

Breeding, survival, and recruitment of Chatham Island pigeon (*Hemiphaga chathamensis*)

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Abstract The Chatham Island pigeon or parea (*Hemiphaga chathamensis*) is an endangered species of pigeon endemic to the Chatham Islands. Effective conservation management of the Chatham Island pigeon required an understanding of its ecology and identification of the causes of decline. We studied the pigeon in their last remaining stronghold; the south-west of Chatham Island, New Zealand, between July 1991 and December 1994. We describe the nesting behaviour, nesting success, and the dispersal, survival, and recruitment of juveniles. The study was confounded by the lack of information on predator numbers or outcomes of pigeon nests from before the start of predator control activities within and adjacent to our study area. Despite a previously reported decline in pigeon numbers up until the early 1990s, during this study there was a 3-fold population increase, and only a low level of predation by possums and rats. Other than predation, no factor which might previously have limited the pigeon population was identified. We assume that the trapping and poisoning of pest-mammals since 1989, has been sufficient to allow the population of Chatham Island pigeon to recover.

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INTRODUCTION

The Chatham Island pigeon or parea, *Hemiphaga chathamensis*, occurs only in the Chatham Islands, 860 km east of New Zealand. *Hemiphaga* is an endemic, monotypic, New Zealand genus of large (500-900 g) fruit pigeons whose relationship to other fruit pigeons is problematic (Goodwin 1983). Three taxa have been described, of which 2 are extant; the kereru (*Hemiphaga novaeseelandiae*) is widespread, though probably declining, throughout the mainland of New Zealand, while the Chatham Island pigeon is considered endangered (Bell 1986).

Chatham Island pigeons remained common well into the period of European and Maori settlement during the nineteenth century (Travers & Travers 1872), but by 1975 were rare and largely confined

to the more forested southern area of Chatham Island (Merton & Bell 1975)(Fig. 1). In 1989 the population was estimated at 40-45 individuals (Grant 1990), though Pearson & Climo (1993) consider that this was an "optimistic" figure. The decline has been attributed to widespread clearance and degradation of the forest habitat by humans and domestic stock, coupled with predation by humans and introduced mammals (Grant 1990). Known, or potential, predators of the pigeon that have been introduced to the islands include cats (*Felis catus*), 3 species of rats (Pacific rat, *Rattus exulans*; ship rat, *R. rattus*, and Norway rat, *R. norvegicus*), brushtail possums (*Trichosurus vulpecula*), pigs (*Sus scrofa*), and weka (*Gallirallus australis*).

Agricultural development on the islands has increased the area of open habitat. Consequently, a predator of pigeons, the Australasian harrier (*Circus approximans*), which was considered rare on

Chatham Island in 1872 (Travers & Travers 1872), is now common. Given this predation pressure, concern was expressed over the plight of Chatham Island pigeons by Grant (1990) and Pearson & Climo (1993). To aid management of the pigeons Grant (1990) and Pearson & Climo (1993) recommended research into their biology and ecology, and the relative impacts of predators on their breeding and survival.

Our study aimed to determine causes of decline and to investigate at which life-history stage(s) reduced survival contributed most to the decline. It became clear during the 3 years of this study, that the pigeon population was no longer declining. Breeding success, juvenile recruitment, and adult survival were all high and the population increased 3-fold in that time (Grant *et al.* 1997). We suggest that this may be attributed to the success of a predator-control programme, aimed at cats and possums, which began in this area during 1989 and was expanded throughout the pigeon habitat during the course of our study (Imber *et al.* 1994; Grant *et al.* 1997).

This paper, therefore, describes the breeding biology and survival of the Chatham Island pigeon between 1991 and 1994. Information that we present on nesting requirements may be used to encourage landowners to protect further lands by fencing and removal of stock. The fledging rate will provide a baseline from which to determine the success of future management of the species. Related topics, such as distribution, abundance, and diet and its relationship to breeding have been presented elsewhere (Grant *et al.* 1997; Powlesland *et al.* 1997).

STUDY AREA AND METHODS

Study area

The study area, (c.400 ha), was in south-west Chatham Island (Fig. 1) and included the catchments of the Awatotara Creek, Tuku-a-tamatea River, Kawhaki Creek, and Waipurua Creek to about 3 km inland. The main habitats of Chatham Island pigeon in the Awatotara and Tuku-a-tamatea catchments were partially fenced in 1985 to exclude grazing animals. During 1992-93 the fenced area was extended to include more habitat (Grant *et al.* 1997). A mosaic of regenerating low forest, scrub, fern, and rough grassland (Powlesland *et al.* 1997) now covers areas within the fence.

