Aspects of habitat selection, population dynamics, and breeding biology in the endangered Chatham Island oystercatcher (Haematopus chathamensis)

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ASPECTS OF HABITAT SELECTION, POPULATION DYNAMICS, AND BREEDING BIOLOGY OF THE ENDANGERED CHATHAM ISLAND OYSTERCATCHER (*HAEMATOPUS CHATHAMENSIS*)

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Frontispiece

"When the last individual of a race of living things breathes no more,
another heaven and another earth must pass before such a one can be born again."
- Charles William Beebe, 1877-1962

Adult Chatham Island oystercatcher, north coast, Chatham Island.
(Photo by Don Hadden)

This thesis is dedicated to
all the conservation workers who have
endured the hardships and
had trouble planning their days.

and to the late

Gerry Clark (1927 - 1999)
ornithologist, naturalist, adventurer,
and a wonderful inspiration.

If the world were merely seductive, that would be easy,
If it were merely challenging, that would be no problem.
But I arise in the morning torn between a desire to improve the world,
and a desire to enjoy the world.
This makes it hard to plan the day.
-EB White

"Studying animals in the field can sometimes involve both physical and mental hardship because of the need to work in remote places with harsh climates. The field worker may have to live for extensive periods in difficult circumstances, facing isolation, possible ill health, poor diet and occasional physical danger. The advice and facilities which are taken for granted in an academic environment are rarely available. Problems with logistics and bureaucracy may mean that less research is done than expected, because everything takes more time...."
-Paul Martin and Patrick Bateson
Measuring Behaviour, Cambridge University Press, 1986

Abstract of a thesis submitted in partial fulfilment of the
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Background

In the late 1980s the endangered Chatham Island oystercatcher (*Haematopus chathamensis*) (CIO) was estimated at less than 110 individuals. Endemic to the Chatham Islands, New Zealand, it was feared to be declining and, based on existing productivity estimates, in danger of extinction within 50-70 years. These declines were thought to be caused by numerous changes since the arrival of humans, including the introduction of several terrestrial predators, the establishment of marram grass (*Ammophila arenaria*) which changes dune profiles, and increased disturbance along the coastline. The New Zealand Department of Conservation has undertaken recovery planning and conservation management to increase CIO numbers since the late 1980s.

Recovery planning raised some key research questions concerning the population dynamics, habitat selection, and breeding biology of Chatham Island oystercatcher (CIO), and the critical factors currently limiting the population. The objectives of this study were to collect and interpret data on: 1) population size, trends, and distribution across the Chathams, 2) basic breeding parameters, 3) recruitment and mortality rates, 4) habitat selection at the general, territorial and nest-site levels, 5) habitat factors that are correlated with territory quality, and 6) cues that elicit territorial behaviour in CIO.

Methods

To determine distribution and abundance of CIO a census conducted from 13-18 December 1998. To determine habitat use of CIO, the lagoon shoreline and coastlines of Chatham, Pitt, and Rangatira Islands were mapped and habitat use by CIO recorded. Aspects of breeding biology, nest-site selection and use of habitat types within territories were studied for 15 CIO pairs along north coast, Chatham Island during the 1994, 1995 and 1996 breeding seasons. To identify factors limiting the population, territory quality was explored by comparing breeding parameters between territories and under different levels of management (none, low and intensive), and data on survival of first year birds were also collected. Because territorial behaviour plays such a key role in population dynamics, cues which elicit defense behaviour in CIO breeding pairs were explored using seven different two-dimensional models.

Key findings

Distribution and abundance Along 310 km (97%) of the coastline of the islands, and 100 km (100%) of the lagoon shoreline a total of 142 CIO were counted. About 85% of CIO were located along the coastlines of Chatham and Pitt Islands. The census indicated an increase of about 20-40 adults over any previous count, although variations in methods of past counts made comparisons difficult. The main increases were along the north coast, and there has been a gradual decline on Rangatira Island.

Breeding biology Breeding effort was high with 98% of pairs attempting to breed, (n = 42 pair-seasons). A clutch had a 20% chance of being successful (at least one egg surviving to produce a fledgling). Overall productivity averaged 0.44 fledglings/pair/season. Flooding was the main cause of egg loss (48%), followed by causes unknown (26%). Juveniles dispersed/were evicted from their natal territories within about 33 days (range 24-42) after fledging.

Habitat selection 277 kms of coastline (92%) and 100% of the lagoon shoreline were mapped. CIO used coastline, rather than the lagoon shoreline, almost exclusively (98% of sightings). Intertidal rock platforms and wide sandy beaches were selected in much greater proportions than available . The highest densities of territories were 4 pairs/km at Tioriori, along the north coast, Chatham Island. Depending on the habitat types available within territories some pairs used rocky platform extensively for feeding (up to 60% of the time spent foraging), while others used sandy beach almost exclusively (76-95%). Paddocks were used for foraging up to 22% of the time by pairs. This extensive use of sandy beach and paddock is either a recent development or was previously under-detected.

Territory quality and season of limitations Over-winter habitat is probably not critically limiting based on the high survivorship rates (71% and 83% minimum) of first-year CIO.

Productivity was much higher during periods of intensive management (e.g., predator control, fencing to exclude livestock, nest manipulation). Territories containing only sandy beach were the most productive under all management scenarios (none, low, or high intensity).

Nest site selection CIO chose nest-sites along the widest sections of beach available, mostly on sandy beach (77% of nests), but occasionally on rock outcrops (23%). They avoided nesting within five metres of vegetation or the mean high tide line. The establishment of introduced marram and high predator pressure has probably had a significant impact on nest site availability and quality for CIO on the Chathams.

Territoriality CIO aggressively attacked all the models that were shaped like an oystercatcher, but attacked those with CIO-like colouration most quickly and vigorously. The model with the least asymmetry (i.e. same colours and size) received the most warning behaviours. The pairs in lower quality territories were the least aggressive. Models also proved useful for determining territory boundaries and capturing birds.

Key words: breeding biology, Chatham Islands, Chatham Island oystercatcher, endangered species, habitat selection, population size, *Haematopus chathamensis*, nest-site selection, New Zealand, territorial behaviour, territoriality, wildlife management

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CHAPTER 1

GENERAL INTRODUCTION

"... successful conservation biology must depend on a detailed understanding of population dynamics and social organisation, so that limiting factors can be identified and alleviated."
Krebs 1994

What factors limit the population of Chatham Island oystercatcher?

The Chatham Island oystercatcher (*Haematopus chathamensis*) is a critically endangered shorebird species found only on the Chatham Islands (Baker 1973; Collar *et al.* 1994). The population was estimated at about 100-110 individuals in 1987, including 44 breeding pairs and, based on past productivity information, feared to be declining and at risk of extinction within 50-70 years (Davis 1988b). The New Zealand Department of Conservation has been managing Chatham Island Oystercatcher (CIO) in order to increase numbers since the late 1980s. Recovery planning identified research into the habitat requirements and breeding biology as high priority research needs (Davis 1988a; Grant 1993).

Key questions raised by the recovery plans included:

- If management intervention increased productivity, would the breeding/total population increase? (Is there enough habitat to support increased productivity, especially over winter?)
- What were the primary causes of clutch and chick losses?
- How could breeding habitat be improved and/or increased?
- What recovery goal should be set, when will the habitat on the Chatham Islands be 'full', i.e., when will CIO reach the carrying capacity of the islands?

Unfortunately, attempting to identify carrying capacity is problematic. Definitions of carrying capacity often vary and create confusion (Dhondt 1988; Caughley and Sinclair 1994). In addition, in order to predict carrying capacity many assumptions must be made about the relationships between current and predicted habitat use, which is fraught with difficulties (see, for example, the review in Newton 1998). Determining limiting factors is suggested as a more fruitful and broader approach to conservation management than simply trying to determine carrying capacity.

Understanding limiting factors can be crucial for effective conservation management of threatened species (Krebs 1994; Newton 1998). There are many examples where breakthroughs in understanding of limiting factors has led to successful management of populations which had previously resisted attempts to increase them. One of the better known and documented cases of this involves the red grouse (*Lagopus lagopus*), an important game bird in Britain. When the red grouse began to decrease in numbers, traditional and intuitive control measures were invoked, such as restrictions on hunting, predator control, the establishment of reservations and refuges, and game farming. Despite this effort the population continued to decrease. Finally, an intensive study of the problem was undertaken to determine the actual limiting factors and as a result of the information obtained, several unorthodox control measures were applied: patches of heather were burned, many older breeding grouse were removed, grit was provided, and wet areas drained. Following the instigation of these measures, the grouse population increased 30-fold (Leopold 1933; Welty and Baptista 1988). A more recent example is the Aleutian Canada goose (*Branta canadensis*) which had been declining throughout the 20th century and breeds on most of the outer Aleutian islands in the Bering Sea. This decline was attributed to Arctic foxes (*Alopex lagopus*) taking eggs and goslings. Foxes were eliminated from four islands, but this did not stem the decline. Captive-bred birds did not survive, and translocation of wild birds to fox-freed islands did not reverse the decline either. Only when hunting was closed in 1975 on the wintering grounds did the goose population triple (Springer *et al.* 1978). Another excellent example of breakthroughs in managing endangered species is the red-cockaded woodpecker of the SE United States where managers and scientists realized that populations could be enhanced by the addition of artificial cavities (reviewed by Walters 1991).

Understanding limiting factors is also essential for predicting responses of populations to changes in the environment (eg. changes in habitat, predator pressures, etc.). For example, to understand the response of CIO to past habitat changes, or to determine the most effective conservation management strategies, requires an understanding of the limiting factors; and, as the population changes, how these factors come into play at different densities and under different environmental conditions (e.g. different weather patterns or predators).

The potential pitfalls of not understanding limiting factors includes placing high levels of resources into management that does not ultimately increase the population equilibrium level. For example, in birds species, high levels of management during the breeding season is almost always successful in increasing fledging success, but this often does not translate into larger breeding populations or a long term increase in population equilibrium level (Côté and Sutherland 1997). This is because survival rates of first year birds over winter may be low. Identifying the limiting factors and any bottlenecks at different stages is essential for effective conservation management. To determine the factors limiting a population it is essential to gain an understanding of basic breeding biology, recruitment, survival at different life stages, and population numbers and distribution.

Insights into limiting factors allows for modelling various management options, and determining which ones would be the most effective. An understanding of the factors limiting a population also allows for predictions to be made and then tested, which can then add to the knowledge base. This is in contrast to a trial and error approach where many different management practices may simultaneously be applied (on top of a background of many varying environmental and biological conditions), and even positive responses add little to an understanding of what drives the systems. Making refinements to management are then difficult because there is no understanding of which of the many management practices created the positive responses, or the role of various environmental and biological conditions. Understanding of limiting factors also aids in predicting which demographic parameters would be most useful to monitor. For example, monitoring the total population in spring may be far more useful if the goal is increasing the total population than conducting a census in the autumn, especially if over-winter habitat and survival of first-year birds is limiting.

Most birds, including CIO, are highly territorial, which can regulate populations by limiting the number of breeding pairs and recruitment rates. Aspects of avian territories including size and productivity are influenced by the biotic and abiotic environment. Site dependent regulation as proposed by Rodenhouse (1997) offers an elegant model for understanding the interactions between the roles of territorial behaviour and various environmental and biological limiting factors, and how together they can lead to tight density dependent population regulation. Based on this model, the greater the variations in territory quality, the tighter the population will be regulated. As a population increases additional pairs will be forced to breed in lower quality territories, or will forgo breeding, reducing the overall productivity of the population until equilibrium is reached. Conversely, if the population declines, only the best quality territories with the highest rates of productivity will be occupied and keep recruitment rates high, stabilising the population.

Determining the environmental factors which are present, and affecting the population, is central to understanding the population dynamics of the species. Food resources are the ultimate limiting factor for a population, but populations may stabilise well below the confines of food resources due to limitations in nest-sites, predator pressure, disturbance, or pathogens (Newton 1998). These factors may act individually or interact and the main limiting factor may operate only in one season (i.e., the breeding season or over-winter), or may interact and operate in both (Fretwell 1972; Sutherland 1996a; Sutherland 1996b; Newton 1998; Sutherland 1998). On the Chatham Islands many factors may be limiting the CIO population including native and introduced predators, lack of suitable nest-sites due to the loss of habitat, disturbance from humans and livestock, and ultimately foraging habitat.

