

Breeding biology of the Kakerori (*Pomarea dimidiata*) on Rarotonga, Cook Islands

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ABSTRACT

The breeding biology of Kakerori, or Rarotonga Flycatcher, (*Pomarea dimidiata*) was studied during ten years (1987-97) of experimental management aimed at saving this endangered monarch flycatcher from extinction. Kakerori remained territorial all year and were usually monogamous. Most birds kept the same mate from year to year, but pairs that failed to raise any young were more likely to divorce than successful pairs. Despite living in the tropics, Kakerori breeding was strictly seasonal, with eggs laid from early October to mid-February, and mostly in late October and early November. Nesting started earlier in years when October was very sunny. Most pairs (74%) laid only one clutch, but some pairs laid up to four replacement clutches when nests failed. Three pairs (1%) successfully raised two broods in a season. Rat (*Rattus* spp.) predation was the principal cause of nest failure, especially of nests in pua (*Fagraea berteriana*), the main fruiting tree used by rats during the Kakerori breeding season. Annual breeding productivity was initially poor (0.46 fledglings per breeding pair over two years) and the population was declining, but intensive management since 1989 has led to a great increase in productivity (1.07 fledglings per breeding pair over eight years) and the number of Kakerori has increased from 29 birds in 1989 to a minimum of 153 birds in 1997. Their IUCN conservation status can therefore be lowered from 'critically endangered' to 'endangered'.

KEYWORDS: Kakerori, *Pomarea dimidiata*, breeding, conservation, Cook Islands, monarch flycatcher.

INTRODUCTION

The Kakerori, or Rarotonga Flycatcher, (*Pomarea dimidiata*) is a small endangered monarch flycatcher, endemic to Rarotonga, Cook Islands. No published information is available about the breeding biology of the Kakerori or the other four species of *Pomarea* flycatchers in eastern Polynesia.

Kakerori were very common throughout Rarotonga until the middle of the 19th century; however, their numbers declined rapidly and their range became restricted to the forested interior in the late 1880s (Gill 1885). By the early 1900s they were thought to be extinct, but were rediscovered in 1973, and the first nest of the species was found in 1983 (Robertson *et al.* 1994). Rod Hay and Gerald McCormack colour-banded eight Kakerori in 1984, and searches from 1984 to 1987 showed that the small population of Kakerori was restricted to dense forest at medium altitude (100-250 m) in rugged terrain on the wettest side of the island (Robertson *et al.* 1994).

Kakerori are unusual among passerines in exhibiting an extreme form of delayed plumage maturation. The age of birds can be determined from bill and plumage colours for the first three years, until the definitive basic plumage is attained at the

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start of the fourth year (Robertson *et al.* 1993). Birds of both sexes are, however, capable of breeding as yearlings. Males are larger than females, and although there is some overlap in measurements, most birds can be sexed from bill length and/or head+bill length measurements (Robertson *et al.* 1993). In the field, size differences are usually indistinguishable, but the sex of birds can be determined from their behaviour during the breeding season.

Since 1987, we have studied the breeding of Kakerori as part of a recovery programme aimed at saving Kakerori from extinction, by firstly determining why they were critically endangered, and then experimentally managing their main threats. We found early in our study that Kakerori were declining because ship rats (*Rattus rattus*) and possibly Pacific rats (*Rattus exulans*) preyed on eggs and nestlings. Our management since 1989 has been to improve breeding success of Kakerori by seasonal poisoning of rats in the 155 ha of forest occupied by the remnant Kakerori population, and by banding trees to prevent rats from reaching nests (Robertson *et al.* 1998). Our observations on the breeding success of Kakerori have been used as a measure of the effectiveness of our experimental management. Since 1989, the number of Kakerori has increased more than five-fold, from 29 birds to at least 153 birds in 1997.

Because of the critical state of the Kakerori population we maintained a policy of minimal disturbance to nesting birds, so, as many of the nests were high and inaccessible, some of our data on breeding biology are incomplete. Also, as the population has grown, it has become increasingly difficult to follow the breeding attempts of all pairs.

METHODS

Study area

Rarotonga (21°14'S, 159°46'W) is the highest (653 m) and largest (6700 ha) of the 15 islands in the Cook Islands group. Most of the rugged basaltic interior of Rarotonga is forested and uninhabited. Almost all of the approximately 9000 residents live on the narrow (<1 km wide), fertile, coastal ring-plain.

Kakerori are largely restricted to 155 ha in the southeastern part of Rarotonga. This area, known as the Takitumu Conservation Area, comprises lower foothills and steep V-shaped valleys between 100 m and 250 m above sea level (Robertson *et al.* 1994). Most birds are in the upper catchments of the Totokoitu, Turoa and Avana Streams (Fig. 1), but a few are found in the lower parts of these valleys. This is the wetter side of the island, as it faces the south-east trade winds. Annual rainfall averages 3250 mm in the study area compared with 2021 mm at Rarotonga Airport on the opposite side of the island (Thompson 1986); about two-thirds of the rain falls in the wet season (November through April). Seasonal and diurnal variation in temperatures are minor, with the winter being dry and cool (94 mm rainfall and 21.9°C in July) and the summer being wet and warm (253 mm rainfall and 25.8°C in January) at Rarotonga Airport (Thompson 1986).