Predator control

A line of predator control traps was set periodically, from 1989, to protect Chatham Island taiko (*Pterodroma magentae*) nesting on the margins of the pigeon study area (Imber *et al.* 1994). The trapping may have reduced predator densities within the pigeon habitat. From 1992/93, brodifacoum bait-

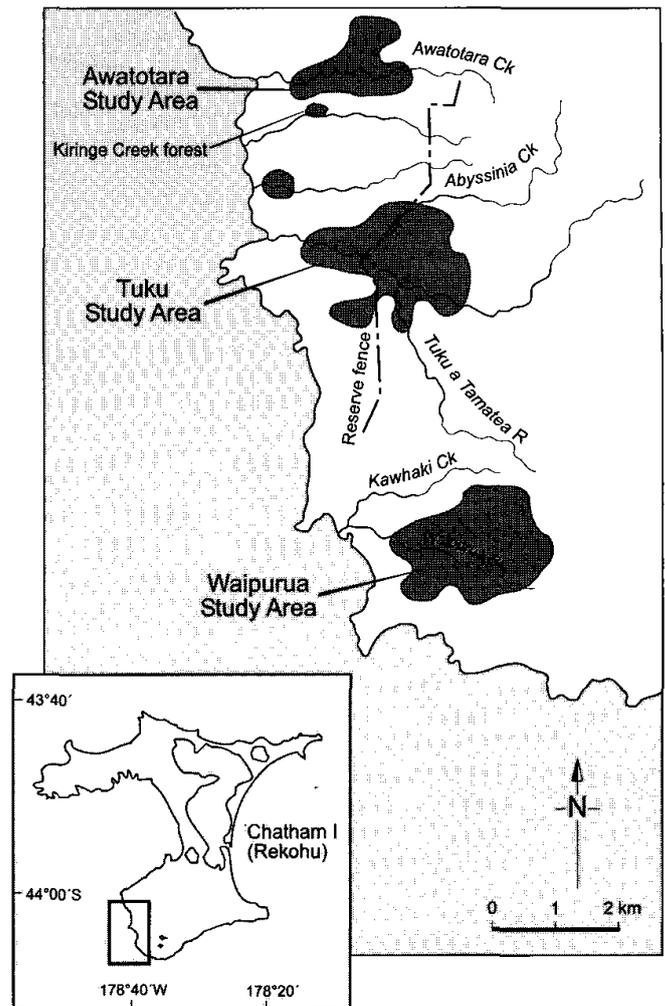


Fig. 1 Chatham Island, showing locations of Chatham Island pigeon (*Hemiphaga chathamensis*) study areas (shaded).

stations set throughout the pigeon breeding area and baited 6-monthly (Grant *et al.* 1997) kept possums at very low densities ($<1\text{ha}^{-1}$) over most of the study area for the remainder of our study (Grant *et al.* 1997). During 1991 we protected all nests. Six rat traps and 6 bait stations containing brodifacoum bait were spaced evenly within a 25 m radius of each nest. The following year we protected only half the nests located, and from 1993 on we did not protect nests.

Capture and marking

Three-week field trips were made 4 times each year from 1991 to 1994, with additional trips when pairs were breeding. Over this time 27 adult pigeons were captured using mist-nets and 37 nestlings were marked shortly before fledging. Captured birds were weighed, then individually marked with numbered metal leg-bands and coloured leg-flags (jesses), of nylon-reinforced PVC. No sexual dimorphism was evident visually or in the weights recorded. Sex was assigned only after observing

courtship, nest-changeovers, or copulations. Nine adults and 6 nestlings were also fitted with radio transmitters using a back-mounted harness design (Karl & Clout 1987).

Monitoring of adults and nests

During each field trip we searched for pigeons to determine survival, breeding activity, and the presence of juveniles. Radio-tagged individuals were located using radio-telemetry. Others were detected by searching suitable habitat within and beyond the study area, where particular foods were abundant. All day watches from hilltops identified where birds were active. The rate of display flights provided an indication of breeding activity and careful observation of these flights was often useful in locating pair territories and nest sites. Individually colour-jessed birds could be identified from considerable distances and all sightings were logged.

For up to 8 months after fledging, juvenile pigeons could be readily distinguished from adults by their dull, brown-tipped bill, dull feet, dark eyes, and a less well-defined border between the dark chest and white breast feathers (Powlesland *et al.* 1994; Mander *et al.* 1998).

Nests were located by observing pairs, noting nest changeovers or carriage of twigs, and following individual birds or locating birds with radio-transmitters (Powlesland *et al.* 1997). We recorded a description of each nest site, including location, the species of the supporting plant, vegetation type, nest height vertically above ground, canopy height above the nest, and an estimate of the vegetation cover (proportion of sky concealed) directly above the nest. All possible nests, and where possible their contents, were examined at least weekly to determine their fate. In addition a sample of nests at different stages of the breeding cycle was observed from dawn to dusk to record times when adults changed over at the nest and when they fed chicks.

RESULTS

Gender roles

Gender was not independently determined for most pigeons during the course of this study. However, we determined that 1 member of each study pair consistently incubated at night and the other by day. We assume throughout this paper that day-incubating birds from all pairs were male and night-incubating birds were female. Our observations of nest building (below) support this assumption in that gender roles were consistent with those described for other pigeon species (Goodwin 1983). Confirmation of our gender assignment was obtained for 3 pairs from their positions during copulations.

