dilks, *pers. obs.*), and 2 years elapsed without breeding at Big Bush, adjacent to the Rotoiti study site (Wilson *et al.* 1998). Of the other 2 large and related species of New Zealand parrots, the kakapo is also an episodic breeder dependent on fruit from masting tree species during breeding, with 2-7 years elapsing between breeding seasons (Powlesland *et al.* 2006). However, the kea, the species most closely related to the kaka, usually breeds annually with an occasional missed year (Elliott & Kemp 1999). In contrast, of the large (> 300 g) Cacatuidae parrot species of Australia whose breeding has been well studied (red-tailed black-cockatoo (*Calyptorhynchus banksii*), yellow-tailed black-cockatoo (*Calyptorhynchus funereus*), short-billed black-cockatoo (*Calyptorhynchus latirostris*), galah (*Eolophus roseicapillus*), Major Mitchell's cockatoo (*Cacatua leadbeateri*) and sulphur-crested cockatoo (*Cacatua galerita*)), all have been found to breed annually, even if the timing of egg-laying has occasionally been delayed by lack of rainfall and/or availability of food (Higgins 1999). A few parrot species are opportunistic breeders, breeding annually during a typical breeding season but also breeding at other times when food is readily available, such as the budgerigar (*Melopsittacus undulatus*) and scarlet-chested parrot (*Neophema splendida*) of Australia, and the brown-throated conure (*Aratinga pertinax*) of South America (Forshaw 1989). Two parakeet species, both of which feed on *Nothofagus* flowers and/or seed, are opportunistic, but not episodic, breeders in relation to the phenology and productivity of *Nothofagus* species; the yellow-crowned parakeet (*Cyanoramphus auriceps*) of southern New Zealand (Elliott *et al.* 1996a) and the austral parakeet (*Enicognathus ferrugineus*) of southern South America (Diaz & Kitzberger 2006; S. Diaz, *pers. comm.*).

The consistent factor associated with breeding of kaka at our study sites was the mast fruiting or seeding of tree species. In the 2000/01 summer, when no masting occurred and few kaka nested at Waipapa and Whirinaki, no females laid replacement clutches after failed breeding attempts, in contrast to when masting occurred. Similarly, at Rotoiti, when little viable beech seed was available (2000/01), no kaka nested. Likewise, the breeding of female kakapo has occurred in synchrony with the abundant fruiting of the masting species rimu and pink pine (*Halocarpus biformis*) (Powlesland *et al.* 2006).

Nest sites

Kaka are secondary-cavity nesters, using natural cavities, usually within the trunks and large branches of trees. Like most other parrot species, such as the *Calyptorhynchus* species (Higgins 1999), kaka make no attempt to construct their own cavities or line the nest cup with foreign material. In comparison, double-eyed fig parrots (*Cyclopsitta diophthalma*) excavate cavities in a tree-trunk or limb (Juniper & Parr 1998), hooded parrots (*Psephotus dissimilis*) and golden shouldered parrots (*Psephotus chrysopterygius*) excavate nest cavities in termite mounds (Higgins 1999), galahs line their nests with sprays of green leaves (Rowley 1990), and peach-faced lovebirds (*Agaponis roseicollis*) line their nests with strips of bark, leaves or grass (Forshaw 1989).

While we did not determine the abundance of cavities suitable for kaka to nest in, the impression from the low incidence of re-use (< 20%) from 1 breeding season to the next at 3 study sites (except for the high level of re-use at Waipapa in the 2001/02 season) was that suitable cavities were readily available. This low frequency of re-use possibly is a function of the relatively low density of the kaka population such that there is little, if any, competition for nest sites. Likewise, the low incidence of cavity re-use by nesting mohua (9.4%) and yellow-crowned parakeets (14.3%) in *Nothofagus* forest in Fiordland was also considered to be as a result of the ready availability of suitable cavities (5-9 per ha) (Elliott *et al.* 1996b).

Blakely *et al.* (2008) found that of silver, mountain and red beech trees at Lewis Pass, New Zealand, red beech trees had the greatest number and largest cavities. Since large cavities (> 10,000 cm^3) were relatively rare in the beech forest (Blakely *et al.* 2008), and were required by kaka to nest in (c. 170,000 cm^3, Table 2), it is not surprising that almost all kaka nests at Rotoiti and Eglinton were in red beech trees.

