THE INFLUENCE OF THE TUATARA ON FAIRY PRION BREEDING ON STEPHENS ISLAND, COOK STRAIT

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SUMMARY: Fairy prions, *Pachyptila turtur,* breed in large numbers on Stephens Island in north-western Cook Strait. The 1974-75 breeding cycle was followed with the aid of observation burrows. Laying, hatching and chick departure times were between those previously observed by Harper (1976) on the Poor Knights Islands and Richdale (1945, 1965) in Foveaux Strait. Tuatara, *Sphenodon punctatus,* are also numerous on the island and often share burrows with the prions. They were directly responsible for the loss of more than one quarter of the eggs and chicks, by predation and interference in the nesting chamber. This mortality is not considered to be a major factor in the regulation of fairy prion populations. That the tuatara-petrel relationship is complex, frequently aggressive, and almost exclusively favours the reptile, is emphasised by this study.

INTRODUCTION

Naturalists have noted for over a century that throughout their range tuatara *(Sphenodon punctatus)* have an intimate relationship with burrowing seabirds. The effect of tuatara on the breeding success of small petrels has been the subject of considerable speculation but little field study. The significance to tuatara of petrel eggs, chicks and adults as food is unknown, as are the spatial relationships between the two animals below ground.

It is well established that tuatara frequently occupy seabird burrows despite being able to construct their own (Mair, 1871; Reischek, 1881). The birds will attack tuatara in defence of their nest chambers, but the two animals may keep separate quarters within the same burrow (Mair, 1872; Reischek, 1885; Kinsky and Sibson, 1959). Many instances of predation by the reptiles of eggs, chicks and adults of the smaller petrel species have been described (Reischek, 1885; Thomson, 1915; Falla, 1924; Sutherland, 1952; Chambers, 1956; Wright, 1961: Campbell, 1967).

Dawbin (1962) expanded the recorded view of tuatara-petrel relationships to encompass the effects of the petrels on the physical environment. Their burrowing activities and enrichment of the soil with minerals and organic matter create easier digging conditions and may encourage a profusion of the invertebrate species upon which tuatara feed. Also, the presence of large numbers of breeding petrels maintains a ground surface free of low-growing vegetation, as substantiated by Campbell (1967), enhancing the ability of the tuatara to forage at night for prey.

Breeding activity of the fairy prion *(Pachyptila turtur)* has been studied in detail twice before; by Richdale (1945, 1965) at Whero Island, Foveaux Strait, and by Harper (1976) on the Poor Knights Islands, North Auckland (Fig. 1). Less complete

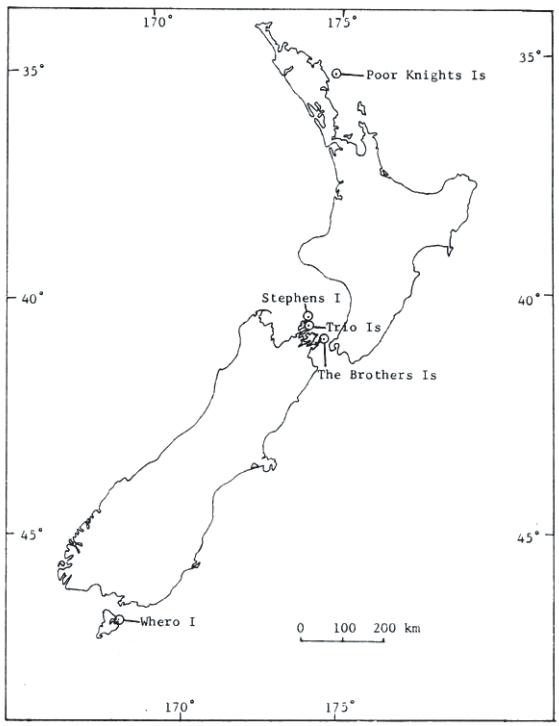

FIGURE 1. *Areas used for study of fairy prion breeding in New Zealand.*

records have been compiled for Trio Islands (Campbell, 1967) and The Brothers Islands (Sutherland, 1952) of Cook Strait.