Nests

Between 1991 and 1994, 101 active nests were located. Initially, both members of pairs collected material and built nests. However, when nest building intensified, males collected most of the material while females accepted and arranged twigs at the nest. Twigs up to 50 cm long were used, of tarahinau (*Dracophyllum arboreum*), karamu (*Coprosma chathamica*) or, less commonly, kopi (*Corynocarpus laevigatus*), supplejack (*Ripogonum scandens*), and matipo (*Myrsine chathamica*).

Twelve nests were observed during site selection or early building stages. Pairs visited potential nest sites together, frequently displaying and breaking off and carrying twigs. Nest building over 1-3 days established the basic nest structure that was added to sporadically over the following 2-12 days before egg laying.

Nests were built between ground level and 10.1 m above ground, (mean 3.9 m, SD = 2.2 m, $n = 101$). Two nests were built on the ground and a further 5 were within 1 m of it. Average canopy height above nests was 5.6 m (SD = 2.1 m, range 1.1 - 10.5m, $n = 101$), thus most nests were well within the forest canopy or in understorey vegetation. Nests were usually on firm bases such as shallow-branched forks, near-horizontal trunks, dense clusters of twigs, overlapping bases of tree-fern fronds, tangles of supplejack vines, or combinations of these. Most (89%) of nests were robust platforms of twigs with a shallow bowl, whilst the remaining 11% were insubstantial structures. Nests were commonly in valley bottoms (41%) or lower slopes (55%) in dense, mixed broadleaf and tree-fern vegetation. Fourteen plant species provided nest sites either individually or in combination. Site details were recorded for 98 nests, 20.4% were in *Dicksonia* tree-ferns, 13.3% in tangles of tree-fern (*Dicksonia*) fronds and supplejack vines, 15.3% in matipo, 10.2% in kopi, 9.2% in hoho (*Pseudopanax chathamica*), and 9.2% in tarahinau. Parea were rarely seen feeding in groves of *Dicksonia* tree ferns, yet 34% of nests were in such sites. Hardwood trees supported 56% of nests, and a further 9% were in bracken, low scrub, or on the ground. In general, Chatham Island pigeons selected sites concealed by dense tangles of overhead vegetation and only 7% of nests had little (<60%) cover overhead.

Pairs were territorial and favoured particular parts of their territory for nesting. Nests were often situated within 100 m of previous nests but reuse of nest sites was uncommon (14%, $n = 63$ nests, where a pair's previous nest site(s) was known). Only on 3 of the 9 such instances did old nest material remain at the site as a base on which new nesting material was arranged.

Eggs

Parea eggs were smooth, oval and matt white (length, $\bar{x} = 50.7$, $SD = 1.96$, $n = 13$, range 46 – 53; width, $\bar{x} = 34.3$, $SD = 1.03$, $n = 13$, range 32.5 – 35.5). The fresh weight of an egg was estimated to be 31.9 g [weight = $k \times \text{length} \times (\text{breadth})^2 / 1000$, with $k = 0.535$, averaged from data on the Columbidae; Robertson (1988)] which represents 4.0% of mean adult weight (789 g, $n = 38$). Weights of known males and females did not differ significantly (authors' unpubl. data). Three intact eggs, which had been incubated for 5–10 days, were found on the ground below nests and weighed 32, 31, and 30 g respectively. Four eggs that failed to develop and had been abandoned after full-term incubation weighed 29.0, 28.1, 27.0, and 26.4 g. Clutch size was 1 in all 17 nests where the egg was seen, and brood size was invariably 1 ($n = 73$).

Fifteen of 22 pairs (68%) were actively nest-building up to 4 days before the known or estimated date of laying (as determined by hatch date), and at least 5 pairs were intensively nest-building up until the date of laying. Seven pairs (32%) had pre-laying periods of 6–14 days from the completion of intensive nest-building activity until the egg was laid. In the pre-laying period, females were found sitting on nests during the day, and males occasionally brought twigs to the nest. At 2 nests, pair changeovers were observed even though eggs had not been laid.

Incubation and early brooding

For 8 nests where the date of laying was known, incubation began immediately at 5, while at 3 the egg was left for up to 20 min. at a time during the first few days. The incubation period was recorded for 4 nests. Time between start of incubation and first sighting of either eggshell fragments below the nest or a chick was 27, 27, 28, and 29 days.

Seventy-seven nests were observed during incubation. Male pigeons incubated for about 50% of daylight hours, from 0.5–1h before solar midday until 0.5–1h before sunset (Fig. 2). Changeovers were rapid, with the egg exposed usually for less than one min. During incubation and while the chick was being constantly brooded (<10–15 days old) Chatham Island pigeons brought a twig, usually leafy tarahinau, to their nest at changeovers on 69.4% of 62 occasions. There was no difference between the sexes in this behaviour; males brought twigs on 68.7% of occasions ($n = 32$) and females on 70% of occasions ($n = 30$).