Most trees in which kaka nested were entirely alive or included a few dead branches. Whether female kaka had a preference for nesting in live trees or whether this finding reflects the availability

of trees, live or dead, containing suitable cavities, is unknown. A few females at each of our study sites squeezed through narrow entrances (40-60 mm) to access suitable cavities, and this was also noted of a North Is kaka on Hen Is where the maximum entrance width to her cavity was just 55 mm (Moon 1967). Given that kaka are 460 mm in length (beak tip to tail tip, Heather & Robertson 2005), the base of each nest cavity needed to be at least that diameter in order to accommodate the incubating or brooding female. While a few cavities were smaller than this, the majority were much larger. As long as the cavity was large enough at the base, most other cavity characteristics were quite variable, for example size of entrance or depth of cavity. Possibly the minimum diameter of the cavity base meant that most nests had to be in trunk cavities of large canopy or emergent trees.

While the mean height of nest entrances in our study sites ranged from 8.3 to 13.4 m, some nest entrances were within a few metres of the ground. This meant that at least some nests were readily accessible to mammalian predators that were adept climbers, such as ship rats, brushtail possums and stoats. Kaka are known to nest much lower, with 40% of 25 nests on Kapiti Is being at ground level (Moorhouse 1991), and 2 ground-level nests were found on Little Barrier Is (T.C. Greene, *pers. obs.*). It is of note that in the Eglinton Valley, mean height of successful kaka nests was not significantly different from unsuccessful nests. Rather than nest height it was mean distance from the nearest trap that had a significant influence on whether a nest was successful or not, successful nests being closer to traps than unsuccessful nests (Dilks *et al*. 2003).

Female kaka expended much effort to create a deep layer of friable, free-draining litter on which to nest. Such nest-preparation activities are also typical of large Cacatuidae parrots (Higgins 1999). Generally these activities did not appear to modify kaka nest cavity dimensions within live trees to a noticeable extent, but some cavities in trees with dead heartwood were enlarged by female wood-stripping activity.

Breeding season
In summers when mast fruiting of podocarp trees occurred at Waipapa and Whirinaki or mast seeding of beech trees at Rotoiti and Eglinton, kaka had long breeding seasons. In these circumstances 3 females at Waipapa, 2 at Rotoiti and 1 at Eglinton each reared 2 broods within a breeding season. Since egg-laying occurred as late as Mar, and as a successful breeding cycle from egg-laying to fledging took *c*. 14 weeks, a few pairs fledged broods as late as Jul, mid-winter. Thus the kaka breeding season extended over 8 months in some years.

The Eglinton population was the most southern of those we studied and there kaka usually started breeding 2 months later than the others. The later start of breeding by the Eglinton population is related to the autumn maturation of beech seeds, rather than the summer maturation of seeds at Rotoiti. The high nutritional content (Beggs 1999) and abundance of beech seed (Fig. 2), when available, sustains kaka breeding in the South Is. Variations in the timing and length of breeding seasons of other parrot species in relation to food availability and climatic conditions have been recorded elsewhere (Smith 1991, Forshaw 1989, Garnett *et al*. 1999, Robinet & Salas 1999), but not to the extreme whereby nesting occurs episodically.

Eggs
Kaka eggs look much like those of other parrots; white and slightly oval. Mean length and maximum breadth of 12 eggs from Whirinaki (41.5 x 31.5) were similar to those of 3 North Is kaka eggs (42.1 x 30.8) reported by Oliver (1955) and 18 eggs (41.2 x 31.0) reported by Forshaw (1989) for which the provenances were not indicated. Estimated mean fresh weight of 22.4 g for the eggs from Whirinaki represents 5.6% of mean female body weight. In comparison, the fresh egg weight as a proportion of female body weight for the closely related kea is 3.5% (estimated from figures in Higgins 1999) and for the kakapo is 3.2% (Powlesland *et al*. 2006). Likewise, the fresh egg weights of 6 Cacatuidae species are 3.7 – 5.1% of female body weight (Saunders 1974, Saunders & Smith 1981, Higgins 1999). Why the eggs of the kaka are a slightly greater proportion of body weight than the other species is unknown, but may relate to its irregular breeding in accordance with an abundance of food provided by mast fruiting or seeding of some tree species.