The species in context

The family Haematopodidae in general

The oystercatchers are a fairly small, conservative family with only a single genus (reviewed in Hockey 1996a; Hockey 1996b). Much research has been done on oystercatcher species around the world, especially Eurasian, American and African species; with the European subspecies of oystercatcher (*H. o. ostralegus*) being one of the most studied shorebirds in the world (Hockey 1996b). Morphologically all oystercatchers are similar in spite of a large geographical range, so much so that the taxonomy of several taxa are in dispute. There are two colour phases, one pied and one black, except for the variable oystercatcher (*H. unicolor*) which is polymorphic, containing black, pied and intermediate colour morphs. In all species the female is heavier and has a longer bill than the male. Oystercatchers are long-lived birds, reaching 40 years for Eurasian oystercatchers (Ens *et* *al.* 1996) and for CIO at least 28 years old (this study). They do not normally breed for the first time until at least three to four years old (Davis 1988b; Ens 1992; Hockey 1996b; Heg *et al.* 2000).

On the open coast and in estuaries they have a varied diet in which bivalves, gastropods and polychaetes figure prominently, but they also eat amphipods, crabs, ascidians, echinoderms and, occasionally, fish (reviewed in Hockey 1986). On rocky shores, the diet is usually dominated by molluscs, especially mussels, limpets, snails and chitons, whereas on soft substrates, bivalves and polychaetes are the dominant prey. Oystercatchers foraging inland eat mostly arthropods, especially earthworms and insect larvae.

The information for the following sections are drawn from the following sources: Harris 1967; Heppleston 1972; Hartwick 1974; Nysewander 1977; Summers and Hockey 1977; Hockey 1982; Davis 1988b; Lauro and Burger 1989; Lauro *et al.* 1992; Vermeer *et al.* 1992; Ens *et al.* 1993; Lauro and Nol 1993; Andres and Falxa 1995; Lauro and Nol 1995; Hockey 1996a; Hockey 1996b; Banks 1998. All oystercatcher species are territorial during the breeding season and are predominantly monogamous, with both the male and female sharing in incubation and chick-rearing duties. A few species are migratory, most are not. Both migratory and sedentary oystercatcher species show both high mate and site fidelity.

Some oystercatcher species breed inland, but most are coastal breeders. The coastal breeders nest in a range of open coastal habitats from rocky shores to shingle and sand beaches, and salt-marshes. Oystercatcher nests are often located close to high tide lines or on the shore side of vegetation lines, even though the risk of flooding is higher in these sites. Extensive inland breeding by Eurasian and South Island pied oystercatchers (*H. ostralegus*) has evolved only during the last century, concomitant with major population increases of both species. Pied species of oystercatcher usually nest on sandy beaches that are light in colour, and black species usually nest where beaches are dark and rocky (reviewed in Lauro and Nol 1995, p 926 Many oystercatcher species chose nest-sites that have more small objects (e.g. shells, gravel, shingle) than random sites, and which are located near objects or clumps of vegetation (Vermeer *et al.* 1987; Andres and Falxa 1995; Lauro and Nol 1995; Hockey 1996a).

With very rare exceptions all are single-brooded, but lay replacement clutches if the nest is lost early in the breeding season. In the northern hemisphere the modal clutch size is three, in the southern it is two except for variable oystercatcher and South Island pied oystercatcher, which have a modal clutch size of three. Oystercatchers are the only birds with young that have full precocial mobility (most chicks leaving the nest within 24 hours of hatching), yet receive food from their parents, some until well after fledging. Chicks fledge at around 33-49 days, not normally breeding for the first time until at least 3-4 years old. Piping seems to play a similar function in all species, as an aggressive behaviour between pairs, although it may be used in other contexts as well (such as greeting when a member of a pair returns from being away).

CIO in particular

The CIO is a pied, non-migratory, coastal breeding oystercatcher and is considered to be only one of two pied coloured rocky-shore specialists (Hockey 1996a). Endemic to the Chatham Islands group, fossil bones have been found in the dune layers, suggesting that the oystercatchers are not recent immigrants to the Chatham Islands (A. Tennyson, Te Papa/National Museum of New Zealand, pers. comm., see also Holdaway *et al.* 2000). CIO are considered to be most closely related to variable oystercatcher and South Island pied oystercatcher (*H. ostralegus finschi*), although the systematics of oystercatchers is uncertain (Baker 1972; Hayman *et al.* 1986; Sibley and Monroe 1993; Hockey 1996a).

Historic numbers of CIO are unknown, although it was never considered common. Travers and Travers (1872) reported that CIO were not common and usually found on sandy beaches. Fleming (1939) was more specific, reporting that, "the CIO is not particularly abundant on the Chatham Islands, but is widely distributed on the rocky shores near Kaingaroa and other northern areas, and from Ouenga [Owenga] to the Tuku in the south. It is present also on Pitt, Mangere and South East [Rangatira] Islands. It is seldom if ever seen on sandy shores, many of which would be considered suitable feeding and nesting grounds for oystercatchers in New Zealand." The first attempted estimates of total numbers were by Baker (1973) based on a brief visit to the islands in the early 1970s, and by Best (1987) in 1987 who visited rocky shoreline which were considered most likely to have CIO present. These counts resulted in estimates of 50-75 individuals. The first complete census was conducted by Davis (1988b) in 1987 resulting in an estimate of 103-110 individuals. A 1992 census by the NZ Department of Conservation resulted in an estimated 69-73 individuals. Unfortunately all these surveys were conducted using different methods, and often in different areas, making comparison difficult (see Chapter 2).

The major prey items reported for CIO foraging on rocky shores were limpets (*Cellana strigilis*), and for birds foraging on sandy beaches, sandhoppers (Amphipoda) and round worms (Nermertean) (Davis 1988b). Other prey items included blue mussel (*Hytilus edulis*), paua (*Haliotis spp*), whelks (*Haustrum haustrorum*), and ribbonworms (Polycheates). They also fossicked among wrack (washed up kelp and organic matter), feeding on sea tulips (*Pyura pachydematina*) and ribbed mussel (*Aulacomya ater*). Other bivalves and chitons have also been recorded as prey items.

Location

The Chatham Islands

The Chatham Islands are located in the Pacific Ocean 850 kms east of Christchurch, New Zealand (44.5°S, 176.5°W). There are two larger islands (Chatham and Pitt), several small islands, plus numerous stacks and islets. CIO are known to breed on four islands, with the majority of pairs (85%) breeding on Chatham and Pitt Islands (Davis 1988b; Page 1992). Chatham Island is around 96,500 ha (965 km^2) in area, with approximately 320 km of coastline. Te Whanga lagoon occupies an area of 186 km^2 in the northern half of the island with around 100 kms of shoreline (Hay *et al.* 1970). The second largest island, Pitt, is around 6,190 ha (63 km^2) in area. Chatham and Pitt Islands are inhabited, extensively farmed, and the vegetation is extensively modified over most of the land and coastal areas (Atkinson 1996). Coastal and dune vegetation is highly modified with most of the coastal forest and dune vegetation now replaced by the introduced marram grass (*Ammophila arenaria*), a sand binding species (Atkinson 1996). Both islands also have a large suite of introduced predators and free ranging livestock (sheep and cattle). Rangatira or Southeast Island (218 ha) and Mangere (113 ha) Islands were both cleared for pastoral farming but, as protected nature reserves for the last three decades, are rapidly becoming re-forested, and are free of introduced mammalian predators and weka (*Gallirallus australis*), a flightless, predatory rail native to the New Zealand mainland.

The islands experience frequent strong winds and occasional high storm swells. The prevailing winds are from the south and west. Mean average wind speed is 25 km/h with gale force winds (greater than 63 km/h) averaging 14 times per year. Frost is rare and temperatures are moderate. Summer temperatures (mean daily maximum) reach 17-18° C; maximum temperatures exceed 20° C about 14 days each year. Winter minima are 5-6° C (Thompson 1983).

North Coast study area

The north coast of Chatham Island has a high concentration of breeding pairs of CIO between Waitangi West and Taupeka Point, and between Whangamoe and Whangatete Bays (see Chapter 1, Figure 1). The New Zealand Department of Conservation has managed pairs in the Tioriori and Wharekauri areas since the early 1990s to increase productivity (Murman 1991; Sawyer 1993; Sawyer 1994; Bell 1998). The primary management action has been control of predators, but has also included artificial incubation of eggs, intermittent exclusion of livestock in some areas, and moving of nests away from the tide line to decrease risk from tidal flooding. The coastline in this area is a mix of sand and shell beaches, wave cut rock platform, low schist rock, or cliffs. Small areas contain boulder beaches or broken rocks. Grazed paddock, cliff, and marram grass covered sand dunes are found behind the coastline.

Key questions and overview of chapters

In order to answer the questions raised by recovery planning several key questions need to be answered including:

- What are the factors limiting the population of Chatham Island oystercatcher (CIO) on the Chatham Islands?
- What is the abundance and distribution of the population and is it increasing, decreasing or stable?
- What are the recruitment and mortality rates, and within which segments of the population are they acting and during which season(s)?
- What habitats are CIO selecting at the general, territory and nest-site level?
- What are the links between productivity and habitat characteristics (what is high quality habitat?)

To answer these questions, objectives for this study were set to collect and interpret data for CIO on: 1) population size, trends, and distribution across the Chatham Islands, 2) basic breeding parameters for 15 pairs along the north coast, 3) recruitment and mortality rates, 4) habitat selection at the general, territorial and nest-site levels, 5) habitat factors that are correlated with territory quality as reflected in breeding success, and 6) cues that elicit territorial behaviour in CIO.

Overview of the chapters

To identify the factors most likely to be limiting the CIO population, information on the basic demography of the population is needed; information such as distribution and abundance, population trends over time, and the age structure of the population. Information on the age structure, and the proportion of the population which is non-territorial, can provide important information about the limitations imposed by low productivity within the breeding population and on mortality rates of different cohorts (e.g. breeders, nonbreeders). Chapter 2 addresses the current distribution and abundance of the CIO population. Determining population trends over time, or the age structure of the population, would have been desirable, but was outside the scope of this study due to lack of historical data or individually marked CIO. Colour bands were not an option during this study due to past problems with colour bands on CIO.

Data on basic breeding parameters such as breeding success, causes of clutch and chick losses, and timing of the breeding season are essential to understanding limiting factors and monitoring management outcomes. This information can also be used to model population responses to various management intervention scenarios. Chapter 3 reports on a range of breeding parameters for 15 pairs of CIO along the north coast, Chatham Island. Highly precise data on this topic was outside the scope of this study as the data were collected incidentally to the habitat use information and pairs could not be visited daily.

Ultimately, the upper limit for any population is determined by habitat quality and availability. The two key seasons when habitat limitations operate are the breeding season and over winter (Fretwell 1972; Goss-Custard 1996; Newton 1998). Habitat use is also influenced by interactions between individuals and other factors such as predators or disturbance. Habitat selection is thought to occur at three levels. General habitat selection involves choice within a broad geographic area. For example, coastal birds commonly show a preference for nesting on islands, where predators and human disturbance may be low compared to mainland sites (Buckley and Buckley 1980; Williamson 1981; Blondel 1985; George 1987). Territory selection involves acquisition of an area vigorously defended by the pair. A territory is generally defended to protect critical resources, usually nest-sites or food supply. Factors that influence nest-site selection include physical and vegetation characteristics that protect adults, eggs and chicks from predators, conditions of abiotic environment, and conflicts with neighbours (Burger 1977; Burger 1985).

Food and nest-sites are two critical resources found within territories which can limit populations. General habitat selection and territory selection, the habitat composition of territories, and the use of microhabitats within territories are examined in Chapter 4. Territory quality and its relationship to habitat types is explored in Chapter 5. In CIO, loss of clutches due to flooding often raises the question as to why they do not nest in areas less prone to flooding. Chapter 6 addresses nest-site selection in CIO and the implications to population regulation.