Chick rearing

Chicks were brooded constantly until well feathered at about 10–15 days old. Thereafter, brooding was erratic, with chicks left unattended for long

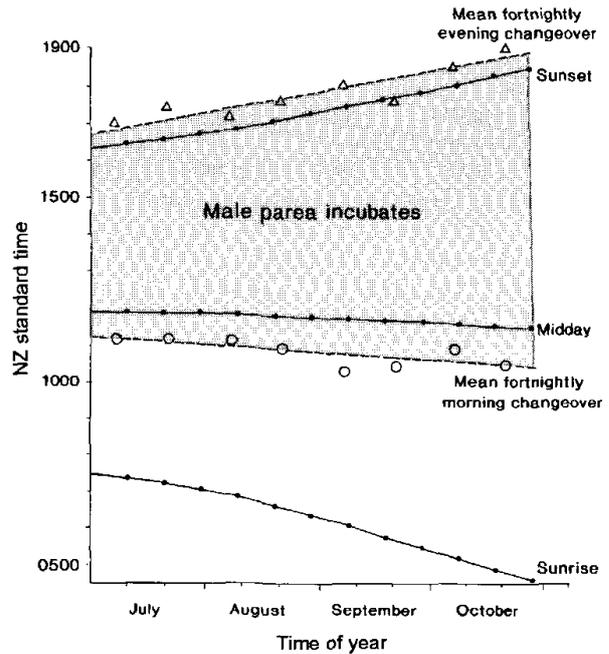


Fig. 2 Period of the day that male Chatham Island pigeon (*Hemiphaga chathamensis*) incubated (shaded) relative to New Zealand Standard Time at sunrise, midday, and sunset during the main nesting months (July–October); $n = 77$ nests.

periods. Nestlings were fed infrequently during the first 2 weeks. One 7-day-old chick was fed only once during the day, and 2 chicks aged 12 and 15 days were each fed twice. A chick 36 days old and another aged 37 days were fed 3 and 5 times respectively, by day. It is not known whether nestlings were also fed at night. The incoming parent usually initiated food regurgitation; chicks encouraged feeding at times by pecking around the adult's bill and neck, flapping wings and emitting low begging calls. Feeding progressed as a series of bouts of regurgitations over 5–20 min.

In their 1st week, chicks were sparsely covered with down. Plumage developed rapidly and by 14 days of age chicks were well covered. Remiges, rectrices, and head feathering were the last to develop. Chicks had no feathering at the base of the bill (i.e. over the forehead and cheeks), which gave the bill an elongated appearance (Mander *et al.* 1998). Feathers developed in this area after a fledgling reached independence. Fledging age was known, to within 5 days, for 20 chicks, which fledged at an average of 46 days (range 36–53 days) though many moved about in the nest tree up to 5 days before. After fledging it became difficult to locate the fledglings. Nevertheless, subsequent sightings of 16 known-age fledglings showed that parents continued to feed them for at least 1 week following fledging. The age at which fledglings

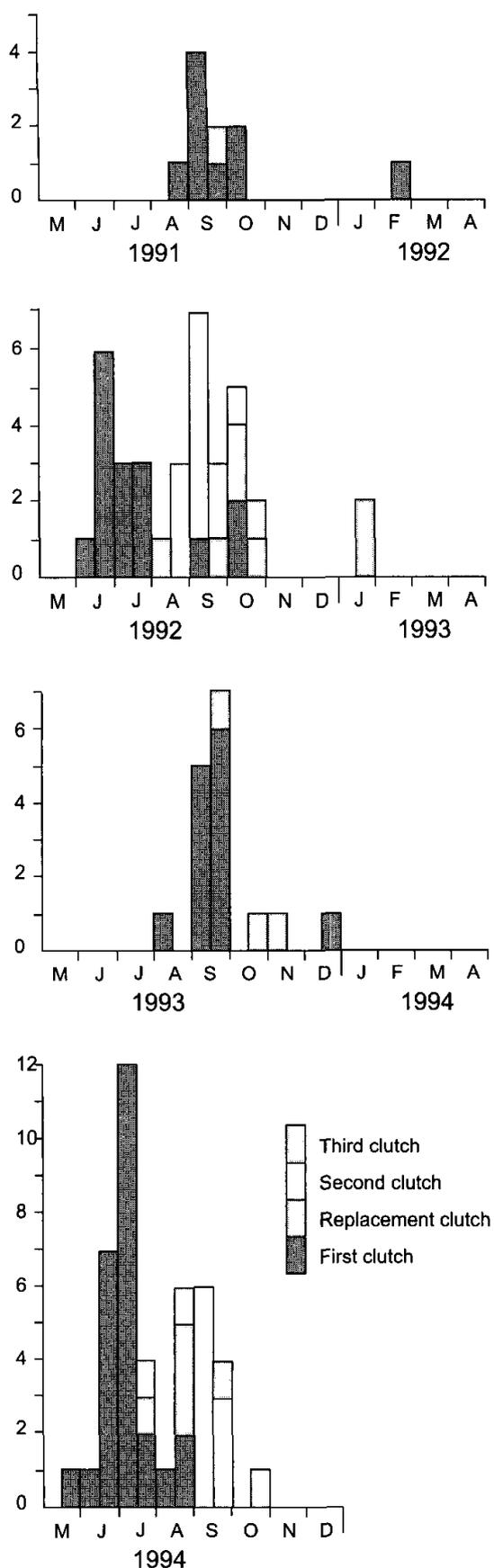


Fig. 3 Fortnightly distribution of egg-laying dates for Chatham Island pigeon (*Hemiphaga chathamensis*) during 4 nesting seasons, from May 1991 to December 1994 (after Powlesland *et al.* 1997). y-axis, no. of pairs; darkest shading, 1st clutch; medium shading, replacement clutch; light shading, 2nd clutch; = "diagonals", 3rd clutch.

