

BREEDING BIOLOGY OF THE NEW ZEALAND SHORE PLOVER *Thinornis novaeseelandiae*

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ABSTRACT

The endemic New Zealand Shore Plover (*Thinornis novaeseelandiae*) is confined to a small population on Rangatira (South East Island) in the Chatham Islands. There are about 43 breeding pairs and 130 adults. The population is sedentary. Shore Plover form monogamous breeding pairs in separate defended territories. Clutch size, parental behaviour, courtship, and defence displays are similar to those of other plovers. Shore Plover have several unusual breeding characteristics which may be responses to the relatively constant environment and limited area of habitat on Rangatira, low prey abundance, differences in habitat quality, no mammalian predators, and the presence of certain avian predators. Shore Plover are unique among plovers in nesting under cover, which protects their nests from avian predators and temperature extremes, but which would make nests very vulnerable to predation by mammals. Environmental conditions on Rangatira may also be a reason for the high hatching rate, low chick survival, and differing breeding success within the population.

INTRODUCTION

The New Zealand Shore Plover *Thinornis novaeseelandiae* has only a small remnant population on Rangatira (South East Island) in the Chatham Islands, where there are no introduced mammal predators. Shore Plover are sedentary. The population has been stable at about 43 pairs and 130 adult birds since at least 1969 (Davis 1994).

Charles Fleming made the first observations of Shore Plover breeding biology and territorial behaviour in 1937 (Fleming 1939). He recorded that Shore Plover breeding pairs strongly defended discrete territories. Population counts, begun in 1961 and continued sporadically until the early 1980s by B. D. Bell and others of the New Zealand Wildlife Service, confirmed that the birds were strongly territorial and that breeding birds formed constant pairs. Flack (1976) also briefly described pairings and territory occupation among breeding Shore Plover. Territory arrangement and behaviour of plovers was discussed in detail by Davis (1987).

In this paper, I present baseline information on Shore Plover breeding biology, and consider factors that influence its breeding behaviour. Aspects of breeding biology covered include the timing of the breeding season, pairing and occupation of breeding territories, courtship, nest building, egg laying, incubation, chick hatching and rearing, and breeding success.

METHODS

I studied the breeding biology of Shore Plover on Rangatira during breeding seasons from 1984/85 to 1986/87. Colour banding had begun in the early 1970s. By the start of this study, c.90% of the Shore Plover population had individual combinations of colour bands. During the study, unbanded birds and birds which had lost bands were fitted with colour bands. Most birds in the population were individually recognisable. I recorded the location and activity of all birds in the population at 3-day intervals in 1984/85 and 5-day intervals in 1985/86.

I selected three study areas in the main habitat types in different parts of the island and recorded breeding and territorial behaviour, and habitat use. All birds in each area were watched twice monthly for 12 h during each breeding season. In the 1984/85 breeding season, I also watched almost all breeding pairs for 3 h each. Data on the number and location of breeding territories, and the identity of breeding birds before 1984 were obtained from New Zealand Wildlife Service records.

STUDY SITE AND HABITAT

Climate

The climate of the Chatham Islands is mild, windy, and cloudy (Thompson 1983). Winter and early spring months tend to be cooler, with higher rainfall. On Rangatira, the prevailing southwesterly winds make the southern shore cooler and windier than the northern, and spray and wash from large swells are commoner in the south.

Habitat

Lower prey densities, harsher climate, and greater exposure to swells mean that the quality of Shore Plover habitat was probably lower on the southern shore than the northern shore. Shore Plover occupied two areas of habitat with contrasting characteristics. The 'northern shore' area consists of extensive shore platforms with densely vegetated margins. The 'southern shore' area contains more dissected and narrower shore platforms and is backed by a large, gently-sloping salt meadow and area of tussock grassland.

Food

Shore Plover prey included copepods, insect larvae, and amphipods <2 mm long. The invertebrates were patchily distributed but species composition and abundance varied little during the plover breeding season (Davis 1987).

Shore Plover preferred to feed on wet, bare or algae-covered intertidal rock platforms, and brackish seeps, all of which had high densities of potential prey. The sea edge of the intertidal platform and pools had the highest prey densities. The invertebrates were, however, not always available because the pools were deep and frequent swells washed across the edge of the platform. Preferred habitats were less abundant on the southern shore. Prey densities were also lower than for the same habitats on the northern shore.