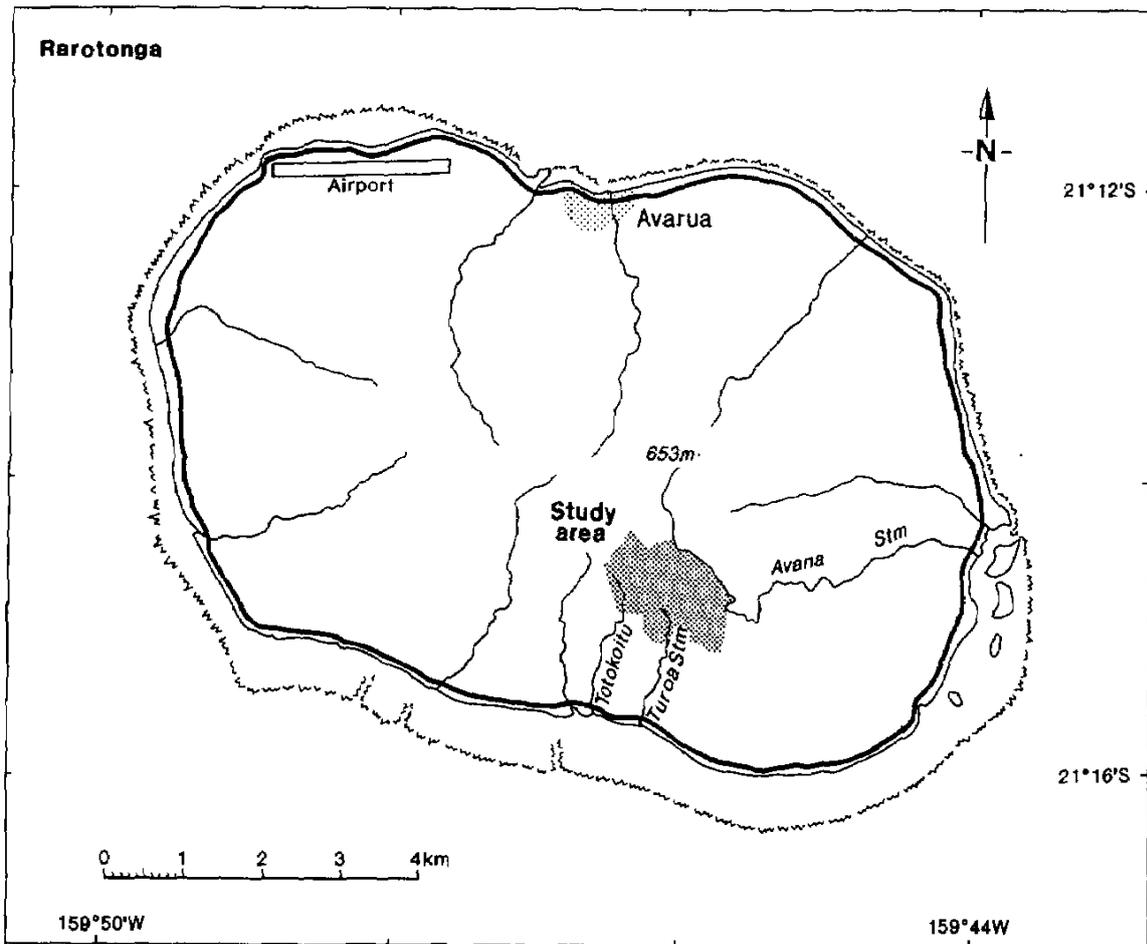


FIGURE 1 – Map of Rarotonga, Cook Islands, showing the location of the study area.

The vegetation has been described by Merlin (1985) and Sanders *et al.* (1995). The tall (up to 25 m) vegetation on the moderate to steep slopes is dominated by mato (*Homalium acuminatum*), koka (*Bischofia javanica*), karaka (*Elaeocarpus tonganus*) and matira (*Cyclophyllum barbatum*), with a dense understorey of the giant kingfern or ana'e (*Angiopteris evecta*), kavakava atua (*Macropiper latifolium*), and kiekie (*Freycinetia wilderi*). Near the valley floor the main trees are mato, pua (*Fagraea berteriana*), and 'au (*Hibiscus tiliaceus*), with a few emergent i'i (*Inocarpus fagifer*) and coconuts (*Cocos nucifera*), and a few scattered mountain lantern-tree or turina (*Hernandia moerenhoutiana*). On the ridges the vegetation is generally shorter (3-5 m tall) and dominated by pua, neinei (*Fitchia speciosa*), mato and rata (*Metrosideros collina*).