This paper summarises observations on the breeding of fairy prions on Stephens Island during the entire 1974-75 season. Tuatara coexisted in the study area with the birds, often using the same burrows, and their effects on the breeding success of the prions are presented. The study was one part of an investigation by the author into the ecology and behaviour of the tuatara on Stephens Island, particularly in relation to its food, habitat structure and weather conditions.

STUDY AREA AND METHODS

Stephens Island (Fig. 2), in north-western Cook Strait, was chosen as a study site because of its relative accessibility and the profusion of both tuatara and fairy prions. The island is exposed to frequent stormy weather but rarely experiences extremes of temperature. Encircled by steep rocky cliffs, which rise almost to the summit (280 m) on the north-western side, it has a total area of about 150 ha.

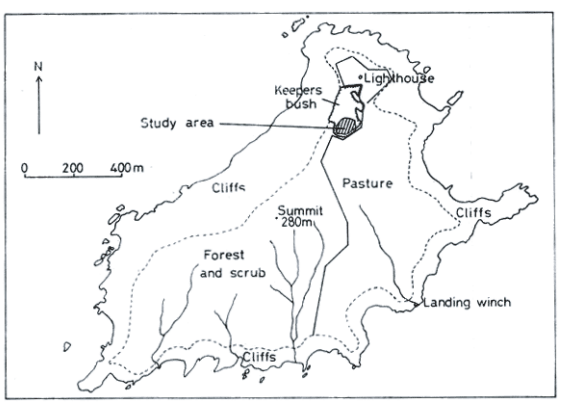

FIGURE 2. *Map of Stephens Island.*

Only small patches of the original forest cover remain following the establishment of a lighthouse station with associated farm in 1894. The cliffs contain a distinctive low-growing vegetation of shrubs (including an endemic form of the kowhai *Sophora microphylla),* herbs and grasses. Most of the rest of the land area is covered in mixed successional scrub, herbland and tussock, with about one third in pasture grazed by sheep and cattle belonging to the lighthouse station. Soils are either clayey and shallow or, where burrowing seabird activity is greatest, very deep, acidic and friable (Ward, 1961). The latter conditions appear to be responsible for the wealth of invertebrate life, many species of which are preyed upon by both the tuatara and the numerous skinks *(Leiolopisma nigriplantare. L. zelandicum. L. infrapunctatum* and *L. lineoocellatum)* and geckos *(Hoplodactylus pacificus. H.* sp. and *Heteropholis manukanus;* A. H. Whitaker, *pers. comm.).* Prions breed all over the island, but are notably in low numbers on the cliffs and in small areas occupied by colonies of sooty shearwaters, *Puffinus griseus.* Tuatara are found almost everywhere.

Between 21 May 1974 and 7 April 1975, alternate fortnights were spent on the island. Regular fieldwork included counts on set transects and general observations of fairy prions, tuatara and other animals, both within the study area (Fig. 2) and elsewhere. In particular, feeding behaviour of tuatara, breeding progress of fairy prions, and above-ground and subterranean activities of both species (especially in interaction) were investigated. A headlamp was used for night observation.

Observations on the breeding of fairy prions were based largely on 50 observation burrows situated in "Keepers Bush", a forest remnant on the north end of the island. In mid-August 1974, before fairy prion breeding had begun, vertical observation shafts were dug to connect with existing prion burrows. The shafts, about 8 cm in diameter, entered the burrows just forward of the nesting chamber, and each was fitted with a wooden lid at ground level. Each burrow had a single terminal enlargement, the nesting chamber, and although some burrows were straight, most curved towards the end so that the chamber was well sheltered from light, wind and rain coming in the entrance (Fig. 3). Burrows varied in total length from about 60 cm to 200 cm, averaging about 120 cm. At approximately 5-day intervals during every second fortnight between 18 August 1974 and 5 April 1975, the burrows were checked in the daytime (using a mirror and headlamp) for prion or tuatara activity. During the period of study, 39 adult birds and 32 chicks were banded.