Finally, behaviour plays a key role in regulating bird numbers through territorial behaviour (reviewed in Newton 1998). CIO were found to respond to two-dimensional models that resemble oystercatchers, which allows for exploration of territorial behaviour within the species. The cues that CIO respond to and the reasons for responding to these cues are explored in Chapter 7.

Thesis context

This thesis was conducted under contract to the Science and Research Division, New Zealand Department of Conservation. The author was supported by a Lincoln University Doctoral Scholarship. Additional funding was received from Lincoln University and the Gordon Williams Biological Fellowship.

This thesis represents work that commenced in October 1994 under the supervision of Drs Adrian Paterson and Chris Frampton, Lincoln University, with external supervision by Ralph Powlesland, Science and Research, New Zealand Department of Conservation. All data collection , analysis, and writing is original and was done by myself for all chapters. I received assistance with the data collection for two weeks from Alastair Freeman, Lincoln staff and about six weeks from Rachel Peach, summer student scholar. Assistance with scanning photos and layout of the plates was received from Rhonda Pearce, Lincoln staff. Assistance with the figures containing maps was received from Adrian Paterson and Rhonda Pearce. The original research questions came from Andrew Grant, New Zealand Department of Conservation, who also assisted with the original funding application. The concept of testing various types of models was originally suggested by Adrian Paterson (Chapter 7). Shaun O'Connor, New Zealand Department of Conservation, provided the funding and logistical support to conduct the 1998 census (Chapter 2).

There were several constraints that limited the scope of the research. Colour banding of adult CIO was not an option due to past problems with bands. Experimental powder-coated metal band was trialed on two cohorts of juveniles, but the colour wore off within less than two years. The timing and amount of data collected was constrained because the study area was remote and travel times to several CIO study pairs was about three hours return. Transportation was limited, especially the first season, and field work had to be suspended several times for transport or administrative reasons. (Inclement weather and changes in beach or river courses also regularly delayed or altered data collection.) Because of the long field seasons (about six months each season), logistics of organisation, and the difficulties with data entry and analysis while on the islands, some data collection and analysis that would have been desirable (such as the effect of storm patterns on productivity and population modeling) were outside the scope of this study. Determining the areas and habitat composition of each territory along the north coast was attempted, but because of a variety of technical obstacles involving aerial photography and GPS/GIS technology, the results could not be included in this thesis. Finally, there was only a short lead time before data collection commenced the first season, due to the terms of the contract, and the time between seasons was also limited (due to the logistics of the study and data entry). Communications by phone and email while on the Chatham Islands was limited due to cost and logistics. Therefore, I must take full credit for any flaws in study designs as I did not have many opportunities to adopt them from other sources.

These chapters, excluding the General Introduction and General Conclusions, have been published or prepared for submission to journals, and so are not entirely consistent in their layout and style. As a result there is, unfortunately for the reader, some repetition of basic information in the introduction and location sections of several chapters, although I have attempted to minimise it. The term 'season' or 'year' refers to the CIO breeding season, which begins in October and ends in the following calendar year. Seasons are given as the year in which breeding begins (e.g., 1994 refers to the 1994/5 breeding season).

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CHAPTER 2

DISTRIBUTION AND ABUNDANCE OF THE CHATHAM ISLAND OYSTERCATCHER (*HAEMATOPUS CHATHAMENSIS*)

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ABSTRACT

From 13 to 18 December 1998, we counted Chatham Island Oystercatchers (*Haematopus chathamensis*) on approximately 310 km (96 - 97%) of the coastlines of Chatham, Pitt, Rangatira, and Mangere Islands, and 100 km (100%) of the shore of Te Whanga Lagoon, Chatham Island. A total of 142 adult Chatham Island Oystercatchers, including 34 confirmed breeding pairs and seven additional possible breeding pairs, were found. This is an increase of 20 to 40 adults over any previous count or estimate. Some of this increase may be due to efforts by the Department of Conservation to increase productivity of breeding pairs since the early 1990s along the northern coast of Chatham Island. Approximately 70% percent of the breeding pairs were on Chatham Island, 15% on Pitt Island, the remaining 18% on Rangatira and Mangere Islands. Most of the oystercatchers (79% of individuals and 74% of the breeding pairs) were in areas we broadly defined as containing rocky wave-cut platform or other rocky coastline or outcrops. Thirty individuals and nine breeding pairs were on sandy beaches. One immature bird was on the shore of Te Whanga Lagoon.

KEYWORDS: Chatham Island Oystercatcher, *Haematopus chathamensis*, Chatham Islands, population size, endangered species.

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INTRODUCTION

The Chatham Island Oystercatcher (*Haematopus chathamensis*) is an endangered species endemic to the Chatham Islands (Baker 1973, Davis 1988, Collar *et al.* 1994, Department of Conservation 1994). Counts from 1986 to 1996 estimated the population to be between 65 and 120 adults, including 30 - 44 pairs (Best 1987, Davis 1988, Davis 1989, Page 1992, Sawyer 1993, 1994; Schmechel, unpubl. data). Because only one or two people conducted these counts, they were done over limited areas and/or over relatively long periods (6 - 13 weeks) thus increasing the likelihood of undercounting or double-counting birds. This census is the first to be conducted within a relatively short time-frame (1 week) over all four islands where Chatham Island Oystercatchers breed.

Chatham Island Oystercatchers are non-migratory, and almost strictly coastal in their distribution (Baker 1973, Davis 1988). Breeding pairs appear to be fairly sedentary and defend their territories strongly during the breeding season, although individuals may move to other areas to feed (Davis 1988). As with many other oystercatcher species, they do not breed until at least two or three years old (Davis 1988, Marchant & Higgins 1993, Hockey 1996). Occasionally pairs defend territories but do not breed (Davis 1988); these pairs usually breed the following season (Sawyer 1983, 1984; Schmechel, unpubl. data). Territorial and breeding pairs often respond to a cardboard model of an oystercatcher placed inside the boundaries of their territories, displaying the same aggressive behaviours they do towards an intruding floater or neighbouring pair of oystercatchers (e.g., piping displays, object tossing, physical attacks) (Schmechel, unpubl. data). Non-breeding and immature birds do not defend territories during the breeding season and ‘float’ around, moving from area to area, even island to island, occasionally forming small flocks of up to a dozen birds (Davis 1988; S. Sawyer, pers. comm.; Schmechel, unpubl. data). Floaters may form pairs, which forage, roost and travel together.

METHODS & LOCATION

Census

We searched the coastline of four islands (Chatham, Pitt, Rangatira and Mangere) inhabited by Chatham Island Oystercatchers (Fig. 1) from 13 to 18 December 1998. This

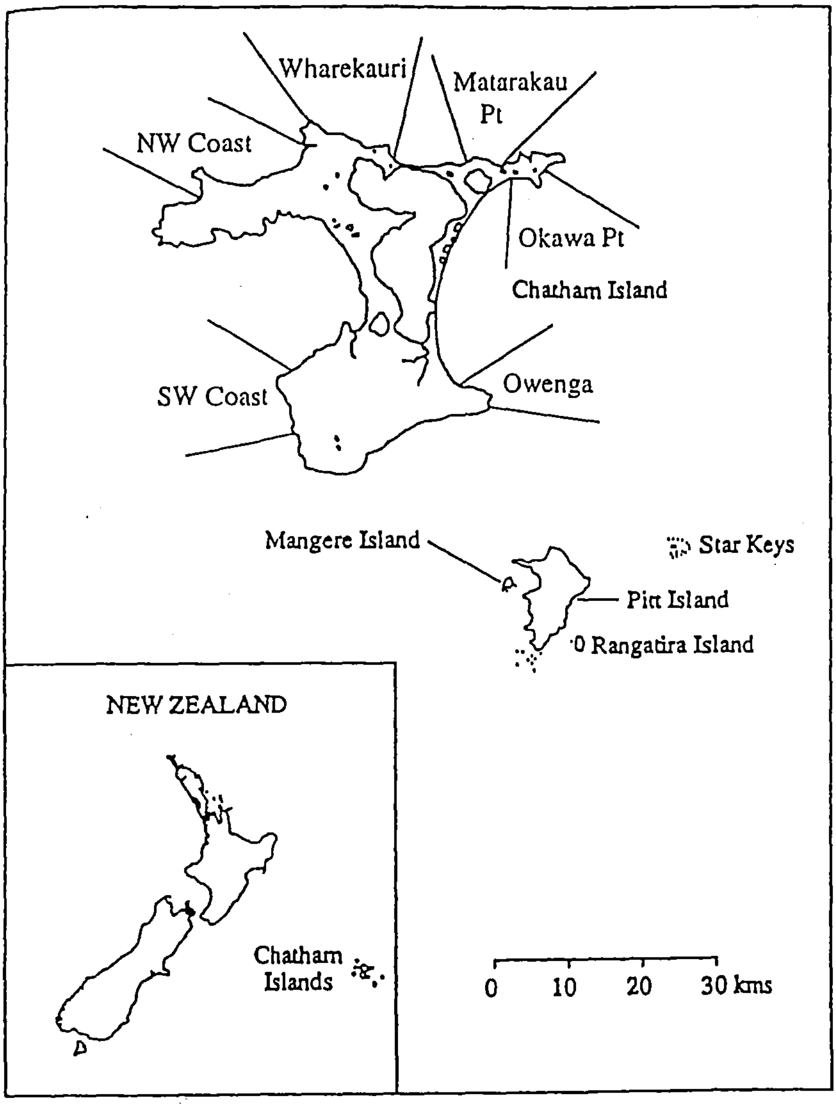

FIGURE 1 - Map of the Chatham Islands and the areas used for comparison with past counts (Table 2).

is within the breeding season, when all pairs are defending territories along the coast. We attempted to cover the islands in as short a time as possible to minimise the chance of miscounting birds.

Census team members collected data on numbers of birds, band combinations, location, age class, habitat type, and made notes on breeding status and behaviour. The presence of nests or chicks was noted, but is not reported in this paper. Age class was estimated by colour of eyes, bill, and legs, i.e., oystercatchers with orange bill tip (possibly brown in some individuals), brown-orange eyes (versus scarlet) and pale legs were classified as immature birds; those with scarlet red/orange eyes, no brown on the bill tip, and reddish-pink legs as adults (Marchant & Higgins 1993, Heather & Robertson 1996; Schmechel, unpubl. data). Colours can be difficult to distinguish from a distance and ageing birds becomes progressively more difficult as they approach adulthood. When in doubt, we assigned birds to the general category of adult. (Adults in this context were birds not identifiable as immature, but not necessarily of breeding age yet.) A cardboard model of an oystercatcher was sometimes used to determine territoriality of pairs if breeding could not be confirmed.

Department of Conservation staff and contractors, members of the Ornithological Society of New Zealand, the Taiko Team, and volunteers from the local community (a total of 35 people) participated in the census. We explained identification, ageing, behaviours, and data recording to the team before the census and some of the less experienced members were teamed up with more experienced people. However, some areas of the coastline and lagoon edge were surveyed by trained but inexperienced observers.

