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Breeding biology of red-crowned parakeets (*Cyanoramphus novaezelandiae novaezelandiae*) on Little Barrier Island, Hauraki Gulf, New Zealand

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Abstract The reproductive biology of red-crowned parakeets (*Cyanoramphus novaezelandiae novaezelandiae*) was studied on Little Barrier Island (Hauturu) during the 1989/90 and 1990/91 breeding seasons. Nests sited in cavities of pohutukawa (*Metrosideros excelsa*) and puriri (*Vitex lucens*) trees accounted for all but 1 nest which was found in a hole in the ground. Breeding activity was recorded from Nov to Mar with peak egg laying in Dec. Mean clutch size was 7.0 eggs (range 4-9). Replacement clutches were rare and only followed the loss of young broods. Female parakeets were entirely responsible for incubation that lasted about 23 days. The nestling period averaged 40.8 days (range 32-49) with about a 30% probability of an egg resulting in a fledgling. The main cause of nestling mortality was starvation. Infestation of nests by mites and predation of nestlings were also occasionally recorded. Post-fledging mortality was high, particularly in the 1st 2 weeks, and was attributed mainly to aerial predators such as morepork (*Ninox novaeseelandiae*). Aspects of nest and roost site characteristics, brood reduction, mortality, and vulnerability to predation are discussed in relation to the conservation of the species.

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INTRODUCTION

The red-crowned parakeet (*Cyanoramphus novaezelandiae novaezelandiae*) is 1 of 7 extant species of mainly forest-dwelling parakeets found in the Southwest Pacific from the tropics to the subantarctic. Of these, 3 species are endemic to the main islands of New Zealand – the red-crowned parakeet, yellow-crowned parakeet (*C. auriceps*), and orange-fronted parakeet (*C. malherbi*) (Boon *et al.* 2000). New Zealand's native parakeet populations declined rapidly in the face of persecution as crop pests, deforestation, disease, and introduced predators (Buller 1888; Oliver 1955; Harrison 1970; King 1984). Red-crowned parakeets seem to have been especially vulnerable to predators; they have disappeared almost completely from the North and South Is, and are now common only on Stewart Is and several, largely predator-free, offshore islands (Falla *et al.* 1978; O'Donnell & Dilks 1986; Greene 1998).

Most of New Zealand's hole-nesting birds are particularly vulnerable to predation during the breeding season (Rasch 1989; O'Donnell 1996; Elliott *et al.* 1996). Investigations of yellow-crowned parakeet productivity and mortality in Fiordland have demonstrated the vulnerability of parakeets to predators while nesting (Elliott *et al.* 1996). However, despite this vulnerability, yellow-crowned parakeets still persist on the mainland where red-crowned parakeets do not (Elliott *et al.* 1996).

Systematic studies of red-crowned parakeet biology have been few and, because of the species' current distribution, confined to populations on offshore islands where significant predators are usually absent (Taylor 1975; Dawe 1979; Nixon 1982; Bellingham 1987; Greene 1998). Assessment of the precise role of predators in the decline of mainland red-crowned parakeet populations must, therefore, be based largely on inferences derived from an understanding of their biology and ecology.

This paper describes the reproductive biology of red-crowned parakeets on Little Barrier Island. Factors affecting productivity and mortality are compared to those affecting other parrot species in New Zealand and elsewhere.

STUDY AREA

Little Barrier Island (Hauturu) (36°12′S 175°7′E) lies at the entrance of the Hauraki Gulf, *c.* 24 km

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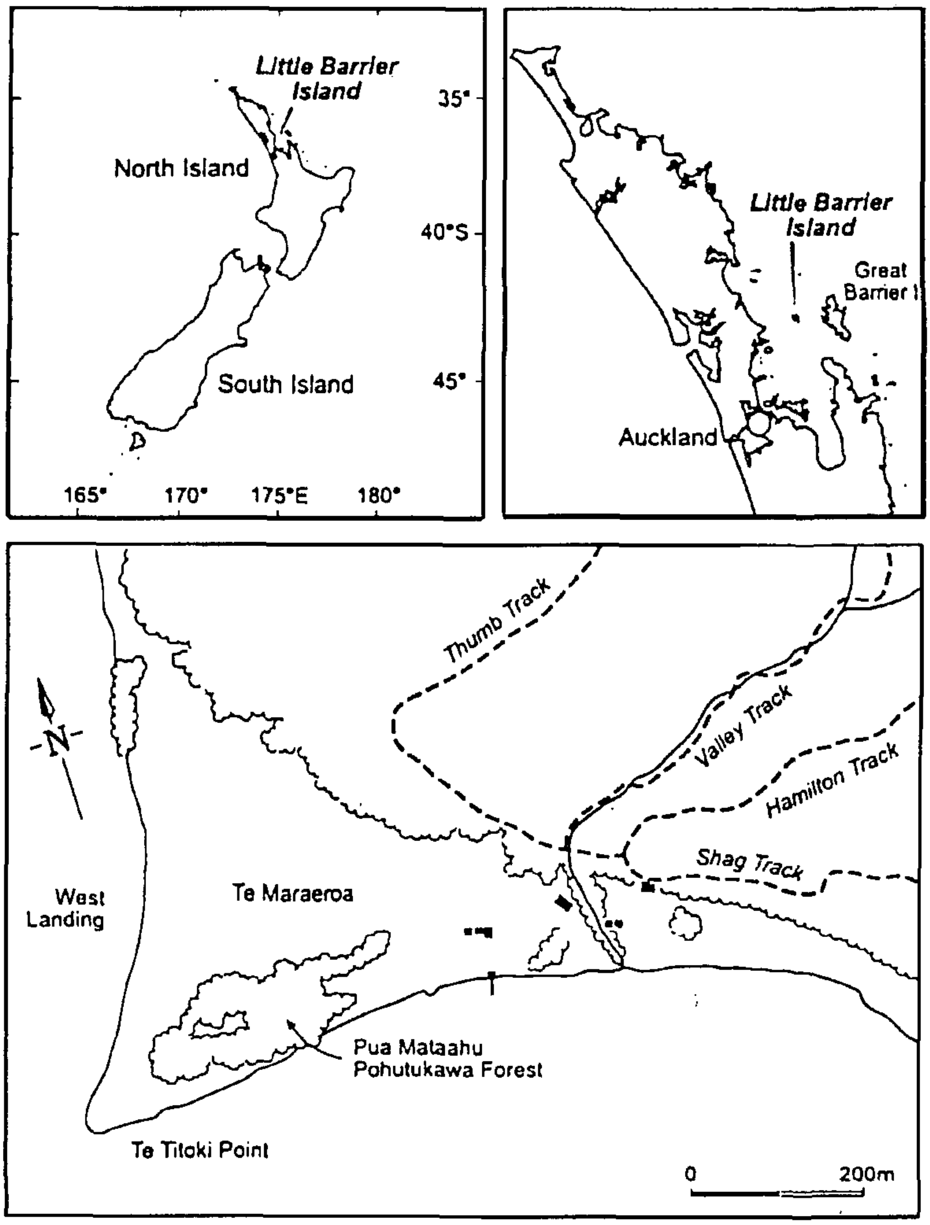


Fig. 1 Study area on Te Maraeroa, Little Barrier Island (Hauturu).

east of Cape Rodney (Fig. 1). A rugged remnant of an ancient volcano, the island is covered in several relatively undisturbed and highly diverse forest types (Hamilton & Atkinson 1961). Te Maraeroa and Te Titoki Point, an area of flat land in the south-west corner of the island, were selected as the main study area for several reasons. The area is flat and fairly open, making both the observations of birds and nests (as well as movement through the area) relatively straightforward. Mist nets could be operated in most of the area. Red-crowned parakeets are common there throughout the year. The concentration of large trees (especially on Te Titoki Point) provided a high density of potential and accessible nest sites within a relatively small area.