RESULTS AND DISCUSSION

Territory

Shore Plover form monogamous pairs; each pair vigorously defends a territory during the breeding season. Non-breeding birds - including immatures - occupy areas that often overlap with breeding territories. Individuals tend to remain in the same location for long periods.

The differences in habitat between the two shores influenced the arrangement of Shore Plover breeding territories. Each territory on the northern shore was discrete, whereas most southern shore territories were fragmented, having separate areas for feeding, nesting, raising chicks, or various combinations of these activities in one area. Some southern pairs raised their chicks in the nesting area; others moved their chicks at varying ages to a feeding area on the shore. The pattern of territories on the southern shore may be explained by the large area of salt meadow and tussock grassland being available for nesting, but with low densities of prey compared to the shore.

Mate and site fidelity

Shore Plover have high mate and territory fidelity. Of the birds breeding in 1981/82, in 1986/87 20 males and 18 females bred at the same site, 2 males and 4 females bred at different sites, and 36 birds had died. Few birds changed their breeding sites or mates in the five years after 1981/82. Changes in mate or breeding site resulted mostly from the death of a partner. Most birds that left their mate or moved breeding site over the five years were females.

From 1981/82 to 1986/87, 94% of birds returned to the same site and 86% returned to the same mate. The high mate and site fidelity can be explained by their being sedentary, and having a high survivorship, in a limited area of habitat with an equable climate. As birds stay on Rangatira, they can remain together. Although most breeding birds move about Rangatira after a breeding season, competition for limited breeding spaces may encourage experienced breeders to settle in territories they occupied in the previous breeding season well before the start of the next.

Timing of the breeding season

The Shore Plover breeding season lasted seven months, from September to April (Figure 1). This is a long season for a plover breeding at low latitudes and altitudes, and where seasonal difference in climate and food supply are small.

Shore Plover food supply varied little with season (Davis 1987), despite the cooler and damper winter and early spring. Shore Plover start their breeding season when the weather begins to improve in late spring.

Breeding started at about the same date each season. For example, breeding began within a few days of the same date in the 1984/85 and the 1985/86 breeding seasons. Although the onset of breeding was constant between seasons, within a season not all pairs began at the same time. Differences in time of breeding may have been related to differences in habitat