RESULTS

General observations

The numbers of fairy prions on the island at night varied seasonally (Fig. 4). Virtually absent in autumn, the birds began to arrive in June and numbers increased spasmodically thereafter. On nights when they were numerous they were very vocal and active. Pairing and burrow excavation began in late July. The highest counts at night were recorded in mid-September, when mating, excavation and fighting over burrows reached a peak. There was a decline in numbers just before laying, but the

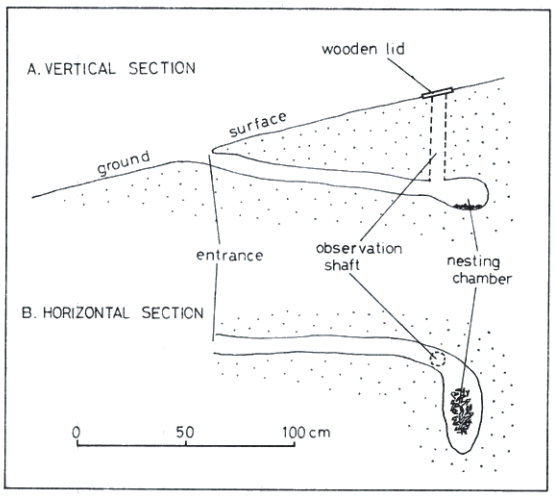

FIGURE 3. *A typical fairy prion study burrow.*

adult population returned in full during early November. In mid-December, adult numbers fell markedly, and declined still further as the chicks matured. Numbers at this time were probably underestimated because the birds were virtually silent, whereas earlier they had been calling constantly. By late February, all prions had left the island, and it was not until the end of March that adults began returning by night.

Aggressive encounters between prions and tuatara were noted throughout the year, though they were very infrequent in comparison with the total number

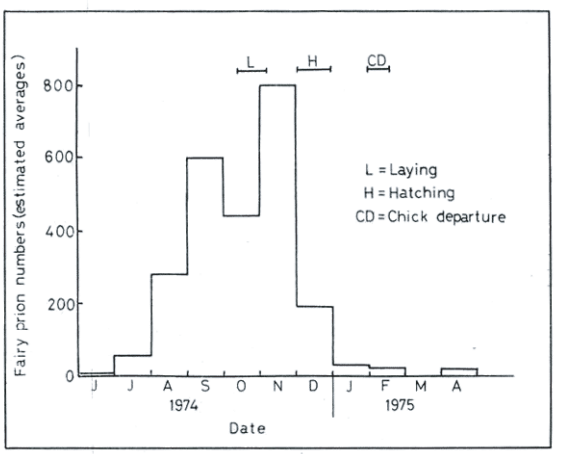

FIGURE 4. *Seasonal abundance of adult fairy prions on Stephens Island as shown by counts at night along set transects.*

of observed interactions between the two species. Prions were only observed attacking tuatara which had entered their nest burrow. The prions attacked by pecking vigorously. On the other hand, eggs, chicks and adult prions were all eaten by tuatara, both above ground and in burrows.

Tuatara faecal pellets containing prion egg shells, and beaks, bones, claws and feathers of chicks and adults were frequently found. Although never observed, it is likely that whole eggs were ingested by tuatara, since scraps of shell and yolk were rarely found. The capture and killing of prions by tuatara were observed. The reptile invariably seized part of the chick or adult (usually the head, though sometimes a wing, a foot or part of the body) in its jaws and maintained a grip until the prey was dead. Occasionally, the prion's pecking, kicking, flapping and struggling forced the tuatara to release it. Adult birds were less frequently attacked than chicks and escaped more often. Those that had been injured by flying into wires or illuminated windows at night, often fell prey to tuatara. Dead and injured birds were sometimes found, having crushed or missing limbs or heads.

During late January - early February when the prion chicks were leaving for sea, predation of chicks by tuatara was especially prevalent: over 50% of all chick predation noted occurred during this fortnight, although chicks were present on the island for about two months. This high predation corresponded to a period when chicks were dying all over the island in numbers unprecedented in recent years (M. Aplin, *pers. comm.).* Dead chicks could be found in hundreds on the ground and those examined were emaciated and had empty guts. Live chicks were often found in a weak state, both above and below ground by day or night. It is probable that enforced fasting during a prolonged period of southerly gales, when adults would have had difficulty gathering food. had debilitated the fledgling birds sufficiently to kill them or make them easy prey to tuatara.