Saunders *et al*. (1984) investigated the relationship between egg weight and body weight of 4 orders of birds, and predicted that a 400 g parrot should produce eggs weighing 19.9 g. Female kaka have a mean weight of 400 g (Moorhouse *et al*. 1999) and a mean egg weight of 22.4 g, 12.6% heavier than Saunders predicted.

The mean egg-laying interval of the kaka at 3.5 days is similar to that of large (> 400 g) Cacatuidae parrots that lay clutches of 1-4 eggs for which information is available. The mean egg-laying interval of the kakapo was 3.4 days (3-7 days) (Eason *et al*. 2006), 2-3 days for the Major Mitchell's cockatoo (Higgins 1999), and 2.7 days for the galah (Rowley 1990). However, Rowley (1990) noted that the egg-laying interval varied between female galahs, and so our small sample size of 5 means our estimate of 3.5 days for kaka may not be reliable.

Clutch-size

Mean clutch-size varied from 3.8 to 4.9 (4.2 overall), and the largest clutch-size was 8. In comparison, kaka on Kapiti Is during the 1988/89 and 1989/90 breeding seasons had a mean clutch-size of 3.7 eggs (*n* = 25), with the largest clutch being of 5 eggs (Moorhouse 1991). The mean clutch size and largest clutches of kaka were greater than those of the other 2 related New Zealand parrots: kea (2.5, 4) (Higgins 1999, Eason *et al*. 2006), and kakapo (2.5, 4) (Eason *et al*. 2006). The large (> 400 g) Cacatuidae parrots have clutches of 1-4 eggs (Saunders *et al*. 1984, Murphy *et al*. 2003). We presume that the larger mean clutch size of the kaka, compared with those of similar-sized parrots, reflects the kaka's irregular breeding. When breeding in years when fruit or seed of masting species was available, kaka fed almost entirely on the fruit or seeds of these species (authors *unpubl. obs.*). While kakapo (lek breeder) also breed irregularly in response to masting events, presumably the fact that the species is flightless and the female alone forages to meet her food requirements (Powlesland *et al*. 2006, Eason *et al*. 2006) results in that species' modest clutch-size.

Incubation

As has been previously reported (Jackson 1963), we found that incubation was carried out only by the female, with the male calling her off the nest at regular intervals and feeding her nearby. Similarly, female kea undertook all incubation, with the male feeding his mate several times during the day (Higgins 1999). Of the Cacatuidae, parrots of the genus *Calyptorhynchus* have the same incubation behaviour, the female incubating and her mate feeding her. However, for each of the 4 *Calyptorhynchus* species (red-tailed black-cockatoo, yellow-tailed black-cockatoo, short-billed black-cockatoo, glossy black cockatoo (*C. lathamii*)) for which information is available, the number of times females were fed during the day was 1-4 (Higgins 1999), much less often than the 8-12 times of the kaka.

Saunders *et al*. (1984) found that 400 g parrots on average have a 25 day incubation period. Although their method used to calculate incubation period was not detailed, the figure of 25 days is slightly longer than ours of 20-23 days for just 2 nests for kaka (mean 400 g; Moorhouse *et al*. 1999). Similarly, Franklin & Wilson (2003) concluded from their study of the breeding parameters of altricial species that the larger New Zealand parrots had shorter incubation periods compared to their Australian counterparts.

Although it was not unusual to see more than 1 male kaka associating with a female or perched near occupied nests during incubation, there was no evidence of polygamy (2 or more males having mated with or feeding a female during incubation) or extra-pair copulations. The main reason for this occurrence is likely to have been male biased population sex ratios where little or no control of introduced predatory mammals had occurred (Moorhouse *et al*. 1999). While sex ratios of kaka populations on pest-free islands have been almost 1:1, those of mainland populations without pest control have been 1:2 to 1:6 (female: male) (Greene & Fraser 1998).