reached independence was highly variable, but was usually 52 - 65 days. When pairs did not re-nest, some fledglings were seen with their parents and were occasionally fed by them for up to 179 days. If parents re-nested, fledglings from previous broods were sometimes driven from the territory, but in other instances fledglings up to 75 days old were found near the new nest and were still fed by the parents. Twenty-two of 69 nests (31.9%) had disintegrated by the time the chick fledged, chicks then perched at or near the nest site.

Reproductive effort and timing of breeding

Chatham Island pigeons bred mainly in winter but active nests were found in 10 months of the year. Peak laying in different years ranged from July to September (Fig. 3). The proportion of monitored pairs that attempted to breed varied from 44% in 1993/94 to 100% in 1991/92 and 1994/95. The mean number of breeding attempts pair⁻¹ varied from 0.5 (range 0-2, SD = 0.7, $n = 12$) in 1993/94 to 2.3 (range 1-4, SD = 1.1, $n = 16$) in 1992/93. A summary of reproductive effort is given in Table 1. In the 8 re-nesting attempts for which we know the date of previous failure, pairs began nest building in as little as 4 days (and all within 14 days), after their previous nest failed.

During the 1992/93 and 1994/95 seasons, 75% ($n = 16$) and 50% of pairs ($n = 26$) respectively, re-nested after successfully fledging a chick. In both years at least 1 pair successfully raised 3 consecutive chicks, but the pairs were different on the 2 occasions. During the 1992/93 season, 12 pairs fledged a chick and then re-nested. On 7 (58.3%) of these occasions the pairs built nests, laid, and began incubating before the nestling in their earlier nest had fledged. Similarly, during the 1994/95 season, 3 (37.5%) of 8 re-nestings involved overlapping clutches. Parents began incubating at new nests up to 15 days before their previous chick fledged; both parents fed that nestling when not incubating at the 2nd nest.

Success rate and causes of nest failure

From 1991/92 to 1994/95, 33.8% of 101 located nests failed (Table 1). Because nests were difficult to locate we may have missed those that were lost early in incubation during 1993 and 1994 when many pairs were breeding. Causes of the 32 failures were predation (46.9%), insecure nests (18.7%), no visible embryo development (15.6%), unknown (6.3%), abandoned egg (6.3%), chick death (3.1%) and human disturbance (3.1%). Of 62 1st and 2nd nests, 28% failed as against 32.5% of subsequent attempts ($n = 39$).

During the 1st year of this study we had attempted to control rats at every nest but during the

Table 1 Outcomes of Chatham Island pigeon (*Hemiphaga chathamensis*) nesting attempts on Chatham Island, 1991 to 1995. P, predation; H, handling; I, insecure nest; F, failed to develop; A, abandoned egg; D, dead chick; ?, unknown cause.

Nesting season	Pairs		Nests		% pairs fledging young	Mean no. of young		Cause of failure
	No	% breeding	Found	% failed		Pair ⁻¹	Breeding pair ⁻¹	
1991/1992	11	(91%)	11	36	70	0.64	0.70	P,H,I,?
1992/1993	16	(100%)	37	35	94	1.5	1.5	5P,3F,A, 3I,?
1993/1994	27	(44%)	15	46	53	0.29	0.67	5P,F,I
1994/1995	29	(100%)	45	18	93	1.03	1.03	4P,F,I, A,D

2nd year we employed traps and bait stations at only half of the nests. We observed no significant difference (Fisher's Exact test, $p > 0.1$) in predation rates between protected (58% fledged, $n = 17$) and unprotected nests (66% fledged, $n = 15$).

Predation occurred at egg and chick stages (Table 1). We confirmed harriers (*Circus approximans*) as the predator at 3 nests; 1 with an egg and 2 with chicks. At 1 nest, faeces and finely nibbled eggshell suggested that the predator was a rat (*Rattus spp.*). Coarsely crushed egg remains were thought to indicate predation by a brushtail possum (Brown *et al.* 1996) at another nest. However, at most preyed-on nests we could not determine the predator. The rate of predation was highest (33% of 15 nests) in the poor breeding year of 1993/94, and lowest (4% of 46 nests) in 1994/95.

The presence of 5 eggs on the ground beneath nests was attributed to the insecurity of the nests. Two nests were so sparsely made that the egg fell through or rolled off the material, and in 3 others the surrounding vegetation did not securely support the nests. Such nest collapses may have been caused or accentuated by predator visits or by windy weather.

