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Cook's petrel (*Pterodroma cookii*): historic distribution, breeding biology and effects of predators

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Abstract Cook's petrel (*Pterodroma cookii*), a New Zealand endemic, now breeds on only three islands at the extremities of its former range. Holocene fossil bones have indicated sites of 11 extinct colonies on North and South Islands, showing that Cook's petrels preferred hills <1000 m high and 20-30 km inland. This is a forest-breeding, burrowing petrel. Atypically for a seasonally breeding gadfly petrel, some birds visit Hauturu (Little Barrier Island) nocturnally through the non-breeding season, but do not land. The breeding season extends from September to April at its northern-most colony on Hauturu but is a month later in the south at Whenua Hou (Codfish Island), where birds are heavier. The pre-laying exodus lasts about 28 days. Egg-laying extends over 38 days in the large northern colony, but barely 15 days in the smaller southern one. Incubation is mainly done in three 14-day spells. Chick-rearing takes about 87 days. Chicks attain almost twice the non-breeding adult weight. There is a desertion period of about 10 days before fledging. Pacific rats (*Rattus exulans*), feral cats (*Felis catus*) and weka (*Gallirallus australis*) have endangered these last colonies. Breeding success, most affected by rat predation of eggs and chicks, deteriorated seriously after extermination of feral cats from Hauturu, but improved significantly after eradication of rats from Whenua Hou. Rats are now a major threat on Hauturu. Cook's petrels should be considered for reintroduction to suitable mainland reserves, to enhance biodiversity and restore nutrient inflows.

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INTRODUCTION

Cook's petrel (*Pterodroma cookii*) is one of a group of the smallest (150-220 g) gadfly petrels sometimes placed in the subgenus *Cookilaria*. They are restricted to the Pacific Ocean, and most migrate northwards or eastwards after breeding in the South Pacific. Four species breed in summer (*P. pycrofti, P. longirostris, P. leucoptera, P. cookii*), one in autumn (*P. brevipes*) and one in winter (*P. defilippiana*). There are published studies of some aspects of the breeding biology only of Pycroft's petrel *P. pycrofti* (Bartle 1968; Dunnet 1985) and Gould's petrel *P. leucoptera* (Marchant & Higgins 1990; Priddel & Carlile 2001) (see Discussion).

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Historic distribution of breeding colonies

Previous knowledge of Cook's petrel's biology derives from limited observations by Reischek on Hauturu (Little Barrier Island) in 1882-85 (Oliver 1955) and by Stead (1935, 1936) on Whenua Hou (Codfish Island) in 1934. Cook's petrel still breeds at both locations, as well as on Aotea (Great Barrier Island), islands at the extremities of its former range in New Zealand (Fig. 1, Table 1). However, palaeontological research, supported by Maori oral history and published accounts by early European explorers, reveals that formerly there were at least 11 colonies on North and South Islands between the present remnant colonies (Fig. 1, Table 1).

In the North Island, evidence for breeding in the western hills of Waikato – North Taranaki (colonies 3, 4: Fig. 1, Table 1) comes from Holocene fossil bones found in 18 sites, mainly in karst limestone

Table 1 Present and former breeding colonies of Cook's petrels (*Pterodroma cookii*), with details of status, location, altitude range, distance from the coast and the sources of information. Numbers refer to Fig. 1. * precise location of the colony inferred ** existence and location of this colony uncertain.

Sequential no.	Name	Status	Location °S	Location °E	Altitude range (m)	Distance from coast (km)	References
1	Hauturu	Unstable	36° 12′	175° 05′	30 - 720	0.2 - 3.0	present paper
2	Aotea	Decreasing	36° 12′	175° 25′	300 - 600	5.0 - 9.0	present paper
3	Waikato*	Extinct	38° 12′	175° 00′	up to 565	23 - 30	Millener 1981
4	Herangi*	"	38° 33′	174° 47′	up to 750	c. 13	Medway 1971; Millener 1981
5	Mangaehu*	"	39° 17′	174° 39′	up to 390	c. 43	Taylor 1855; Mead 1966
6	Waikaremoana*	"	38° 48′	177° 05′	up to 1180	c. 40	Colenso 1894; Millener 1981
7	Te Waka	"	39° 14′	176° 39′	up to 1020	c. 27	Worthy *et al.* 2002
8	Maniaroa	"	39° 19′	176° 33′	up to 700	c. 30	Worthy & Holdaway 2000
9	Puketoi*	"	40° 28′	176° 07′	up to 800	c. 30	Millener 1981
10	Aorangi**	"	41° 27′	175° 21′	up to 980	c. 14	Millener 1981
11	Punakaiki*	"	42° 03′	171° 26′	up to 450	c. 5	Worthy & Holdaway 1993
12	Weka Pass*	"	43° 00′	172° 43′	up to 570	c. 20	Worthy & Holdaway 1996
13	Kakahu*	"	44° 08′	171° 04′	up to 695	c. 27	Worthy 1997
14	Whenua Hou	Increasing	46° 46′	167° 38′	30 - 300	0.2 - 2.0	present paper