Hatching success

Kaka hatching success for all sites and seasons varied from 39 to 66%, and was up to 88% at Waipapa in 1 season. In comparison, hatching success of large (> 400 g) Cacatuidae parrots in Australia varied from 60 to 76% (Murphy *et al*. 2003). Hatching success of kaka eggs was least at Whirinaki (39%), where there was no systematic predator control, while it was greater but variable (49 – 66%) at the other 3 sites where predator control was carried out. In comparison, at the Mt Bruce National Wildlife Centre near Masterton, North Is, where kaka have been re-introduced (Berry 1998) and nest in predator-proof sites (artificial nest boxes and natural sites that predators are unable to access), hatching success was just 41% of 167 eggs laid between 1998 and 2006 (R. Berry, *pers. comm.*). Similarly, the hatching success of the kakapo was 42% of 146 eggs laid between 1981 and 2002 (Elliott *et al*. 2006). Poor hatching success, such as evident for the kakapo, is characteristic of bird populations with low genetic diversity (Briskie & Mackintosh 2004). Sainsbury *et al*. (2006) found that despite substantial levels of genetic variation, there was little genetic difference between kaka populations through New Zealand. This suggests that low genetic diversity is not the reason for the poor hatching success of kaka at Whirinaki and Mt Bruce. Predators probably contribute considerably to the low hatching success we observed, and in our study areas possums and stoats are the most likely predators (Moorhouse *et al*. 2003). On Kapiti Is, Moorhouse (1991) observed Norway rats (*Rattus norvegicus*) preying on kaka eggs and chicks. However, given that hatching failure at Whirinaki was 41.5%, a considerable proportion of eggs remained unhatched for unknown reasons.

Nestling rearing

Even though our sample size is small, the mean hatching interval was just 1.1 days compared with the mean egg-laying interval of 3.5 days. This has also been noted for the galah, with a mean egg-laying interval of 2.7 days, and that most of the clutch hatched on the same day (Rowley 1990). Presumably little warming of the first egg, and perhaps even the 2nd egg, occurs until the 2nd or 3rd is laid.

Nestlings of the genera *Nestor* (kaka and kea) and *Strigops* (kakapo) are well covered in down on hatching (Higgins 1999). This dense layer of down on *Nestor* and *Strigops* hatchlings is probably not just an adaptation to cool ambient temperatures because hatchling black cockatoos (*Calyptorhynchus* spp.) of temperate and tropical Australia are also covered in dense down (Higgins 1999).

This study provides no explanation for the long night-time absences of females from nests with 11-20 day old chicks at Whirinaki. While food shortage is known to modify female incubation and brooding attentiveness in parrots (Saunders 1982), no female kaka returning to their nests at night were observed feeding chicks, so it seems unlikely that night time female absences were for food gathering.

The behaviour of female kaka when in the nest cavity attending nestlings was similar to that of other parrots, spending most time feeding, brooding and preening the young. However, once nestlings were older that 10 days and the brood consisted of 2 or more nestlings, most female kaka spent little time in the cavity by day. Presumably this was because by this age kaka nestlings with their thick covering of down were able to thermoregulate reasonably effectively. By comparison, nestling galahs were not able to thermoregulate until about 4 weeks of age and their feathers began to burst from the sheaths (Rowley 1990). Similarly, nestling yellow-tailed black-cockatoos were 3-4 weeks old before they were left unattended by day, and 8-9 weeks old before they were not brooded at night (Saunders 1982).

The stripping of bits of wood from the internal walls of nest cavities by female kaka when rearing nestlings seemed to be to provide clean material for the nestlings to rest on. While nestlings older than 14 days of age moved to the edge of the nest bowl to defecate, the nest base soon became compacted, and so the new material probably helped to keep the nestlings clean and dry. Black cockatoos (*Calyptorhynchus* spp.) strip bits of wood from the walls of their nest cavities and use them as a lining for the floor of the nests (D.A. Saunders, *pers. comm.*), but whether this activity is carried out when rearing nestlings is not known.

Kaka nestlings fledged at *c*. 70 days of age. Amongst the large (> 300 g) Cacatuidae parrots that often lay 3 or more eggs, the age at fledging for the sulphur-crested cockatoo was similar at 66-73 days, but that of the galah (50 – 52 days) and Major Mitchell's cockatoo (53-66 days) were shorter (Murphy *et al*. 2003). However, some Cacatuidae species that lay 1- or 2-egg clutches have much longer fledging periods, such as *c*. 90 days for the glossy black cockatoo, red-tailed black-cockatoo and yellow-tailed black-cockatoo (Murphy *et al*. 2003). Saunders *et al*. (1984) derived a figure of 58 days for the nestling period of 400 g parrots. The longer

duration of the kaka nestling period, also noted by Franklin & Wilson (2003) for New Zealand parrots in general, may relate to the kaka's slightly larger brood size compared to that of similar-sized Australian parrots. It may also have evolved because there were few predators capable of accessing kaka nests prior to the arrival of mammals in New Zealand.