Records from observation burrows

1. Prion breeding cycle

Because of the alternate fortnightly regime of field-work, there are gaps in the records. This means that precise incubation and nestling times could not be determined. Table 1 summarises the situation within the burrows at each inspection date in terms of fairy prion and tuatara numbers.

Each pair of breeding prions took possession of one burrow, which they scraped out and often enlarged, using their bills and feet. Leaves (green

TABLE 1. *Fairy prion and tuatara numbers in burrows during* 1974-1975 *prion breeding season (total number of burrows = 50).*

Date	Prion numbers							Tuatara numbers
	Adults	Eggs	Eggs preyed upon*	Live chicks upon*	Chicks preyed	Dead chicks †	Departed chicks ‡	
18 Aug	20	0	0	0	0	0	0	7
12 Sep	0	0	0	0	0	0	0	4
16 Sep	29	0	0	0	0	0	0	6
22 Sep	2	0	0	0	0	0	0	5
13 Oct	3	0	0	0	0	0	0	5
19 Oct	7	6	0	0	0	0	0	3
8 Nov	39	44	0	0	0	0	0	4
12 Nov	36	46	0	0	0	0	0	5
13 Nov	43	44	2	0	0	0	0	3
3 Dee	40	41	1	1	0	0	0	7
9 Dec	28	25	1	15	1	0	0	7
15 Dec	8	7	1	32	0	0	0	6
1 Ian	0	0	2	32	0	0	0	6
6 Ian	0	0	0	32	1	0	0	3
12 Ian	0	0	0	32	0	0	0	2
29 Ian	0	0	0	12	2	2	16	7
2 Feb	0	0	0	6	0	1	5	2
6 Feb	0	0	0	1	0	1	4	8
10 Feb	0	0	0	0	0	0	1	8
23 Feb	0	0	0	0	0	0	0	8
2 Mar	0	0	0	0	0	0	0	7
26 Mar	0	0	0	0	0	0	0	7
5 Apr	0	0	0	0	0	0	0	5

* Killed or destroyed by tuatara

† Found dead in burrow from other causes

‡ Assumed to have fledged and left the burrows

or dead) and twigs were carried in from the forest floor to make a sparse lining in the nesting chamber. Only one adult of each pair was present in the burrow by day during mid-August; in mid-September birds were found occupying burrows in pairs; thereafter only one adult was ever present in a burrow at a time.

The first eggs appeared (in 12 % of the burrows) on 19 October, though one was found on the surface the day before. By 8 November, 88% of the burrows contained eggs (one egg in each). Incubation was shared by the parents, but was not always continuous since sometimes both birds were absent at once. The first chick appeared on 3 December, and by 15 December 80 % of the eggs had hatched. A few days after hatching, chicks were left alone during the day and adults returned to feed them at night. Feeding consisted of a transfer of regurgitated material from adult to chick, and continued until the chick left the burrow. In all cases examined, the food brought from sea was composed almost entirely of euphausiid crustaceans 1-2 cm long. Chick departure began in late January when fledglings departed seawards at night. By 10 February all burrows were empty of birds.

Details of fairy prion breeding success in the 50 study burrows are given in Table 2. In total, 55 % of the pairs (26 out of 47) successfully reared a chick. Desertions, interference (by other prions or tuatara), predation by tuatara and other mortality were responsible for the failures.

TABLE 2. *Data from 50 observation burrows: fairy prion breeding success and the effects of tuataras*

	No.	% Burrows	% Eggs laid	% Chicks hatched
Burrows laid in by prions	46	92		
Burrows used by tuatara	27	54		
Prion eggs laid	47	94		
Chicks hatched	34	68	72	
Chicks departed (maximum)	26	52	55	76
Eggs eaten by tuatara	7	14	15	
Eggs deserted due to tuatara	2	4	4	
Eggs deserted due to other causes	4	8	9	
	-	-	-	
	13	26	28	
	-	-	-	
Chicks killed by tuatara	4	8	9	12
Chicks died (starvation?)	4	8	9	12
	-	-	-	-
	8	16	17	24
	-	-	-	-
				% All losses
Egg losses due to tuatara (minimum)	9	18	19	43
Chick losses due to tuatara (minimum)	4	8	9	19
Total egg and chick mortality due to tuatara (minimum)	13	26	28	62
Total egg and chick mortality due to other causes	8	16	17	38