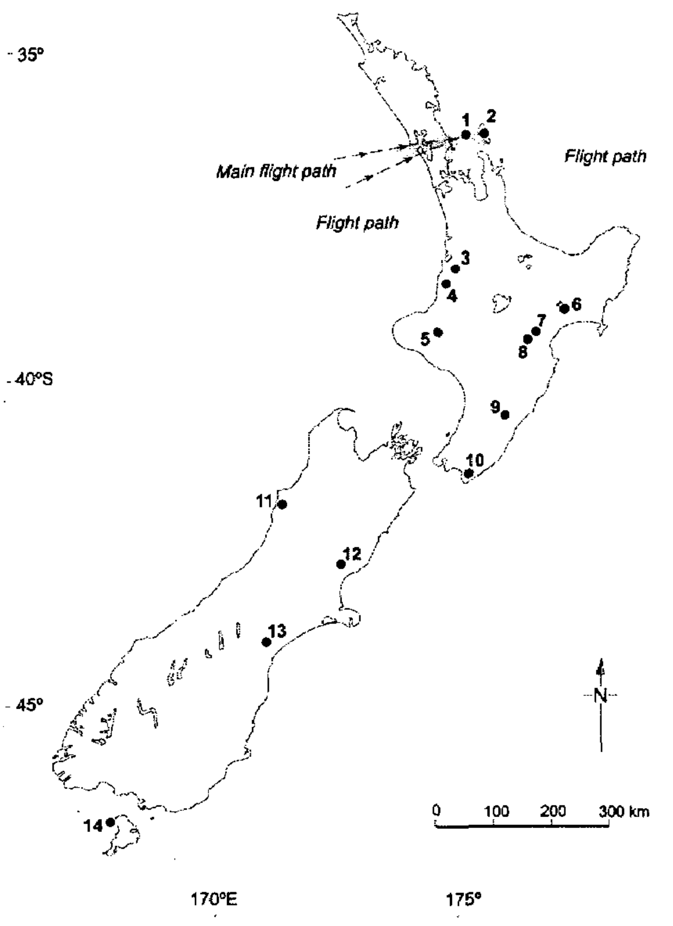

Fig. 1 New Zealand showing the sites of present and former colonies of Cook's petrels (*Pterodroma cookii*) as described in Table 1. The flight paths to the Hauturu (Little Barrier I.) colony are also shown.

caves (Medway 1971; Millener 1981; D.G. Medway, R. J. Scarlett, T.H. Worthy pers. comms.). This is consistent with Maori history of the capture of adult petrels ("titi", which were usually Cook's petrel in North Island) by lighting fires to attract them on ridge tops between the west coast and the Waikato colony (Phillipps 1958). The disoriented birds landed or were knocked down with sticks. This method seems always to have been associated with capture of Cook's petrels (see also Taylor (1855) and Mead (1966) (Taranaki); Colenso (1894) (Lake Waikaremoana); Oliver 1955). The timing of this activity in November (Phillipps 1958) coincided with high activity of Cook's petrels visiting Hauturu (pers. obs.). A stream which flows from the highest part of the inferred Waikato colony is the Mangatiti (manga = branch of a river). There is also a Mangatiti stream flowing from Puketoi Range (colony 9: Fig. 1, Table 1), where Millener (1981) found Holocene fossil bones of Cook's petrel at two sites.

Another breeding site was well inland in Taranaki (colony 5: Fig. 1, Table 1), and probably associated with Holocene bones from rock shelters 20 km to the north-west of this site (D.G. Medway pers. comm.).

Holocene fossil bones of Cook's petrel have also been found by Lake Waikaremoana (colony 6: Fig. 1, Table 1) (Millener 1981), where Colenso (1894) reported petrels calling at night in 1841-43 (the described calls could have been of Cook's, as he thought, or of mottled petrels (*P. inexpectata*)). Colenso also describes the petrels being caught there by Maori using brush fires on ridges to attract them.

Palaeontological studies indicate the existence of past breeding colonies on Te Waka and on and near Maniaroa Ranges (colonies 7,8: Fig. 1, Table 1) (Worthy & Holdaway 2000; Worthy *et al.* 2002). The fossil deposits from Te Waka included many immature bones of Cook's petrel but this colony, at relatively high altitude, did not survive the glacial maximum of about 18,000 years ago (Worthy *et al.* 2002).

The possible Aorangi colony (colony 10: Fig. 1, Table 1) is at a very likely site but supported by only 1 bone (Millener 1981).

In South Island, there is evidence for past breeding on the west coast north from Punakaiki (colony 11: Fig. 1, Table 1), and in North Canterbury near Weka Pass (colony 12: Fig. 1, Table 1). In South Canterbury there are Holocene fossils from hills inland from Temuka (colony 13: Fig. 1, Table 1). There are bones from other South Island sites such as Mt Cookson (Worthy & Holdaway 1995), coastal Otago (Worthy 1998a) and inland Southland (Worthy 1998b), but there are so few bones from these sites that they seem insufficient as evidence of breeding rather than of transient, prospecting or stray birds.

Several of the records from eastern South Island are of bones associated with laughing owl (*Sceloglaux albifacies*) nest sites or roosts (Worthy & Holdaway 1996; Worthy 1997, 1998a), indicating that this extinct hawk-owl was a predator of Cook's petrel and would have occurred in similar areas. In descriptions of the calls of laughing owls in South Canterbury (Williams & Harrison 1972), one of the calls described (by Black) is so perfect a description of Cook's petrels' flight call as to suggest it possibly was this petrel, which also calls often on wet, misty nights. Potts (1871: 63) was aware of a similarity between the calls of Cook's petrel and this owl, but could distinguish them. T. Worthy (Higgins 1999: 886) also suggested there had been confusion between petrels' and owls' calls, especially when heard on wet, misty nights.

