# STATUS, DISTRIBUTION, AND POPULATION TRENDS OF THE NEW ZEALAND SHORE PLOVER Thinornis novaeseelandiae

# by ALISON DAVIS

Department of Zoology, University of Auckland, Private Bag, Auckland

#### ABSTRACT

The New Zealand Shore Plover Thinomis novaeseelandiae is colourful and sexually dimorphic, which is unusual among plovers. T. novaeseelandiae is confined to Rangatira (South East Island) in the Chatham Islands. The sedentary population is relict. The mainland New Zealand population declined over the past century, probably as a result of predation by introduced rodents and feral cats. The population of about 130 birds includes 43 or 44 breeding pairs. There is no migration or dispersal from Rangatira. The population has been stable at least since 1969, but could increase by 12% per annum. Shore plover are long-lived. Survival and productivity are age-dependent. Mortality was highest among juveniles and for all birds in winter. Compared to other shore birds, adult mortality is low, and productivity high. The high proportion (20-35%) of non-breeding adults suggests that population increase may be constrained by a shortage of suitable habitat. Although the population appears to be stable at present, a single small population of a species is always in danger of extinction. A recovery programme now under way is aimed at establishing new populations.

#### INTRODUCTION

The Shore Plover *Thinornis novaeseelandiae* is endemic to New Zealand, where it was once widespread around the coast of both main islands. During the 19th Century its range contracted, until a single small population remained, on Rangatira (South East Island; 44°20' S, 176°10' W) in the Chatham Islands.

Little information was recorded on the Shore Plover until Fleming visited Rangatira in December 1937 (Fleming 1939). Fleming estimated that there were about 70 pairs, and noted that their distribution included coastal as well as inland areas (Fleming 1939). No further work was done until New Zealand Wildlife Service personnel (B. D. Bell and others) began counting and banding birds in the 1960s.

I began studying Shore Plover distribution, behavioural ecology, and population dynamics in November 1984 (Davis 1987). Research on various aspects of the behavioural ecology of Shore Plover was necessary so that a sound management and recovery programme for the species could be devised and implemented.

In this paper, I describe the Shore Plover, and summarise its former distribution and decline, and its present population trends, using information from my study, and from Department of Conservation reports and file notes.

## **METHODS**

I studied Shore Plover on Rangatira from November 1984 to December 1986. I measured and weighed all birds caught. Measurements were made with vernier calipers, to 0.1 mm. Birds were weighed using a Pesola balance (0-100 g), accurate to  $\pm 1$  g.

Colour banding of Shore Plover began in the early 1970s. At the start of my study, about 90% of the population was colour-banded. During my study, I colour-banded unbanded birds and birds which had lost their colour bands. Every individual's location and activities could be monitored.

I observed Shore Plover breeding, territorial behaviour, and habitat use in three study areas in the main habitat types in different parts of Rangatira. All birds in each area were watched twice-monthly for twelve hours, during the breeding season.

Information on the former distribution of Shore Plover was collated from historical records, and labels on museum specimens. Population data for Rangatira were augmented with earlier counts, territory mapping, and banding records. Counts and banding records for years after 1986 are from my own further work and from that of others.

Population trends were analysed using a modification of the Leslie Matrix population model (Usher 1978). The Leslie Matrix population model is deterministic and predicts future population characteristics, including the natural rate of population increase and future age distribution or structure. Shore Plover population age structure, survivorship and estimated productivity or fertility in December 1986 were used in the model. The modified Leslie Matrix model incorporates data on males as well as females in the population data; the form of the model was chosen because male Shore Plover contribute a significant proportion of the parental care.

# **RESULTS AND DISCUSSION**

### **Description and taxonomy**

#### Description

Shore Plover are small wading birds with a 'squat' appearance, and a rather long tail. The sexes are similar in size and weight. Measurements (mm) and weights (g) for a combined sample of adult males and females (n = 24) are as follows: total body length c. 200; wing chord 116.24 ± 1.02 (mean ± SE; range 106.8-123.0); tarsus 26.35 ± 0.18 (24.8-28.1); bill length 23.88 ± 0.33 21.8-28.4); weight 60.98 ± 0.67 (52.0-68.5).