Team members checked the majority of the coast and lagoon edge on foot. Some long stretches of beach and the northern edge of Te Whanga lagoon were surveyed from four-wheel farm bikes, and a section of the southern cliffs of Chatham Island between Cape Fournier and Otawae Point, where land access is difficult, was searched from a boat running close to the shore (Fig. 2). The swell was too large to complete a section of coastline of about eight kilometres between Otawae Point and an unnamed point east of Green Point, and the team did not cover a few small sections of the Pitt Island coastline (approximately four kilometres) (Fig. 2). Altogether, we checked an estimated 310 km of coastline, about 96 - 97% of the total coastline, and 100 km of lagoon edge (100%). This

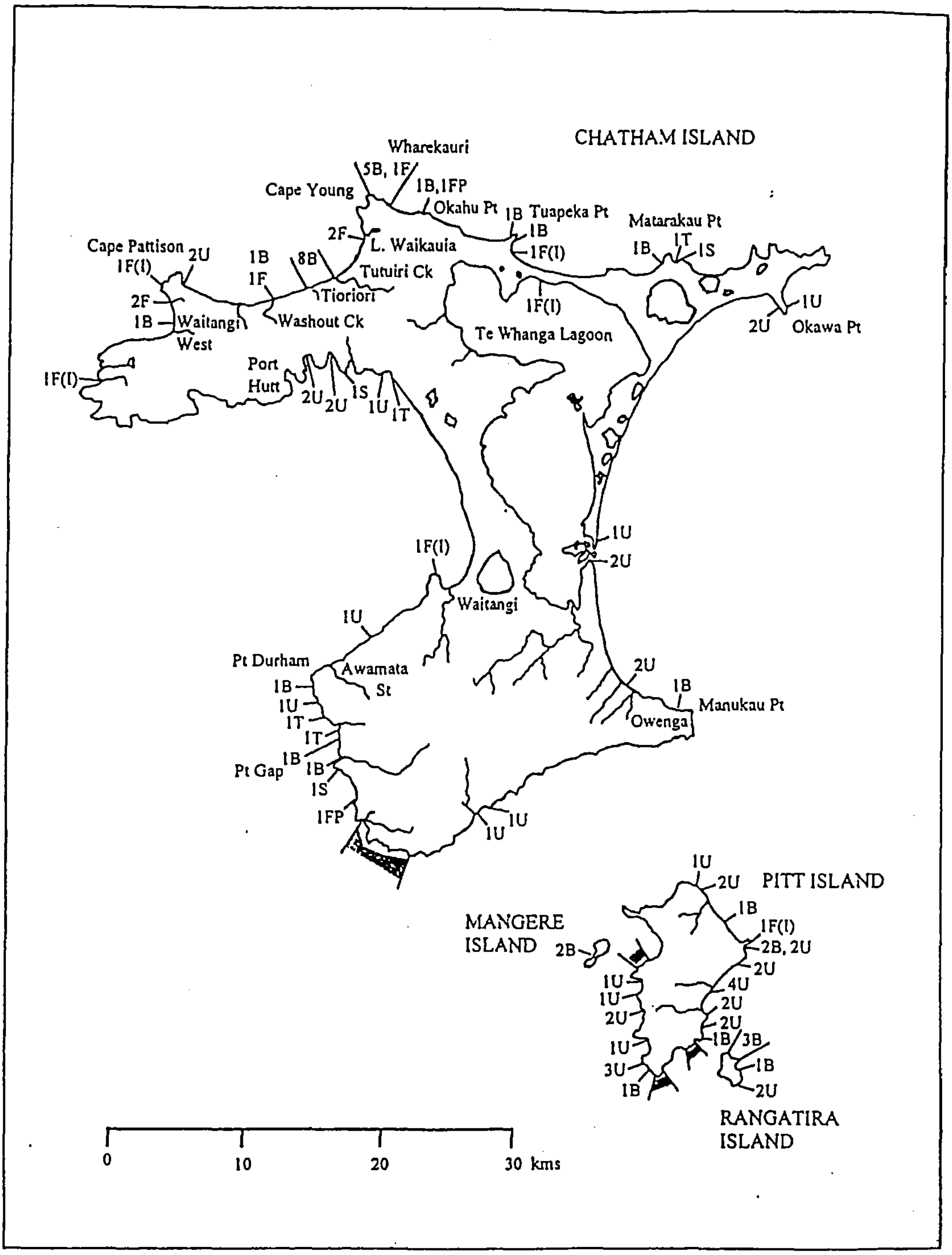

FIGURE 2 - Location of oystercatchers sighted during the 1998 census and the areas not covered by the 1998 census (stippled). Codes: B = confirmed breeding pair, S - suspected breeding pair, T - territorial pair, FP - floating pair, F - floater, I - immature, U - status unknown.

survey covered the known range of the Chatham Island Oystercatcher except for the Star Keys, small rock outcrops about 10 km east of Pitt Island, and the Muramur stacks of Pitt Island, where one or two oystercatchers have been reported (Davis 1988; M. Bell, pers. comm.; S. Sawyer, pers. comm.).

Mapping and analysis

We assigned oystercatchers, for the purposes of data analysis, to one of the following categories:

1) <u>confirmed breeding pair</u> - breeding confirmed for that season by sighting of either a nest or chick;

2) <u>territorial pair</u> (a good predictor of breeding in either the current or next breeding season) - pair seen to defend territory against either floaters, other pairs, or a model oystercatcher but not confirmed to be breeding;

3) <u>suspected breeding pair</u> - pair not confirmed as territorial, but they are either displaying breeding behaviours (e.g., alarm calls, distraction displays) however nest or chicks were not found, or have been reported breeding from earlier in the season (but reports are unconfirmed);

4) <u>floaters</u> - singles, or pairs travelling around together but not displaying territorial or breeding behaviours; and

5) <u>breeding status unknown.</u>

Where observers noted two adults together but had no additional information on their status, we recorded them as two individuals of unknown status at the same location, rather than as a 'pair'. We used this approach to avoid calling floaters 'pairs', since the term 'pair' can lead to an assumption of more breeding pairs than actually exist. This is a conservative approach and may underestimate the number of breeding pairs in areas seldom checked. In this paper the general term breeding pair includes confirmed and suspected breeding pairs, and territorial pairs.

RESULTS & DISCUSSION

Distribution and abundance

We counted a total of 142 adults (including those with immature colouration) on the four islands, including 34 confirmed breeding pairs and seven additional possible breeding pairs (Fig. 2). Together, Chatham and Pitt Islands (96% of the area searched) accounted for 90% of the total number of adults seen and about 85% of the breeding pairs (Table 1). Per unit area of coastline, Rangatira Island had the highest density of individual birds and breeding pairs (Table 1). The number of breeding pairs on Pitt Island may be an underestimate because many were observed infrequently and/or from a long distance, making determination of breeding status difficult.

TABLE 1 - Number (and percentages) of Chatham Island Oystercatchers seen on each island in the Chathams, December 1998. Individual oystercatchers includes both adults and those with immature plumage. Lower estimates of breeding pairs are confirmed breeding pairs only, upper estimates includes suspected breeding pairs and territorial pairs.

Location	Total individual oystercatchers			Number of breeding pairs		
	No.	(%)	per 10 km of coastline*	No.	(%)	per 10 km of coastline*
Chatham	94	(66)	4	23 - 30	(67 - 73)	1
Pitt	34	(24)	6	5	(15)	1
Rangatira	10	(7)	12	4	(12)	5
Mangere	4	(3)	6	2	(6)	3
Total	142			34 - 41		

* rounded to the nearest whole number

Six (4%) of the oystercatchers seen had immature colouration, the remainder had adult or undetermined colouration. The number of birds with immature colouration will be a minimum, as those viewed from a distance, or where the observer was uncertain, were assigned to the adult age class.

Fifty-one birds had metal bands, 49 were unbanded, 29 unknown (e.g., legs not seen), and 13 had either colour bands or jesses. There were no cases of individually recognisable birds being sighted twice, but there were two cases when birds not originally seen were later sighted (M. Bell, pers. comm.). Individuals (especially floaters) can move considerable distances from month to month, even between islands (Davis 1988;

Schmechel, unpubl. data), but details of how often birds move around and the patterns of movement are unknown. With only a small proportion of birds individually identifiable, it is difficult to estimate the likelihood of birds having been double counted or missed in this census. We attempted to minimize miscounting by checking adjacent survey areas on the same day as much as possible.

Population trends

Thirty-nine more adult Chatham Island Oystercatchers were seen during the 1998 census than in any previous count, and the total was 22 more than the highest previous estimate (Table 2). Many past surveys were only partial (e.g., 1970/71, 1986/87, 1995/96) and covered different areas from one another. However, if a comparison is made of the number of adult oystercatchers seen in areas that have been counted most consistently over the last 12 years, it shows that numbers have increased in the northern half of Chatham Island, have remained steady in the southern half of Chatham Island and on Pitt Island, and decreased on Rangatira Island (Table 2). There is also good evidence that the number of breeding pairs has increased on the north coast of Chatham Island since 1987, but decreased on Rangatira Island since the 1970s (Table 3).

Increases in the numbers of birds observed on the northern coast may be due, at least in part, to management activities since the early 1990s by the Department of Conservation designed to increase the productivity of breeding pairs, especially between Waitangi West and Okahu Points. Changes in weather patterns that effect the direction of high winds and storm tides during the breeding season could also have a significant effect on productivity over time in particular areas (Lauro & Nol 1993). The decline of breeding pairs on Rangatira Island since the mid 1980s is difficult to explain and could be due to a variety of causes including changes in habitat, weather patterns, lack of local recruitment, skua numbers, disturbance factors, or a combination of these or other factors.

TABLE 2 - Numbers of adult Chatham Island Oystercatchers in selected areas over 12 years of surveys (including those with immature plumage for 1998). Numbers in parentheses indicate that only a portion of the area was surveyed. Areas (see also Fig. 1): NW Coast - Waitangi West to Waikauia Lake mouth, Wharekauri - Cape Young to Taupeka Point, SW Coast - Awamata Stream to Point Gap. Sources: 1970/71 = Baker (1973), 1986/87 = Best (1987), 1987 = Davis (1988), 1992 = Page (1992), 1995/96 = Schmechel (unpubl. data).

Areas	1970/1[1]	1986/7[1]	1987	1992	1995/6[1]	1998
NW Coast	4 - 20	n/a	14	14	22	28
Wharekauri	6 - 30	10	16	11 - 12[2]	12	19
Matarakau Point	0	0	0	2	4	6
Okawa Point	0	0	0	0	3	3
Owenga	2 - 10	2	3	1	5	4
SW Coast	0	12	11	2 - 6	9	13
Pitt Island	8 - 40	(8)	23	9	(10)	34
Rangatira	11 - 50	n/a	17	12	12	10
All other areas	4 - 20	15	19	18	20	24
TOTAL count	25+	65	103	69	97	142
TOTAL estimate	50	65 - 75	103 - 110	69 - 73	100 - 120	140 - 150

1 partial surveys only

2 upper range includes 'unconfirmed sightings'

TABLE 3 - Changes in the number of 'pairs' of Chatham Island Oystercatcher along the north coast of Chatham Island (Washout Creek to the east end of Tioriori beach and Cape Young to Okahu Point) and Rangatira Island. The term 'pair' may have not been defined in the source documents and could include floating (i.e. non-breeding) pairs. Sources: a = Fleming (1939), b = *in* Davis (1988), c = Davis (1988), d = Page (1992), e = Sawyer (1993), f = Nilson *et. al.* (1994), g = Sawyer (1994), h = Schmechel, unpubl. data, i = 1998 census.

	North coast of Chatham Island		Rangatira Island		
Year	Total pairs[1]	Known breeding	Total pairs[1]	Known breeding	Source
1937			3		a
1970-84			10 - 13[2]		b
1984-87			9		b
1987/88	11		8		c
1991/92	11		6		d
1992/93	13	10	6		e,f
1993/94	13	9	6		g,f
1994/95	13	11			h
1995/96	14	14	6		h
1996/97	14	14			h
1998/99	15	15	5	4	i

[1] includes territorial, known and suspected breeding pairs

[2] except in 1978/79 when only 9 pairs were recorded (H. Robertson, pers.comm.)

Variables and potential biases

There are potential biases in the data from both this census and previous counts. The time of day, tide, weather, and observer's skill, knowledge and experience may bias the number of birds sighted (Bibby *et al.* 1992). The weather during this census was mixed with light or no winds (less than 40 km/h) on most days and stronger winds (estimated 40 to 60 km/h) on two other days. Light rain delayed the start times on two days (14 and 15 December), but there was no precipitation the remainder of these days. Only one section of coast was checked during occasional showers on the morning of 15 December. Most days were a mix of cloud and sun, except 16 and 17 December, which were fine.

High tide peaked between 02:52 - 06:34 and 15:17 - 18:54 during the dates of the census. The majority of the survey work was carried out between 09:00 - 18:00 resulting in portions of the rocky coastline being checked around low tide when birds may be more difficult to observe because they are foraging on rock platforms out of sight.