Surviving colonies

Hauturu (Table 1) is a long-dormant volcanic island of 2817 ha and rising to 722 m. It has perhaps New Zealand's best example of pristine sub-tropical rainforest, having been virtually unaffected by introduced herbivores, and suffering only logging of kauri (*Agathis australis*) in the late 1800s on its west and south flanks. Feral cats (*Felis catus*) were eradicated by 1980 (Veitch 2001). Hauturu holds by far the largest colony of Cook's petrel, estimated at 50,000+ breeding pairs (MJI unpubl. data), the vast majority occupying burrows above 350 m a.s.l., as they did when Reischek studied them in 1882-85 (Oliver 1955).

On Aotea (Table 1), about ten times the size of Hauturu, only 12 scattered burrows have been found despite extensive surveys during the last 25 years, and these are the first burrows reported from this island. Cook's petrels commonly fly over this inhabited, highly-modified island, presumably passing to and from Hauturu. Some land on Aotea, as shown by the widespread corpses of cat kills in numbers disproportionate to numbers breeding locally. Dogs (*Canis familiaris*), wild pigs (*Sus scrofa*) and two rat (*Rattus*) species are other threats.

Whenua Hou (Table 1) is a granite island of 1369 ha and rising to 348 m. It has temperate rainforest, somewhat modified by past impacts of possums (*Trichosurus vulpecula*) and of sealers and their cattle around Sealers' Bay. Its Cook's petrel colony, estimated as occupying 20,000+ burrows when discovered in 1934 (Stead 1936), and reportedly then spread over much of the island, was approaching extinction when our study began there in 1982. Removal of weka (*Gallirallus australis*), mainly responsible for this demise, was in progress then and completed 2.5 years later (D.A. Brown unpubl.). Pacific rats (*Rattus exulans*) were eradicated in 1998. The Cook's petrel population has been recovering for over 15 years and probably already numbers 1000+ breeding pairs (pers. obs.).

Scope of this study

The observations of Reischek on Hauturu in 1882-85 (Oliver 1955) and of Stead (1935, 1936) on Whenua Hou in 1934 identified the egg-laying peaks as early November and early December respectively. On Hauturu, Reischek observed disturbing levels of mortality of this petrel caused by introduced predators (feral cats, dogs, wild pigs – the latter two were removed within 25 years). Thereafter, this petrel was studied only casually until this study began, preliminary results of which have been published by Marchant & Higgins (1990). Thus our paper provides the first detailed information on the breeding biology of Cook's petrel, and the effects of predators on it. The data were obtained mainly on Hauturu, but we include comparative data from Whenua Hou on the egg-laying period, breeding success and effects of predators.

METHODS

During 6-12 November 1971, 50 study burrows of Cook's petrels were established on the summit ridge of Hauturu near the junction of summit and Herekohu tracks, at about 700 m a.s.l.. An observation shaft to the nest chamber was dug, then sealed with a flat rock. Burrows varied in length from 1.0 to 4.6 m, and in depth from 10 to 70 cm. Each burrow was marked with a numbered tag.

Petrels when first found during daytime nest inspections were banded, and colour-banded according to sex if one of the pair was caught around, or within a few weeks after, egg-laying, when they can be sexed cloacally. Fledglings were also banded. Birds were usually weighed (to the nearest g) if removed from the nest. Eggs were also weighed when fresh, and candled by daylight well

Table 2 Weights (g) of male and female breeding Cook's petrels (*Pterodroma cookii*) on Hauturu and Whenua Hou during courtship/mating, at laying and at beginning of 1st, 2nd and 3rd incubation spells on Hauturu and 1st spell on Whenua Hou; and of Hauturu fledglings.

	Hauturu			Whenua Hou		
Sex, status	No.	Mean ± SD	Range	No.	Mean ± SD	Range
Male, courtship/mating	8	197 ± 8.8	185 – 213	6	212 ± 15.7	190 – 232
Female, " " " "	11	185 ± 8.9	175 – 208	4	202 ± 6.2	193 – 207
Unknown, " " " "				5	192 ± 8.2	182 – 205
Female, laying	16	202 ± 8.5	180 – 214	13	219 ± 13.9	195 – 244
Male, starting 1st spell	13	253 ± 14.4	224 – 275	18	276 ± 12.7	257 – 302
Female, " " 2nd "	7	253 ± 7.2	240 – 261			
Male, " " 3rd "	30	247 ± 15.5	215 – 273			
Fledgling, departure	17	205 ± 12.2	175 – 221			

into incubation to determine fertility. Eggs with unaltered contents were judged infertile; those with sloppy, smelly contents or inactive older embryos were considered as embryonic deaths.

Activity at burrows was monitored by screening the entrance with twigs. Burrows with undisturbed screens were not inspected unless a weighing or other observation was required. These petrels were very tolerant of handling: only 2% of 102 captures of breeders from nests resulted in desertions (one temporarily – the chick was reared; the other from a wet burrow which produced no chick in any year of study). Thus we believe that our studies had only a minor effect on these petrels' behaviour and breeding success.