The farmed area (now retired) of Te Maraeroa covered *c.* 16 ha and was dominated by a paspalum (*Paspalum dilatum*) and white clover (*Trifolium repens*) sward, many weed species, and a few large trees such as puriri (*Vitex lucens*), pohutukawa (*Metrosideros excelsa*) and kanuka (*Kunzea ericoides*). There are exotic fruit trees (peach, guava, fig, walnut, grapefruit, orange) near the ranger's residence. Sedge tussocks, herbaceous weeds, grasses, and manuka (*Leptospermum scoparium*)/kanuka scrub dominated an area of coastal scrub behind the western boulder bank. Large areas of the boulder bank itself were covered in a mat of pohuehue (*Muehlenbeckia complexa*). Te Titoki Point was dominated by a stand (1.2 ha) of large, old pohutukawa, which form an almost complete monoculture. Adjacent to Te Maraeroa and covering almost 1/3rd of the island is a *Leptospermum*/*Kunzea* forest; a mature secondary growth community (dominated by kanuka) with a well-developed subcanopy and scattered, large emergent trees (Hamilton & Atkinson 1961).

METHODS

Catching and banding

Red-crowned parakeets were either captured in mist nets or trapped around dawn using small nets placed over roost sites. Birds were individually colour banded using 2 cut-down D-bands to allow for both a greater range of combinations and their short tarsometatarsi. Sex was determined using measurements of culmen length and width, which are reliable indicators of significant differences in both measurements between males and females (Sagar 1988). A metal band was placed on the right leg of males and the left leg of females. Juveniles were given a metal band on the left leg and a single colour band, denoting their nest, on the right. All birds were weighed and measured.

Nest monitoring

Before 1989, >20 holes in trees had been identified within the study area as having been used by parakeets (Dawe 1979). Tree species, height, diameter at breast height (DBH) and status (dead or alive) were recorded for each nest tree. Height of the nest entrance above the ground, entrance aspect, degree of shelter, nest entrance dimensions (width × height), and depth of the nest hole were also recorded.

From early Oct to late Dec all potential nest sites within the study area were checked every 3-4 days for the start of breeding activity. Checks usually involved the observations of nest chamber excavation or increased activity by adult birds near the nest hole. Subsequent checks were made every 1-2 days before the 1st egg being laid, using a Reichert FS-236 fiberscope. Of the active nests identified in the 1989/90 and 1990/91 breeding seasons, 20 were chosen as study nests. The choice of study nests was largely determined by location sufficiently early in the breeding cycle so that a relatively unbiased estimate of nesting success could be calculated and ease of access or visibility of the nest chamber.

Following the appearance of the 1st egg, each nest was visited every day until the last egg had hatched. Incubation period was measured as the interval between the laying and hatching of the last egg in the clutch (Rowley 1990). Subsequent visits were made every 2-3 days to assess the developmental progress of the nestlings and to record any mortality. Nests under observation from hides (see below) were visited every day from the 1st signs of nest occupation to the fledging of the last chick and provided information on behaviour of the female within the nest, laying dates, incubation temperatures, hatching dates, and measurements of the growth and development of chicks.

Every effort was made to reduce disturbance to nesting adult parakeets to an absolute minimum. Nests were inspected internally using either the fiberscope or hides only after the male had called the female from the nest.

Modification of selected nests

More detailed examination of red-crowned parakeet breeding biology was achieved by modifying 3 nest holes with a history of known use (chewed entrance hole, presence of dried faeces) to allow direct access into the nest chamber. Small holes were cut into nest chambers where a removable perspex window, red and white lighting controlled by a dimmer switch, and a temperature probe were installed. A hide of plywood was constructed around the window excluding light and allowing observation throughout the day. To limit disturbance at nest holes, modification and hide construction was completed 3-4 months before the start of the breeding season.

RESULTS

A total of 24 adult red-crowned parakeets (10♂♂, 14♀♀) was banded in the study area between 29 Sep and 20 Dec 1989.

Pre-nesting behaviours

From mid-Oct 1989, about 2 months before the 1st eggs being laid, courtship feeding and other pair bond maintenance activities were observed. The number of instances of male birds regurgitating food to begging females increased in both frequency and duration. These behaviours became particularly noticeable as parakeets began selection and initial occupation of nests.

Most parakeet pairs remained within fairly specific parts of the study area before and throughout the breeding season. These areas were centred about regularly occupied roosts and, later on, nest sites. Many of these sites were traditional and used continuously over many years. At several sites the entrances were well worn and accumulations of dried faeces were present.

Roost sites varied considerably, including holes (25-240 cm^2), split branches, vegetation-covered overhangs (on banks or in trees), and dense foliage, and were used by both sexes. Two birds were never seen to occupy the same roost at once. The roost sites of a pair of parakeets were 10-200+ m apart and often different in character. Unpaired male and female parakeets occasionally occupied roosts in the same tree before breeding. Of the 11 different nest sites monitored in this study, 10 were regularly occupied (>80% of nights) as roosts before both breeding seasons. At least 6 roost sites were later used as a nest by either the regular roost occupant or its mate. Only 2 instances were observed in which individuals occupied holes as roosts before the breeding season, but those holes were nested in by different birds.

Nest selection and preparation

Pairs of red-crowned parakeets began inspecting potential nest sites during the 1st week of Oct. The process of nest selection followed a fairly consistent pattern. Male birds actively escorted their mates between a variety of sites, while keeping up a constant stream of soft contact calls. Each potential site was checked by both birds from the entrance and cautiously entered by females for short periods. Males responded to any interest shown by the female by rushing back and forward near the entrance, often beginning the "side-switching" and pupil dilation behaviour described by Dawe (1979). If the female moved off, the male quickly escorted her to other potential sites nearby and repeated the performance. As relatively few holes were examined in an area (usually within that area most often frequented by the pair), several visits may be made to each site before the final choice was made. On locating a suitable site the female indicated her intention to occupy it by entering and exiting the hole repeatedly with decreasing caution. Sometimes the male persisted in introducing her to other sites, but his efforts were generally ignored from this point. A period of 4 weeks usually passed before a site was selected; although 1 pair spent 12 weeks selecting a nest site.

During nest preparation the female parakeet excavated a depression up to 10-12 cm deep and 15 cm wide in the floor of the nest chamber, usually at the point most distant from the entrance or in the darkest corner. The upper mandible was used to loosen the substrate and the feet to vigorously rake it back out of the way. If the nest chamber was close to the entrance, showers of debris were often seen being flung out at regular intervals. The walls of the chamber were also chewed and the resulting chips dug into the nest floor substrate. Larger pieces of debris were chewed by the female until the substrate was reduced to a fine, well-aerated tilth several cm deep. No external sources of nest material, such as grass and leaves, were used. Immediately before egg laying, the depth of the excavated depression usually decreased by 30-40 mm as a result of the female's movements. There are usually some contour feathers within or around the depression, presumably plucked from the female. A large proportion of the female's time within the nest tree during this period was spent sleeping, interrupted only by bouts of preening. Throughout this period the male of the pair remained in the general vicinity of the hole, but gave no assistance in nest preparation. Instead, much of his time was spent feeding, returning occasionally to feed his mate, and chasing other parakeets from the area.

Site fidelity

Five of the 7 pairs identified as nesting during the 1989/90 season bred during the 1990/91 breeding season. The other 2 pairs of parakeets were not seen again after the 1989/90 breeding season and their nest sites remained unused during the 1990/91 season. Roost and nest site fidelity did not appear to be particularly strong, with only 3 of the 5 pairs that nested in both years using the same hole. The 2 pairs that moved holes lost their entire broods in the 1989/90 breeding season and moved to different holes <50 m away. The 2 vacated holes were subsequently occupied by other pairs of parakeets.

Nest site description

Twenty-nine parakeet nests were located in 24 known nest sites during this study. Nine of these sites were used in both the 1989/90 and 1990/91 breeding seasons and one was used 3 times. Twenty-eight nests were found in 23 holes in trees and 1 nest was found in a hole on the forest floor formed by the roots of a fallen tree. Nests were found 0-6.4 m above the ground (mean = 2.9 m, SD = 1.5 m, n = 24), in predominantly large old trees (mean height = 12.9 m, SD = 3.0 m, n = 23, mean DBH = 120 cm, SD = 50 cm, n = 23). None of the nests located in trees had a DBH of <30 cm. Nests were located in only 2 species of tree, pohutukawa (56.5%), and puriri (43.5%). All nest trees were alive and healthy.

Nests in trees were either in the hollow centres of trunks (78.3%) or in large branches (21.7%) with access via the ends of broken branches and knot holes (87%) or splits (13%). Nest entrance dimensions ranged from 20 cm^2 to 341 cm^2 (mean = 99.6 cm^2, SD = 86.6 cm^2, n = 22). The smallest dimension of any hole was 30 mm. More nests faced north (45%) than any other direction. Only 12.5% of nest chambers were level with the entrance hole with the deepest or longest reaching 1.9 m from it. The average drop from the nest entrance to the chamber was 750 mm (SD = 450, n = 24).