Travelling slowly on foot may increase the chances of observing and hearing birds compared with travelling by farm-bike or boat, particularly along locations with rocky coastline. The majority of rocky coastline was checked by foot during this census; however, if farm-bike or boats were used more extensively during any of the past surveys, it may explain some of the variation in numbers between years (e.g., 1992).

The overall potential bias for this census may be towards a slight undercounting of birds due to: the likelihood of missing birds on rocky coastline during low tide, effects of winds and swell on detecting birds (especially the south coast), areas of coastline that were not checked and may have contained birds, and the use of inexperienced observers in some areas. Countering this bias is the possibility of double-counting birds, especially since few have unique band combinations. As a result of this a range of 140 - 150 has been estimated for the population (Table 2).

Differences in methods between counts over time (e.g., the amount and areas of coast-line and lagoon edge covered, the number of days over which the count was conducted, the experience of the observers, the definition of pairs, the method of travel) increase the risk of bias and make trends in numbers of breeding pairs, floaters, and the total population difficult to detect (Table 4). This census and the 1987 surveys are probably the most comparable in terms of methods of travel, experience of observers, and areas covered. Many of the other surveys may have underestimated total numbers of birds in at least portions of their range due to lack of complete coverage of areas (1970/71, 1986/87, 1995/96), or lack of experience of observers and/or methods of travel used (1992). In spite of this, the magnitude of the changes on the northern coast of Chatham Island and Rangatira are too large to be explained by variations in survey intensity alone, especially for breeding pairs, which tend to be reasonably sedentary and may be checked several times per season.

TABLE 4 - Comparison of time-frames and number and experience of participants for past survey efforts. Experience of observers: H = high, U = unknown, M = mixed. Sources: a = Best (1987), b = Davis (1988), c = Page (1992), d = Schmechel, unpubl. data, e = 1998 census.

Survey dates	Duration (weeks)*	Number of participants	Approx. percent of coastline surveyed	Experience of observers	Source
22.12.86 - 2.2.87	6	1	30	H	a
12.10.87 - 5.12.87	8	1	95	H	b
9.1.92 - 20.2.92	7	2	100	U	c
11.11.95 - 11.2.96	13	4	75	H	d
13.12.98 - 18.12.98	1	35	98	M	e

* rounded off to the nearest week

Habitat use

All oystercatchers were seen along the seacoast (e.g., within 0.5 km of the ocean) apart from one apparently immature bird that was seen on Te Whanga Lagoon on a substrate of sand and mud with low vegetation. Thirty adults (21% of the total), including nine breeding pairs (26%), were on sandy (or sand and shell) beaches. Many of the sandy areas used by oystercatchers were near stream mouths, and had wide beaches and abundant kelp deposits. All other sightings (79%) were in areas broadly defined as having some wave-cut rock platform (relatively flat volcanic or sandstone platforms exposed only during low tide) or intertidal rocky areas (volcanic, schist or sandstone) associated with them (see also Davis 1988 for descriptions and maps of habitat types). Approximately 40% of the coastline of the four islands surveyed is classified by Davis (1988) as some type of intertidal rocky platform, 35% as sandy beach, and 25% as cliff or boulder. The oystercatchers are selecting for intertidal rocky habitats (79% use / 40% availability), using sandy beaches less than would be expected based on availability (21% use / 35% availability), and avoiding cliff and boulder areas (0% use / 25% availability).

CONCLUSIONS

The 1998 census was the most intensive to date, providing a base-line from which to compare both past and future Chatham Island Oystercatcher counts. Variations in census effort, methods, timing, and data collected between counts make it difficult to determine how much of the increase in numbers recorded is the result of actual changes in the population, changes in the census effort and accuracy, changes in management, or a combination of these and/or other factors. However, the estimated increase in total numbers (20 - 100% over previous estimates) and the nature of the data for some areas (e.g., the northern coast of Chatham and Rangatira Islands) provide good evidence that changes have occurred in the numbers of Chatham Island Oystercatchers and are not just the result of increased census effort.

Careful and intensive monitoring is essential to detect changes in numbers, especially if numbers begin to decline. Because Chatham Island Oystercatchers, like other oystercatchers, appear to be long-lived, do not begin breeding until at least two or three years old, and a proportion of the Chatham Island Oystercatcher population is non-territorial, it would be easy to miss early changes, such as a decline in the floater population, if periodic, comparable censuses were not conducted. Undetected declines in portions of the population, or concluding the population is increasing when it is not (a Type II error), could have serious implications for the conservation and management of the species if undetected for too long.

Future surveys should be designed to minimise potential biases and make those counts as comparable as possible with this census. If partial surveys are done between complete censuses, the same areas should be covered each time and standard methods used. If birds are individually marked, future counts could also provide information on adult and fledgling survival, movements, fidelity, population structure, and fecundity. Future surveys, combined with individual colour-banding, could also reveal whether management on the northern coast is benefiting the species at other sites.

The number of Chatham Island Oystercatchers appears to have increased significantly. However, because reliable comparisons with past estimates cannot be made, trends in the overall population will remain uncertain until further comparable counts are undertaken.

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CHAPTER 3

ASPECTS OF THE BREEDING BIOLOGY OF CHATHAM ISLAND OYSTERCATCHER (*HAEMATOPUS CHATHAMENSIS*)

ABSTRACT

In order to support conservation management efforts and better understand the population dynamics of the endangered Chatham Island Oystercatcher (CIO) aspects of the breeding biology of the CIO was studied on the north coast of Chatham Island during the 1994/5, 1995/6 and 1996/7 breeding seasons. Reproductive activity was monitored regularly for 5 to 6 months each season on 13 to 15 territories, or approximately 27-44% of the total estimated breeding population of the species. Data were also collected on colour changes of soft parts in immature birds.

Breeding effort was high. Only one pair apparently did not attempt to breed in one season over the total 42 pair-seasons. On average 33% of all pairs successfully raised at least one chick to fledging per season (range 14-47%). Damaged eggs left in the nest ended or shortened 17% of the breeding CIO pair seasons due to pairs incubating these eggs rather than re-nesting. These mostly intact eggs were either cracked or had small holes in them from a variety of possible causes.

Hatching success per clutch averaged 41% (range 28-62%), and fledging success (of those clutches which hatched at least one chick) averaged 56% (range 43-63%). Over the three seasons a clutch had a 20% (range 9-38%) chance of being successful (at least one egg surviving to produce a fledgling). Overall productivity averaged 0.44 fledglings/pair/season, but varied widely between years (range 0.14-0.73 fledglings/pair/season). A total of 20 fledglings was produced over the three seasons in the study area (Waitangi West to Okahu Point). Tidal flooding and storms were the cause of almost half (48%) of all egg losses, followed by causes unknown (26%). Other mortality factors included predation, trampling, abandonment, and infertility. The risk of flooding was constant throughout the incubation period; for other causes, the risk of loss was highest the week before and after hatching. All but one chick that died before

fledging simply disappeared (n = 8), and most of the losses (75%) occurred within the first 11 days after hatching.

The breeding season extended over six months (October to March) with peak activity from mid-November to mid-February. Clutches were initiated from mid-October until the third week in January. The latest nest hatched in mid-February. Chicks were present from mid-November to late March. The incubation period was normally 28-29 days. Chicks fledged about 39 days after hatching (range 30-47). One-chick broods fledged more quickly than two-chick broods (midpoint estimates ranged from 30-40 and 42.5-46.5 days respectively). Fledglings were evicted (or dispersed) from their natal territories about 33 days after fledging (range 24-42).

Based on 61 nests with complete records, mean clutch size was 2.20 (range 1-3) eggs per clutch. One-egg clutches were very rare (5% of all clutches) and found only in replacement clutches. Two-egg clutches, and clutches laid early in the season, were the most successful. Up to two replacement clutches were laid if the first clutch was lost.

Immature CIO when under 11 months old had brown eyes, brown bill tips and pale legs. Between 11-16 months of age immature CIO began to resemble mature birds, but could still be distinguished by their brown bill tips, brown or brownish eyes, and legs which were not as red as mature individuals. From 22-25 months distinguishing immature birds from adults was difficult, but subtle differences in eye colour were noted.

INTRODUCTION

Basic information on population dynamics, limiting factors, habitat relationships, and predator/prey interactions underpins advances in understanding the ecology of threatened and endangered species (DeSante and Rosenberg 1998). For threatened bird species, information on the timing of the breeding season, incubation and fledging periods, and breeding success is necessary for most conservation management activities. To determine annual breeding success accurately, for example, it is essential to know how long fledglings remain in their natal territories. Similarly, to target management efforts where they can be most effective, it is essential to understand when losses are occurring and the magnitude of these losses. The Chatham Island Oystercatcher (*Haematopus chathamensis*) (CIO) is an endangered species with an estimated population of only 140-

150 individuals (Schmechel and O'Connor 1999), yet little is known about its breeding biology.

Limited information on breeding success, basic breeding parameters (e.g., clutch size, incubation period, egg measurements) and timing of the breeding season have been collected, mostly incidental to other work (primarily for the Rangatira Island population). However, little or no information is available on several key aspects of the breeding season, especially for pairs outside Rangatira Island, such as clutch replacement times, hatching success rates, productivity, time to fledging and dispersal/eviction of fledglings from parental territories, and causes of egg and chick losses.

The information which is available on the breeding biology of Chatham Island Oystercatcher (CIO) comes primarily from a survey done by Davis (1988, 1989). Information on aspects of breeding was collected in conjunction with a survey of CIO numbers and habitat use during the 1987/8 and 1988/9 seasons (hereafter seasons are given as the year in which breeding begins) across the whole of their range. More detailed data on breeding have been collected incidentally on Rangatira and Mangere Islands from the 1970s by conservation and research workers. Some information was also collected in conjunction with management on the north coast of Chatham Island in the early 1990s. Much of the general breeding information for CIO is in unpublished reports to the Department of Conservation (Merton and Bell 1975; Davis 1988). The primary source of published information (based primarily on Davis' work) is Marchant and Higgins (1993) and Heather and Robertson (1996). Additional data have been published in early accounts of the species of the Chathams (Travers and Travers 1872; Fleming 1939) and by Baker (1973; 1975) as part of a review of the oystercatchers of New Zealand.

The impetus for recent conservation work on the species stemmed from concern that it was rare and possibly declining. The population was estimated at around 100-110 individuals in the late 1980s with productivity too low to maintain the population (Davis 1988). To increase CIO numbers, Department of Conservation drafted a recovery plan and initiated a management programme which included nest manipulations, predator control, and fencing along the north coast of Chatham Island (Murman 1991; Sawyer 1993; Sawyer 1994).

Management intervention (e.g., predator control, nest moving, etc.) was minimal during the course of this study, providing a baseline from which to compare future efforts (DOC 1995). The fence at Tioriori (an area managed specifically for CIO) was occasionally maintained, but breaches often occurred and both livestock and weka (*Gallirallus australis*) were regularly seen inside the fence during all three seasons of the study (pers. obs.).

Breeding of CIO is restricted to coastal areas (Baker 1973; Davis 1988). About 70% of the estimated 40-50 breeding pairs are on Chatham Island, 15-20% on Pitt, and the remainder on Rangatira and Mangere (Schmechel and O'Connor 1999; Moore *et al.* 2000). Each pair vigorously defends its territory during the breeding season, and may defend it all year round in some locations (Davis 1988; pers. obs.). On Chatham Island, nesting is primarily in areas of good visibility for the incubating bird on sandy beaches or occasionally on rocky outcrops (Chapter 6). Nests are either shallow cup-shaped scrapes in the sand or similar depressions in low mat-forming vegetation on rocks. In oystercatchers, the precocial young are fully mobile (most chicks leaving the nest within 24 hours of hatching), yet receive food from their parents, some until well after fledging (Hockey 1986).

The major prey items which have been reported for CIO foraging on rocky shores are limpets (*Cellana strigilis*), and for birds foraging on sandy beaches are sandhoppers (Amphipoda) and round worms (Nermertean) (Davis 1988). Other prey items include blue mussel (*Hytilus edulis*), paua (*Haliotis spp*), whelks (*Haustrum haustrorum*), and ribbonworms (Polycheates). They also fossick among wrack (washed up kelp and organic matter), feeding on sea tulips (*Pyura pachydematina*) and ribbed mussel (*Aulacomya ater*). Other bivalves and chitons have also been recorded as prey items.