Observations

Just before each breeding season, we mist-netted and colour-banded as many yearlings and unbanded older birds as possible. During the concurrent annual censuses, we roughly mapped the territory of each pair and home range of non-territorial birds by plotting locations of birds and their territorial disputes. The proportion of

individually colour-banded birds in the population has increased from 37% in 1987 to about 80% since 1993, and the number of known-age birds has risen from 42% in 1987 to over 92% in 1997.

Through each breeding season, from October to February, we and staff of the Cook Islands Conservation Service and then Environment Service, searched for Kakerori nests. For each nesting pair, we kept detailed notes on the colour-band combinations, bill and plumage colours of the birds, the territory they were using, height of the nest up the tree and vertically to the ground, species of tree, position of the nest, and details on behaviour of the birds that could help to identify the stage of their nesting cycle.

We did not disturb breeding birds except to protect their nests by placing aluminium collars around the trunk of the nest tree and nearby trees to prevent rats from reaching nests. In a few cases, however, the contents of nests close to the ground could be examined with a mirror attached to a long pole, or by climbing an adjacent tree. No attempt was made to climb nest trees, or to band nestlings, for fear of causing desertions. This meant that some of our observations (particularly of the number of chicks present) are incomplete, and so figures given are minimum numbers of successful nests or young fledged. By 1996, there were 38 breeding pairs and we were unable to keep track of about a third of their nesting attempts, and so these were excluded from analysis of breeding success.

Most nests were visited weekly during our rat poisoning rounds, but some nests were visited almost daily, while some remote nests were visited fortnightly or even less frequently. Nest construction, incubation spells, and feeding visits were timed at a few nests, especially during the early years when there were few nests to follow.

Unless otherwise stated, we give mean \pm standard deviation and range of measurements.

RESULTS

Social structure

Typically, adult Kakerori remained in pairs and defended their territory all year. We noted four exceptions to this pattern, all involving additional birds helping to feed chicks or a change in partners. Two pairs had helpers at their nests; in one territory a male helper stayed for at least three successive years (from yearling to 3 years old), and in the other a male (yearling) and a female (2-year-old) helped to defend the territory and feed nestlings. Another pair had a 4-year old male help to feed a fledgling in January 1993 (but he was not seen at the nest), but by August 1993 the 5-year old male of the original pair had disappeared, presumed dead, and had been replaced by the new male. The final exception was a pair (3-year-old male and 2-year-old female) who twice nested unsuccessfully between mid-October 1994 and mid-November 1994, and were then joined by a yearling female. She was incubating on a third nest on 13 December 1994, while the original female stood only 2 - 3 m away; this latter bird was not seen again, and is assumed to have died.

Most Kakerori retained their mates from year to year. During the ten breeding seasons, we recorded 15 (10%) divorces out of 155 pairings where both birds were known to be alive the following year. Divorced birds were more likely to divorce again than non-divorcees; one male divorced three times and three males and three females each divorced twice. Of the 15 divorced pairs only three (20%) had bred successfully the previous season, compared with the 74% success rate of all other breeding pairs ($\chi^2 = 22.7$, $P < 0.001$).

Unpaired subadults (mainly yearlings, but some birds up to 3 years old) were generally found in loose flocks on spurs and ridges, away from breeding territories. These 'clubs' were usually moderately sedentary during each breeding season, but membership was variable as individuals occasionally abandoned one 'club' in favour of another up to 1 km away, or took up temporary residence in unoccupied valleys nearby. These 'clubs' seemed to serve as social gatherings close to, but away from, territory holders, in which young birds formed pairs and later shifted several hundred metres to occupy a territory.

Territories

Most territories were centred on a valley floor and extended up the valley sides to nearby ridges or spurs. Almost all territories were on the leeward side of major ridges and spurs, or in valleys otherwise sheltered from the prevailing south-easterly trade winds. The usual territory size was about 2 ha, but the size and shape was largely determined by topographical features, the presence of adjacent pairs, and the population size. As the population of Kakerori increased, territory size decreased; for example, in the 12 ha upper basin of the Totokoitu Valley, there were five territories (mean 2.4 ha) in 1989, but 11 territories (mean 1.1 ha) in 1996. The breeding range of Kakerori has expanded very slowly compared with their growth in population size, with only a few small adjacent valleys being colonised within the 155 ha study area since 1994.

Breeding season

Clutches were started from 5 October to 12 February, with a peak in late October and early November (Fig. 2). Most of the 75 clutches laid after mid-November were replacement clutches, but a few (11%) were true repeat clutches following successful fledging from an earlier nest. The start of egg-laying varied by up to three weeks between years; birds bred earlier in years with spells of fine settled weather in October. The mean date of first clutches in a year was significantly correlated with sunshine hours recorded at Rarotonga Airport in October ($r = -0.77$, d.f. = 8, $P < 0.05$).