2. Tuatara influence

Table 2 shows that the influence of tuatara on the breeding success of fairy prions can be considerable. By far the greatest effect is through egg predation, 15% of those laid being eaten. Direct interference, causing nest desertion or the exclusion of breeding prions from a chamber, and the predation of chicks, also contributed to breeding failure. The combined effect was to cause failure of 28 % of eggs laid. These figures are minima, since tuatara were suspected of being the cause of some other egg and chick mortality and disappearance. although this could not be definitely attributed to them. For this reason also, the number of chicks recorded as having departed for sea is a maximum. Predation of prion eggs in the burrows was first discovered on 8 November, and of chicks on 9 December. Tuatara, therefore, were quick to take advantage of these new food sources.

The number of tuatara found in the 50 study burrows on anyone day fluctuated between two and eight (mean 5), with no marked seasonal trends (Table 1). Only one tuatara was ever found in a burrow at a time. Larger individuals usually retained residence of a single burrow, but smaller tuatara often came and went and used several burrows for shelter. Marking (with fingernail paint) and night spotlighting indicated that more than 30 tuatara were living within the study area.

Intense competition between prions and tuatara for space was evident in the single-chamber burrows of the study area. Five chambers occupied by tuatara before the breeding season were exclusively taken over by breeding birds, usually over a period of several weeks. Of the five burrows regularly occupied by large tuatara, prions failed to establish in two of them, and in the other three prions laid eggs but failed to rear chicks. Two chambers initially occupied by breeding birds were abandoned before egg-laying when large tuatara moved in. In only two burrows regularly occupied by tuatara did prions breed successfully, and even then the tuatara (both small) were absent more often during the breeding season. After the chicks had departed, tuatara took up residence in nine of the breeding chambers.

TABLE 3. *Fairy prion breeding times on Stephens Island in comparison with those on Aorangi I. and Whero I.*

Island:	AORANGI			STEPHENS			WHERO		
Latitude	35° 30′ S			40° 40′ S			46° 55′ S		
Longitude	174° 44′ E			174° 00′ E			168° 12′ E		
Author	Harper 1976			This study			Richdale 1945, 1965		
Period of study	Dec 1963-Oct 1975			May 1974 - April 1975			Dec 1940 - Feb 1942		
	First	Peak	Latest	First	Peak	Latest	First	Peak	Latest
Laying date	14-24 Oct			18 Oct	± 27 Oct	± 13 Nov	24 Oct	2 Nov	
Hatching date	21 Nov	last week of Nov	4 Dec	3 Dec	12 Dec	± 17 Dec	18 Dec	27 Dec	
Chick departure date	3 Jan	10 Jan	22 Jan	± 19 Jan	± 25 Jan	± 7 Feb		14 Feb	
	Shortest	Longest	Average	Minimum *		Maximum *	Shortest	Longest	Average
Incubation time (days)				44		63			56
Nestling period (days)			±45	45		61	44	55	49
Chick survival rate (%)		74				76 (maximum)		79	

* actual values lie between these extremes, since precise laying and hatching dates were not obtained.

DISUCSSION

Prion breeding cycle

Seasonal fluctuations in numbers of fairy prions visiting Stephens Island closely paralleled those observed by investigators of other fairy prion populations. A rapid drop in adult numbers after chick hatching was also noted by Richdale (1945) and Harper (1976) and presumed to be due to the departure of the non-breeding birds.

The timing of fairy prion breeding on Stephens Island is apparently the same as on the Trio Islands, 18 km to the south (Campbell, 1967). On The Brothers Islands, 61 km south-east of Stephens, Sutherland (1952) did not record laying until 27 October. Table 3 shows the recorded breeding times for prions on Stephens Island, and gives a comparison with the events on Aorangi Island of the Poor Knights group (Harper, 1976) and on Whero Island (Richdale, 1945; 1965). Although similar in pattern the dates differ, and conform to a latitudinal trend in which the breeding cycle occurs earlier in the north and later in the south.