— 1984/85.
 - - - 1985/86

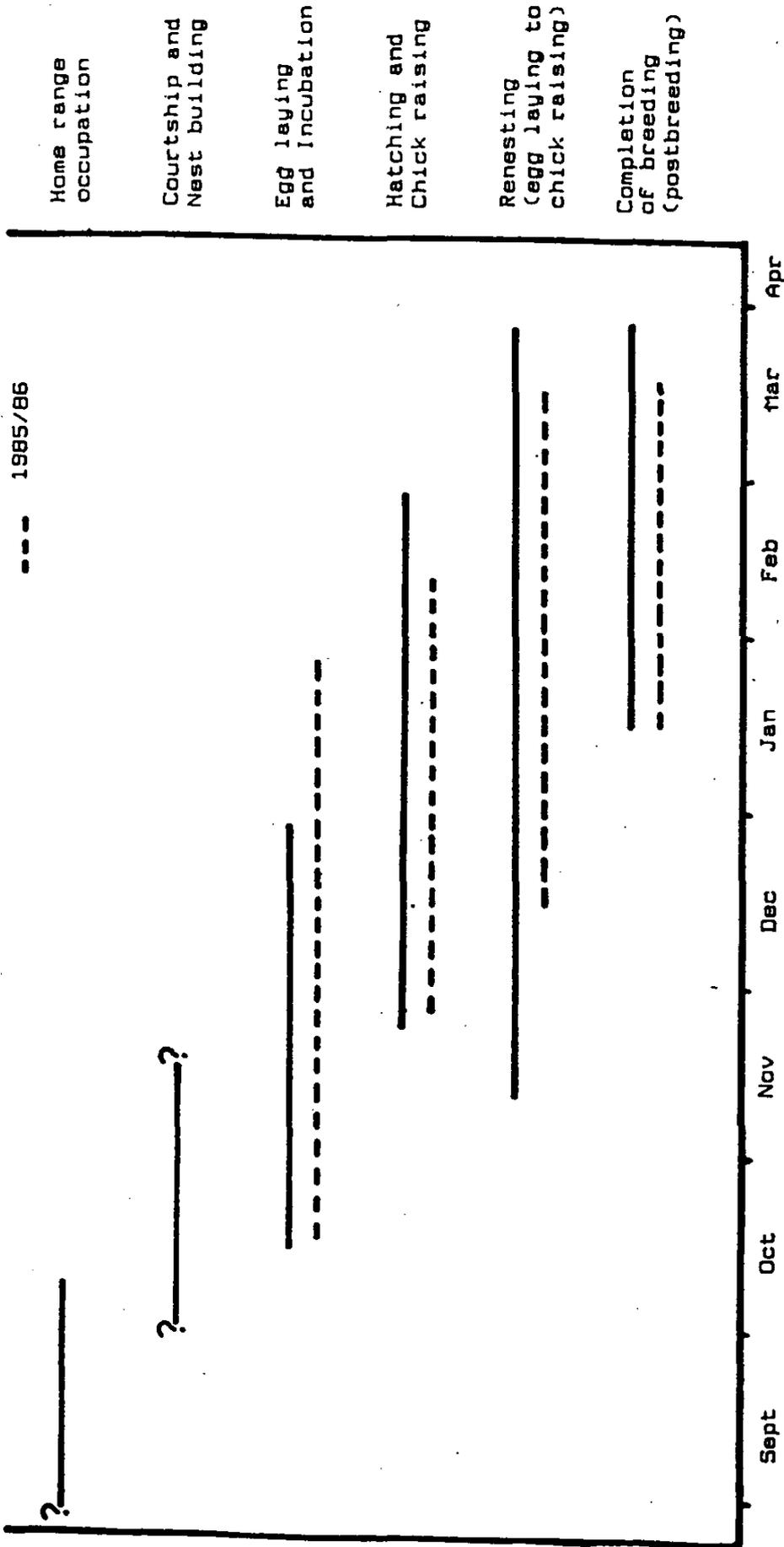


FIGURE 1 - Timing of the 1984/85 and 1986/87 breeding seasons of Shore Plover *Thinornis novaeseelandiae* on Rangatira, Chatham Islands.

quality between territories. In good-quality territories, breeding pairs may have been able to obtain sufficient food to build up energy reserves to start breeding earlier than those in poorer territories. Pairs in territories within a bay or similar discrete area tended to begin breeding at the same time, which suggested that social stimulation may also be important in initiating breeding each season. Further investigation would, however, be required to confirm that social as well as environmental factors influence the start of breeding in Shore Plover.

Courtship

Courtship appeared to be triggered more by the breeding behaviour of neighbouring pairs than by the time of occupation of breeding territories. Courtship started with a period of aggression between the birds of a potential pair. The male lunged repeatedly at the female, which attempted to avoid contact. After the period of aggression, the birds began a series of courtship displays, the *flutter* display and the *crouch*.

During a *flutter* display, males - and occasionally females - faced their potential mate, lowered their heads, lifted their wings in a rapid fluttering movement, and jumped a short distance. The displaying bird called a soft *wheet-wheet*. The *crouch* display was also done mostly by males, which quietly moved up to their potential mate, hunched their body and lowered their head. During both displays, the potential mate stood a few metres away and watched the display before moving off quietly.

Copulation sometimes followed the courtship displays, but more often the male repeatedly chased and lunged at the female until she remained still and he could copulate. Then the male approached the female with his body held almost horizontally, began a rapid, high-stepping walk, while calling a rapid, high pitched *chip-chip*. The male mounted the female when she stood still, and coition occurred.

The post-copulation display by the male included up to eight repetitions of movements similar to a *flutter* display. The male gave a soft crooning *kwee-kwee* call during the post-copulatory display. The female shook her feathers and preened for several seconds after coition, and occasionally head-bobbed as she moved away.

Shore Plover courtship behaviour is typical of that of many other plovers. The *flutter* and *crouch* displays resemble the *tilt* and *wing-raise* displays described for many plovers, including Wrybill and Banded Dotterel (Bomford 1978; Hay 1984), and the high-stepping walk before copulation has also been recorded in other species (Phillips 1980). The post-copulatory display has not, apparently, been reported for other plovers.