Nest building

Both members of a pair helped to build the nest, but the female usually did most construction. Usually the male collected nest-material, and occasionally helped construct the nest if the female was absent. At one partially-built nest, the male and female made 14 visits during 50 minutes of observation. At another three-quarters

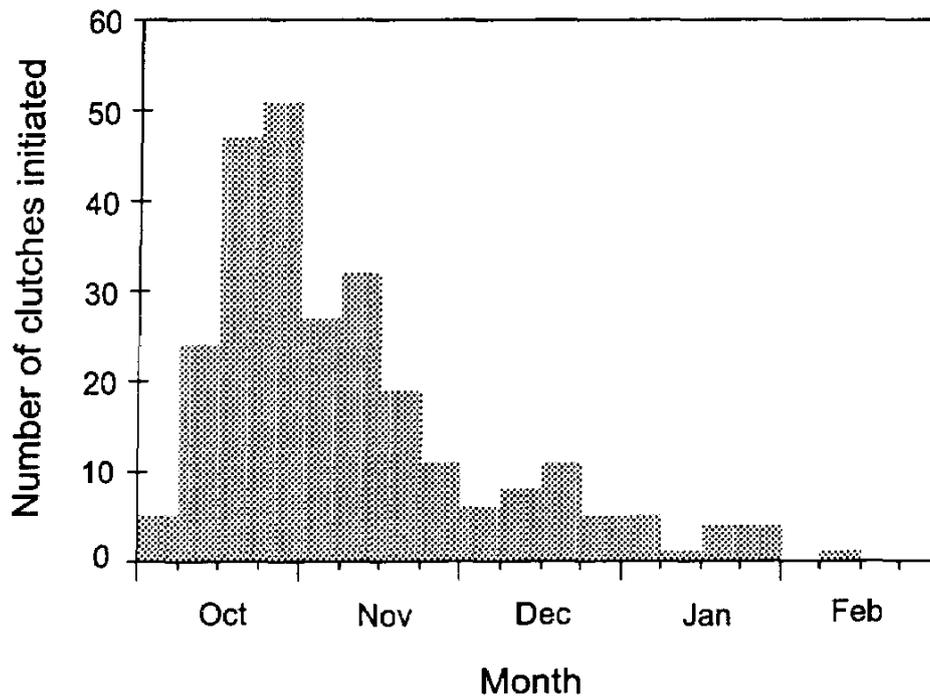


FIGURE 2 – Seasonal pattern of clutch initiation over the ten years, 1987-1997.

completed nest, the female visited the nest 10 times in 45 minutes; she spent 3.0 ± 1.3 (2 - 5.5) minutes collecting nest material, and 21.5 ± 8.2 (10 - 40) seconds fitting the material, while sitting in the incomplete cup; the male did not help, but stood, foraged and preened nearby. During the final stages of nest building at another nest, the female visited the nest 16 times in 62 minutes, she spent 3.4 ± 1.6 (1.5 - 7) minutes collecting nest material, and 28.8 ± 11.8 (15 - 60) seconds fitting the material, while sitting and wriggling in the cup; the male carried nest material to the nest once, during the longest absence of the female, and during his 120 seconds on the nest he did little other than sit and look around. However, during an hour at another well-built nest occupied by a 9+ year-old male and a yearling female, both built and fashioned the nest; the male spent 25.5 ± 16.7 (5 - 65, n=9) seconds at the nest (excluding the nine other visits when he spent extra time at the nest calling and displaying with wings spread and quivering, tail fanned and feet stamping), while the female stayed for 23.3 ± 13.2 (10 - 60, n=21) seconds.

Each nest took about a week to complete, occasionally as little as 1 - 2 days, but some (especially younger) pairs took several weeks, or built a number of incomplete nests before settling on a final nest site and building a complete nest.

Nest structure

The nest was usually in a small triple fork, close under a canopy of leaves, which sheltered the open nest from sun and rain. Often several branchlets were incorporated into the nest for increased stability. The nest was like a large version of a Fantail *Rhipidura fuliginosa* nest; the external diameter and depth of the nest was generally about 110 mm, and many had a small (50 cm) 'beard' hanging underneath. The cup measured about 60 mm across and 40 mm deep. The nest was made of interwoven

strands of moss (especially live *Aerobryopsis*), lichen and liverwort, with spider egg-cases woven into the outer layers, camouflaging the nest by disrupting the shape of the otherwise bulky, green structure. The cup was lined with short pieces of coarse plant fibre mostly derived from strips of 'au bark.

Usually a new nest was built for each breeding attempt, but sometimes birds returned to a nest used earlier in the season, or built on the remains of a nest used earlier in the season or in a previous year.