Shore Plover have brightly coloured 'soft parts'; they have an orange eye ring, the rather fine and pointed bill is orange-red with a black tip, and the legs are pale orange. The colours of the eye ring, bill, and legs contrast with the predominantly black, white, and grey plumage. Shore Plover are sexually dimorphic; females have more brown on the cheeks, and a more extensive black tip to the bill.

Newly fledged birds are pale grey-brown, and have black bill and legs. By the beginning of the next breeding season, the legs have begun to turn pale orange, and the base of the bill red-orange. Immature birds at first resemble adult females, but at about one year old (about two months into the next breeding season, in November or December) plumage differences become apparent.

# Taxonomy

Gmelin (1789) described the Shore Plover as *Charadrius novaeseelandiae*. Gray (1845) erected the monotypic genus *Thinornis* for it, based on the long, thin, pointed bill, which is unusual among plovers. Peters (1934) retained this classification, but Bock (1958) returned it to *Charadrius*. Today, the Shore Plover is placed in either *Charadrius* or *Thinornis* by different authorities (e.g., Phillips 1980; Johnsgard 1981). A review of the relationships and taxonomy of the Shore Plover is needed.

# Previous distribution, and decline

There are few historical records of Shore Plover distribution, habitat, or behaviour. Before the 1880s, Shore Plover were regarded as moderately plentiful in most coastal parts of the North and South Islands of New Zealand, and on the Chathams Islands, New Zealand (Oliver 1955) (Figure 1).

Hutton (1868) and Buller (1882) suggested that Shore Plover were migratory, breeding in the South Island and moving to northern estuaries in mixed flocks with Wrybills Anarhynchus frontalis for the winter. There is some doubt as to whether these records refer to Shore Plover, or to Turnstone Arenaria interpres (R. Sibson pers. comm.).

The decline of Shore Plover in mainland New Zealand was not documented, but by the 1880s they had vanished from the mainland. The last mainland sightings were by Potts (1872), who recorded three birds in Otago, and an unconfirmed record from Okarito in 1878 (Hamilton 1878).

Shore Plover were first recorded in the Chathams by Travers (1871) who saw them on Pitt and Mangere Islands. Shore Plover have never been recorded on Chatham Island itself, although both Fleming (1939) and Oliver (1955) assumed that they had been present there. Shore Plover disappeared from Pitt Island sometime in the 1880s. The last record on Mangere Island was in 1898 (Fleming 1939). The species was then confined to a single island - Rangatira.

Unlike many threatened species in New Zealand, the habitat of Shore Plover on the mainlamd has remained largely intact, although it is now occupied by introduced mammals. Predation by Norway Rats *Rattus norvegicus* and feral cats *Felis catus* is the most likely cause of the decline and extinction of mainland populations. The introduction and spread of these mammals through New Zealand coincides well with the period of decline in Shore Plover distribution. Ship Rats *Rattus rattus* and mustelids *Mustela* spp. spread through New Zealand after Shore Plover had declined or disappeared. DAVIS