Laying

Of the 20 study nests closely monitored over the 1989/90 (n=10) and 1990/91 (n=10) breeding seasons, 13 were located before laying, the remainder were found with complete clutches. The 1st egg of the 1989/90 season was laid on 29 Nov. The remainder of the eggs in the 10 study nests were laid over the following 27 days. M-YG also laid the 1st eggs of the 1990/91 breeding season, during the 1st week of Nov 1990, *c.* 3 weeks earlier than in the previous year. Eggs in the remaining 9 nests were laid between 23 Nov 1990 and 31 Jan 1991. Egg laying peaked in Dec in both seasons. This long egg-laying period (70 days) can be attributed to at least 1 instance of re-nesting and possibly another. The mean time taken to lay a clutch (mean of 7 eggs) was 12.6 days (SD = 3.75, n = 12, range = 7-19).

Table 1 Intervals (days) between red-crowned parakeet (*Cyanoramphus novaezelandiae*) eggs laid on Little Barrier Is during the 1989/90 and 1990/91 breeding seasons.

		Laying intervals between eggs						
		1 and 2	2 and 3	3 and 4	4 and 5	5 and 6	6 and 7	7 and 8
1989/90	Median	1	1	1	2	2	3	2
	Range	-	1-2	1-2	-	1-3	3-8	1-3
	n	6	6	6	6	6	4	2
1990/91	Median	1	2	2.5	2	3	3	4
	Range	1-4	1-2	2-3	1-2	2-3	-	-
	n	7	6	6	5	5	5	1

Table 2 Clutch size of red-crowned parakeets (*Cyanoramphus novaezelandiae*) on Little Barrier Is during the 1989/90 and 1990/91 breeding seasons.

	Clutch size									
	4	5	6	7	8	9	Total	Mode	Mean	SD
1989/90	0	0	4	3	3	0	10	6	6.9	0.88
1990/91	1	0	1	4	3	1	10	7	7.1	1.4
Total	1	0	5	7	6	1	20	7	7.0	1.1

Table 3 Dimensions (mm) and weight (g) (ranges in parentheses) of eggs of red-crowned parakeets (*Cyanoramphus novaezelandiae*) laid on Little Barrier Is, compared with those measured in previous studies.

	Source				
				Dawe (1979)	
	This study	Fleming (1939)	Oliver (1955)	Adults	F1 & F2
n	10	3	5	19	17
Length	25.8 ± 0.4	26.2 ± 2.5	25.5 ± 0.8	-	-
	(25.3-26.4)	(23.5-28.5)	(24.5-26.6)	-	-
Width	20.7 ± 0.3	21.0 ± 0.5	21.2 ± 0.6	-	-
	(20.2-20.9)	(20.5-21.5)	(20.5-22.0)	-	-
Weight	6.1 ± 0.2	-	-	6.1	5.2
	(6.0-6.5)	-	-	(5.3-7.0)	(4.7-5.6)

Laying intervals were determined for 6 clutches in 1989-90 and 7 in 1990/91 breeding seasons (Table 1). With one exception in the 1989-90 season, the 1st 3-4 eggs in each clutch were laid on successive days. Subsequent eggs (usually the 5th and 6th) were laid at intervals of 48 h, followed by intervals of 72 h for the remaining eggs (7th and 8th). In 1 clutch, 8 days passed between the penultimate and last (6th) egg being laid; this last egg did not hatch. During the 1990/91 breeding season laying intervals were more erratic with only the 1st 2 eggs laid on successive days for 3 of the 6 nests examined. Intervals of 1-3 days between the laying of the 1st and 2nd eggs were recorded. As for the 1989/90 season, laying intervals increased from the production of the 5th egg to the last egg but this interval was generally longer (72 h).

All eggs were laid within the prepared depression. Larger clutches of eggs (>5) were generally arranged in pairs under the female in a fairly regular rectangular pattern. This pattern changed throughout incubation, particularly for smaller clutches, as the female turned the eggs.

Clutch size

A total of 140 eggs was laid in the 20 nests during the 1989/90 and 1990/91 breeding seasons (Table 2). The mean clutch size for both years was 7.0 (SD=1.21, range=4-9, *n*=20) and varied little between years — 6.9 (SD=0.9) and 7.1 (SD=1.4) eggs, respectively. Eggs were elliptical-ovate and, when laid, were white with a slight gloss. As incubation proceeded, the gloss was lost and the eggs became discoloured. Ten eggs from 3 nests were weighed and measured (max. width × length) during the day they were laid. Mean egg weight was 6.14 g (SD=0.21, range = 6.0-6.5 g, *n* = 10); the smaller eggs were usually being laid later in the clutch. Weights and measurements of red-crowned parakeet eggs are compared with data from other authors in Table 3, and show strong similarities for all measurements.

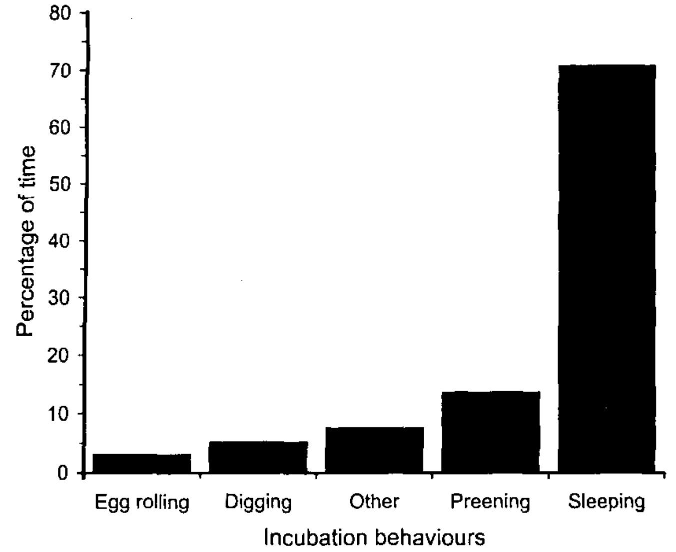


Fig. 2 Behaviours exhibited by 2 female red-crowned parakeets (*Cyanoramphus novaezelandiae*) throughout the incubation period (n = 120, over a total of 3 h observation).

Incubation

Only female parakeets incubated. Observations of 2 females suggested that the start of incubation may be delayed until the appearance of the 4th egg. Before the laying of the 4th egg females would often leave the nest to feed for up to 35 min intervals (Table 4). Also, before laying the 4th egg, females spent time preening and chewing the nest chamber walls while standing above or to one side of the eggs. Egg turning did not start until the 4th egg was laid, after which females left the nest only when their mates called them off. On average, females spent 118 min (SD = 47.1, range = 43-224 min, n = 20) inside their nests during each incubation stint (Table 4) after laying the 4th egg.

Table 4 Incubation and brooding attentiveness (mean ± SD, range, n) of female red-crowned parakeets (*Cyanoramphus novaezelandiae*) on Little Barrier Is. *, includes visits by male birds.

	Period (min) Female on nest	Female off nest
Pre-incubation	40.7 ± 18.2	25.7 ± 9.7
	20-70 (10)	4-35 (10)
Incubation (after 2nd egg)	118.1 ± 47.1	43-224 (20)
	6.6 ± 3.6	1-16 (67)
Chicks <14 days old	47.9 ± 37.3	13.7 ± 15.1
	6-224 (20)	2-56 (60)
Chicks >14 days old	12.9* ± 20.4	25.3* ± 23.1
	1-103 (102)	1-98 (50)

Throughout incubation, males visited nests at regular intervals to feed their mates. The length of incubation stints usually reflected the rate of male visits (Table 4) but stints of >120 min usually resulted from the refusal of females to leave the nest rather than neglect on the part of their mates.

On returning to the general vicinity of the nest the male would either approach the entrance immediately or spend several minutes nearby feeding, preening or perching before doing so. In either case the male made the final approach to the nest entrance by foot, usually calling softly until the female emerged. Males were also seen to call some distance from the nest with the same result. Any attempt to enter the nest chamber by the male was restricted by his mate who would sometimes resort to physical aggression.