Of the 50 study burrows originally prepared seven, found to be unsuitable for breeding for various reasons, were excluded. Between the 1980s and late 1990s many of the nest chambers became inaccessible for study because of burrow extensions by the birds, loss of study lids through leaf litter accumulation, or landslips. Thus, in January–February 2001 a new set of 50 study burrows was established near Orau hut, at a similar altitude but further east than the originals. In February 2003, 22 study burrows were set up near the base at 60 m a.s.l., in an isolated, atypical lowland site.

Study burrows were set up similarly on Whenua Hou from 1982, when those prepared were among the first found as active burrows on the island since 1934 (Stead 1936). More study burrows were found in succeeding years. The 36 study burrows on this island were in two groups about 2 km apart. The low study area (30-100 m a.s.l.) had burrows in pure sand under consolidated forested dunes, or in peaty loam at the higher extremity. The high study area (about 250 m a.s.l.) had burrows in heavier, peaty soil under tall podocarp/rata forest. As this area was adjacent to pakihi bogland, a few burrows suffered drainage problems.

Studies on Whenua Hou concentrated on assessing breeding success (% of study burrows with fledglings), with typically one visit only each year about late March, three-four weeks before fledgling departures. Chick mortality subsequent to visits was probably minimal, as nearly all were in good condition, and late chick deaths could be detected from remains found next year.

In November-December 1998 we determined laying dates in the low study area on Whenua Hou. Fresh eggs were weighed to the nearest g, and measured to the nearest 0.1 mm. Adults were sexed and weighed on their first day on the nest. The pattern of incubation around laying was observed.

Since all weighings were done by day, yet the petrels arrived and departed at night, all weights were derived by adding (arrival weight) or subtracting (departure weight) the average weight loss/half day of that particular bird or category of bird. For example, all birds arriving to incubate had 2 g added to the weight taken on the first day, as they lost about 4 g/day.

Unless stated otherwise, the results presented in this paper were obtained on Hauturu. Means are given ± 1 standard deviation. Statistical tests used were Student's t-test for weight comparisons, and chi-square tests for ratios.

RESULTS

Weights on Hauturu and Whenua Hou

Comparisons of weights of adult Cook's petrels at various stages of the breeding cycle showed that Whenua Hou birds were consistently heavier than Hauturu birds (Table 2). This was so for all adults weighed during mating/pair formation ($t_{32} = 3.042$, $P<0.01$). The Whenua Hou data included five unsexed birds which, from their weights, seem to have been mainly females, so there was probably a similar female bias in the mating/pair formation weights from both islands. Whenua Hou females were heavier at laying ($t_{27} = 4.165$, $P<0.001$), and males beginning their first incubation spell were heavier ($t_{29} = 4.663$, $P<0.001$) than their counterparts on Hauturu.

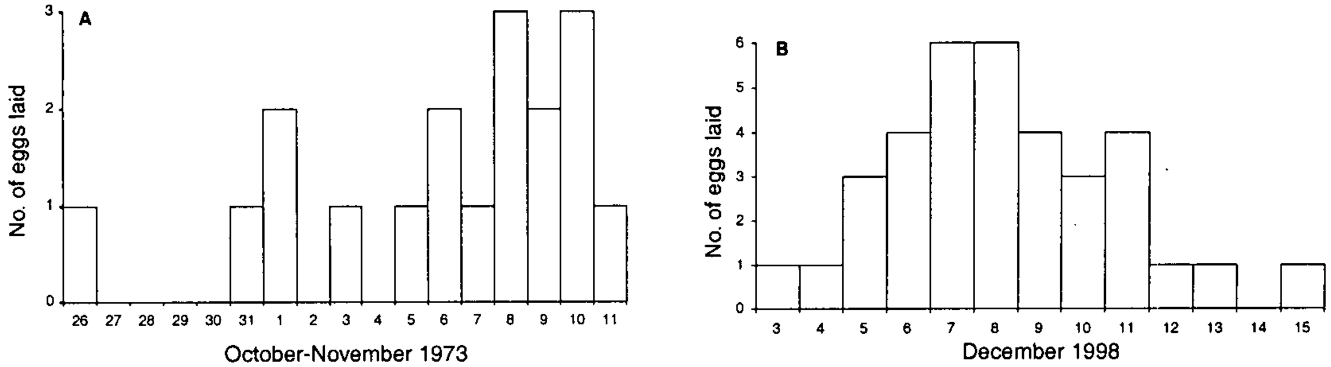

Fig. 2 Laying dates of Cook's petrels (*Pterodroma cookii*): **A.** Hauturu (Little Barrier I.) in 1973 until 11 November when 50% of eggs had been laid; **B.** Whenua Hou (Codfish I.) in 1998.

Activity on the breeding grounds

Colony attendance (aerially, at night) during the non-breeding season is documented for Hauturu, but thus far not for Whenua Hou. Cook's petrels calling over the high parts of the Hauturu colony have been recorded as follows: one to a few at a time, heard every night above tops, 25 Apr.-13 May 1986-88 (Tennyson 1989; MJI pers. obs.); mid-June 1982, "a lot were flying around and calling all night" (M. Shepard pers. comm.); 30 July 1962, "first calls heard at base" (Blanshard 1972); heard "before end August 1958" (Heather 1959).