Nest-building

Shore Plover built nests under cover in dense vegetation, either *Muehlenbeckia australis*, grass tussocks, or sedges. A few nests were under boulders. Only two of 141 nests were completely open to the sky.

The habit of nesting under cover in dense vegetation is unusual in plovers. Most select nest sites in open areas of sand, gravel, or in low turf. Nesting under cover reduces the ability of the nesting bird to see predators

approaching the nest, and the bird could not escape the nest as quickly as it could if nesting in the open. Nesting under cover probably made Shore Plover vulnerable to mammalian predators when they arrived in mainland New Zealand and Chatham Island.

The long laying period for a complete clutch (see below) may explain the choice of covered sites. Eggs are left unincubated, but they are under cover and so are protected from temperature extremes. It is also possible that covered nests may be peculiar to Rangatira. Several other shore-nesting birds - White-fronted Tern *Sterna striata*, Red-billed Gull *Larus scopulinus*, Chatham Island Oystercatcher *Haematopus chathamensis* - nest under cover on Rangatira as well, so the habit may be a response to predation by Brown Skua *Catharacta skua lonnbergi*, which regularly prey on nests in open sites (pers. obs.).

Pairs investigated nest sites together or independently; up to 7 days passed before a nest site was chosen. Both birds built the nest, preparing the scrape and carrying pieces of nearby vegetation and occasionally feathers, shells, and pebbles to line it. To build nests in soil, birds made the scrape by lowering their breast to the ground and kicking soil out from behind them. Nests were bulky for a plover, being up to 8 cm across and 4 cm deep.

For most pairs, nests sites were less than 6 m apart for breeding attempts both within and between seasons. About 15% of pairs used exactly the same nest sites for each nesting attempt.

Laying and incubation

Clutch Size

Of 119 clutches in the 1994/85 and 1986/87 breeding seasons, 23 contained two eggs and 96 contained three eggs. No clutches of four or more were found. The ancestral clutch size in shore birds (Charadrii) is thought to be four (Maclean 1972), but reduced clutches of two or three eggs in response to a limited food supply are common in plovers (Ricklefs 1970; Cody 1966).

Egg dimensions

Fresh Shore Plover eggs weighed 12.6 ± 0.19 g ($n = 27$). Egg dimensions (mm) tended to vary with the order of laying: 1st, $36.3 \pm 0.2 \times 25.6 \pm 0.1$; 2nd, $35.6 \pm 0.2 \times 25.5 \pm 0.1$; 3rd, $35.7 \pm 0.2 \times 25.8 \pm 0.1$, but the differences were not significant (Length, $F = 2.76$, $p > 0.07$; Width, $F = 1.16$, $p > 0.32$). For birds in general, the first egg tends to be longest and the second or third egg to be widest (Coulson 1963; Gochfield 1977).

The mean clutch mass as a percentage of female body weight was 42% for a two-egg clutch and 63% for a three-egg clutch. Both are high percentages of adult female weight, but the long intervals between successive eggs may reduce the need for females to build up considerable reserves of body fat before laying.

Laying interval

The mean laying interval for a three-egg clutch was 4.1 ± 0.6 days ($n = 20$), but laying interval varied between and within clutches. The interval between the first and second eggs tended to be longer for than the second and third, but the difference was not significant ($t = 1.59$, $p > 0.13$).

Pairs on the southern shore, however, took significantly longer (4.8 ± 0.5 days, $n = 10$) to lay clutches than those on the northern shore (3.3 ± 0.2 days, $n = 10$) ($t = 2.32$, $p < 0.03$). Southern shore females may have taken longer to build up body condition for egg-laying because of the lower quality habitat there. Egg formation may then have taken longer, so that intervals between successive eggs laid in a nest were prolonged.

The within-clutch interval of Shore Plover is long in comparison to that of other plovers, such as Piping Plover *Charadrius melodus* (2 days, Cairns 1982) or White-fronted Plover *Charadrius marginatus* (2-4 days, Summers & Hockey 1980).

The interval between the laying of the last egg and the start of incubation was <1-5 days; from the first egg until incubation took 7-15 days. These delays are very long in comparison to other plovers. Eggs are left unprotected in the nest for a considerable period, increasing the time that Shore Plover eggs are exposed to predation.