Nestling-rearing success
Kaka nestling survival varied between breeding seasons in each study site, and between study sites, mainly as a result of predation (Moorhouse *et al*. 2003), although an occasional brood died of starvation or exposure when a cavity was flooded during heavy rain. Lack of mammalian predator control at Whirinaki resulted in significantly lower nestling-rearing success there than at the other sites. Even though predator control was carried out in the Eglinton, Waipapa and Rotoiti study sites, nestling-rearing success was much greater in Eglinton (81% compared with 52 & 58%). We suspect this relates to the low density populations of brushtail possums, ship rats and stoats in Eglinton during the 2 kaka breeding seasons of this study (Moorhouse *et al*. 2003), compared with lesser success at maintaining predator densities at low levels at Waipapa over 5 breeding seasons and at Rotoiti over 4 breeding seasons. In addition, the densities of ship rat and possum populations, and probably stoat populations too, are generally greater in North Is podocarp forests (Pureora: Powlesland *et al*. 1999; Whirinaki: Powlesland *et al*. 2003) than in South Is beech forests (Rotoiti & Eglinton: Moorhouse *et al*. 2003), except following mast-seeding events of beech forests after which rodent and stoat populations irrupt (Moorhouse *et al*. 2003). Thus, predator populations in beech forests leading up to and when kaka are breeding are usually lower and therefore more readily controlled than those in podocarp forests. There is no comparative information on nestling-rearing success from other studies of wild kaka populations. In comparison, at the Mt Bruce National Wildlife Centre, near Masterton, where kaka nested in predator-proof sites, 79.1% of nestlings survived to fledge during the 1998/99 to 2005/06 breeding seasons (R. Berry, *pers. comm.*).

Breeding productivity
Productivity (proportion of eggs that resulted in fledglings) was lowest at 19% at Whirinaki, 26-28% at Waipapa and Rotoiti, and greatest at 53% at Eglinton. Overall, both site and predator control had nearly significant effects on productivity during our study. In comparison, at Karori Wildlife Sanctuary, Wellington, where kaka bred within a site fenced to exclude introduced predatory mammals and received food supplements, 57% of 84 eggs resulted

in fledglings being produced (R. Empson, *pers. comm.*). Similarly, at the Mt Bruce National Wildlife Centre, where kaka also bred in predator-proof sites and receive food supplements, 40.7% of 167 eggs resulted in fledglings being produced (R. Berry, *pers. comm.*). Thus, breeding productivity of kaka at the predator-free sites of Karori and Mt Bruce was on a par with that at Eglinton, where predators were successfully controlled to very low levels.

The predatory activities of stoats and brushtail possums have resulted in many nesting female kaka being killed (Beggs & Wilson 1991, Wilson *et al*. 1998, Moorhouse *et al*. 2003), and so unmanaged mainland kaka populations have become male dominated (Greene & Fraser 1998). While neither of the 2 females that were filmed actively attempting to oust stoats from their nests was killed, their aggressive response to stoats could have readily brought about their demise. Similarly, Henry (cited in Hill & Hill 1987) found that female kakapo were fiercely protective of their young, repeatedly charging his dog (*Canis familiaris*) when it approached their nests. Such aggressive behaviour by female kaka, even after their broods had been killed and removed from the nest, presumably reflects the relatively short time (since mid 1880s) in which kaka have co-occurred with the stoat (100-150 years (King 2005)). Given the high selection pressure from the loss of breeding female kaka, we would have expected them to promptly abandon their nests after chick predation, thus removing themselves from danger, rather than attack predators in the confined space of their nest cavities. Given the high proportion of nesting females killed at sites without pest control (Moorhouse *et al*. 2003), it suggests that the 2 females seen attacking stoats on video possibly survived because they were absent when stoats first entered their nests, rather than asleep incubating or brooding.