Nest site

Most of the 309 nests we found were close to the territory centre, in the outer branches of subcanopy trees overhanging a streambed, although a few were on ridges or on steep slopes away from streambeds. The height of the nest above the ground averaged 9.9 ± 5.0 m (2-30), but varied considerably depending on the plant species used, ranging from a mean of 3.0 m in ana'e to 17.3 m in outer islands karaka *Pouteria grayana* (Table 1).

Of the 227 nests definitely laid in and with a known outcome, there was no significant difference ($t=0.4$, $P>0.05$) in height between successful nests (10.4 ± 5.2 m; 2 - 30, $n=135$) and unsuccessful nests (10.1 ± 5.1 m, 3 - 28, $n=92$).

The majority of nests were in mato (108, 35%) or turina (62, 20%), with lesser numbers in pua (21), kavakava *Pittosporum arborescens* (18), karaka (17), ana'e and neinei (16 each), ka'i'atea *Weinmannia samoensis* (7), candlenut or tuitui *Aleurites moluccana*, *Alstonia costata*, and koka (6 each), guava *Psidium cattleianum* (5), i'i and outer island karaka (4 each), 'au (3), venevene tinito *Ardisia humilis*, ma'ame *Glochidion concolor* and rose apple *Syzygium jambos* (2 each), and *Allophylus timoriensis*, *Charpentiera australis* and *Meryta pauciflora* (1 each).

It was clear that Kakerori preferred to nest in turina; they built 20% of their nests in it although it comprised only 9% of the trees (and 4% of all plants) near a sample of 14 nests (Sanders 1993; p.43). Mato, the most commonly used tree, was used roughly in proportion to its abundance in the area (35% of nests cf. 40% of trees in the area). Conversely, Kakerori avoided koka, and 'au trees which held 2% and 1% of nests compared with their relative abundances of 15% and 7% respectively. Kakerori completely avoided kavakava atua, which was the most common shrub in the study area (Sanders 1993; p.48), matira and itoa *Ixora triflora*. Although 16 nests (5%) were found in ana'e, this fern made up 58% of all vegetation near nests (Sanders 1993; p.43). Kakerori probably prefer to nest in turina trees because their large leaves provide good shelter from sun and rain. Conversely, they avoid koka, 'au, kavakava atua and matira because these trees have relatively sparse and/or small leaves which provide little overhead protection.

The success of nests varied considerably depending on the tree species used. Nesting success in turina, the preferred nesting tree, and in mato, the most common tree in the area, were both 63%, similar to the overall average of 59% (Table 1). Nesting success in pua, the third most commonly used species, was less (28%) than average ($\chi^2=8.0$, $P<0.01$). Nesting success in three of the less preferred species –

TABLE 1 – Number of Kakerori nests found, their height and nesting success in different plant species.

Plant species used	No. nests found	% nests found	Height to ground (m)	s.d. (m)	Min (m)	Max (m)	% success	n
<i>Aleurites moluccana</i>	6	2	9.8	4.3	7	18	100	6
<i>Alstonia costata</i>	6	2	6.0	2.1	4	10	25	4
<i>Angiopteris evecta</i>	16	5	3.0	0.9	2	5	55	11
<i>Bischofia javanica</i>	6	2	12.3	5.1	5	18	40	5
<i>Elaeocarpus tonganus</i>	17	6	9.1	3.6	4	15	71	14
<i>Fagraea berteriana</i>	21	7	11.1	5.7	3	25	28	18
<i>Fitchia speciosa</i>	16	5	6.5	2.6	3	11	42	12
<i>Hernandia moerenhoutiana</i>	62	20	12.3	4.5	3	23	63	41
<i>Homalium acuminatum</i>	108	35	10.5	4.8	2	30	63	81
<i>Inocarpus fagifer</i>	4	1	7.0	1.4	5	8	100	4
<i>Pittosporum arborescens</i>	18	6	9.4	5.5	3	20	62	13
<i>Pouteria grayana</i>	4	1	17.3	3.2	15	22	100	2
<i>Psidium cattleianum</i>	5	2	5.2	1.6	4	7	50	2
<i>Weinmannia samoensis</i>	7	2	11.6	5.4	3	18	71	7
Other/unknown	13	4	7.2	3.5	3	12	38	8
TOTAL	309		9.9	5.0	2	30	59*	228'

* excludes 15 successful nests that were not found

koka (40%), 'au (0%) and ana'e (55%) – was also lower than average, but samples were too small to test statistically.

Eggs

Eggs were a pale coffee colour with an irregular circle of dark brown spots and blotches at the larger end. A single addled egg measured 21.5 x 15.3 mm and weighed 2.5 g at least 3 weeks after it had been laid, and two eggs in an abandoned clutch measured 23.3 x 15.9 mm and 22.6 x 17.7 mm. Using Hoyt's (1979) method of estimating the fresh weight of an egg with the formula: $Wt = K_w \times Length \times Breadth^2$, and using the average constant (K_w) from 26 species of 0.548, a Kakerori egg therefore weighs about 3.3 g, or 15% of the weight of a 22 g adult female.