Female parakeets usually flew rapidly from the nest to a sheltered perch nearby where their mate joined them. The female crouched with her head held slightly back and her bill open while uttering a high-pitched begging call. The male jerked his head up and down several times to bring food up from his crop then placed his bill crosswise over the female's before regurgitating. This process was repeated 6-21 times and was accompanied by short squeaks from the female following each "mouthful" received. Once the female exhausted the available food supply, the male turned away and ignored further begging. The female usually performed any maintenance behaviours such as preening and defecation before re-entering the nest. Only a short period was spent by female parakeets off the nest (mean = 6.6 min, SD = 3.6, range = 1-16, n = 67; Table 4).

Observations of incubating females showed that they were quite active. Four general behaviour types were most frequently observed within nests: egg turning; preening; digging; and sleeping (Fig. 2). Egg turning was the least frequently observed of these behaviours, as a percentage of incubation time over a total of 3 h of observations. An egg was turned on average every 7.2 min (SD = 5.5, n = 99). Eggs were moved from the periphery to the centre of the clutch using only the bill and 2 or 3 eggs were moved during each episode. Almost invariably the female would then reorientate her body position at least 90° relative to the clutch. Preening was also observed at frequent intervals and was often quite vigorous. Digging and chewing of nest material was seen throughout incubation, but considerably less frequent than observed before laying. These activities were confined to the immediate area surrounding the eggs and appeared to be responsible for the maintenance of the nest depression throughout incubation. Sleeping was, however, the most frequent behaviour observed for incubating birds. Almost 75% of the incubating female's time was spent lying across the eggs with its bill resting on the ground, apparently asleep. These periods of sleep were often very deep as surprising amounts of disturbance, both inside and outside the nest, were ignored. In 1 instance a pair of parakeets was

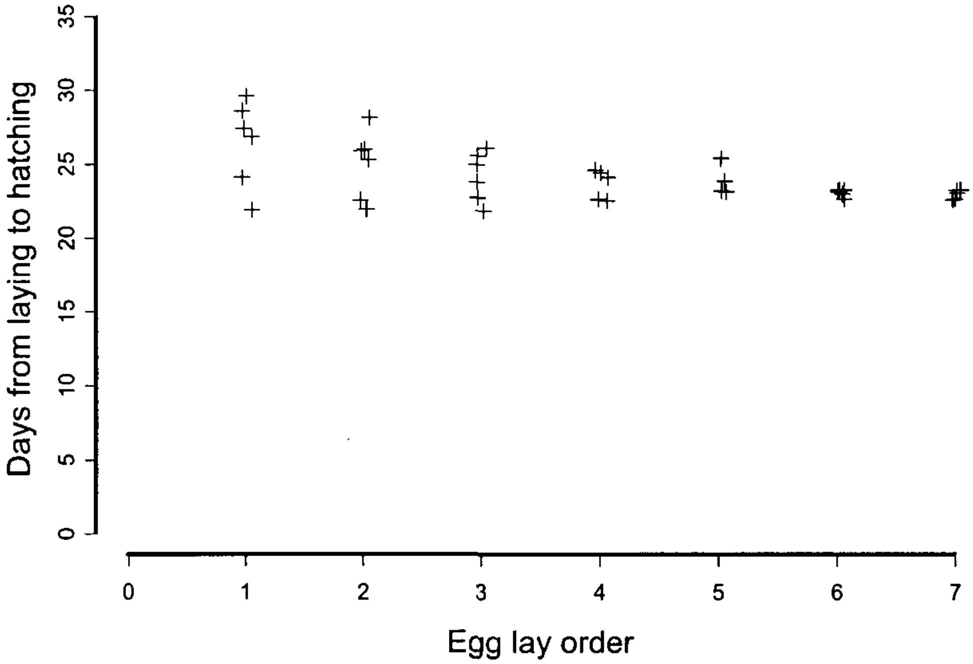


Fig. 3 Incubation period (laying to hatching) for each egg in order laid for 6 clutches of marked red-crowned parakeet (*Cyanoramphus novaezelandiae*) eggs (n = 30 eggs). Points have been jittered slightly for clarity.

Table 5 Variation of surface temperature (°C) of red-crowned parakeet (*Cyanoramphus novaezelandiae*) eggs on Little Barrier Is (taken at centre of clutch) and ambient air temperature (°C) within nests throughout incubation and initial chick rearing. Pre-incubation, range; egg temperature. Mean ± SD (n)/range; -, no data.

	Temperature		
	Ambient air in nest	Egg, female incubating	Egg, female off nest
Pre-incubation	-	-	-
	18.3-19.3	20.9-21.4	18.3-19.3
Incubation	-	-	-
Full clutch to 1st egg hatching	20.9 ± 0.6 (10)	32.6 ± 1.2 (35)	29.2 ± 1.0 (10)
	-	29.8-34.5	27.7-30.4
1st to last egg hatched	20.8 ± 0.9 (10)	33.6 ± 1.6 (49)	29.5 ± 2.1 (10)
	-	31.5-36.2	26.9-31.9
Chick until 10 days of age	21.3 ± 0.6 (10)	33.2 ± 3.5 (49)	30.5 ± 3.3 (10)
	-	29.8-37.1	25.0-35.2

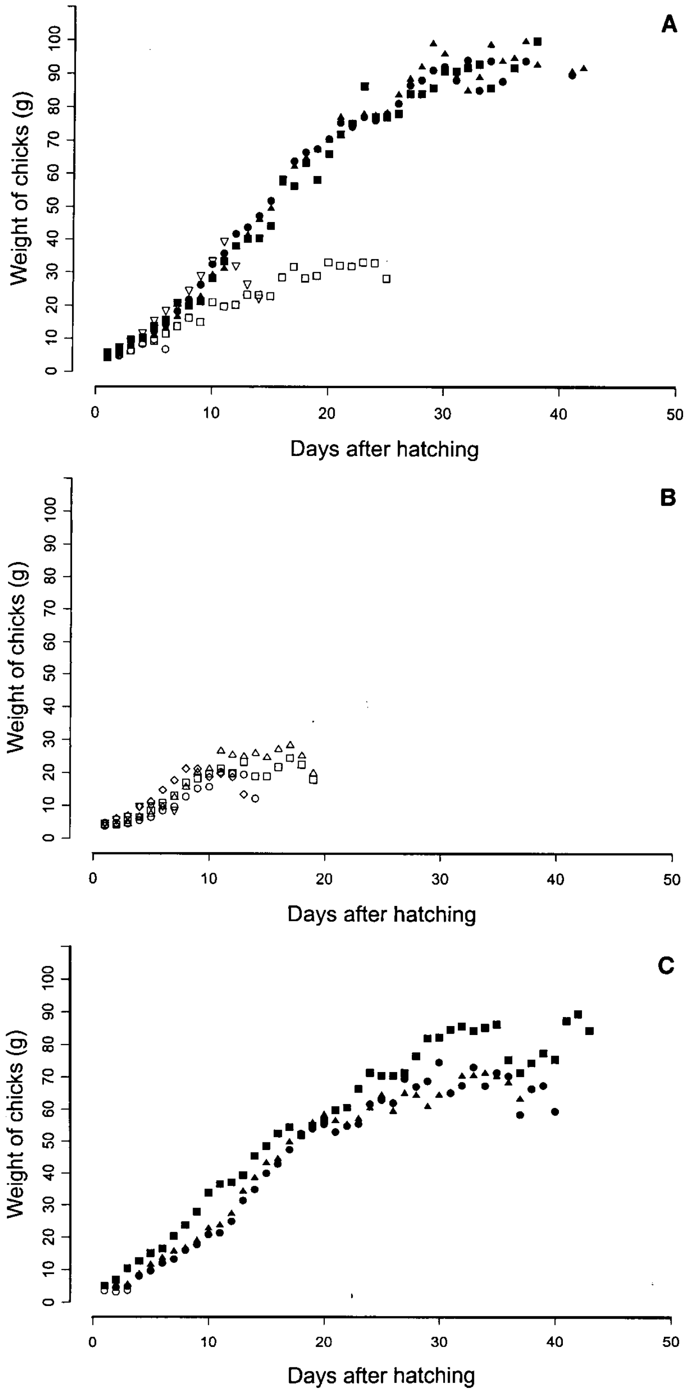
seen to enter a nest, inspect the nest chamber and even walk over the back of the incubating female without disturbing her.