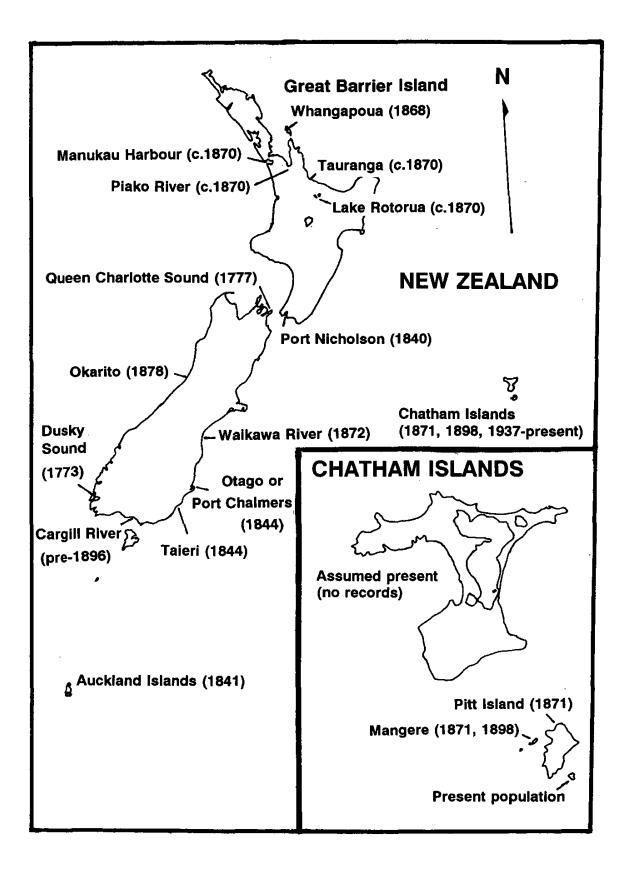
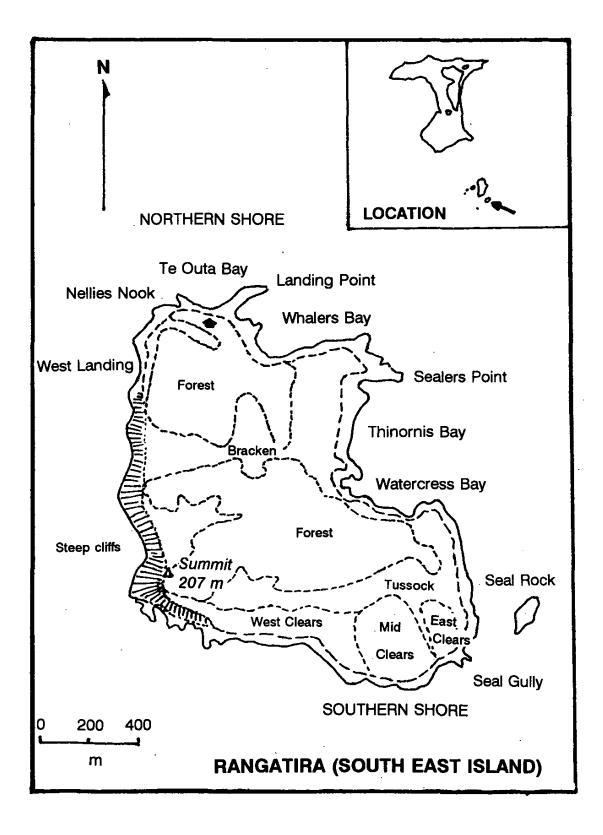


FIGURE 1 – Distribution and dates for historical records of New Zealand Shore Plover *Thinornis novaeseelandiae*.



# FIGURE 2 – Distribution of major areas of habitat on Rangatira (South East Island), Chatham Islands.

#### Distribution and habitat today

Shore Plover have existed as a single population on Rangatira for over 80 years. Although the nearest island, Pitt, is no more than 2 km from Rangatira, Shore Plover are rarely seen there, and then mainly juveniles.

Rangatira is a nature reserve of 218 ha (Figure 2) and is free of mammalian predators. Shore Plover live on the extensive shore platforms that surround the northern and eastern coasts (referred to here as the northern shore), and on the more dissected shore platforms backed by a large gently sloping salt meadow and tussock-land on the southern coast (the southern shore).

Habitat quality on the southern shore was lower than on the northern shore. The difference was reflected in the different rates of breeding success and distribution patterns on the two shores (Davis 1994).

Disturbance to, and destruction of, the forest on Rangatira after European settlement resulted in an increase in the area of salt meadow and tussock grassland which provided additional habitat for Shore Plover. The meadows and grassland were grazed, but the sheep were removed in 1961 and the areas have gradually become overgrown and are now mostly unsuitable as habitat for Shore Plover.

Shore Plover form monogamous pairs, and each pair occupied a separate home range during the breeding season (Davis 1994). On the northern shore, breeding territories were arranged linearly in an almost continuous chain around the coast. Breeding territories on the southern shore were clustered in several discrete sites. Most breeding pairs had nesting territories that were separate from their feeding and chick-raising territories.