Clutch size

Of the 12 nests where it was possible to examine the eggs and where clutch was certainly complete, one contained 1 egg and 11 contained 2 eggs (1.92 ± 0.29 eggs). In 21 other nests with chicks of various ages, three had one chick, and the other 18 had two chicks (1.86 ± 0.36 chicks). It appeared that two eggs is the normal clutch size.

Breeding effort

Because we missed some breeding attempts and could not always be sure whether birds had definitely laid in the nest, the following are minimum estimates. Most (74%) Kakerori pairs laid one clutch per season (1.27 ± 0.60 ; 1-5, $n = 215$). Replacement clutches were laid after 48% of the 93 nesting failures, but six (4%) of 146 successful pairs laid repeat clutches, and three of them raised two broods in a season (two pairs raised two single fledglings, and one pair raised two fledglings and then a single fledgling). Exceptionally, in 1989-90, one pair fledged a chick and then built four further nests and laid in at least one of them, but none was successful.

Incubation

Birds started incubating when the first egg was laid. Incubation spells were noted at five nests for a total of 446 minutes. Spells lasted 9.3 ± 5.2 (0.5 - 18, $n=42$) minutes, but were occasionally broken by brief (0.5-2 minute) excursions from the nest, or the nest was left unguarded for longer spells (5-12 minutes), usually when both birds were chasing Long-tailed Cuckoos (*Eudynamys taitensis*) from the territory. Incubation spells of females (11.6 ± 4.6 minutes; 0.5 - 18, $n=19$) were significantly longer ($t=2.83$, $P<0.05$) than those of males (7.4 ± 4.9 minutes; 0.5 - 18, $n=23$). During these timed observations, females incubated for 49% of the time, males for 38%, and the eggs were unattended for 13% of the time. Because we visited nests infrequently and made few direct observations on nest contents, the incubation period was never determined precisely, but was about 12 - 14 days.

Chick care

The chicks hatched 1 - 2 days apart. For the first 2 - 3 days, they were brooded and fed by the female only, and she ate the faecal sacs; the male often fed the female on the nest and he usually remained near the nest while the female was away feeding. From the fourth day, both parents brooded and fed the nestlings and removed faecal sacs, but the male occasionally continued to feed the brooding female on the nest. Brooding spells were typically 3 - 12 minutes, but the young were left unattended for increasingly longer periods as they developed. Single nestlings at two nests were fed about eight times per hour during 177 minutes. Two half-grown chicks were brooded by the female for 29 of 47 minutes, and she fed them three of the nine times. Chicks near to fledging were not brooded, but were fed on average 17 times per hour over four hours; the female fed the chicks 12 times per hour and the male fed them five times per hour. The nestling period was never determined accurately, but was about 11 - 15 days.

Nestling development

We did not measure the growth of nestlings, but chicks were black, naked and blind when they hatched; and they remained black and naked even into the second half of the nestling period. When chicks left the nest, their body was covered in loose grey-brown down with light grey or light yellow feathering on the head and

nape, and their bill was black with a prominent yellow-orange base to the lower mandible. Chicks fledged with short wings and tail: a freshly dead fledgling weighed 13 g (cf. adult weight of 23 g) and had 46 mm wings (cf. yearling mean of 77 mm) and 21 mm tail (cf. yearling mean of 63 mm) - measurements of adults and yearlings from Robertson *et al.* (1993). Where two chicks fledged from a nest, they usually differed markedly in size. This suggests that hatching order influenced growth rate and hence survival of chicks, as does the observation that although 92% of clutches had 2 eggs, only 25% of nests produced 2 fledglings.

Fledglings

As soon as fledglings left the nest, they fluttered to the top of the nearest tree with a dense canopy, and then continued to move uphill through the surrounding canopy. Thus, although the nest may have been in the bottom of a gully, within 2-3 days of fledging the young were often found on the ridge above the nest. Fledglings were fed by both parents for at least five weeks and sometimes up to eight weeks, but they were cared for mostly by the female, especially if only one chick had fledged. During the fledgling's first week out of the nest the parents were inconspicuous and made only fleeting visits to feed their young, which usually sat quietly in a sheltered spot high in the canopy. The young gave occasional high-pitched begging calls when their parents appeared and this was often the only clue to their presence. As they became increasingly adept at flying, they begged more, and after about 10 days they started following their parents around and chasing them for food. The chicks were cared for in different ways by different pairs; some pairs fed both chicks indiscriminately, some split their brood, with one adult assigned to each chick; and other pairs fed one fledgling until it was satiated and went to sleep, and then fed the other chick. When a month old, the youngsters were still being fed by their parents, but also caught their own food. Most young were independent two months after fledging and started forming loose flocks or 'clubs' on nearby spurs and ridgetops. An exception to this pattern was a male that fledged in December 1987 and was still in his parents' territory in September 1988. By October he had started to establish a territory 400 m downstream; however, on 14 December 1988 he returned briefly and was fed at least once by his mother.