During the period from April (after the last chicks had departed) to August, no Cook's petrels were reported seen on the ground. There was no evidence of activity at burrows in this period, and no bird was found killed by cats in this period prior to 1980. Beach patrol scheme reports of the Ornithological Society of NZ reported none beach-cast during May to August (see also Powlesland 1987). This indicates that the numbers visiting Hauturu in winter were small, and that they did not land.

On Hauturu during September, birds were heard regularly at the island ranger's base, indicating that the level of activity of Cook's petrels was increasing. Birds were first heard by the resident ranger at his base on 17 September 1947 (Parkin 1948) and by a subsequent ranger on 7 September 1960 (Blanshard 1961). They were also reported overhead at Kaipara Flats, on the western flyway to the island (Fig.1), on 20 September 1958 (Hudson 1960).

Nocturnal activity, as indicated by the volume of calling over Hauturu, was at a high level throughout October- February. It then tailed off to reach its lowest level at the end of March (silence on some nights), though late chicks were still being fed.

Courtship and the pre-laying exodus

Adults that subsequently incubated did not visit their burrows during at least the two weeks before laying. No studies were made through the main period of the pre-laying exodus (October), but anecdotal evidence suggests that the exodus lasted about 26-31 days. In 1973, a male was found freshly cat-killed on 1 October. His mate laid on 31 October, deserting the egg five days later. She probably would not have laid had she not mated. A late pair was in their burrow on 4-5 November 1973, and the female laid about 1 December.

Egg-laying

Laying extended over about 38 days on Hauturu (extreme dates 23-24 October and about 1 December in two years). In 1973, 50% of 36 eggs had been laid by 11 November (Fig. 2A), as also in 1971 when 33 eggs were observed. With a third of eggs laid during 6-11 November 1973, a broad laying peak within 6-16 November was indicated. On Whenua Hou, laying occurred a month later but during a period of just 13 days (Fig. 2B), with a peak on 7-8 December.

On Hauturu, fresh eggs weighed 43.3 ± 2.5 g (n=20, range 39-48) and were 21.7 ± 1.4% (19.1-24.0%) of females' post-laying weight; correlation between egg weight and female weight was positive but weak (r^2 = 0.26, 14 df, *ns*). On Whenua Hou, fresh eggs weighed 46.3 ± 3.8 g (n =19, range 40-52) and were 20.9 ± 1.6% (18.3-23.1%) of females' post-laying weight; correlation between these was positive but weak (r^2 = 0.43, 11 df, *ns*); 20 eggs there measured 52.9 ± 2.1 mm (range 49.2-56.2) x 39.1 ± 1.2 mm (range 37.6-40.8).

Incubation and hatching

In 17% of 35 monitored layings (both colonies combined), males arrived before or with females (mean 1 day, range 0-2) to initiate incubation. Thus, females initiated incubation in 83% of nests, their first incubation spell averaging 2.3 days (range 0-6, n = 35). Results from Hauturu (16 layings) and Whenua Hou (19) were similar.

On Hauturu, the mean incubation period was 47.3 ± 1.4 days (range 46-50; n = 7). In 11 pairs monitored in 1973 there were 33 main incubation spells, three for each pair and conducted by male, female and male again. The average duration was 14.0 days (range of within-pair means: 12.7-15.0).

Although 25% of eight hatchings occurred at the end of males' second spell, 75% were undertaken in a final brief spell by females averaging 2.8 days (range 0-6, n = 8).

Weights of males and females at the beginning of incubation spells are shown in Table 2.

On Hauturu, the rate of weight loss during incubation in 1972 and 1973, for 23 males over 131 days was 4.24 ± 0.75 g/day; for 14 females over 90 days it was 4.24 ± 0.99 g/day.

Occasionally eggs were left unattended between change-overs, usually when the incubating bird's weight declined to a critical level. This occurred particularly at the end of females' main spell in 1973 (Imber 1984), when 26% of 31 eggs were left unattended before the males' return. These females attained the lowest mean weight recorded for any group of adults in our study: 172.2 ± 9.7 g (range 156-183, n = 6). Although one desertion was for only <1-5 h (the female departed before the male arrived on the same night), all unattended eggs were eaten by Pacific rats. The frequency of temporary egg neglect varied between years: 2.1% of egg-days in 1972 (376 egg-days, 36 eggs) compared to 8.2% in 1973 (330 egg-days, 36 eggs).

After predations among the 72 eggs laid, the fertility rate of 56 eggs inspected (28 in 1972, 28 in 1973) was 91%, and hatchability (infertility and pre-hatching mortality deducted) was 88%. Of the two embryonic deaths, one resulted from intermittent incubation as the burrow was prone to flooding. There were seven losses due to infertility plus embryonic death against at least 12 egg losses caused by rat predations.

The time from first pipping until hatching of the egg averaged 4.8 days (range 4-6, n = 4).

Hatching dates recorded on Hauturu ranged from 10 December to 20 December (n = 4) but the majority were later than this. The guard stage was 1-2 days (n = 2), both by females.

Chick-rearing

Chick weight reached its peak in late February (Table 3). The mean maximum weight attained by 18 chicks between 18-25 February 1973 was 346.5 ± 43.8 g (range 275-436). The frequency of feeds to 19 chicks over 129 nights during 18-25 February 1973 was one feed per 3.1 nights. The mean overnight weight-gain of 15 fed chicks was 39.1 ± 15.3 g. However, two of these probably received a feed from both parents on the same night. Excluding these, the mean weight of 13 meals was 37.4 ± 9.8 g (range 17.7-48.7), similar to half the weight of the two putative double feeds (67.4 and 72.7 g).