Before incubation the egg temperature was closely correlated with ambient air temperature within the nest. When the female was present in the nest air temperature increased slightly (Table 5). However, with the onset of incubation, egg temperatures increased to *c.* 9-14°C above ambient. During incubation, egg temperatures taken from the centre of the clutch suggested that the rate at which eggs cooled following the female's departure was not constant with initial small decreases in temperature (~0.3°C min^{-1}) followed by a rapid decrease after an absence of 2-3 min (~0.9°C min^{-1}). However, in most instances females returned to the nest before egg temperatures dropped below 27°C. Temperatures taken of the nest material directly below the eggs (n=7) showed that although the nest temperature was similar to that of the eggs (albeit slightly lower) when the female was incubating, as soon as the female left the nest the rate of cooling of the substrate was considerably slower than that of the eggs (~0.1°C min^{-1}).

The incubation period (interval between the laying and hatching of the last egg) averaged 23.6 days (SD = 0.82, range = 23-25 days, n = 6). Intervals between the laying and hatching of all eggs laid in these 6 nests (Fig. 3.) confirmed observations (see above) that incubation usually commenced following the laying of the 4th egg.

Hatching

Hatching was asynchronous, although the degree of hatching asynchrony varied between clutches. The longer the delay in commencement of incubation, the more likely eggs hatched at the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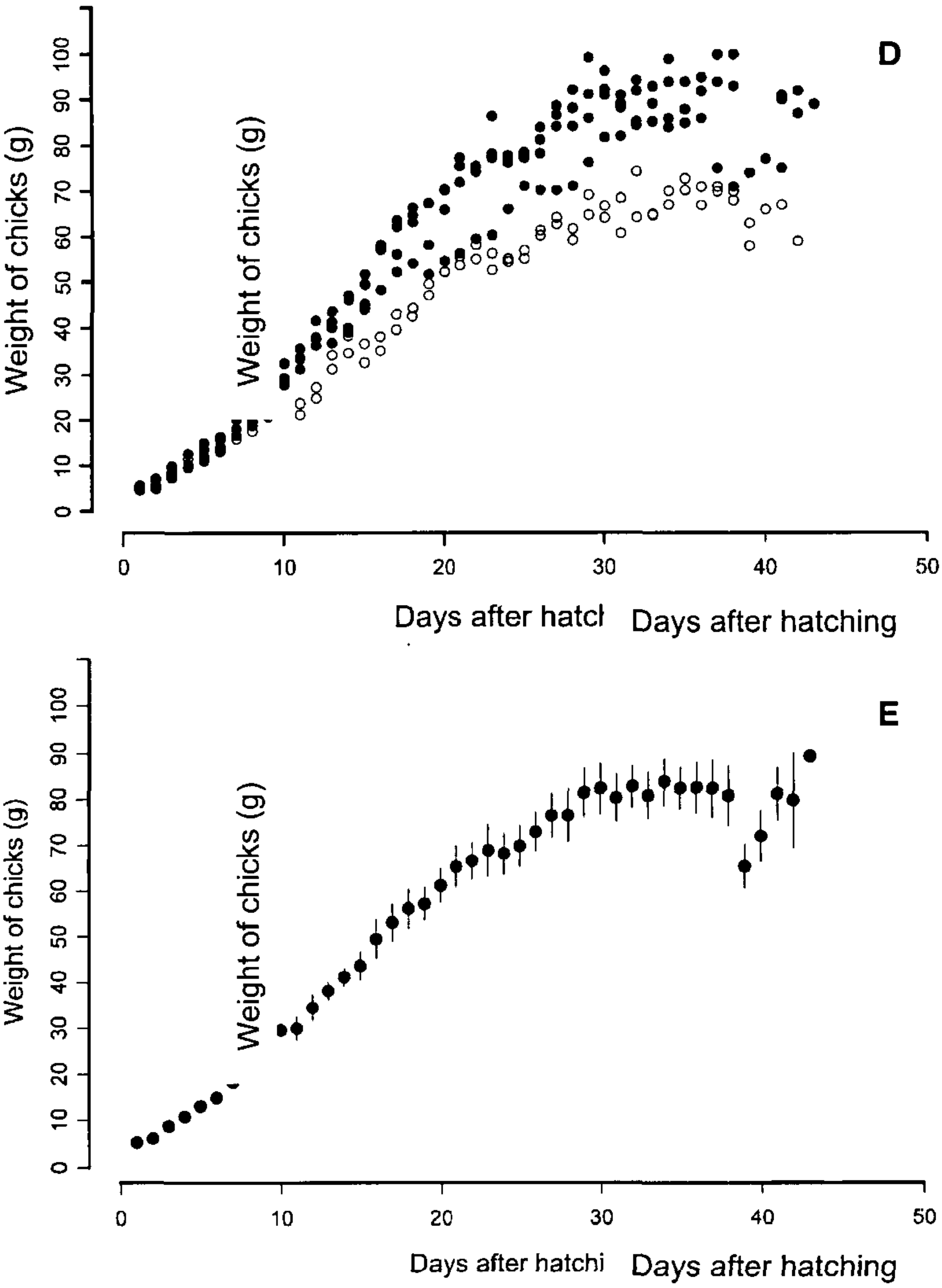

Fig. 4 Rate of chick weight increase from hatching to fledging for red-crowned parakeets (*Cyanoramphus novaezelandiae*). **A-C**, results for 3 different broods; open symbols, chicks that died before fledging (3, 5, 1, respectively); closed symbols, chicks that survived (3, 0, 3, respectively) to fledging. **D**, weight increase for the 6 chicks surviving to fledgling (open symbols, ♀; closed, ♂). **E**, mean weight increase (+/- 1 $SE_{\bar{x}}$) for all 3 nests.

same time. For example, in one nest 4 of the 5 eggs hatched on the same day. In most clutches the 1st 2 eggs hatched within the same 24-h period (63.1%, *n*=19). However, the intervals between the hatching of subsequent eggs became increasingly variable as the laying interval between eggs increased, with up to 11 days between the hatching of the 1st and last eggs. Hatching intervals for eggs often did not coincide with the intervals in which they were laid, even taking into account delays in the initiation of incubation. Not surprisingly, there were significant differences in the ages and weights of chicks within broods. For example, in one nest 4 eggs (out of the 5 that hatched) hatched on the same day whereas in another nest the last egg hatched (the 7th) 7 days after the 1st 2 eggs of the clutch.

Of 140 eggs laid in the 20 nests 117 eggs hatched successfully (83.6%), an average of 5.85 (SD = 1.3) clutch^{-1} (Table 6). In only 4 nests (*n*=20) did all eggs hatch (clutch sizes of 6, 6, 7, 8). Of 20 eggs that were accessible via hides, 5 failed to hatch, 3 were infertile, 1 embryo died during development, and 1 chick died during the hatching process.

Incubating parakeets became more restless 1-2 days before hatching. The frequency of egg-rolling increased slightly (about once every 10 minutes to once every 7 min, n.s.) and there was a corresponding decrease in time spent sleeping. Cracking noises could also be heard to which females responded by giving soft whines that persisted for 30 min and were repeated at intervals of up to 2 h. Once, cracking was heard for several minutes followed some 15 min later by the female eating part of an eggshell.

On hatching, chicks were wet and exhausted, but their sparse covering of light grey down soon dried and they could be seen lying together amongst older siblings or the remaining eggs. Even at this early stage they could vocalise strongly (a high-pitched peeping) and were highly sensitive to light, which they tried to avoid. As the number of chicks within a nest increased, there was a marked tendency for them to clump together. This behaviour persisted for the next 3 weeks by which time feather growth was well advanced.

Nestling growth and development

The initial covering of wispy down thickened and darkened over the 3-4 days after hatching. By days 5 and 6 feather tracts began to appear as dark lines under the skin and were particularly prominent on the wing, tail, and scapular areas. Nine days after hatching the eyes began to open and continued to open slowly over the following 10 days. At 12-13 days, pin quills began to break the skin and feather tracts on the head began to darken. At 18 days the 1st feathers emerged from secondary wing quills and tail quills. Primary wing feathers and the first contour feathers (particularly those over the ears) generally appeared about day 21-22 and emerged from the innermost quills 1st. At 25 days, feather growth over the remainder of the body had advanced rapidly although down feathers were still obvious. By day 30 most nestlings were well feathered apart from their flanks and rump, which was usually downy, and the face which was covered in quills. This plumage pattern often persisted for some days after fledging.