Fledgling survival

Variation in fledgling survival to 4 months (44-100%) between our study sites seemed to relate mainly to the success of pest control operations in reducing predatory mammal populations to low levels. Fledglings that ended up on the ground at sites where no pest control had been carried out (Whirinaki) were particularly vulnerable to being preyed upon by stoats, ferrets (*Mustela furo*) and feral cats (*Felis catus*). For example, in the Waimanoa Ecological Area, central North Is, where there was no pest control during the 2001/02 breeding season, 63% of 11 radio-tagged fledglings were killed within 2-3 days of fledging (Greene *et al*. 2004). Their cryptic behaviour of remaining quiet and still under cover when approached by us would provide little defence against mammalian predators with a good sense of smell. Also, fledglings perched

in trees called noisily while begging for food from their parents. This behaviour advertises their presence to predators, particularly stoats which are adept arboreal climbers. As a result considerable commitment and funding are required to maintain mammalian predator populations low enough over a sufficient period (up to 10 months of the year) to ensure high levels of kaka fledgling production and survival.

Native avian predators, such as New Zealand falcon (*Falco novaeseelandiae*) and the Australasian harrier (*Circus approximans*), have both been observed hunting and feeding on kaka fledglings where they still co-occur (T. C. Greene, *pers. obs.*). In 1 instance a falcon was seen on the ground actively hunting a recently-fledged kaka hiding among the roots of a fallen tree. This falcon was only prevented from finding the fledgling by the aggressive intervention of the female kaka returning and chasing the predator from the area. Australasian harriers have also been observed feeding on the remains of recently-fledged kaka on the ground, often in areas of dense vegetation. Given the current scale of depredations by introduced mammals on kaka populations, natural predation events are likely to be of relatively minor importance.

Implications for conservation

Kaka eggs, chicks, fledglings, and incubating or brooding females were vulnerable to predation by introduced mammalian predators. Rats, stoats and brushtail possums are all known to prey upon eggs and chicks, and the latter 2 species kill nesting females as well, resulting in declining and sex-biased populations (this study; Moorhouse 1991; Greene & Fraser 1998; Wilson *et al*. 1998; Moorhouse *et al*. 2003). This predicament is not confined to the kaka, with populations of several other New Zealand forest bird species, such as the North Is robin (*Petroica australis longipes*) (Powlesland *et al*. 1999) and North Is kokako (*Callaeas cinerea wilsoni*) (Innes *et al*. 1999) being in decline and male biased as a result of predation by introduced mammalian predators. Populations of such species have recovered, and population sex ratios have returned to 1:1, where pest control operations have reduced predator populations to very low densities (Powlesland *et al*. 1999, Innes *et al*. 1999, Moorhouse *et al*. 2003).

While such pest control operations are expensive to carry out (Saunders 2000), once a population has been restored to the habitats' carrying capacity, year-round or annual breeding season control operations are no longer required (Greene *et al*. 2004). Pulsed pest control for the conservation of North Is kokako populations is presently being tested (Basse *et al*. 2003), and if successful, will free up much-needed funding for other species

conservation programmes in the intervening years. In the case of the kaka, pulsed management is likely to be most cost-effective if pest control is timed to coincide with the masting of kaka food species, as suggested by Powlesland *et al*. (2003). Kaka in beech-dominated forests bred only when seeding of beech trees occurred (this study; Wilson *et al*. 1998). Likewise, kaka in podocarp-dominated forests at Waipapa and Whirinaki bred most intensively (> 50% of radio-tagged females nested) in years when podocarp trees produced abundant fruit crops. Masting events of rimu can be predicted from phenology observations 18 months prior to fruit ripening (McEwen 1988), but probably less than 6 months prior to seed formation in beech species (Wilson *et al*. 1998). Other forest bird species also breed most intensively during such masting events, such as the kereru (*Hemiphaga novaeseelandiae*) (Powlesland *et al*. 2003) and yellow-crowned parakeet (Elliott *et al*. 1996a). Therefore, timing expensive pest-control operations to coincide with masting events would benefit a variety of native forest-dwelling bird species.

Kaka fledglings that ended up on the ground after leaving their nests were particularly vulnerable to being killed by a variety of introduced predators, including stoats, brushtail possums, feral cats and ferrets. In order to provide some protection for these young birds, it is vital that pest control operations take into account all species of predators present and the months when kaka nestlings are likely to fledge.

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