Richdale (1945) reported that rarely was an egg left cold in the nest chamber. On Stephens Island though, eggs were quite often left unattended and felt cold, but subsequently hatched normally. Harper (1976) recorded similar behaviour and suggested that incubation absences of three days could affect chick survival.

Since the 1974-75 breeding season, checks have been kept on the study burrows by D. Newman and L. Moran *(pers. comm.)*. Several of the banded prion adults, but no chicks, have been recaptured. From these records, it is apparent that the adults return yearly to the same burrows to breed and pair for more than one season, although partners can be changed. These findings duplicate those of Harper (1976) on the Poor Knights.

Tuatara influence

This study has really only begun to reveal the complexity of the tuatara-petrel relationship in terms of predation, breeding success and spatial interaction below ground.

In the firm, clayey soil of the study area, the strong competition between the two species for available subterranean space is probably keenest. Burrow density averaged 0.7 burrows per sq. m. (range 0.2-1.3 per sq. m.), which was fairly low for Stephens Island but within the range that appears to provide conditions for optimum tuatara numbers (Crook, 1975). In more easily burrowed ground elsewhere on the island, multi-chambered burrows are the rule and burrow densities are greater (up to 4.5 per sq. m., I. Crook, *pers. comm.)*. Here, a more flexible and less competitive arrangement seems to occur in that tuatara and prions more often share the same burrows, although using separate chambers. This latter situation is being examined on Stephens Island (D. Newman and L. Moran, *pers. comm.)*.

Although tuatara certainly have a deleterious effect on the breeding success of fairy prions, they are unlikely to be a major cause of population regulation of the birds. Competition for breeding burrows is fierce among the prions, and possibly only the minority of the adult population is engaged in breeding, the rest comprising the 'unemployed' birds described by Richdale (1945, 1965). Mortality at sea through starvation and fatigue during rough weather is probably the most significant control. Fledglings and young adults are frequently washed ashore in large numbers following prolonged storms (Buller, 1888; M. Imber, *pers. comm.)*.

In the study area, tuatara were responsible for many more prion egg and chick losses than were all other means (desertions, interference by other prions, starvation, disease and accidents). However, the figures for chick survival rate (Table 3) from Aorangi Island and Whero Island are very similar to those from this study. It is possible that the tuatara, like many predators, is responsible for a part of the mortality of its prey that would otherwise occur anyway. Aorangi Island also possesses tuatara, but in much smaller numbers than Stephens Island (L. Moran, *pers. comm.),* and Harper (1976) considered that their influence on prion breeding there was slight. Whero Island has no tuatara.

The significance of the presence of breeding petrels to tuatara is undoubtedly far greater than that of the reptiles to the birds. Not only do the birds provide a source of food, but also shelter in the form of burrows, improved surface hunting conditions through the depletion of the vegetation understorey, and a numerically~stimulated invertebrate prey fauna through soil enrichment. During late summer tuatara are physically most active, and, especially in times of drought, predation on prion chicks could alleviate a desperate need for nutrients and water. At this time, there are few soft-bodied invertebrates available (Walls, in prep.), particularly in open pasture, and the birds could thus be important to the survival of tuatara.

ACKNOWLEDGEMENTS

Mr I. G. Crook and Mr L. R. Moran of the N.Z. Wildlife Service were instrumental in initiating the study and offering practical advice. The Ministry of Transport, Marine Division, allowed me to travel to and from Stephens Island on the lighthouse tender M.V.

'Enterprise', to the crew of which I am grateful. Financial support was given through both the N.Z. Wildlife Service and the University Grants Committee, and my work supervised through the Zoology Department of Victoria University of Wellington. Without the presence of the Aplin family, my periods spent on the island would have been much less pleasurable and my studies more difficult. Mr R. H. Taylor, Mr P. C. Harper and Mr S. R. June made useful criticism of the manuscript.

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