The mean hatch weight of red-crowned parakeet chicks was 4.6 g (SD = 0.58 g, *n* = 15). Of the 15 eggs hatched in 3 closely-monitored nests, only 6 nestlings fledged (Fig. 4A-C). In the 2 successful nests (Fig. 4A, C) nestlings rapidly increased in weight over the 1st 25 days then began to decrease slowly followed by a period of fluctuating weights before fledging. In most instances chicks fledged at a weight lower than the asymptotic weight (*c.* 83 g). Those nestlings that perished either showed an initial weight increase similar to their successful siblings followed by dramatic declines over a 24-48 h period ending in death (*n*=8) or the growth rate was severely retarded from hatching (*n*=1).

Interpretations of growth curves based entirely on weight are limited by variation in crop and stomach contents, the feeding regimes of the parents and the apparent differences in growth rates exhibited by male and female nestlings (Fig. 4D). However, chick weights do provide a composite measure of chick size and condition (Krebs 1999). Although the weights of these nestlings varied considerably both within and (more markedly) between nests, the average weight immediately before fledging was 81.3 g (SD = 16.6 g, range = 59.0-100 g, *n*=6). The absolute rate of growth increased to a point of inflection then decreased with large fluctuations until fledging (Fig. 4E). Small sample size and difficulties in fitting logistic curves because of these fluctuations meant only crude measures of asymptote weights could be estimated. The average weight of a nestling parakeet reached the asymptotic weight of *c.* 83 g about 30 days after hatching (Fig. 4E).

Nestling care

On hatching, nestlings are almost completely helpless, uncoordinated and entirely dependent on the brooding adult for warmth and nutrition. Throughout the hatching period the average brooding interval decreased dramatically from that recorded during incubation and continued to decline as chicks aged and their demands for food increased (Table 4). When the brooding female left the nest, the nestlings congregated in the middle of the nest depression with their heads draped over the necks of their siblings. Any nestling removed from these groups would actively make its way back to the clump.

Although the precursors of maintenance behaviours in nestlings can be observed after only 3-5 days (i.e. rudimentary wing and head movements typical of adult preening actions), the brooding female was largely responsible for this role for the first 14 days.

Young nestlings appeared to be sensitive to movements by the brooding female. If uncovered for even a short period, nestlings immediately began vocalising using high-pitched squeaking calls. At the same time both the neck and body were extended fully as nestlings attempted to make contact with the female. For the 1st 2 days following hatching, food delivered to chicks consisted of a clear, fairly viscous liquid dribbled into the gape of chicks by the female. Subsequent feeds were usually more solid consisting of finely ground particles. Until the eyes of the nestlings began to open (*c.* 9 days) and co-ordination improved, the nestlings were fed almost lying on their backs with their heads resting for support on the sides of the nest depression. The female actively maintained the nest depression for up to 3 weeks after hatching.

Despite marking individuals within 3 broods, accurate determination of feeding intervals was not

Table 6 Productivity and mortality of red-crowned parakeet (*Cyanoramphus novaezelandiae*) eggs, nestlings, and fledglings during the 1989/90 and 1990/91 breeding seasons on Little Barrier Is.

	1989/90	1990/91	Total
Nests	10	10	20
Eggs laid	69	71	140
Eggs hatched	59 (85.5%)	58 (81.7%)	117 (83.6%)
Egg mortality	10 (14.5%)	13 (18.3%)	23 (16.4%)
Chicks surviving to fledging	20 (33.9%)	26 (44.8%)	46 (39.3%)
Chick mortality in nest	*39 (66.1%)*	32 (55.2%)	71 *(60.7%)*
Chicks reaching independence	14 (70.0%)	18 (69.2%)	32 (69.6%)
Post fledging mortality	6 (30.0%)	8 (30.8%)	14 (30.4%)
Overall mortality	55 (79.7%)	53 (74.6%)	108 (77.1%)
Probability of survival (egg to independence)	20.3%	25.4%	22.9%

possible. Most nestlings were initially fed once h^{-1} (Table 4). Each feed consisted of anywhere between 2 and 10 regurgitations. Observations of chick feeding also suggested the female attempted to divide the available food amongst all nestlings regardless of size, particularly in the early stages.

After 9 days the eyes of the nestlings began to open. As their co-ordination and size increased, nestlings became considerably more active. A corresponding change in the behaviour of the adult female was also seen. The time spent brooding the nestlings declined (Table 4) as the demand for food increased. The female then began to forage for herself again and the male was allowed into the nest to feed the chicks. By 15-21 days old begging becomes increasingly vigorous as chicks competed for food when the male and female return to the nest. From 14 days of age the average rate at which nestlings were fed (the number of visits made to the nest by the parents) was every 25 min (SD = 23 min, *n*=50). The rate was highly variable and although most visits were made independently, adults began to visit together more frequently as fledging approached. Usually 1 adult then the other fed the nestlings (the male deferring to the female), but at one nest both adults were seen feeding the nestlings simultaneously.

As fledging approached, adults only made brief visits to the nest. The period between visits varied from *c.* 2 min to > 2 h. Three weeks after hatching most nestlings began to congregate at the nest entrance and vocalise loudly when a returning adult was detected. Nestlings would then compete vigorously and noisily to be fed. Consequently, the oldest or largest chicks were invariably fed first, often clambering over their smaller siblings in the process.

Nestling survival and mortality

Of 117 eggs that hatched over both breeding seasons, 46 (39.3%) chicks fledged, (mean = 2.3, SD = 1.6) from each nest (Table 6). Best estimates of nestling periods were 32-49 days (mean = 40.8 days, SD = 4.8, *n* = 45), with only slight differences between years. Five (25%) of the 20 nesting attempts failed at the nestling stage. Causes for complete loss of broods included a massive mite infestation, kiore (*Rattus exulans*) predation of nestlings (33-35 days old), and starvation. Partial loss of a brood was far more common and was observed in all of the other nests. Partial brood mortality was 25-80% and accounted for 46 of the 117 chicks hatched. Much of this nestling mortality was assumed to be starvation. One chick died as a result of an infection from a broken leg.

Fledging and independence

Fledging was observed once. Adult parakeets played a limited role in encouraging their offspring from the nest. Instead of flying off immediately after having fed the nestlings, the adult or adults flew to a nearby perch and chattered softly. If, after a few minutes of the adult flying between this perch and the nest, the nestlings showed no interest, the adult usually flew off and repeated the process at its next visit.

The ability of the fledglings to fly immediately after leaving the nest was extremely variable. Birds fledging at 32-36 days were both extremely weak and inept at flying or were unable to fly at all. After 40 days fledglings could fly much more strongly and were often found perched above the ground only minutes after leaving the nest. Initial flights were closely monitored by adult birds, which followed the fledglings until all were perched in areas of thick cover. Fledglings with limited or no flying ability remained on or close to the ground for 1-3 days until their feathers had grown sufficiently. One fledgling remained on the ground beneath a pile of branches for 7 days.

For the 1st 3-5 days after fledging parents appeared to co-ordinate their efforts by feeding specific fledglings. However, once the fledglings were able to fly reasonably well, adults become less discriminating and fed all fledglings.

Thirty-five fledglings were colour banded and attempts were made to follow them until they became independent from their parents. In the 2 weeks immediately following fledging, young parakeets remained in well-defined areas ≤100 m from their nests. These birds spent most of their time perched quietly or sleeping within trees. Fledglings living on the ground sought refuge in holes or areas of dense ground cover. Parent birds returned periodically to feed them but despite their often close proximity and loud begging calls only one of the juveniles was usually fed during each visit. Begging fledglings with their wings slightly spread were often seen following a feeding parent along a branch.

Although fledglings were seen nibbling bark and leaf bases only a few days after leaving the nest, they were not seen feeding for themselves for at least 10 days after fledging, and then only in the presence of an adult (but not necessarily a parent). From this point the frequency and duration of the feeds provided by adult birds decreased. In response, the fledglings pursued their parents (often as groups of siblings) over a wide area, but returned at frequent intervals to their natal areas throughout the day to feed, and to roost at night. Three to 4 weeks after leaving the nest, most fledglings were rarely fed and adults ignored much of their begging and began to act aggressively toward them.