From 93 breeding attempts for which egg development was ascertained, 5 (5.4%) eggs failed to develop a visible embryo. Three of these failed eggs were recovered in the 1992/93 season; 2 were 2nd clutches from pairs that laid viable eggs in their 1st and 3rd clutches of the season. No pair consistently laid eggs that failed to develop.

Fledgling survival

Of 35 nestlings banded and individually jessed during the first 3 seasons (Table 2), 31 (88.6% of those fledged) were seen when 10–12 months of age. Of the remaining 4, a 7-month-old juvenile was killed by a cat, and the other 3 were not seen again, but may have moved beyond our study area. Several jessed pigeons, both adults and juveniles, have remained undetected by us for periods in excess of a year before being seen again.

Dispersal

In each of the first 2 seasons, 3 nestlings were fitted with radio-transmitters. The movements of these birds after fledging and chance observations of marked juveniles show that 2 females paired on territories within 1 km of their natal areas, and a 3rd female paired on a territory 4 km away from her natal area. The maximum distance recorded was for a male that took up a territory 5.5 km from its natal area. The other 4 males known to have bred moved 0.2, 0.3, 0.6, and 1.5 km. All recorded movements were within 3 km of the coast, but birds which may have moved inland from the study area were less likely to have been located because it was difficult to search there.

Recruitment

Age at first breeding was unknown for most fledglings. Fourteen (40%) of the fledged young paired and bred within the study area. Three females were found breeding at 8, 11, and 21 months of age (mean, 13.3 months), and 5 males bred at 20, 24, 32, 32, and 34 months of age (mean, 28.4 months). A further 5 birds of unknown sex bred at 21, 24, 25, 28, and 29 months of age (mean, 25.4 months).

All 6 fledglings from the 1991/92 season were sighted with mates, and 5 were known to have bred at least once before the end of the study. One female of this cohort successfully fledged 4 young in the 3 seasons following her pairing; the other female fledged a chick in the 1992/93 season, but was not monitored subsequently.

None of the 1992/93 cohort was known to breed in the following season which was a season of poor fruit availability (Powlesland *et al.* 1997) and only 44% of the already established pairs attempted to breed. Of 21 pigeons that fledged in 1992/93, 19 (90%) were sighted subsequently and 9 (43%) were located with nests or dependent fledglings in 1994–95. Of 9 young that fledged during May to September 1992, 7 were found breeding in the study area during the 1994/95 season. In contrast, only 2 of

Table 2 Number of juvenile Chatham Island pigeons (*Hemiphaga chathamensis*) marked as nestlings during the 1991-92, 1992-93 and 1993-94 seasons that were seen again during the 1992-93, 1993-94 and 1994-95 seasons, Chatham Island.

Season	Nestlings marked	Marked juveniles resighted (recruited)		
		1992/1993	1993/1994	1994/1995
1991/1992	6	6(2)	4 (2)	5 (5)
1992/1993	21	-	19 (0)	13 (9)
1993/1994	8	-	-	6 (0)

the 12 young that fledged after the start of October were subsequently found breeding within the study area. None of the young that fledged in 1993/94 was found breeding in 1994/95 despite that being a major breeding season.

DISCUSSION

Nesting biology

The nesting biology of the Chatham Island pigeon, including the roles of the sexes during nest-building and incubation, was similar to the New Zealand pigeon (Moon 1967; Dunn & Morris 1985; Clout *et al.* 1988; James 1995) and other pigeons (Goodwin 1983). Chatham Island pigeon nest-building behaviour was typical of tree-nesting pigeons; the male brought material to the site and the female accepted it and built the structure (Goodwin 1983). Chatham Island pigeons chose nest sites that offered horizontal support for the material and where the nest was well screened from above and the sides by vegetation. Presumably good cover was important to reduce the likelihood of the adult or nestling being seen by avian predators such as the Australasian harriers, which prey on nestlings of a variety of species, including Chatham Island and New Zealand pigeons (Dunn & Morris 1985). Before European settlement, the New Zealand falcon (*Falco novaeseelandiae*) is likely to have been a key predator of the Chatham Island pigeon (R. Holdaway pers. comm.).

The Chatham Island pigeon commonly nests low to the ground. This is rare for New Zealand pigeons but has been reported on the Hen and Chickens Islands (Moon 1967; Pierce & Graham 1995) where the Pacific rat was the only predatory mammal. The contents of pigeon nests built on, or within 1 m of the ground, were readily accessible even by less arboreal introduced predators such as Norway rats and weka. Such nests may also be put at risk by stock movements in areas that are not adequately fenced. Higher nests can be reached easily by possums, cats, and ship rats, which readily climb to the canopy.

Chatham Island pigeons lay a single white egg.