The rate of weight loss between meals of nine chicks measured over 22 chick-days (18-25 February 1973) was 12.7 ± 2.7 g/day (range 9.5-18 g/day). The rate of weight loss in chicks approaching departure was 5.5–9.5 g/day, and averaged 7.7 g/day over 37 chick-days.

Table 3 Weights (g) of Cook's petrel (*Pterodroma cookii*) chicks through February-early March on Hauturu during 1972-74.

Period	No. chicks	Weight (g) Mean ± SD	Range
7 Feb. 1974	5	245 ± 55	182 – 315
11-14 Feb. 1974	9	295 ± 75	204 – 420
17-18 Feb. 1973-74	30	312 ± 47	200 – 422
24-26 Feb. 1972-73	36	323 ± 49	210 – 420
2-3 March 1972	18	320 ± 45	220 – 404

There was a desertion period before chicks departed during which they were not visited by parents. Between 18 and 27 March 1973, 11 of 12 fledglings observed were not visited before their departure; for two, at least nine and about 11 nights elapsed without a parental visit. Only the youngest was fed (twice) during 18-27 March, resulting in a weight increase from 233 to 295 g.

Departure of fledglings

Fledglings emerged from their burrows on average on 2.6 nights before the night of departure (range 1-5 nights, n = 7). In one instance a fully-feathered fledgling of departure weight was found by day in a vacant burrow near its own.

Of 13 fledglings observed on Hauturu in 1975, 11 departed between 14-31 March, the remaining two on or about 2 and 7 April (estimated from weight loss rate and plumage state). Over half (54%) departed between 23-27 March. The mean weight at departure of 17 fledglings (Table 2) was 107% of the mean breeding adult weight during courtship. On Whenua Hou, single fledglings were seen leaving on 25 and 26 April 2000.

The length of the chick-rearing period (hatching to departure) was not measured for any individual chick. The interval between the mid-point of egg-laying (11 November) and that of departure (25 March), less 47 days of incubation, indicates a fledging period of about 87 days.

Breeding success and population trend

Breeding success is defined as the number of fledglings reared per usable breeding burrows and expressed as a percentage. This measure assumes a similar occupancy rate by breeding pairs each year; it was 86% in two consecutive years on Hauturu (Table 4).

On Hauturu (Table 4), average breeding success during 1971-82 (7 years) was 33%, but it was less than 13% during 1984-2003 (5 years) (Table 4; χ^2=20.6, 1 df, P<0.001). However, 68% breeding success was achieved in the isolated, 22-burrow low study area in 2003. A slow, downward population trend was noticed, temporarily reversed by the increased recruitment following cat eradication.

On Whenua Hou (Table 5), breeding success in the presence of rats was significantly lower (χ^2=50.4, 1 df, P<0.001) in the high study area than in the low study area, but it increased significantly (χ^2=29.3, 1 df, P<0.001) in the high study area following eradication of rats. In the low study area, breeding success with or without rats did not differ (χ^2=1.36, 1 df, *ns*), and it did not differ between high and low study areas without rats (χ^2=0.28, 1 df, *ns*). After 1982-84, numbers of active burrows began to increase.

Table 4 Breeding success of Cook's petrels (*Pterodroma cookii*) on Hauturu between 1971 and 2003 (* % of burrows).

Year	No. burrows	No. eggs	% laid	No. chicks	% departed*
1971/72	43			17	40
1972/73	42	36	86	17	40
1973/74	42	36	86	11	26
1974/75	42			12	29
1976/77	41			11	27
1978/79	40			14	35
1981/82	39			12	31
1984/85	40			≤9	≤22
1997, 2000	21			1	≤5
2000/01	50			≤9	≤18
2002/03	55			≤5	≤9

Table 5 Breeding success of Cook's petrels (*Pterodroma cookii*) in the low and high altitude study areas of Whenua Hou in 1982-1998 (1989 excepted) when Pacific rats were present, and in later years (1999, 2000, 2003) following rat eradication.

	Low area			High area		
	No. burrows	No. chicks	% success	No. burrows	No. chicks	% success
1982	6	5	83	5	2	40
1983	14	10	71	5	0	0
1984	12	8	67	7	2	29
1985	12	9	75	11	6	55
1986	13	9	69	10	6	60
1987	13	11	85	13	0	0
1988	19	11	58	13	8	62
1990	19	13	68	13	8	62
1991	20	10	50	13	1	8
1992	20	12	60	12	1	8
1993	20	11	55	13	1	8
1994	20	14	70	13	2	15
1995	20	14	70	13	9	69
1996	22	12	55	13	8	62
1997	22	17	77	13	2	15
1998	22	14	64	13	1	8
1999	23	18	78	13	7	54
2000	23	13	57	13	11	85
2003	41	32	78	17	15	88
1982-98	274	180	66	180	57	32*
1999-2003	87	63	72	43	33	77 ‡

*Low vs High areas, 1982-98: χ^2=50.4, 1 df, P<0.001
‡ 1982-98 vs 1999-2003, High area: χ^2=29.3, 1 df, P<0.001

Impacts of predators

Hauturu

During three years of intensive breeding study (1971-74), cats killed five (7%) of 72 breeding adults from study burrows in 1973/74, but none in the two previous seasons. Cats killed one fledgling in 1973 and one in 1975 from the study burrows, but occasionally killed fledglings *en masse* along tracks, e.g. 14 on 18 March and 6 on 23 March 1975.