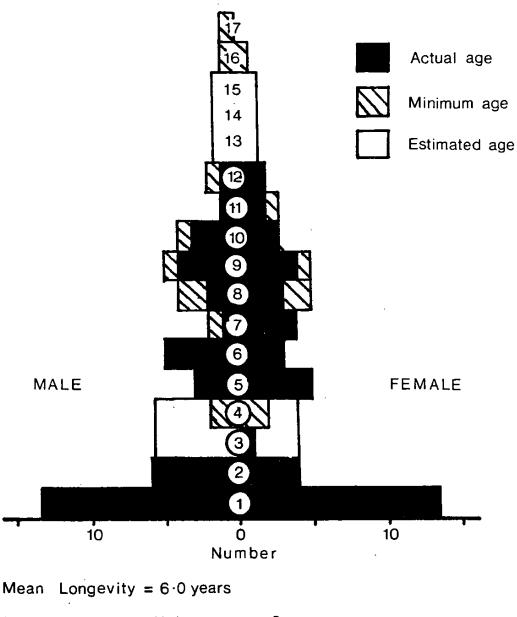
Non-breeding birds, including immatures, often occupied areas that overlapped with breeding territories. Breeding birds nearby frequently attacked non-breeding birds and attempted to drive them away from the area. Although non-breeding birds tended to keep to the same general area over the breeding season, they occasionally moved around the island. The lower quality habitat on the southern shore meant that more space was available for non-breeding birds.

At the end of breeding in March, most pairs abandoned their breeding territories and formed flocks with other post-breeding pairs, non-breeding birds, and juveniles during the winter. Some pairs on the northern shore remained in their territories all year. Territories were reoccupied by breeding pairs in late winter, four to six weeks before the start of the next breeding season.

#### **Population dynamics**

#### Age structure

To see whether a population a stable, it is important to know the age distribution of the birds. A population with a large proportion of older birds, and few birds in younger age classes, has a greater chance of declining in numbers and possibly going extinct, than a population in which young birds predominate, which is usually stable or expanding.



Known age 124, Unknown age 8.

FIGURE 3 – Age structure of New Zealand Shore Plover *Thinornis novaeseelandiae* population on Rangatira (South East Island) in February 1986. Age classes shown in years; actual-age birds, birds of known age; minimum-age birds, banded as adults; estimated-age birds, were minimum-age birds averaged over number of years when no banding was done.

DAVIS

The age structure of the Shore Plover population on Rangatira in February 1986 is shown in Figure 3. Information is shown for known-age birds, as well as for birds banded as adults (minimum- and estimated-age individuals). Minimum-aged birds were probably close to their real age because fewer than 10% of birds remained unbanded for more than one season. Some birds lost their colour bands, but could be identified by their metal bands. Ages could be determined for most birds in the population because 98% were banded in February 1986.

Shore Plover are long-lived; the mean age was six years. The oldest bird, a male banded as an adult, was at least 17 years old. The overall sex ratio was 533:472; it did not differ markedly from parity for most age classes.

The largest cohort was the first-year juveniles. Only 26% of birds survived to their second year. The survival rate of juveniles was typical of that for many bird species (Davis 1987). Numbers in cohorts from two to 10 years of age were similar. Numbers in the 11-year-old cohort were abruptly lower than for younger birds, but then were similar for each age cohort up to 15 years. The reason for the abrupt decline in numbers for birds after 10 years of age is not known.

High juvenile mortality appears to be compensated for by low adult mortality, reflected in the longevity of breeding adults, and by high productivity rates (see below). Sufficient birds were being recruited into the breeding population to prevent a population decline in the years immediately after the period analysed, unless other factors intervened.

#### Survivorship

A survivorship curve was calculated for the population from the observed age structure (Figure 4). Shore Plover survivorship was age-dependent. Survivorship was low for juveniles; it was highest in the two- to six-yearold cohorts. Survival rate peaked at three years of age, when most Shore Plover began to breed. Shore Plover over six years old had a lower survival rate than younger birds (except juveniles).

Shore Plover survivorship was similar to that of most bird species, being low for juveniles and higher for adults (Davis 1987), but the small sample of older Shore Plover means that the results should be treated with caution.

#### Mortality

Shore Plover are not known to disperse or migrate from Rangatira, so any losses from the population can be attributed to mortality. Mortality was highest in juvenile Shore Plover, lower in non-breeding adults, and lowest in breeding adults (Figure 5). Only 8% of the annual mortality occurred in winter, when mortality in plovers should be highest as a result of the rigours of migration and harsh climatic conditions. The sedentary habits of Shore Plover and the equable climate of Rangatira did not lead to high winter mortality. A more important cause of mortality of Shore Plover was likely to have been competition for space during the breeding season, particularly for immature birds, and for non-breeding adults searching for territories. Birds in both categories were driven off higher-quality feeding areas by territory-holders.