Incubation

The incubation time of 27.8 ± 0.3 days ($n = 21$) is typical for plovers (e.g., 32 days for Wrybill *Anarhynchus frontalis* (Hay 1984) and 28 days for Piping Plover (Cairns 1982)). Eggs were incubated for c.90% of daylight hours; females were incubating in 71% and males in 29% of 2393 observations. The proportion varied between pairs, but females always did the greatest proportion of incubation during daylight. In addition, single incubation stints by females averaged twice as long as those of their male partners. All nests checked at night had an incubating bird, usually the male. Males defended their territory to a greater extent than females during the day, which may explain the sexual differences in incubation behaviour.

Incubating birds commonly stayed on the nest when avian predators such as Brown Skuas or Black-backed Gull walked close to the nest, but usually ran off the nest when humans approached. Birds flushed from the nest usually stood in an alert posture, bobbing their head rapidly and giving shrill beeping calls. Some birds continued to head 'bob', and occasionally false brooded as they followed the person away from the breeding territory. At night, Shore Plover were slow to leave the nest and rarely called. The reluctance to move off the nest at night would make Shore Plover vulnerable to predation by nocturnal mammals.

Hatching and Rearing of chicks

Hatching

Almost all eggs within a clutch hatched within 6-12 h of each other, although there was sometimes a delay of up to 24 h before the last chick hatched.

Both parents stayed close to the nest from when the eggs began to pip until the chicks were ready to move away (1-2 days after hatching). Both parents brooded newly-hatched chicks. Parents called the chicks off the nest with a soft *chip-chip-chip*.

Newly-hatched chicks spent longer on the nest than most plovers, such as Mountain Plover *Charadrius montanus* (Graul 1975) and Banded Dotterel *Charadrius bicinctus* (Bomford 1978), which leave the nest 3-6 h hours after the last egg hatches. The longer delay must increase the vulnerability of chicks and brooding adults to predation at the nest.

After they left the nest, chicks were led by their parents to the closest area suitable for rearing, the distance moved varying from a few metres for territories on the northern shore to several hundred metres for some territories on the southern shore. Chick-rearing habitat included brackish seeps, algae-covered intertidal rock platforms, or salt-meadows, which were close to boulders or dense vegetation.

Chick rearing

Both sexes shared parental care, which is common in monogamous plovers. The parents cared for the chicks together for the first week. After the first week of intensive care, parents mostly took turns to care for the chicks alone. Parental care consisted of guarding the chicks from approaching predators, leading chicks to feeding habitat, and brooding chicks. Parents continued to brood chicks until they fledged.

Chicks pecked the ground within minutes of leaving the nest, but captured few prey until they were a few days old. Chicks hunted prey for themselves. Parents only led chicks to good feeding habitat. No interactions between siblings were observed.

Females contributed more parental care than males (females, 83% of 1250 observations; males, 62% of 1275; $\chi^2 = 299$, $p < 0.001$). Females spent most of their time roosting near or brooding the chicks. Males also spent most of their time roosting near the chicks, but spent more time than females scanning the area for approaching predators and other Shore Plovers moving into the territory.

Birds on the northern and southern shores spent significantly different amounts of time on parental care (northern, 72%, $n = 1528$; southern 76%, $n = 997$; $\chi^2 = 277$, $p < 0.001$). Southern shore birds brooded their chicks less, roosted more, and scanned less while guarding chicks, and chased fewer intruding Shore Plover. Many southern shore pairs could not feed and care for their chicks at the same time because they had to move away from the chick-rearing territory to feed. As a result, chicks on the southern shore were less frequently attended simultaneously by both parents than were northern chicks. The decreased level of parental care could have increased the chicks' vulnerability to predation. When both parents were present, one could lead the chicks to safety while the second distracted the predator. Differences in parental care resulting from habitat differences may explain some of the difference in breeding success between northern and southern birds (see below).

Parents alerted chicks to danger from avian predators and humans by giving a shrill rapid chipping call that caused chicks to seek cover under rocks and vegetation. Parents with very young chicks often performed distraction displays (injury feigning, crouched rodent-like run). Birds also stood in an alert posture and bobbed their head rapidly until the predator or human left the area. Distraction displays such as head bobbing, false brooding, crouched running, and injury-feigning performed by Shore Plover with nests or chicks have been observed in Banded Dotterel (Bomford 1978), White-fronted Plover (Summers & Hockey 1980), and Piping Plover (Cairns 1982).