Throughout this fledging period, juvenile parakeets tended to associate only with their siblings. They responded to the begging calls of their nest mates and ignored calls of other fledglings in the near vicinity. Adult parakeets other than the parents generally tolerated fledglings whilst foraging or near nests for 3 weeks after leaving the nest, but other species were not as tolerant. Kingfishers (*Todiramphus sanctus*), bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*), and even welcome swallows (*Hirundo neoxena*) were all seen chasing juvenile parakeets.

Significant post fledging mortality was noted. Of the 45 chicks fledged from the 20 study nests, 13 (28.9%) died before achieving independence, almost all of these within 2 weeks of leaving the nest. Post-fledging mortality for each study nest was estimated to be 0-66% (median = 25%). Although no corpses were found, the plucked feathers of at least 7 juveniles were found in the more open scrubby areas of Te Titoki Point suggesting that morepork (*Ninox novaeseelandiae*) were responsible for many of these losses. The chewed remains of at least 1 juvenile parakeet (and a kingfisher) were also found in a stream pool inhabited by a 1-m-long long-finned eel (*Anguilla dieffenbachii*).

Fledglings became independent from their parents after 4-5 weeks. Juveniles were commonly seen with small groups of adult parakeets foraging throughout the study area (generally close to their natal range) before dispersing over a much wider area. Although independent, juveniles were still recognisable as such by their more "pristine" plumage, shorter tails, pale bills, and poorly developed vocalisations. Although some effort was made in subsequent years to relocate banded juveniles none of these birds was seen after becoming independent.

Length of breeding season

The breeding season for red-crowned parakeets from the production of the 1st egg through to the departure of the last fledgling lasted just over 2 months (mean = 67.3 days, SD = 6.9, n = 11). The period was, however, shorter in the 1989/90 breeding season (62.8 days, SD = 5.8, n = 5) than in the 1990/91 season (71.0 days, SD = 5.7, n = 6). If the period of nest-site selection (up to 2 months) and the period from fledging to independence (4-5 weeks) are also included, the breeding season is *c.* 5 months long. Depending on the timing of nest failure and subsequent re-nesting (if any), breeding season duration could be extended by a further 1-2 months.

Peak egg laying was in Dec and fledging in Feb although there was a 2-3 week difference in the commencement of laying between the 1989/90 and 1990/91 breeding seasons. Despite the study area being atypical of most of the island, the length or timing of the breeding season differed little in other habitat types. Later instances of egg laying and fledging than that described above were rare (see above) and invariably involved re-nesting attempts following the failure of eggs to hatch or the death of entire broods of young chicks. There was no evidence that more than 1 brood pair^{-1} was raised in either the 1989/90 or 1990/91 breeding seasons.

DISCUSSION

Breeding season

Red-crowned parakeets started breeding in late spring and early summer with most eggs laid in late Nov and Dec, which is consistent with other observations of red-crowned parakeets (Dawe 1979; Taylor 1985). Generally only 1 successful breeding attempt is made each year year, probably triggered by a combination of increasing day length, climatic conditions, and the increasing seasonal availability of food (Forshaw 1980; Taylor 1985; Greene 1998). Seasonal and annual variations in food availability and utilisation (Greene 1998) resulted in females being in better condition earlier or later in the season and directly influence the timing of the onset of nesting. Breeding activity has, however, been recorded in all months of the year in several New Zealand forest and grassland ecosystems (Higgins 1999) and appears to be related to the episodic super-abundance of food, such as the "mast" seeding of beech and some podocarp tree species. "Mast" events generally result in the production of multiple clutches and rapid increases in numbers subsequently followed by steep population declines typical of an "*r*-selected" species (Elliott *et al.* 1996). Given their current restricted distribution such events are rarely recorded today for red-crowned parakeets (a function of remote or relatively small offshore island habitats and stable food supplies), but were regularly recorded in the past (Buller 1888; Oliver 1955). Captive red-crowned parakeets are known to have raised at least 4 consecutive broods where the food supply was unlimited (Dawe 1979). Extended breeding seasons with multiple consecutive clutches are still commonly seen in populations of yellow-crowned parakeets inhabiting southern beech forests that periodically experience mast production of beech seed (Elliott *et al.* 1996). Variations in the timing and length of breeding seasons of other parrot species in relation to food availability and climatic conditions are also commonly recorded (Smith1991; Garnett *et al.* 1999; Robinet & Salas 1999).

Nest site selection

The period of nest site selection and preparation by red-crowned parakeets was prolonged. Sites used included habitually-used roosts and nest sites used successfully in previous years. Selection of nest sites appeared to be part of a ritualised set of behaviours that contributed to reinforcement of the pair bond and the stimulation of nest preparation. Such behaviours have also been reported in other members of the genus, particularly yellow-crowned parakeets (Taylor 1985; Elliott 1996; Higgins 1999).

A variety of nest sites have been recorded for red-crowned parakeets ranging from holes in cliffs, cavities amongst the roots of trees and aerial epiphytes, to abandoned seabird burrows, man made structures and natural hollows in large trees (Kinsky & Sibson 1959; Taylor 1985; Bellingham 1987; Hicks & Greenwood 1989; Higgins 1999; pers. obs.). Sites on the ground or in cliffs are generally recorded on offshore islands where few or no trees are of a suitable size for cavity formation and where there are no introduced mammalian predators (Taylor 1985; Greene 1999). Nest site selection, therefore, appears to be based entirely on the availability of suitable hollows with minimal structural prerequisites, including height, depth, and orientation, within their home range but with a general preference for cavities in large trees.

On Little Barrier Is, the many red-crowned parakeet nests in puriri and pohutukawa trees resulted from their natural propensity to develop cavities as well as their abundance as large trees within the study area. Similar trends have also been found in species such as superb parrots (*Polytelis swainsonii*) where 92% were found in river red gum trees (*Eucalyptus camaldulensis*) that, because of their size and proximity to water, provided an abundance of natural sites (Webster 1989; Higgins 1999). It is unclear, however, why 45% of nests faced north. It is possible that this simply reflects the accelerated decay of wounds caused by burrowing invertebrates or the breakage of branches where it was warmer and humidity remained elevated. In contrast, yellow-crowned parakeet nests usually faced southeast (Elliott *et al.* 1996).

Although red-crowned parakeets used cavities of many sizes, cavity height, DBH, and nest tree height all differed from those recorded for yellow-crowned parakeets (Elliott *et al.* 1996). The 2 different forest structures and growth patterns (short squat pohutukawa and puriri as against tall beech forest) easily explain such differences. Similarly, the internal dimensions of cavities broadly overlap and are also likely to result mainly from the physiognomy and growth patterns of the main hole-producing tree species. However, on average, red-crowned parakeet nest cavities were larger and deeper, probably reflecting both the larger size of the red-crowned parakeets and the ability of yellow-crowned parakeets to exploit smaller sites (Elliott *et al.* 1996).

Because they rely on natural cavities, nest-site limitation and increased intra- and inter-specific competition have been reported for many secondary-cavity-nesting parrots (Saunders *et al.* 1982; Snyder *et al.* 1987; Rowley 1990; Beissinger & Bucher 1992; Munn 1992; Garnett *et al.* 1999; Robinet & Salas 1999). Competitive interactions at, and even in, nest sites during this study were conspicuous and numerous, particularly at the beginning of the breeding season, and was probably exacerbated by the relatively low number of potential nest sites within the highly modified study area. Nest site competition may have been less in unmodified forests with higher densities of large, cavity-containing trees. Red-crowned parakeets were common over the entire island along with other hole-nesting species, such as yellow-crowned parakeet, kaka, kingfisher, and stitchbird (Rasch 1985; pers. obs.). Scarcity of suitable nest cavities probably limited the size of the red-crowned parakeet population on Little Barrier Is, and may also explain why nest spacings of <10 m were tolerated, and why some birds nested in apparently sub-optimal subterranean cavities accessible to kiore (see below).

Of the 7 pairs that could be identified and followed throughout the 2-year study, 2 divorced. Although there were too few data on the stability of pair bonds to examine its impact on productivity, breeding failure (usually with young nestlings) was a critical factor. In both instances breeding failure seemed to be a function of the inability of the male of a pair to provide sufficient food for both the brooding female and the young chicks. Females often paired with other males and almost immediately attempted to re-nest following such failures. Presumably such behaviour could have some degree of adaptive significance if either members of a pair can re-mate and breed successfully (Smith 1991).