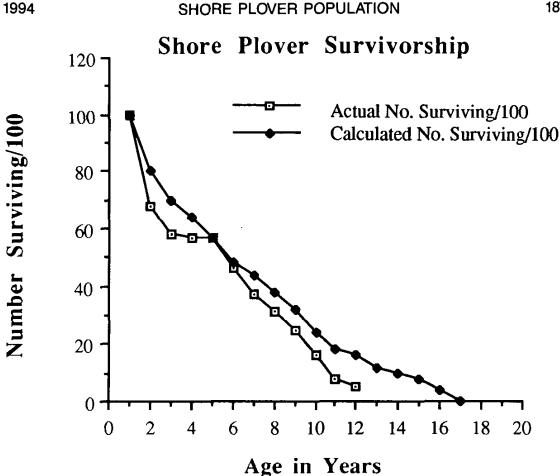


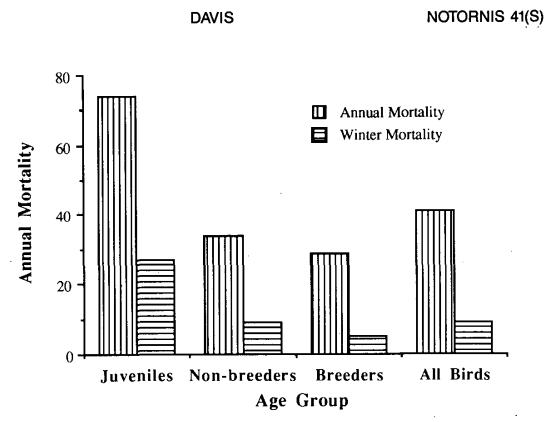
FIGURE 4 - Survivorship curve for New Zealand Shore Plover Thinornis novaeseelandiae population on Rangatira (South East Island), drawn from age structure pyramid as at February 1986. Curves drawn separately for known-age and calculated-age birds (combination of actual-age, minimum-age, and estimatedage birds) Conventions as in Figure 3.

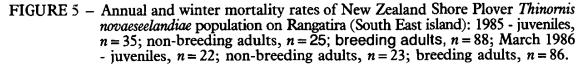
Mortality rates of adult Shore Plover were low in comparison with other plover species such as breeding Wrybill (17%, Hay (1984)) or Ringed Plover Charadrius hiaticula (42%, Boyd (1962)). As noted above, the low mortality of Shore Plover probably results from their sedentary habits, the relatively stable environment, and a lack of mammalian predators on Rangatira.

#### **Productivity**

My measure of productivity was the number of fledged young per breeding bird. It was obtained by direct observation and could be compared with productivity rates of other species.

Annual productivity for Shore Plover was consistent over six years of observations. Productivities for individual years (fledged young pair<sup>1</sup>, all from author's data except 1992/93 (J. Dowding pers. comm.) were: 1984/85, 0.89; 1985/86, 0.64; 1986/87, 0.58; 1987/88, 0.49; 1988/89, 0.62; 1992/93, 0.61. The mean was 0.64 fledged young pair<sup>1</sup>, equivalent to a breeding pair producing one chick every two years. Shore Plover productivity was similar to that of the Wrybill (0.78, Hay (1984)), but higher than that of other plovers, such as Ringed Plover (0.17) or Little Ringed Plover Charadrius dubius (0.41) (Boyd 1962).





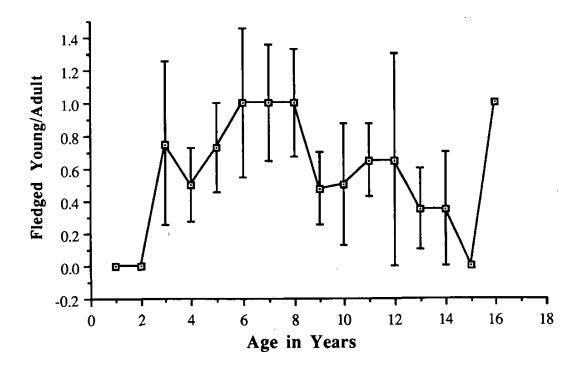


FIGURE 6 – Age-related productivity (mean  $\pm$  SE) of New Zealand Shore Plover *Thinornis* novaeseelandiae population on Rangatira (South East Island), calculated over the 1984/85 to 1986/87 breeding seasons (n = 162).

1994

Age-related productivity could be estimated, because many birds in the population were of known age. Although values overlapped, Shore Plover productivity was age-dependent (Figure 6). First year breeders had a low productivity, but productivity increased with age until birds were between five and eight years of age. Productivity then declined.