The main effect of cats on the population was in killing non-breeders and pair-forming breeders. In 1975/76, 156 cat-killed Cook's petrels were counted along 8 km of track (C.R.Veitch pers. comm.). Most of these were presumably non-breeders. This could be extrapolated to the *c*.50 km of tracks that then penetrated the island's interior (Veitch 2001). In the study area we counted 4 corpses off the tracks for each corpse on the adjacent tracks. Thus, cats probably killed about 5000 Cook's petrels that 1975/76 breeding season. The level of mortality seemed to peak in 1973-1976, as it did for black petrels (*Procellaria parkinsoni*) (Imber 1987).

Non-breeding Cook's petrels on the ground uttering the 'purrr' call must have fatally attracted cats, as they probably did weka on Whenua Hou. The 'purrr' call was almost unknown to MJI on Hauturu till after cats were removed, but is now often heard during the breeding season on both islands.

The predation rate on eggs by Pacific rats was 12.5% and 32% in 1972/73 and 1973/74 respectively. Equally detrimental was rat predation of chicks, particularly just after the brief guard stage, but also of chicks up to 50 days old and weighing 300+ g. We have not studied the full chick-rearing period, so are unable to provide an overall rate of rat predation of chicks. Of three chicks observed until 1-3 days beyond the guard stage, one was killed. Among eggs with live embryos during late incubation, 32% of 28 were lost in 1972/73 (16 December-17 February), and 48% of 21 in 1973/74 (22 December- 4 February). We believe most of these losses were caused by rats because *Pterodroma* spp. in New Zealand rarely suffer above 10% chick mortality in the absence of rats (pers. obs.). Combining egg and chick losses, up to 40% (1972/73) and up to 64% (1973/74) of fertile egg losses were caused by rat predation at the egg or young chick stage.

In 2001, only 12 chicks survived in 50 burrows on 27 January, and 25% were killed by rats in the

Table 6 Aspects of the breeding biology of three *Cookilaria* gadfly petrels: Pycroft's petrel (*Pterodroma pycrofti*) (Bartle 1968; Dunnet 1985), Gould's petrel (*P. leucoptera*) (Marchant & Higgins 1990; Priddel & Carlile 2001), and Cook's petrel (*P. cookii*) on Hauturu. Data refer to mean values.

	Pycroft's petrel	Gould's petrel	Cook's petrel
Non-breeding weight (NBW) (g)	153	181	191
Breeding season	Oct. - April	Oct. – May	Sept. - Apri
Incubation period (days)	45		47.3
Weight of males beginning first incubation spell (% NBW)	128		129
Weight loss during incubation (g/day)	3.6		4.2
Fertility of eggs (%)	93		91
Hatchability of eggs (%)	87		88
Peak weight of chicks (% NBW)	*c.*163	138	169
Chick-rearing period (days)	81		*c.*87
Mean weight (g) of feeds to older chicks		35	37
Fledgling departure weight (% NBW)	110	90	107
Peak of fledgling departures	30 March	14 April	25 March

next two weeks. In 2002/03, only five survived in 55 burrows on 3 March. We estimated that rats ate the eggs or killed chicks of 70-90% of potentially successful pairs in those two breeding seasons.

Whenua Hou

Weka, introduced probably during 1895-1920, threatened this petrel population's survival (Blackburn 1968). By 1982, when our study began, the removal of weka was well advanced, having been most intensive in 1980-81. Even though only four weka persisted during 1983-84 (D.A. Brown unpubl.), they killed 15 adult Cook's petrels in part of the low study area (6 in 1982/83; 9 in 1983/84), where there had been only about 26 breeding petrels. Two 1982/83 breeding burrows (where all adults were killed in 1983/84) have remained disused since. The weka believed solely responsible was shot 1 km away late in 1984, thus completing eradication. This demonstrates the destructive potential of the 2500-3000 weka estimated present on this island before 1980 (Brown unpubl.).

Breeding success before and after eradication of Pacific rats is shown in Table 5. The rats had little effect in the low study area, although one case of predation of a large chick was observed there. Their greatest effect was in the high study area, even though this varied greatly from year to year. Pacific rats were eradicated in October 1998, after which petrel breeding success improved significantly.

The lowest breeding success in the high study area (but not in the low study area) coincided with El Niño phases of the El Niño - Southern Oscillation (ENSO). Thus, in El Niño years of 1982/83, 1986/87, 1990-94 and 1997/98 (Wolter 2003) the breeding success in the high study area was 7.3% compared to 52% in other years till rat eradication (Table 5; χ^2=41.3, 1 df, P<0.001).

Two predatory birds formerly had a minor impact on Cook's petrels on Whenua Hou. The island held one-two pairs of southern skua (*Catharacta lonnbergi*) in the 1970s, but these were apparently poisoned by eggs intended for weka in 1982. Skua have not re-colonised. Stead (1935) observed two pairs of New Zealand falcons (*Falco novaeseelandiae*) breeding there, and noted that Cook's petrels were their main prey. Falcons no longer frequent this island.