The egg weight relative to mean body weight is similar for the 2 New Zealand pigeons (4.0% for CIP and 4.3% for NZP; Robertson 1988). The incubation pattern of males and females closely resembled that of the New Zealand pigeon (Moon 1967; James 1995). Time off the nest allowed each gender roughly equal daylight hours for provisioning. Although other observers have noted that New Zealand pigeons add twigs to the nest at changeovers during the incubation and early in the nestling-rearing phases (Moon 1967; Dunn & Morris 1985), the frequency of such additions has not been quantified. Twigs were carried on 69.4% of occasions that a Chatham Island pigeon came to the nest to relieve its partner. As the twig was not presented to the mate as part of a pair-bonding or greeting ceremony, but was added to the nest, possibly the activity helped to maintain the nest structure.

The incubation period for the Chatham Island pigeon was 27-29 days, close to or within the ranges reported for New Zealand pigeons; 29-30 days (Moon 1967), 29-30 days (Dunn & Morris 1985), 28-29 days (Clout 1990), and 25-30 days (James 1995). Infrequent feeding of nestling Chatham Island pigeons by day, especially when less than 2 weeks old, has also been noted for New Zealand pigeon nestlings (Moon 1967), but probably under-represents total feeding. Using a video camera and recorder with infra-red lighting, James (1995) showed that nestling New Zealand pigeons less than a fortnight old were fed mainly between midnight and sunrise. Perhaps chicks are fed infrequently by day to reduce the frequency of visits to the nest and therefore the likelihood of the nest being found by avian predators such as harriers. Certainly chicks' crops can accommodate a considerable quantity of rich food in the form of crop milk and partly digested food fed by their parents. The large volume given probably sustains the chick when left for long periods of the day after it is 2 weeks old.

Length of nesting cycle

Both surviving species have low productivity given that the clutch size is 1, and the nest cycle from nest building to the chick fledgling lasts about 3 months.

Even after fledging, young Chatham Island pigeons continue to depend on their parents for food for at least a further 3 weeks. Clutch-overlap is a means by which a species can increase its reproductive output when it cannot increase clutch size, or has a brief energetically limiting phase in the nesting cycle. Both species have a herbivorous, low-protein diet so production of crop milk for the young chick may be energetically limiting (Clout *et al.* 1988). Clutch-overlap has been recorded for several of the Columbidae (Robertson 1985), including the New Zealand pigeon (Clout *et al.* 1988). Chatham Island birds were able to sustain overlapping clutches only in those breeding seasons when nutritious food was particularly abundant (Powlesland *et al.* 1997). Clutch-overlap decreased the time taken for a pair of pigeons to complete 2 nesting cycles from about 240 days (nest-building, 3 days; pre-laying period, 5; incubation, 28; nestling, 45; fledgling, 40) to about 185 days, a 23% reduction. Clutches were overlapped in half of the 20 occasions that pairs fledged a chick and re-nested.

When pairs overlapped clutches, they fed their first fledglings for only about 20 days compared with about 40 days when raising only 1 brood. Chatham Island pigeons overlapped clutches only in years of abundant food. It is possible that the shorter provisioning period in those years resulted in lighter chicks, but given the abundant food this may have been of no consequence to chick survival. Our data were insufficient to detect any difference in the survival of these fledglings. The Mauritius pink pigeon (*Columba mayeri*) rarely raised more than 1 chick and never overlapped clutches, but fledglings whose parents had access to food supplements reached independence at 10-20 days, whereas young of pairs without access to supplementary food took 60-90 days (Jones *et al.* 1992).

Food determines nesting season

Quality and quantity of food were the main factors controlling nesting in the Chatham Island pigeon (Powlesland *et al.* 1997). During the winters of 1992 and 1994, when fruits were abundant, most pigeons began their nesting in winter (Fig. 3) when other environmental factors would have been at their least favourable (i.e. shortest day-length and coldest temperatures). Although New Zealand pigeons have been recorded nesting in winter (Genet & Guest 1976; Pierce & Graham 1995), most nests have been found during spring and summer (Dunn & Morris 1985; Clout *et al.* 1988). James (1995) concluded from his study at Wenderholm, Auckland, that the ultimate factors controlling the breeding of pigeons there were most likely food availability and temperature. Results from other studies indicate that food has a pronounced impact on the timing and duration of pigeon and dove nesting. For example Mauritius pink

pigeons that fed on food supplements nested 3 months earlier than those that did not (Jones *et al.* 1992). Captive New Zealand pigeons at the National Wildlife Centre, Wairarapa, with *ad libitum* access to nutrient-rich foods frequently raised 2 or 3 chicks year⁻¹ (M. Bell, pers. comm.). The ability of Chatham Island pigeons to nest earlier and for longer in years with abundant food (Powlesland *et al.* 1997) was important in enabling them to increase their numbers quickly after feral cat, rat and possum population densities were reduced (Grant *et al.* 1997). As well as preying on nests, rats and possums overlap considerably with pigeons in their use of plant species (Tisdall 1992). Their feeding on fruit competes directly with the birds and their damage to bark and foliage of some species (notably hoho) undoubtedly has an impact on fruiting ability. Though not quantified, it seems likely that the amount of fruit available to Chatham Island pigeons may have increased as the pest populations declined.