# Age of first breeding

The youngest age of first-breeding for Shore Plover on Rangatira was two years, but many adults bred first at three to four years old. Age of first breeding did not differ between sexes. Some adults never bred. Captive Shore Plover have bred at one year old (H. Aiken, pers. comm.).

# **Population trends**

The first census of Shore Plover on Rangatira Island was made by C. A. Fleming in 1937 (NZ Wildlife Service files). Counts were next made in the 1960s and 1970s. The population has been counted annually on Rangatira since spring 1978. From the 1981/82 breeding season, the distribution of individually colour-banded birds has been recorded.

The Shore Plover population has remained nearly constant over the 50 years since the first count (Table 1). The 1937 count is likely to have been an underestimate, because even though regeneration of vegetation has reduced the area of Shore Plover habitat, and numbers of Shore Plover have dropped slightly recently, counts are still higher than in 1937.

The small fluctuations in the population most likely reflect changes in the ease of survey and variations in survey effort, rather than changes in the size of the population. A reduction in the numbers banded in the late 1980s and early 1990s has resulted in a rise in the proportion of birds with only metal bands and of unbanded birds, which are difficult to count accurately. The population on Rangatira may decline with further habitat loss as salt meadow regenerates towards forest, and as a seal colony on the southern shore expands.

Few bird populations have been regularly monitored with such precision over a long period as has that of the Shore Plover on Rangatira. Although not presented here, regular counts of the population have been made at the end of the breeding season, as well as at the start. As the Shore Plover is endangered, it is important to monitor population numbers closely, including individual survival, and location of individually-marked birds. The monitoring will also provide information on the long-term population trends of a shore bird.

# **Population model**

The format, assumptions, and results from applying the modified form of the Leslie Matrix population model (Usher 1972) to the Shore Plover population are as follows. The Leslie Matrix model predicts the natural rate of population increase (R), and the stable age distribution at n year intervals.

TABLE 1 – Population numbers of Shore Plover on Rangatira Island from 1937 to 1993. Counts were made early in each breeding season (Oct-Nov), except in 1992/93 (early Feb, most young of the year still with parents; not included in count). Non-breeding birds and total adults include immature birds surviving their first winter.

Year	Breeding pairs	Non-breeders	Total adults	Observer
1937/38	52 (est. 70)	?	104 min.	C. A. Fleming
1961/62	47 (est. 52)	?	94 min.	B. D. Bell
1968/69	?	?	c.100	B. D. Bell
1970/71	?	?	c.100	D. Merton
1972/73	40	?	80 min.	D. Flack
1978/79	?	?	83 min.	D. Merton
1980/81	?	?	111	J. & B. Seddon
1981/82	40	26	106	D. Crouchley
1982/83	c.35	43	113	A. Munn
1983/84	40	8 min.	88 min.	A. Munn
1984/85	44	37	125	A. Davis
1985/86	43	38	124	A. Davis
1986/87	43	32	118	A. Davis
1987/88	43	24 min.	110 min.	A. Davis
1988/89	39	42	120	A. Davis
1989/90	?	?	114	A. Davis
1990/91	43	9	95	A. Davis
1991/92	?	?	103	E. Kennedy; S. Phillipson
1992/93	41	24	106	J. Dowding

The model takes the form:

0 0 0 0 0	 0 f1 0 f2 0 0 0 0 s1 0 0 s2 Matrix	0 0 0 0 0	0 0 0	×	n1 n2 n1 n2 n1 n2 Vector
	Matrix				Vector

where: f1 = no. of males fledged per adult female in the *i*th class; f2 = no. of females fledged per adult female in the *i*th class; s1 = probability that a male alive in the *i*th group will be alive in the *i* + 1th group; s2 = probability that a female alive in the *i*th group will be alive in the *i* + 1th group; n1 = no. of males in the *i*th group; n2 = no. of females in the *i*th group. The assumptions of the model are that: 1) mortality, productivity (fertility), and age structure are constant through time; 2) all birds of breeding age breed; 3) population grows independently of size. For the Shore Plover population, the model gave the following values for R: at 10 years, 0.14; 20 years, 0.12; 30 years, 0.12; 40 years, 0.12; 50 years, 0.12.