A three year study (1994 - 1996) was undertaken to assess which factors may be affecting productivity and which may be limiting the population, and determine actions which could be taken to increase numbers breeding pairs on the north coast of Chatham Island. Additionally basic breeding information was collected to aid in management. Specific objectives of this study included:

1) obtaining more detailed productivity information for CIO pairs outside of Rangatira (breeding success rates and the causes and timing of breeding failures);

2) determining timing of the breeding season (clutch initiation, incubation periods, re-nesting intervals, time to fledging, and timing of eviction/dispersal of fledglings);
3) recording clutch sizes and egg measurements; and
4) determining changes in soft part colouration as immature CIO age.

This paper presents results of research on the breeding ecology of this species and compares CIO with other oystercatcher species.

LOCATION

The Chatham Islands are located in the Pacific Ocean 850 kms east of Christchurch, New Zealand (44°S, 176.5°W). The islands experience frequent strong winds and occasional high storm swells. The prevailing winds are from the south and west. Mean average wind speed is 25 km/h with gale force winds (greater than 63 km/h) averaging 14 times per year. Frost is rare and temperatures are moderate. Summer temperatures (mean daily maximum) reach 17-18° C; maximum temperatures exceed 20° C about 14 days each year. Winter minima are 5-6° C (Thompson 1983).

Chatham Island is around 96,500 ha (965 km^2) in area, with approximately 320 km of coastline. Te Whanga lagoon occupies an area of 186 km^2 in the northern half of the island with around 100 kms of shoreline (Hay *et al.* 1970). The second largest island, Pitt, is around 6,190 ha (63 km^2) in area. Rangatira or Southeast Island (200 ha) and Mangere (100 ha) Islands are protected nature reserves with no permanent human residents nor any introduced mammals or avian predators (e.g., weka). Chatham and Pitt Islands are inhabited, extensively farmed, and the vegetation is extensively modified over most of the land and coastal areas (Atkinson 1996). Both Chatham and Pitt Islands have a large suite of introduced predators and free ranging livestock (sheep and cattle). Coastal and dune vegetation is highly modified with most of the coastal forest and dune vegetation now replaced by the introduced marram grass (*Ammophila arenaria*), a sand binding species (Atkinson 1996).

The study areas were located on the north half of Chatham Island between Waitangi West and Taupeka Point, and between Whangamoe and Whangatete Bays (Figure 1) (hereafter

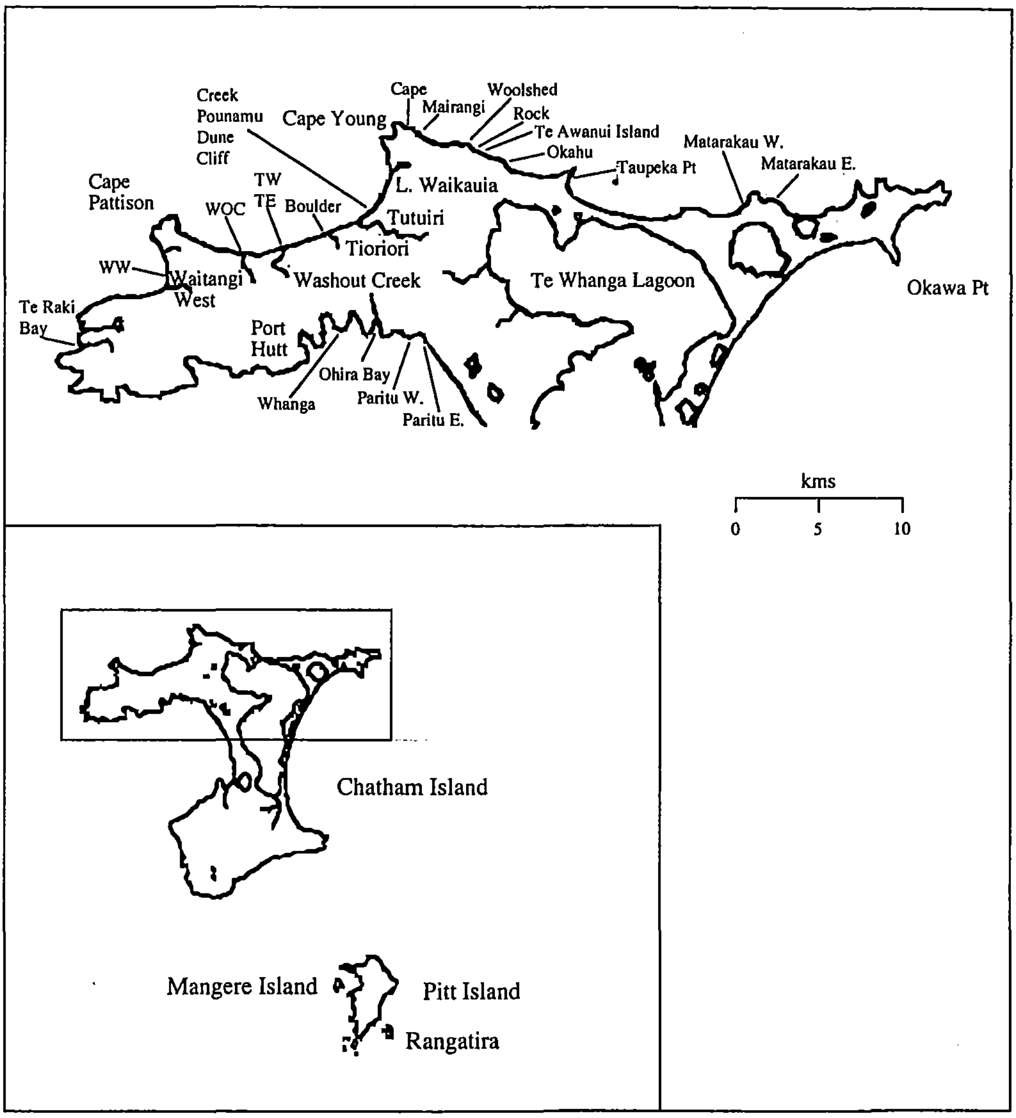

Figure 1 Map of the north coast, Chatham Island with location of study pairs.

referred to as the 'north coast'). The coastline in this area is a mix of sand and shell beaches, wave cut rock platform, low schist rock, or cliffs. Small areas contain boulder beaches or broken rocks. Grazed paddock, cliff, and marram grass covered sand dunes are found behind the coastline. Four of the breeding territories at Tioriori were within a site fenced off to protect CIO nests (i.e., predator control and fencing to exclude livestock).

METHODS

Territories of 13-15 pairs of CIO along the north coast of Chatham Island were monitored for breeding activity over most of the breeding season from October or November until late March or early April (Appendix 1). A record was kept of dates of breeding outcomes; hatching and fledging success; known and suspected causes of losses of nests or chicks; dates of nesting, hatching, fledging, and eviction/dispersal of fledglings; clutch size; egg weights and measurements; and soft part colouration of fledglings.

Pairs were widely scattered along the coastline with access to territories by farm-bike or on foot. Five pairs required three hours travel time to monitor. One pair, which nested on an island, could only be accessed during low tide. Two pairs (Waitangi West and Whanga) not regularly visited during the first season, were visited in subsequent seasons. Some pairs were passed regularly en route to other pairs and were therefore monitored more frequently. A range of 14-23 checks was made per pair per season (Appendix I). Pairs with fewer than eight checks in a season were excluded from some breeding calculations due to the higher likelihood of nests being missed, except clutch size and egg sizes.

For various analyses, clutch data were sometimes excluded. Two pairs were found with chicks for which no nest had been found; these were not included in the hatching success calculations for that season. In five cases, the final size of the clutch was not established with certainty; these clutches were excluded from calculations involving clutch sizes. Additional notes describing the criteria for exclusion are included in the tables and text. Clutch data were compared using a repeated measures ANOVA and one-way ANOVA to determine if there were differences between mean sizes of first, second and third clutches. Fisher's LSD test was then used to make pairwise comparisons between clutches.

Eggs were weighed to the nearest 0.5 grams using a Pesola 100 gram scale. Width and length were measured to the nearest 0.1 mm using Mitutoyo callipers. To reduce possible chilling or over-heating of eggs, care was taken to ensure visits to the nest were as short as possible, and nests were not disturbed during adverse weather.

Breeding success was analysed in terms of individual eggs and clutches. Clutch success was categorised into 'hatching success' (percentage of nests that hatched at least one egg) and 'overall success' (percentage of nests that fledged at least one chick). Hatching and fledging success are presented as a percentage of the number of nests found during the study. Because frequency of checks for nests varied, and some nests were probably lost before being found, a daily survival rate for clutches was calculated using the Mayfield method to ensure that the importance of early losses was not underestimated (Mayfield 1975). Failure of clutches was normally assumed to take place mid-way between the last two checks (Mayfield's original method) except in a few cases where there was very good evidence that clutches had been lost due to a large storm event, in which case the date of the storm (rather than the midpoint) was used as the 'loss date'. Maximum intervals between such checks varied from 4 to 21 days (average 8.92, n = 42). Clutches with damaged eggs (not viable) were considered 'lost' (treated the same as if they had disappeared). Clutches of unknown size were excluded from the data set for calculating survival probabilities. The stage between clutch completion and hatching was the only one reported using the Mayfield method. The data were insufficient to report meaningful daily survival probabilities for the other stages (i.e., laying, hatching, or chick rearing). Both the traditional or naiive methods as well as the Mayfield estimates were reported.

There were numerous clutches where it was not possible to determine if they had hatched before disappearing. In these cases the clutches were assigned to three categories depending on how likely it was that they had hatched: high, unknown, and low. Clutches considered to have a high probability of having hatched were those that were pipping when last seen, or those with a predicted hatch date (based on clutch initiation and completion dates) in the first quarter or less of the period between the last two checks. Clutches assigned to the 'low' category were those with an estimated hatch date in the last quarter of the period between the checks. All others were assigned to the 'unknown' group. These were assumed to have had a 50% chance of hatching. In calculations of hatching success those assigned to the high category were assumed to have hatched, those in the low were assumed to have been lost before hatching, and the unknowns were divided equally between the two groups. For the Mayfield calculations, if the estimated loss dates fell before the estimated hatch dates, the clutch was assumed to have hatched; if after, it was assumed to have hatched.

When a range of dates, rather than the exact date, was known for clutch initiation, hatching, and fledging, the midpoint was normally used for estimating various parameters. If the intervals were at the beginning or end of the season, or simply too large (greater than 20 days), these data were excluded or noted in the appropriate section. Occasionally, if additional information (such as a minimum relaying intervals) was available to narrow the possible range, this was also incorporated.

The following assumptions were used in calculations (based on parameters from my data where it was complete, and from other reported values for various oystercatcher species including CIO): 29-day incubation period from clutch completion to completion of hatching, a 48-hour period between each egg laid with incubation commencing when the last egg was laid, and a minimum 10-day relaying period from loss of clutch to initiation of the next replacement clutch (Baker 1969; Davis 1988; Marchant and Higgins 1993; Heather *et al.* 1996). If an egg had not begun pipping when checked, it was assumed the earliest probable hatch date for this egg was a minimum of two days later. Incubation was defined as the time from clutch completion until the last egg hatched.

The period of nesting was divided into ‘early’, ‘mid’, and ‘late’ season based on breeding patterns of CIO in the study area, specifically when second and third clutches were initiated. 'Early season' nests were those initiated before 29 November, 'mid-season' nests were those initiated between 29 November and 3 January, and 'late season' nests were those initiated after 3 January.

The fate of failed nests was recorded when possible. Notes were made if large swells had passed over the nest area, or if predator, livestock, or tyre tracks were visible in the area around the nest site. The causes of egg loss were categorised as: ‘unknown', ‘known’ (where there was a high degree of confidence in the cause of loss) and ‘suspected’ (when the evidence was less conclusive).