Adults defended chicks less strongly from predators at night. Brooding birds disturbed at night by people ran off silently, leaving the chicks to fend for themselves.

Fledging and independence

The time to first flight (fledging) varied widely (29-63 days). Fledging was related directly to weight; chicks always fledged when they reached c.37.0 g, regardless of age. The shortest fledging time (29 days) was similar to that in other plovers, such as Wrybill (35-37 days, Hay 1984), Banded Dotterel (35-40 days, Bomford 1978), and Piping Plover (28-32 days, Cairns 1982), but in none of these species was the range in fledging time as great as that in Shore Plover.

The variable fledging period for Shore Plover resulted from differences in chick growth rate related to differences in habitat quality (Davis 1987). Chicks on the southern shore took on average twice the time to fledging as chicks on the northern, reflecting the lower quality habitat on the southern shore.

Fledgling Shore Plover remained with their parents for 4-36 days. Birds therefore reached independence at 41-67 days; those taking longest to fledge usually remained with their parents for a shorter period after fledging. There is little information on fledgling behaviour for other plovers, but fledglings of most species leave their parents and natal territory within a few days of fledging.

Renesting

Shore Plover renested after losing abandoning a nest, losing their first brood, or when their eggs were damaged. The likelihood that a pair would renest was lower if the first attempt failed at a more advanced stage (Table 1). Shore Plover did not attempt to renest a third time if they failed twice in the same season.

The time to renesting after the first failure (renesting interval) was 17.4 ± 1.4 days ($n = 85$, range 9-32 days). The long renesting interval is unusual among plovers, which usually renest within 7 days of losing eggs or chicks. Breeding female Shore Plover may have difficulty replenishing the energy and nutrient reserves necessary for a replacement clutch. There was no relationship between the renesting interval and the date in the breeding season, or the stage in the breeding cycle when the first breeding attempt failed.

TABLE 1 – Incidence of renesting of Shore Plover *Thinornis novaseelandiae* on Rangatira, Chatham Islands, for the 1984/85 and 1985/86 breeding seasons, in relation to the fate of first nests of the season.

Fate of first nest	No. of pairs	No. of pairs renesting (%)
Eggs damaged or abandoned before incubation started	4	4 (100)
Eggs abandoned during incubation or failed to hatch	5	2 (40)
Death of downy chick (1-17 days)	25	13 (52)
Death of pullus (18 days - fledging)	15	4 (26)
Young independent	36	0 (0)
FAILED PAIRS	85	23 (27)

TABLE 2 – Hatching, fledging, and percentage of fledglings raised to independence for Shore Plover *Thinornis novaeseelandiae* pairs on the northern and southern shores of Rangatira, Chatham Islands, for the 1984/85 and 1985/86 breeding seasons.

Season/Area	Total eggs found	% hatched	% hatchlings fledged	% fledglings independent
1984/85				
Northern shore	77	79	43	100
Southern shore	62	84	19	90
1985/86				
Northern shore	78	89	28	95
Southern shore	70	80	7	100

Shore Plover on Rangatira did not double-brood or nest again in the same season after successfully raising chicks. Recent management of Shore Plover in captivity at the National Wildlife Centre at Mt Bruce has resulted in pairs both renesting and double-brooding (H. Aiken pers. comm.). Habitat quality, and in particular food supply, probably limits the ability of Shore Plover to double-brood or renest on Rangatira.

Most plover species renest after a breeding failure, and many will also double brood in the same season after successfully raising a first brood. Instances of renesting and double-brooding in captivity indicate that Shore Plover can renest and double-brood given sufficient food supply.

Breeding success

Hatching success of Shore Plover (Table 2) was high in comparison to most plovers, for example 44% in Banded Dotterel (Bomford 1978), and 61% in Mountain Plover (Graul 1975), although it was within the 63-91% known for Wrybill (Hay 1984). Survival of young chicks was lower than the hatching rate (Table 2). There are few data with which to compare Shore Plover chick survival, but the comparatively high hatching rate and overall breeding success (see below) suggest that the chick survival rate is typical of plovers. After fledging, chicks had a high survival rate to independence when they left their parents' and natal territory.