DISCUSSION

Breeding biology

Of the six species of *Cookilaria* gadfly petrel, there is information on the breeding biology of Pycroft's petrel (Bartle 1968; Dunnet 1985) and Gould's petrel (Marchant & Higgins 1990; Priddel & Carlile 2001) to compare with Cook's petrel (Table 6). Pycroft's petrel is the smaller species and one of the smallest gadfly petrels; much of the comparative data reflect this size difference. In general, however, the available data suggest close similarities in breeding biology among these three species.

Colony attendance outside the breeding season

We know of no other *Pterodroma* species with a seasonally restricted breeding season that visits its breeding colony throughout the year. The numbers visiting outside the breeding season appear quite small and there is no evidence that they land, suggesting that most are young pre-breeders. This habit is similar to, but less developed than, that found in prions (*Pachyptila* spp.), blue petrels (*Halobaena caerulea*), Kerguelen petrels (*Lugensa brevirostris*) and other fulmarine petrels (Marchant & Higgins 1990). Thus, it may be another indication of a phylogenetic link between prions/blue petrel and the primitive *Cookilaria* gadfly petrels (Palma & Pilgrim 2002).

Mortality and breeding success

On Hauturu, cats probably reduced the level of rat predation on Cook's petrel before 1980 because rats were the main prey of cats in August (Marshall 1961), and probably from May-August when Cook's petrels, their main prey in summer (Marshall 1961), were virtually absent. By depressing rat numbers through winter–spring, before the annual rat population increase, cats could have reduced rat predation at the beginning of the petrels' breeding season. The cat population was lowered about 1969 during an attempt at eradication (Veitch 2001), but predation on black petrels indicated that the cat population increased during 1971-75 (Imber 1987). Although Cook's petrels' breeding success declined over that period, thus running counter to the hypothesis that cats could depress rat predation, the higher breeding failure rates in 1973-75 could be attributed directly to cats (predation of adult petrels), and to poor foraging conditions in 1973/74.

Since 1980, breeding success on Hauturu has declined significantly, evidently because of increased rat predation. During cat eradication there would at first have been an increase in the breeding population as a result of diminishing mortality of pre-breeders, many of which would have been produced when breeding success was around or over 33% prior to 1980. But, with decreasing breeding success since 1980, and accentuated since 1984, recruitment would have gradually declined, and is unlikely to be sufficient now to replace adult losses. Recent poor breeding success may have been exacerbated by increased proportions of inexperienced breeders occupying burrows.

On Whenua Hou, the effect of rats fluctuated in the high study area, apparently due to the ENSO. It seems most likely that El Niño phases affected the petrels' breeding success through an effect on the population cycle or foraging and predatory habits of rats. For example, the drier climate of La Nina in southern New Zealand may have enabled the rat population to be more herbivorous. The reversion to El Niño conditions may have caused a deterioration of supplies of plant foods, leading to rats becoming more carnivorous and predatory. The 2002/03 El Niño (Wolter 2003) was accompanied by high breeding success within the high study area, indicating that rats were previously implicated in breeding failures.

Most Cook's petrels breed above 350 m on Hauturu. This distribution may have been induced by cat predation, as well as historical bush clearance during logging of kauri, and past predation by feral pigs, dogs and people. There is evidence of these petrels spreading into areas below 100 m to breed within the last 20 years, and some burrows frequently produced fledglings (A. Dobbins pers. comm.). In 2003, 68% of 22 burrows there produced fledglings, indicating that there is an altitudinal effect on rat predation on Hauturu, as there was on Whenua Hou. This may be related to more carnivory by Pacific rats at higher altitudes on both islands. We could find no indication of a link between the ENSO and petrels' breeding success on Hauturu.

Management implications

On Hauturu, the eradication of cats would initially have benefited the Cook's petrel population by enabling an extra c. 5000 pre-breeders to enter the breeding population every year, but at the cost of liberating Pacific rats from predation by cats. Now, rats are reducing the potential productivity of fledglings by about 83% (from 74% (mean success rate on Whenua Hou since rats were eradicated) to <13% of burrows), equivalent to an annual loss of 35,000+ eggs and chicks, given a breeding population of 50,000+ pairs. Elimination of this threat would not only prevent Hauturu's colony accelerating towards extinction, but also enable it to be a source for colonisation elsewhere, such as Aotea. This island has the potential for a large Cook's petrel colony if predators (feral cats and rats) are controlled.

Removal of rats from Hauturu will also be necessary before other petrels, particularly fluttering shearwaters (*Puffinus gavia*) and diving petrels (*Pelecanoides urinatrix*), can recolonise.

The removal of weka from Whenua Hou during 1980-84 saved this Cook's petrel population from extinction. By the 1990s there were already signs the petrels were recolonising abandoned areas of the island. The extermination of rats in 1998 has had additional benefits for this population, with those birds breeding at higher levels more than doubling their annual productivity.

Mainland 'islands'

Cook's petrel was one of the major species formerly breeding on New Zealand's main islands. Petrels are among few species that increase the fertility, and probably biodiversity, of mainland sites by importing nutrients from surrounding seas (R.N. Holdaway pers. comm.). Managers of mainland 'island' reserves (Saunders 2000) might consider Cook's petrel for introduction to suitable reserves, because of their potentially beneficial effects on the wider ecosystem.

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