Nesting effort and success

The nesting effort of Chatham Island pigeons varied from year to year. Only 44% of pairs nested in 1993/94, but all pairs nested in 1992/93 and 1994/95 when many of them attempted to rear two successive fledglings (Powlesland *et al.* 1997). Similarly, the nesting effort of New Zealand pigeons has been found to vary between years. At Pelorus Bridge, Marlborough, nesting began in summer and eggs were laid as late as June (winter) in good fruiting years (Clout *et al.* 1995a). At the same site no pairs nested in a very poor fruiting season.

Prolific breeding by Chatham Island pigeons, in conjunction with sustained control of feral cats and brushtail possums, resulted in a marked increase in the numbers of pigeons during the study (Grant *et al.* 1997). Pairs re-nested promptly after the failure of a nesting attempt and were found nest-building within a week of a failure. Similarly, New Zealand pigeons will lay again within 8 days of losing an egg (Clout *et al.* 1995a). The most nestings we recorded for a pair of Chatham Island pigeons in a season was 4, 2 of which were successful.

As well as re-nesting promptly, Chatham Island pigeons reared 2 fledglings in some seasons, and exceptionally 3. We suggest that this may be attributed to the populations of frugivores and herbivores (including pigeons) being well below the levels the habitat could sustain after the possum population declined. No comparative information on the reproductive output of pigeons on the mainland is available because a high proportion of their nesting attempts are foiled by predators (Clout *et al.* 1995a; Pierce & Graham 1995).

The overall nesting success of *parea* during this study was 68% ($n = 101$). A very similar result (63%, $n = 16$) was observed for New Zealand pigeons on

predator-free Lady Alice and Coppermine Islands, Northland, where Pacific rats were present but not thought to be a threat to pigeons (Pierce & Graham, 1995). In contrast, the nesting success of pigeons at 4 mainland sites (without any predator or competitor control) was 22.2 % ($n = 45$) at Pelorus Bridge during 1984-91 (Clout *et al.* 1995a), 0% ($n = 9$) at Mohi Bush during 1988-91 (Clout *et al.* 1995a), 0% ($n = 27$) at Wenderholm during 1988-92 (Clout *et al.* 1995b), and 19% ($n = 31$) at Maungatapere, Northland, during 1991-93 (Pierce & Graham 1995). At Wenderholm during the 1992/93 nesting season rats were poisoned and Clout *et al.* (1995b) reported that pigeon nesting success increased from 0% to 45.5% ($n = 11$). These results indicate that predators have a major impact on the productivity of New Zealand pigeons and that predator control can lead to rapid recovery of pigeon populations.

Population recovery

Working with rare species can present researchers with considerable problems in interpretation. In this study, the lack of previous information (on either Chatham Island pigeons or their food-plant seasonality), the lack of a non-managed, control population and small sample sizes limited our ability to draw strong conclusions. With the population of pigeons down to <50 birds at the start of our study we encouraged the management decision to augment control of mammalian pests at the site, based on our knowledge of the impact of mammalian predators on other New Zealand forest bird species. The hoped-for dramatic population increase happened during our study yet the study presents only circumstantial evidence that removal of predators caused the increase.

Once possum and feral cat numbers had been reduced to low levels (Grant *et al.* 1997) several factors enabled the pigeon population to increase. Nesting success was 68% as against 0-22% for pigeons on the mainland (Clout *et al.* 1995a; Pierce & Graham 1995). Chatham Island pigeons were able to reduce the length of the nesting cycle by nearly 25% by overlapping their clutches. If a nest failed part way through the nesting season, pairs quickly laid a replacement clutch. Thus, in 2 of the 4 nesting seasons when fruit (particularly hoho) was abundant, all pairs were able to breed and some reared 2 or 3 broods within a season. Survival to 1 year of age, and recruitment were both high. Nearly 90% of 35 marked nestlings were seen when 10-12 months of age. By this age, 2 of the 3 females had bred, while did not breed before 2-3 years of age. The sexual difference in mean age at first breeding possibly results from males having to acquire and defend a territory for nesting, whereas young females were able to pair with mature, unpaired males that already held a territory. Adult annual survival rate was 0.96 (Grant *et*

al. 1997). The combination of all these factors allowed the number of adult pigeons in the Awatotara and Tuku study areas to increase 3-fold from 1990 to 1994 (Grant *et al.* 1997).

The observed dispersal of juveniles to sites 4-6 km from their natal ranges suggests that sustained pest control will allow the pigeon population to increase and re-colonise distant areas of suitable habitat. Foraging and nesting habitats of the pigeons have been greatly modified in the past by human disturbance. Chatham Island pigeons regularly nest near the ground in relatively young vegetation, so fencing and removal of feral stock, particularly from land with some forest remnants, can rapidly increase the number of suitable breeding sites.

Pigeons are the only large frugivorous birds on the Chatham Islands, and so they play a crucial role in the dispersal of a wide variety of forest seeds. We are optimistic that, given the species' longevity, periodic but intensive control of pest mammals, coupled with further habitat protection, will ensure the conservation of healthy pigeon populations that can perform this vital function.

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