Breeding success

In this section, we have excluded 15 successful nests (1 in 1987, 1 in 1990, 3 in 1992, 4 in 1993, 3 in 1995, and 3 in 1996) that were not found, but have used data from these pairs in estimating the number and percentage of successful pairs and the number of fledglings each year.

On average, 59% of nests were successful, and 76% of pairs fledged at least one young each year. Success varied significantly according to the management we carried out to protect nests from rat predation.

During the 1987-88 breeding season, nesting success was very poor in the Totokoitu Valley; only one of 11 nests studied and at least one other nest was successful, meaning

that two of seven breeding pairs were successful (Table 2); most nests failed during incubation or the early chick stage and the damage was usually attributed to rats (fine eggshell fragments and/or rat droppings in nests). In 1988-89, after rats had been poisoned and metal collars put around most nest trees, breeding success in the Totokoitu Valley improved: chicks hatched in five (63%) of eight nests definitely laid in, and fledged from three nests (38%) belonging to three of the seven pairs. In the Avana and Turoa Valleys, where no poisoning took place, but where we protected some nests from rats by banding trees with metal collars, chicks hatched in three (38%) of eight nests, and fledged from two nests (25%) belonging to two of the six pairs. In marked contrast to 1987-88, we had no direct evidence that rats had destroyed eggs or chicks in the Totokoitu Valley, but we know that rats destroyed eggs in at least four nests outside of the poisoned area, and may have killed young chicks in another nest. Even in the Totokoitu Valley, the level of breeding success would not have sustained the population, and so we trebled the density of bait stations and progressively increased the area of intensive rat control so that by 1990 the whole 155 ha was protected (Robertson *et al.* 1998). We were not able to sustain protection of the whole area in ensuing years, but normally at least 90% of territories received some protection.

In the two seasons (1987/88 and 1988/89) with little or no management of rats, nesting success was $20 \pm 15\%$ (9 - 31), and $34 \pm 6\%$ (29 - 38) of breeding pairs were successful (Table 2). Since intensive rat control began in 1989, the breeding success of Kakerori has been consistently higher. Nesting success in the eight seasons from 1989/90 to 1996/97 was significantly better ($67 \pm 12\%$, 50 - 83; $\chi^2 = 17.4$, $P < 0.001$) and a higher proportion of breeding pairs fledged at least one chick each year ($83 \pm 9\%$, 66 - 92; $\chi^2 = 21.3$, $P < 0.001$). The number of fledglings raised each year increased from 0.46 ± 0.23 (0.29 - 0.62) per breeding pair in 1987-89 to 1.07 ± 0.19 (0.88 - 1.46) per breeding pair in 1989-97 ($t_8 = 3.5$, $P < 0.01$). The recruitment rate, measured as the number of yearlings recruited divided by the total population size (including non-breeders), also more than doubled from 0.13 ± 0.02 (0.11 - 0.14) in 1987-88 to 0.29 ± 0.08 (0.17 - 0.38) in 1989-96.

Reasons for breeding failure

Most Kakerori nests that failed, especially in the first two years before we began intensive rat control, were apparently preyed on by ship rats or Pacific rats. In 1987, the young in one nest died of starvation after one parent was killed, apparently by a cat (*Felis catus*).

Long-tailed Cuckoos in New Zealand forests eat eggs and chicks (Gill 1980, Beaven 1997). Some juvenile Long-tailed Cuckoos were present throughout the Kakerori breeding season, but from late December adults started to appear, presumably returning early from New Zealand. Adult Kakerori reacted strongly to Long-tailed Cuckoos, and often left their nest unattended while they chased cuckoos from their nesting area. Although we never saw cuckoos at nests, we suspected that late in the breeding season adult Long-tailed Cuckoos may have eaten eggs and/or young Kakerori,

TABLE 2 – Comparison of nesting success and breeding productivity of Kakerori in years with and without management of rats in the study area.

Year	Nests found	% nests* successful	Fledglings found	Pairs breeding	% pairs** successful	Fledglings per pair
No management						
1987-88	11	9	2	7	29	0.29
1988-89	16	31	8	13	38	0.62
1987-89	27	20	10	20	34	0.46
With management						
1989-90	22	59	19	13	85	1.46
1990-91	17	65	16	14	86	1.14
1991-92	21	57	15	17	71	0.88
1992-93	11	82	14	14	86	1.00
1993-94	24	83	29	25	92	1.16
1994-95	38	61	26	28	82	0.93
1995-96	40	50	32	35	66	0.91
1996-97	28	75	27	25	92	1.08
1989-97	201	67	178	171	83	1.07

* nests found, that were definitely laid in, which produced at least one fledgling

** pairs that raised at least one fledgling in a season, even if their nest was not found

including a fledgling which disappeared about the time of a major confrontation between the chick's parents and a cuckoo. The damage at nests (seen only when adult cuckoos were back), included the whole nest being shredded and sometimes also being tipped sideways, quite unlike the lack of disturbance recorded at a Tomtit (*Petroica macrocephala*) nest preyed on by a Long-tailed Cuckoo in New Zealand (Beaven 1997).