The presence of chicks was determined by sight. If chicks were suspected as being present, but not sighted, a recording of the behaviour of the parents was made. A fledgling was defined as any juvenile capable of flight. Because fledgling oystercatchers remain with the parents for a minimum of several weeks, and no CIO chicks disappeared between the last check before and the first check after fledging, no corrections were made for fledging success. Fledglings were regarded as being independent once they left their natal territory and had not returned for several days, or if their parents showed repeated aggressive behaviour to them and drove them away from their territories. Some of the chicks were colour banded with experimental powder coated metal bands during the first two seasons of the study and so were individually recognisable for one to two years later before the colour faded.

During this present study most of the adult CIO were not individually recognisable. Some birds had metal bands, but it was not until the third season (1996) that a reliable method for drawing the birds in close enough to read metal bands from a distance was discovered. One colour banded bird was present in the study area during the beginning of the first season (1994). Males and females could sometimes be distinguished by the length and colour of the bill, but bill length of pairs can be quite similar (Schmechel, unpubl. data).

RESULTS

Hatching and fledging success

Summary of breeding outcomes for pairs on the north coast, Chatham Island

A total of 42 breeding pair seasons were monitored closely (i.e., visited over eight times per season). On average, one-third of all pairs were successful (i.e., raised one or more chicks to fledging) over the three seasons. Breeding success was lowest for the 1996 season when only two pairs (14%) raised chicks to fledging, compared with 1994 and 1995, when 38% and 47% of the pairs successfully raised chicks to fledging respectively (Table 1). The low success rate in 1996 was due primarily to two major storms that occurred at key times during the breeding season (just before many nests were due to hatch) (Figure 2).

Table 1 Summary of breeding outcomes for study pairs of CIO, north coast, Chatham Island and causes of unsuccessful breeding seasons.

	Pair seasons				
	Total		**By breeding season (n)**		
Outcomes of breeding effort for the season	**Percent**	**n**	**1994**	**1995**	**1996**
Successful*	33%	14	5	7	2
Unsuccessful	67%	28	8	8	12
no known breeding attempt	2%	1	1	-	-
1 clutch (total for season), failed	5%	2	-	-	2
2 clutches (total for season), all failed	21%	9	2	2	5
3 clutches (total for season), all failed	10%	4	-	2	2
1 clutch, damaged eggs**	12%	5	2	1	2
2 clutches, damaged eggs	5%	2	-	2	-
infertile eggs in clutch	2%	1	1	-	-
lost older chick (over 14 days)	2%	1	-	1	-
suspected pair turnover / new pair	7%	3	2	-	1
Total pair seasons	100%	42	13	15	14

* pair raised one or more chicks to fledging
** damaged eggs left in nest delaying re-nesting

Entire breeding seasons were lost, in effect, due to various causes. Pairs not attempting to breed, loss of older (i.e., over two week old) chicks, or incubation of infertile clutches were rare causes (only once each over 42 pair seasons). Pair turnover, due to divorce or death of one of the members of the pair, was a more common cause, implicated in three instances. Once, a member of a pair disappeared during the breeding season (the only colour banded bird in the study), the nest was abandoned, and there were no further breeding attempts in that territory during the season. In the other two cases, the pairs acted oddly at the beginning of the season. One of these pairs made nest scrapes, but no eggs were ever found; the other pair did not initiate a first clutch until very late in the season (January). Damaged eggs left in nests either shortening or ended the breeding season for seven pair (17% of the unsuccessful outcomes). If eggs were damaged, but still substantially intact (e.g., shell cracked, or small hole in shell), pairs would often continue to incubate them for extended periods, rather than re-nest. Five pairs incubated inviable eggs for as long as 40-55 days (Table 2).

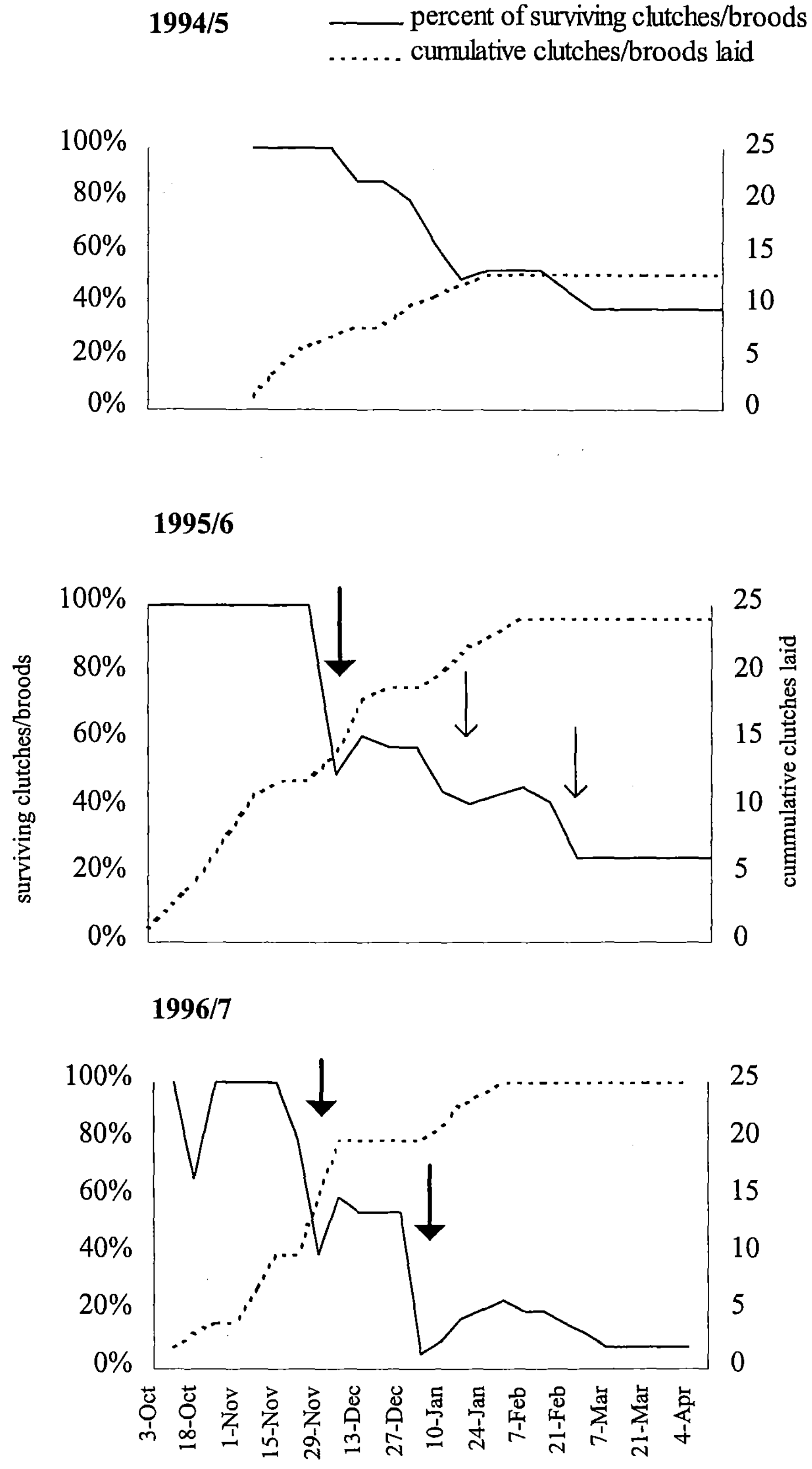

Figure 2 Percent of surviving clutches/broods over time and cumulative clutches laid over the season, north coast, Chatham Island. Bold arrows mark major storms, light arrows indicate less intense storms. (Monitoring began late in the first season, i.e., 1994).

Table 2 Number of pairs incubating inviable eggs (eg. damaged, infertile or dead embryo) for 40 or more days 1994 - 1996, north coast, Chatham Island. Arranged from longest to shortest incubation period. Normal incubation period 28-29 days.

Pair	Season	Minimum number of days eggs incubated	Number of eggs
TE	1994	55	2
Cape	1994	49	1
Creek	1994	42	2
TW	1996	41	1
OTF	1995	40	1

Breeding outcomes and numbers of fledglings produced for the entire north half of Chatham Island (n = 55), including pairs outside the study area, are recorded in Appendix 2. During the first two seasons, 43% and 47% of pairs were successful (raising at least one fledgling) in marked contrast with the final season (1996) when only 9% of pairs were successful (compared with 14% in the study area). Even though a higher percentage of pairs was successful in the second season than the first, there were more fledglings per pair in the first season (0.71) than in the second (0.53), because of the higher number of two-chick broods in the first season (Appendix 3). The total number of fledglings recorded over the extended north coast area was the same for both of these seasons (i.e., 10 each season).

Hatching and fledging success rates

Over the three seasons, 20% of clutches produced at least one independent young, but success rates varied considerably between years, ranging from 9-38% (Figure 3). Of 60 clutches, 41% (± 14%) hatched at least one egg. Of those clutches which hatched at least one egg, 56% (± 20%) fledged one or more chicks. Chicks fledged per pair averaged 0.44 (range 0.14 to 0.73) for the three seasons (Table 3).

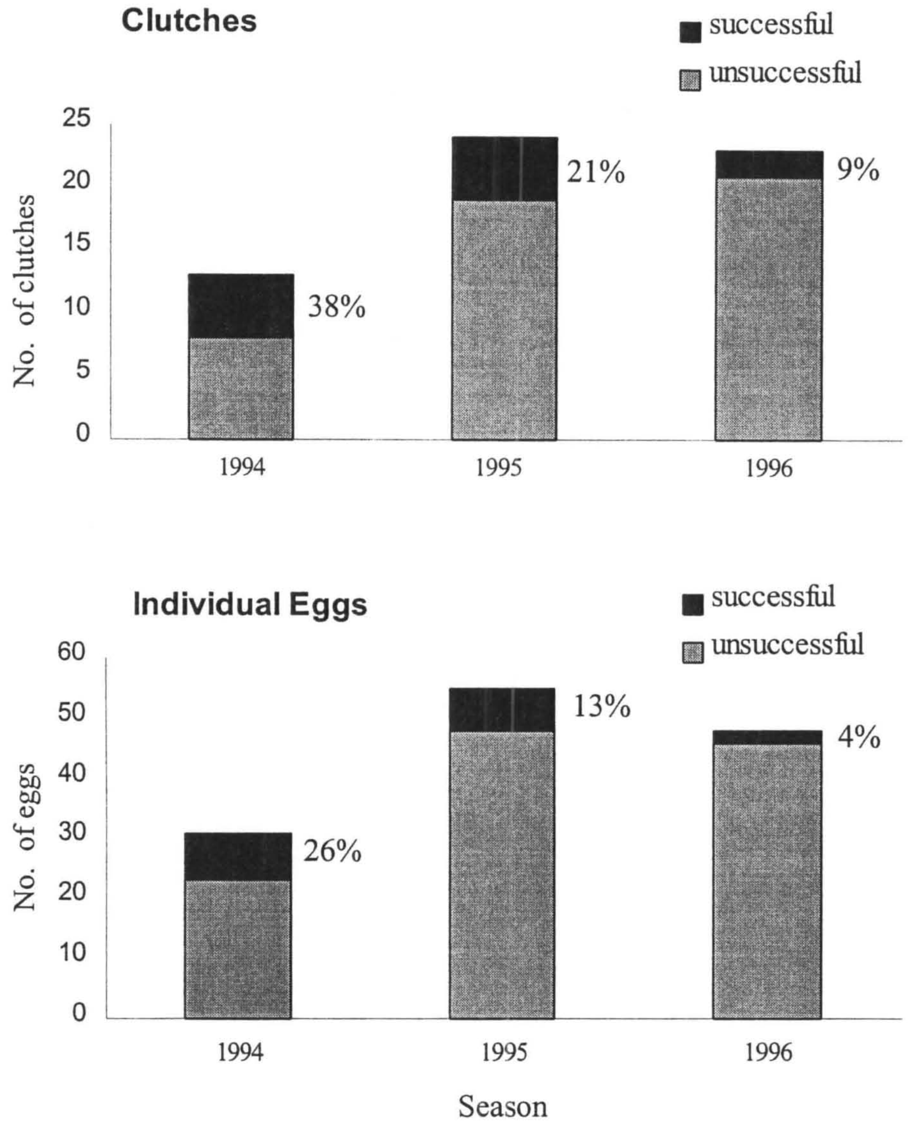

Figure 3 Numbers of clutches and eggs and percent successful by season, north coast, Chatham Island. 'Successful' is defined as any egg surviving to hatching and the resultant chicks surviving to fledging, or any clutch where one or more chicks survive to fledging.