Clutch-size, hatching asynchrony, and productivity Red-crowned parakeets on Little Barrier Is produced large (4-9) clutches. The large modal clutch size (7) may be related to latitude — birds in temperate areas lay larger clutches than those of a similar body size in the tropics (Lack 1968) — or an *r*-selected breeding strategy (Taylor 1985; Forshaw 1989; Elliott *et al.* 1996). Alternatively, large clutch size and short incubation and nestling periods in parrots have been positively correlated with diets of protein- rich seeds (Smith 1975) or as an "insurance" that some nestlings will survive if earlier laid eggs fail (Stinson 1979; Stoleson & Beissinger 1997). Hatching of such large clutches is not, however, synchronous. Red-crowned parakeet broods hatched over 3-11 days, despite incubation commencing after the laying of the 4th egg, and varied between years and for individual females. Such highly asynchronous hatching produced significant size hierarchies within single broods. Generally such size disparity among nestlings meant that some of the last chicks to hatch were competitively inferior to their nest-mates and consequently often died of starvation (O'Connor 1984; Stoleson & Beissinger 1995). Nestling mortality (60.7%) of red-crowned parakeets was extremely high compared to that for Ouvea parakeet (*Eunymphicus cornutus uvaeensis*) (37%), red shining parrot (*Prosopeia tabuensis*) (17%), and green-rumped parrotlets (*Forpus passerinus*) (18%) (Robinet & Salas 1999).

Red-crowned parakeets, therefore, have a hatching pattern that paradoxically reduces fledging success. Several hypotheses, including the Brood Reduction Hypothesis (Ricklefs 1965), on the origin of such an apparently detrimental pattern have been put forward. Most so-called "adaptive hatching pattern" hypotheses (Stoleson & Beissinger 1997) consider the size hierarchy to have some adaptive value for the parents, mediated by food limitations, sibling rivalry, or insurance against the loss of older siblings (Stoleson & Beissinger 1997). For example, it may be better for red-crowned parakeet parents to ensure that a few large chicks rather than several medium-sized chicks fledge when food is limiting, but also to be in a position to take advantage of "mast" food events. The few data for red-crowned parakeets suggest that nestling deaths seem to be spread evenly over all nestling ages rather being a result of hatching asynchrony. Observations within nest cavities also suggest that the female parent attempted to feed young chicks selectively for a period while they remained relatively helpless and older chicks were unable to monopolise food deliveries. Such selective feeding may (at least initially) equalise growth rates of nestlings and so contribute to increased survival of last-hatched chicks and so reduce the cost of hatching asynchrony (Stamps *et al.* 1985; Krebs 1999).

The present data are insufficient to exclude adaptive hatching patterns as an explanation for the extreme hatching asynchrony seen in red-crowned parakeets. However, studies of other parrots with similar hatching asynchrony concluded that reduced growth and survival of later hatching chicks do not inevitably follow (Smith 1991; Stoleson & Beissinger 1997; Krebs 1999). In green-rumped parrotlets, an early onset of incubation of large clutches may increase egg survival, offsetting the costs of asynchronous breeding (Stoleson & Besissinger 1997). Where there were few cavities, female parrotlets may also defend them by starting to incubate before the last egg is laid (Beissinger & Waltman 1991). In crimson rosellas (*Platycercus elegans*) the cost of extreme asynchrony was apparently low and largely a function of maintaining equitable food distribution to the entire brood, thereby equalising growth rates (Krebs 1999). Variations in hatching intervals and the degree of hatching asynchrony between years in red-crowned parakeets may result from differences in age, experience, and condition of females, or the "quality" of her mate.

Red-crowned parakeets had a high hatching success (83.6%) for such large clutches of eggs (all eggs hatched in 20% of clutches). Mortality of nestlings, however, was high: all nestlings died in 25% of the nests examined, rather than gradual attrition through brood reduction. At least 1 nest failed because of predation. More commonly, complete broods (mostly older than 2 weeks) starved as a result of the male failing to provide sufficient food for both the brooding female and offspring. The pair invariably divorced after breeding failure.

Given the cumulative investment in resources for chick growth, losses at chick stage represent significant costs in time and energy to the parents. Causes of mortality could, therefore, be expected to be biased towards factors, such as predation or weather, that may operate at any time and whose expectation of occurrence changes with time (Ricklefs 1969). For example, the population of Kermadec Is red-crowned parakeets (*C. n. cyanurus*) on Macauley Is in 1966 was *c.* 1000, but by Sep 1988 this had risen to 17,000-20,000. Between Sep and Nov 1988 the population declined by 90-95%, as a result of drought (G.A. Taylor pers. comm.).

Mortality was also high immediately following fledging. In some broods up to 50% of fledglings disappeared, mainly as a result of predation by morepork. Nestlings became increasingly vocal when begging at nest entrances as they approached fledging, increasing the risk of attack by morepork, even in daylight (pers. obs.). Horizontal holes in lateral branches further increased the risk of predation because nestlings often remained exposed for some minutes whilst being fed, and a morepork took such chicks at least once.

Post-fledging mortality was highest during the 1st 2 weeks following fledging. All 10 young that fledged before their feathers had developed sufficiently for flight survived to independence. However, not all the 36 fledglings that were able to fly as soon as they fledged, survived. These inexperienced fledglings often roosted in very exposed sites in large trees, where they were vulnerable to morepork, rather than in holes or thick cover. When their flying skills improved, and they chose better roost sites, their chances of survival improved.

Implications for conservation

The red-crowned parakeet is one of 3 *Cyanoramphus* parakeets endemic to the main islands of New Zealand. Aspects of the behaviour and ecological characteristics of red-crowned parakeets and orange-fronted parakeets are thought to have resulted in the almost complete extirpation of the former on the mainland — it is now restricted to several small offshore islands, mostly free of introduced mammals, where they are still common — and the restriction of the latter to small relict populations in the South Island high country. Yellow-crowned parakeets, however, persist in reasonable numbers in several mainland forests.

Introduced predators and browsers, habitat loss, and behavioural differences have been suggested as mechanisms explaining the current distribution of parakeet species on mainland New Zealand (Taylor 1985; Elliott *et al.* 1996; Greene, 1998). The relative vulnerability of red-crowned parakeets to predation appears to be particularly significant. Several features of red-crowned parakeet breeding biology appear to exacerbate this vulnerability and so have significant implications for the conservation of the species.

Red-crowned parakeets are noted for using an extremely wide range of nest sites, ranging from holes in tall trees to underground cavities, holes in cliffs and rock tumbles, and in dense vegetation on offshore islands. Often such sites are used repeatedly as roosts or for nests, and are often very conspicuous because of various behaviours and the accumulation of faeces. Although it is uncertain whether all such sites were used in the past on the mainland, experience on Little Barrier Is suggests that at least some sites such as holes in the ground or in cliffs were used, if population densities were high or there were few large hole-producing trees. Holes near or on the ground were likely to have been extremely vulnerable to predators such as stoats, rats, and perhaps possums. Not only would many of these holes have been within easy reach many would have been substantially larger than those used by the much smaller yellow-crowned parakeet, affording easy access for some predators.

As with other hole-nesting species such as the yellowhead (mohua; *Mohoua ochrocephala*) and yellow-crowned parakeets, given the late start and extended breeding season (Elliott 1996; Elliott *et al.* 1996) and coincident peaks in the populations of rats (Innes *et al.* 2001) and stoats (King *et al.* 1996), predation of red-crowned parakeet nesting attempts are likely to be higher than for many other forest birds. Female parakeets, in particular, are exposed to predation for a considerable period; from nest preparation until chicks no longer need to be brooded. Activities that attract avian and mammalian predators to nests, such as vigorous digging in nest chambers resulting in material being flung out of holes, and nestlings begging loudly for food near the nest entrance only make matters worse. Female red-crowned parakeets in their nest holes also respond poorly to intruders, which increases their vulnerability. Additionally, the red-crowned parakeet's breeding strategy, including large clutches, marked hatching asynchrony, and the associated extended incubation and nestling periods, increases the time that females and nestlings are vulnerable to predators. Increased predation pressure may therefore increase the costs of asynchronous hatching in red-crowned parakeets and increase the rate of population decline (Krebs 1999). Recently-fledged chicks, particularly those fledging before they are able to fly, are also vulnerable to predators.

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