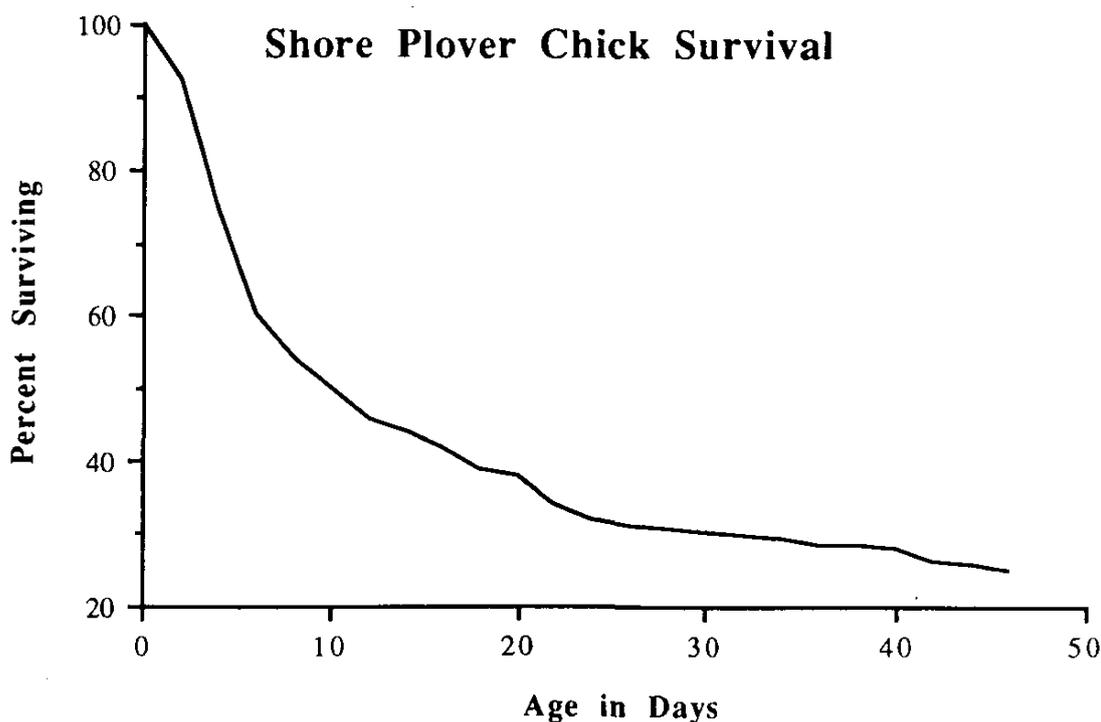


FIGURE 2 – Survivorship curve for Shore Plover *Thinornis novaeseelandiae* chicks calculated from chick mortality observed in 1984/85 and 1985/86 breeding seasons on Rangatira, Chatham Islands.

The absence of mammalian predators meant that losses at the egg stage were usually from infertility rather than predation. Most infertile eggs were from three-egg rather than two-egg clutches. The infertile egg of a three-egg clutch was generally the last egg laid. Clutches were abandoned only if one of a pair died.

Chick mortality was low in the first day after hatching, but increased rapidly and peaked at 4 days when chicks first left the nest (Figure 2). Four-day-old chicks had exhausted their yolk sac, but were still inexperienced at foraging and avoiding predators.

Causes of chick mortality included starvation, drowning by large waves, and predation by Red-billed Gulls, but the major cause of death of chicks on the southern shore was starvation. The food supply in chick-rearing areas was limited. Underweight and malnourished chicks were common on the southern shore. Once young birds could fly, they had better access to food and were less subject to predation, hence the high survival rate of fledglings.

Breeding success differed greatly between seasons and between northern and the southern shores in the 1984/85 and 1985/86 seasons (1984/85: northern, 26 pairs, 1.0 independent young pair⁻¹; southern, 18, 0.5. 1985/86: northern, 25, 0.7; southern, 18, 0.2). Northern pairs produced twice as many independent young pair⁻¹ as southern shore pairs in 1984/85, and three times as many in 1985/86. Although hatching rates and fledgling survival to independence differed slightly between areas and seasons, the greatest differences were in chick survival or hatchling success (Table 2).