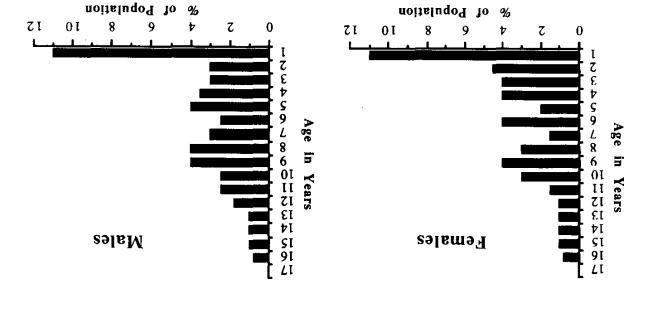
The model predicted that the natural rate of population increase (R) stabilised after 20 years at 12% year<sup>-1</sup>. Such an increase is unlikely given the almost constant population size in the past. However, the model assumes that all adult birds in the population breed, and that the population grows independently of its size. This is clearly not so for the Shore Plover, in which there is a pool of non-breeding adults of breeding age. The pool of non-breeding adults of breeding age. The pool of non-breeding and that the population cannot grow independently of its size. The results do show, however, that the Shore Plover population could increase if there was more habitat available.

A comparison between the initial population age distribution and the predicted stable population age distribution showed that there was a higher proportion of birds in the > 10 years age classes in the stable population than in the initial population (Figure 7). Habitat limitations on Rangatira may also be limiting adult longevity.

Together, the 12% year<sup>-1</sup> increase predicted by the Leslie Matrix Model, the population trends over the past 50 years, and the present and predicted age distribution, suggest that there is no immediate risk that the Shore Plover will become extinct, if Rangatira remains free of predators and the environment does not change.

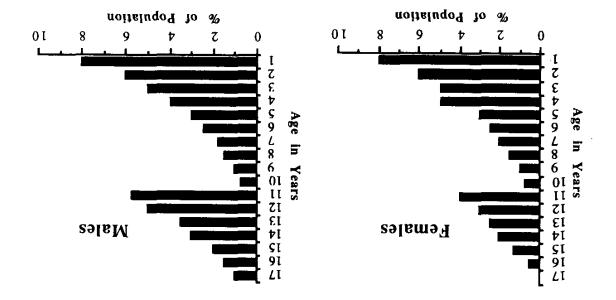
#### CONCLUSIONS

Knowledge of the historical distribution of the Shore Plover allowed the apparent rate and extent of its decline to a single population on Rangatira in the Chathams to be correlated with possible causes, such as the introduction of predators. Counts on Rangatira since 1937 have shown that the population of 120-140 is stable. Shore Plover numbers appear to be limited by the amount of suitable habitat. Changes in the island's vegetation may lead to a slight reduction in Shore Plover numbers in the future. The



SIVAD

# Initial Population Distribution



Stable Population Distribution

FIGURE 7 – Initial and stable population age structures of New Zealand Shore Plover Thinomis novaeseelandiae on Rangatira, from modified Leslie Matrix analysis. characteristics of the Shore Plover population include stable numbers, high longevity, low mortality (greatest during breeding season), high productivity, and delayed breeding. These factors result from the limited area of habitat and the relatively constant environmental conditions on Rangatira. The high longevity of Shore Plover may have led to bird's age-related productivity, and age-dependent mortality.

Data on population trends are useful for management. The population has a predicted capacity to increase at 12% year<sup>-1</sup> at known mortality and productivity rates. The rate of increase could be higher if Shore Plover first bred at two years old rather than three. Stochastic population models such as those used for population viability analysis may be better ways to predict future trends in the Shore Plover population on Rangatira, and elsewhere. The IUCN Species Survival Commission's population viability analysis (PVA) is a stochastic model that takes habitat limits, non-breeding adults, and random events such as large storms into account as well as the standard population parameters. Obviously, information on the Shore Plover population since 1987 will strengthen the analysis.

The Shore Plover Recovery Plan (Davis 1989) proposed several management techniques that could be used to ensure the survival of the species. The plan was based on the premise that the Rangatira population is stable, and could recover from the removal of eggs or non-breeding birds. Knowledge that the Shore Plover's distribution declined rapidly after predators were introduced to New Zealand led to proposals that new populations be established in coastal habitats free of mammalian predators. Such a site may be Pitt Island, near Rangatira, where eradication of feral cats would provide suitable predator-free habitat.