Mynas (*Acridotheres tristis*) in New Zealand eat eggs and chicks (Heather & Robertson 1996), and were present in the study area, but they were not obviously involved in any of the nest failures that we recorded. Kakerori were alert when Mynas were near their nest, but they never chased them away as they did with Long-tailed Cuckoos.

Our disturbance (when banding trees) probably caused a few nesting attempts to fail, and sometimes nest-building ceased if the birds were surprised by us. One nest failed because a photographic hide was built too close to it, and we suspect that a branch holding another nest was accidentally broken off by a photographer.

Several nests failed because eggs were apparently infertile or addled; in one case the parents incubated an infertile egg for more than 70 days.

The sheltered sites chosen for nests meant that very few failed because of storm damage, even though several tropical cyclones (of sufficient strength to cause structural damage to houses on Rarotonga and bring down trees in the study area) passed close to the Cook Islands during the study.

DISCUSSION

This study of the breeding biology of Kakerori is the first carried out on any of the five species of *Pomarea* flycatchers of tropical eastern Polynesia. The breeding biology of Kakerori is likely to be similar to that of the other species (all classified as threatened; Collar *et al.* 1994), except that the breeding season of the three species (*P. iphis*, *P. mendozae* and *P. whitneyi*) living close to the equator in the Marquesas Islands may be more protracted or governed by variation in rainfall (as with passerines in the Galapagos; e.g., Curry & Grant 1989).

The relatively short, regular breeding season from late spring to mid-summer is more typical of temperate zone passerines and probably reflects the seasonal nature of the climate of Rarotonga which lies just within the tropics. The breeding season coincides with increasing daylength, temperatures and rainfall, with a consequent likely flush of invertebrates, but a study of invertebrate availability was beyond our resources. Variation in the start of breeding each year was influenced by the amount of sunshine in October, which may also promote increased invertebrate activity in the canopy and understorey.

The introduction of ship rats to Rarotonga has been profound. Kakerori were numerous in the early 1800s (Gill 1885) although they had presumably lived in the presence of Pacific Rats for thousands of years. Kakerori disappeared rapidly from lowland areas in the mid-to-late 1800s, about the time that ship rats reached New Zealand (Atkinson 1973), and presumably Rarotonga. The remaining healthy populations of the other *Pomarea* flycatchers are found only on islands in French Polynesia without ship rats (Sietre & Sietre 1992).

Kakerori build a large and moderately conspicuous open cup nest, although it is often high and on branches overhanging a stream. The adults change frequently at the nest and even from a young age chicks give very audible begging calls, which makes them especially vulnerable to mammalian predators. The breeding success of Kakerori improved dramatically following intensive poisoning of rats, but predation was not eliminated. In recent years, rat predation was most evident at nests in pua trees. Pua fruit was commonly found in stomachs of rats we trapped during the Kakerori breeding season and it is possible that rats encountered nests when foraging for fruit.

The Kakerori is an exceptionally long-lived passerine (three of the eight birds colour-banded in 1984 as grey (4+ year-old) birds were at least 17.8 years old in September 1998), which evolved in the largely predator-free and environmentally stable forest of an isolated tropical island. As expected from life-history theory (e.g., Lack 1968, Ricklefs 1980, Kulesza 1990, Stearns 1992), the Kakerori shows the pattern typical of tropical passerines in having a low reproductive rate, with a small clutch and usually only one brood each year. This means that when nest predation is substantially reduced, the rate of recovery of the population is still quite slow.

Suitable habitat for Kakerori appears to be available in nearby valleys, but the breeding range has expanded very slowly compared with the increase in numbers of birds. The annual productivity per breeding pair (1.07 fledglings) has now more

than doubled since before rat control (0.46 fledglings), but the productivity per bird has actually declined in recent years to a level similar to that in 1987-89, because there is now a large number of non-breeding subadults in the population, even though some birds are capable of breeding as yearlings. This suggests that the time is right to establish a new population on ship-rat free islands elsewhere in the Cook Islands. Although there are no subfossil or historical records of Kakerori away from Rarotonga, given the wide geographical range of *Pomarea* flycatchers in eastern Polynesia, it seems likely that they have previously lived on smaller islands and atolls elsewhere in the southern Cook Islands, but subsequently died out through chance demographic events or catastrophes such as severe cyclones, droughts or disease.

The long-term survival of Kakerori will depend on continued nest protection in the Takitumu Conservation Area on Rarotonga, and/or the transfer of Kakerori to an island free of ship rats.

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