The lower chick survival and overall breeding success of southern shore pairs in both seasons indicates that the southern shore contained lower quality habitat for chick rearing. Qualities used to define suitable chick-rearing habitat (Davis 1987) included the amount of suitable chick feeding area (brackish seeps, algae-covered platforms, salt-meadow), the amount of cover (boulders or dense vegetation) from predators, the distance from the chick feeding areas to cover, the presence of avian predators, exposure to waves and harsh climatic conditions, and territory arrangement.

Habitat for chick rearing on the southern shore was lower quality because the area experienced cooler and windier conditions, large waves frequently washed over the shore platforms, there were more avian predators (skuas and gulls), and many territories had widely-separated chick-rearing and adult feeding areas. Birds probably needed more energy to maintain body temperature there, and birds were often seen sheltering from the wind rather than feeding. When large waves inundated the shore platforms, they were unavailable for feeding. More energy would be required to move between the different parts of dispersed territories, and birds could not always be present together to care for chicks. Chicks, with their smaller body size and high energy requirements, would have been most affected by the cooler temperatures. Chicks were also at risk of being swept away and drowned by large waves.

The Shore Plover were much more successful in the 1984/85 season than in 1985/86, as nearly they produced nearly twice as many independent young. The difference in breeding success resulted largely from the lower chick survival in 1985/86, but was not linked clearly to environmental factors. No obvious differences in climate, prey availability, or predator disturbance were observed between the two seasons.

Although environmental factors such as habitat quality may strongly influence breeding success of Shore Plover, individual behaviour may affect breeding success to some degree: this possibility was not explored.

CONCLUSIONS

As with many plovers, Shore Plover formed monogamous pair bonds, breeding pairs each established a vigorously defended territory, laid 2-3 eggs per clutch, both sexes incubated the eggs for c.28 days, eggs hatched synchronously, and both sexes raised the chicks. Courtship, and nest and chick defence behaviours were similar in many ways to those in other plovers. Unlike most plovers, however, Shore Plover were sedentary throughout the year, had a long breeding season and high mate and breeding site fidelity. Shore Plover were also unusual in having a high mean clutch mass as a percentage of female body weight, long and irregular laying intervals between eggs within a clutch, a long interval from laying the last egg to start of incubation, delayed departure of chicks from the nest after hatching, a low incidence of renesting (which was then usually delayed), absence of double brooding, a highly variable fledgling period, usually a long period of chick dependence, slow growth rates of some chicks in the population, and high hatching success.

The differences in breeding characteristics may result from the relatively constant climate, limited area of habitat on Rangatira, generally constant but low availability of prey, marked differences in quality within the habitat, freedom from mammalian predators, and the presence of avian predators. The limited area of habitat on Rangatira and lack of migration resulted in high mate and breeding site fidelity and in intra-specific competition for habitat and food. Food may be limiting Shore Plover on Rangatira, as shown by the unusual egg laying and fledging timing and by differences in the chick growth rates and fledging period between the two areas on Rangatira.

It is interesting that New Zealand Snipe *Coenocorypha aucklandica* and Chatham Island Snipe *Coenocorypha pusilla*, species that occupy similar or share the same habitat as Shore Plover, show many of the features of Shore Plover breeding biology. For example, the snipe have a long inter-egg interval, delayed renesting, no double brooding, slow chick growth rates, a long period of chick dependence, and a high overall hatching success in comparison to the Common Snipe *Gallinago gallinago* (Miskelly 1989). As with Shore Plover, the differences were attributed to the absence of mammalian predation, a stable environment, and to intense intraspecific competition for a limited food supply.

Shore Plover are thought to be unique in nesting under cover in dense vegetation or occasionally under boulders. The habit, along with the protracted laying period, and delay before chicks leave the nest made Shore Plover very vulnerable to mammalian predation, and so may explain why Shore Plover disappeared from the New Zealand mainland and Chatham Island soon after rats, cats, and mustelids were introduced. On Rangatira, it may, however, be an advantage to lay under cover; eggs are concealed from avian predators, and protected from temperature extremes. Similar advantages would have been obtained on the mainland before mammals were introduced.

The anti-predator behaviours of Shore Plover have implications for the ability of the species to recover because the displays are unlikely to be effective in the presence of rodents, cats, or mustelids.

Studies of captive Shore Plover may provide information on the influence of food availability on clutch size, laying interval between eggs, incidence of renesting and double brooding, chick growth rates, fledging period, and breeding success.

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