In addition, Davis (1989) recommended that the population on Rangatira, including individually-marked birds, continue to be monitored until further populations can be established. At present, it is essential that mammalian predators are not introduced to Rangatira.

A captive Shore Plover population has recently been established at the National Wildlife Centre, Mt Bruce, North Island, from eggs transferred from Rangatira. The captive population will provide a nucleus of birds from which to establish new populations in the wild, on islands around New Zealand and in the Chatham Islands.

Further research on Shore Plover taxonomic status is necessary, and research on energetics and diet (including chick diet), and incubation temperatures would provide data for the recovery programme.

#### ACKNOWLEDGEMENTS

I thank Brian Bell who first interested me in Shore Plover, and provided encouragement and assistance with my field work. For assistance in my MSc studies I am indebted to: officers of the former NZ Wildlife Service, in particular Don Merton, Allan Munn, Geordie Murman, and the rest of the 'Black Robin Team'; Alan Hemmings and Euan Young (Auckland University); Rob Chappell, Rod Hay, Mark Bellingham. For financial support I thank the Watson Trust and Royal Forest & Bird Protection Society. The people of Pitt Island and Chatham Island provided much assistance without which my work would not have been possible. For assistance and access to information since 1987, I thank the Department of Conservation, in particular Euan Kennedy, Andy Grant, and John Andrews. Paul Sagar and Mark Bellingham provided useful comments on the manuscript. I wish especially to acknowledge Sir Charles Fleming for his enthusiasm and interest in hearing about Shore Plover as my research progressed.

#### LITERATURE CITED

- BOCK, W.J. 1958. A generic review of the plovers (Charadriinae). Bull. Mus. Comp. Zool. 118: 27-98.
- BOYD, H.B. 1962. Mortality and fertility of European Charadrii. Ibis 104: 368-384.
- BULLÉR, W.L. 1882. Manual of the Birds of New Zealand. Wellington: New Zealand Government Printer.

DAVIS, A.M. 1987. The behavioural ecology and management of New Zealand Shore Plover. Unpubl. MSc thesis, Department of Zoology, University of Auckland.

- DAVIS, A.M. 1989. The New Zealand Shore Plover recovery plan. Unpubl. rep., Department of Conservation, Christchurch.
- DAVIS, Â.M. 1995. Breeding biology of the New Zealand Shore Plover. Notornis (Supplement) 42: 195-208.

FLEMING, C.A. 1939. Birds of the Chatham Islands. Part I. Emu 38: 380-413.

- GRAY, G.R. 1844-45. Birds of New Zealand in RICHARDSON, J.; GRAY, J.E. (eds.) Zoology of the Voyage of HMS *Erebus* and *Terror* during the years 1839 to 1843. Vol. 1 Mammals & Birds. London: Jansen.
- HAMILTON, A. 1878. The district of Okarito, Westland. Trans. Proc. NZ Inst. 11: 388-91.
- HAY, J.R. 1984. The behavioural ecology of the wrybill plover Anarhynchus frontalis. Unpubl. PhD thesis, Department of Zoology, University of Auckland.
- HUTTON, F.W. 1868. Notes on the birds of Great Barrier Island. Trans. Proc. NZ Inst. 1: 160-161.
- JOHNSGARD, P.A. 1981. The Plovers, Sandpipers and Snipes of the World. Lincoln and London: University of Nebraska Press.

OLIVER, W.R.B. 1955. New Zealand Birds. Wellington: Reed.

PETERS, J.L. 1934. Checklist of Birds of the World, vol. 2. Cambridge, Mass.: Harvard University Press.

- PHILLIPS, R.E. 1980. Behaviour and systematics of the New Zealand plovers. Emu 80: 177-197.
- POTTS, T.H. 1872. On the birds of New Zealand, Part 2. Trans. Proc. NZ Inst. 5: 171-205.
- TRAVERS, W.T.L. 1871. Notes on the Chatham Islands extracted from letters from Mr H.H. Travers. Trans. Proc. NZ Inst. 11: 388-391.
- USHER, M.B. 1978. Developments in the Leslie Matrix Model. Pages 243-280 in JEFFERS, J.N.R. (ed.) Mathematical Models in Ecology: 12th Symposium of British Ecology Society. Oxford: Blackwell.