Table 3 Breeding success by clutch of Chatham Island Oystercatcher, north coast, Chatham Island 1994 - 1996. Hatching success - percent of clutches that hatched at least one egg, fledging success - percent hatched that fledged at least one chick, overall success - percent of clutches that fledged at least one young. Numbers in parenthesis are the upper and lower range limits of clutches which may have hatched due to some eggs disappearing around the expected hatching date. (Excluded - clutches of unknown size, and pairs with visits under eight in a season.)

	Year			1994 -
	1994	1995	1996	1996
Pairs	11	14	14	39
Clutches	13	24	23	60
Hatching success	62% (54-70)	42% (25-59)	28% (13-43)	41% (27-55)
Fledging success	63% (56-70)	60% (37-83)	43% (20-66)	56% (36-76)
Overall success/clutch	38%	21%	9%	20%
Chicks fledged/pair	0.73	0.50	0.14	0.44
Chicks fledged/successful pair *	1.60	1.17	1.00	1.31

*raised at least one chick to fledging

Total fledgling success depended on a combination of hatching and fledging rates and brood size. If either hatching or fledging rates were very low, overall productivity was significantly decreased. In 1994, both hatching and fledging success rates (using traditional or naiive methods) were high (62% and 63% respectively), resulting in a high proportion of clutches (38%) successfully fledging at least one chick. In the following season, hatching success was lower (42%), but fledging success was still high (60%), resulting in over one fifth (21%) of clutches being successful. In contrast, both hatching and fledging success rates were low (28% and 43% respectively) in 1996, resulting in a low overall success rate (9%). There was a much higher proportion of successful two-chick broods in 1994 than the successive two seasons (33% in 1995 and 0% in 1996) (Figure 4).

The estimated probability of clutches surviving to hatching using the Mayfield method (1975) in 1994 was almost twice that of the next two seasons (62% per day for 1994 compared with 32% and 34% per day for 1995 and 1996 respectively).

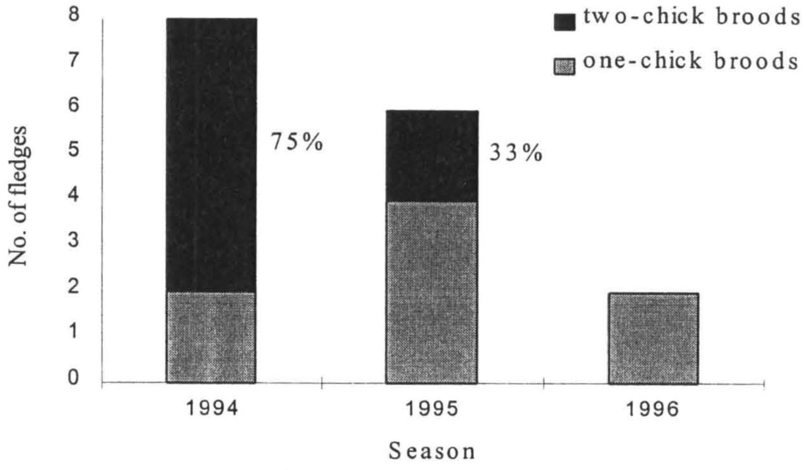

Figure 4 Percent of successful two-chick broods by season, Chatham Island Oystercatchers, north coast, Chatham Island.

Of individual eggs laid, 36% hatched; of those which hatched, 43% survived to fledging (Table 4). Overall, any one egg had a 13% chance of hatching and surviving to fledging. The number of fledglings produced per year in the study area (i.e., between Waitangi West and Te Awanui Island) was: 1994 - 10 fledglings, 1995 - 8 fledglings, and 1996 - 2 fledglings (Appendix 3).

Table 4 Breeding success by individual egg of Chatham Island Oystercatcher, north coast, Chatham Island 1994 - 1996. E - eggs laid; C - chicks hatched; F - fledglings. Numbers in parenthesis include the minimum to maximum number of eggs which could disappeared around the expected hatching date but it is unknown whether they hatched. (Excluded - clutches of unknown size and pairs with visits under eight in a season.)

	Year			1994 -
	1994	1995	1996	1996
Pairs	11	14	14	39
Eggs laid (E)	31	55	48	134
Hatching success (C/E)	52% (39-65)	37% (18-56)	24% (8-40)	36% (19-72)
Fledging success (F/C)	53% (40-66)	46% (23-69)	30% (10-50)	43% (23-63)
Overall success (F/E)	26%	13%	4%	13%

Nest loss

The main cause of egg loss over the three seasons was flooding (48%), especially in the 1995 and 1996 seasons, followed by causes unknown (26%) (Figure 5). Together these two causes accounted for 74% of the total egg loss. This includes both 'known' and 'suspected' losses. Causes of loss were often difficult to determine because eggs frequently disappeared with few traces. This was due in part to frequent strong winds and rain which obscured any tracks or signs, and the habit of CIO of removing shells if eggs are crushed or after hatching (pers. obs.). Only one clutch was thought to be infertile, possibly due to the male being less than three years old. The following year, the pair in that territory (presumably the same pair - a metal banded male, and unbanded female) raised two chicks to fledging. Crushing due to vehicles (once) or livestock caused several losses, plus several additional ‘close calls’ (where vehicle, horse or livestock tracks were seen near the nest). The suspected predation was by weka and possibly spur-wing plover (*Vanellus miles*). In one case, an empty egg shell was found near a nest with marks similar to those on chicken eggs depredated by weka. In another case, a single peck mark was found in an egg and spur-wing plover were suspected because there was no further predation of the egg and because of their presence in the area; but gulls or weka may also have been responsible. One embryo died during hatching (see later section).

The highest risk of loss from any cause for eggs or chicks was during the seven days before, and after, hatching (Figure 6). About 60% of losses occurred during those two weeks.

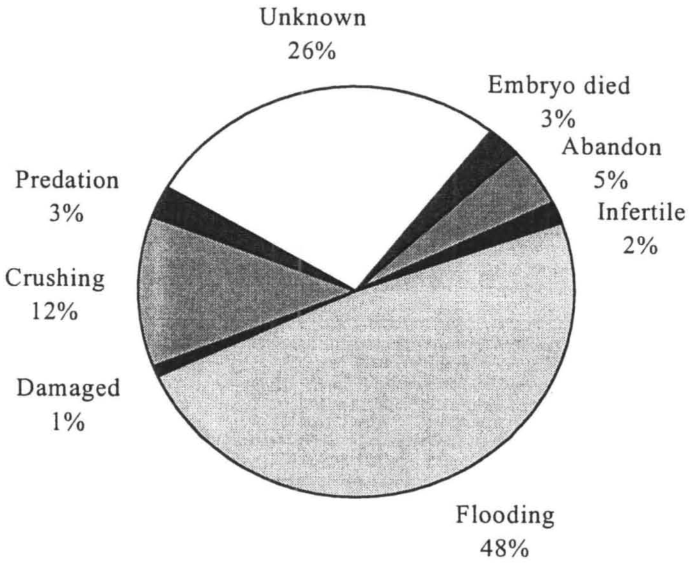

Figure 5 Causes of egg loss, including suspected losses, of Chatham Island Oystercatcher along the north coast, Chatham Island.

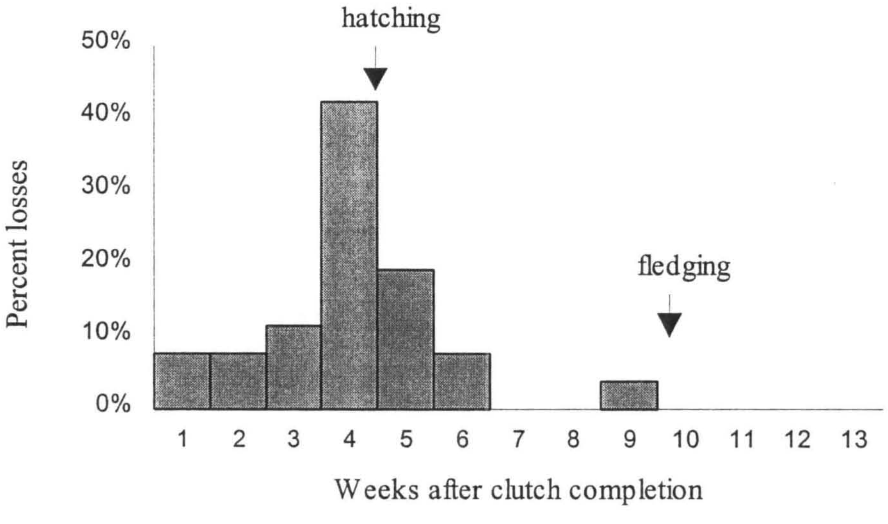

Figure 6 *Percent loss by week after clutch completion for Chatham Island Oystercatchers, north coast, Chatham Island. Pipping and hatching normally occurred around week 4 and 5, and fledging around week 10. Losses were estimated as the midpoint between when nests or chicks were last seen and the first date they were missing or seen dead.*

If the cause of clutch loss was tidal flooding, losses were independent of clutch age (Figure 7). However, if the cause of loss was non-flooding, a large percentage of losses occurred between day 21 and day 37. During the first three weeks after laying, 80% of these clutches remained viable (i.e., at least one, but usually all, eggs surviving). After day 21, survival dropped quickly until only 36% of clutches were viable by day 37. In other words, for clutches lost to causes other than flooding, 62% of these were lost during this critical two-week time period (i.e., day 22 to day 36).

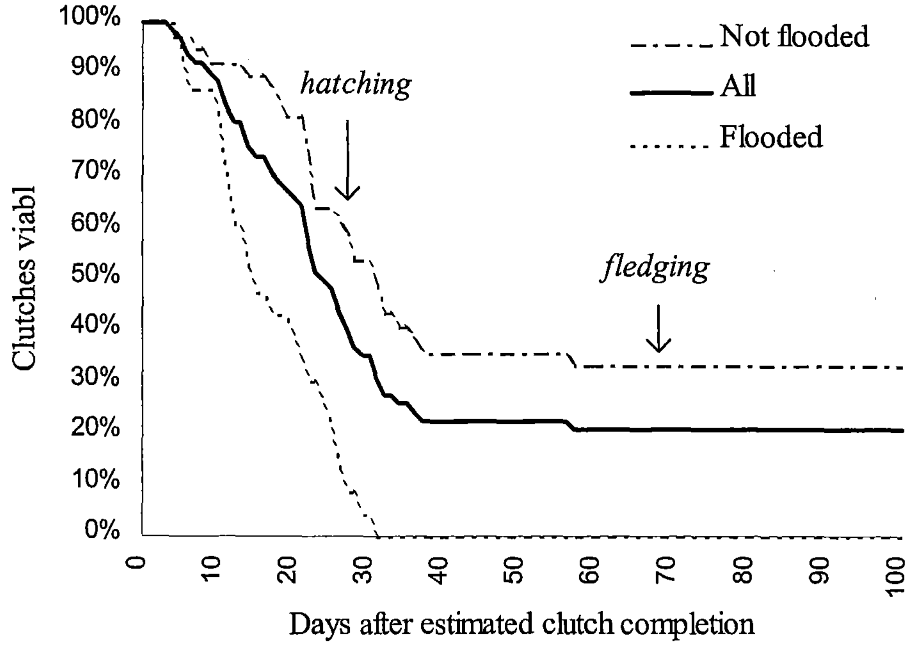

Figure 7 Percent of viable clutches after estimated clutch completion. A viable clutch was defined as any of the eggs or chicks still surviving. Hatching occurs at about 29 days after clutch completion and fledging around 70 days.

Loss of chicks

Most chicks which died before fledging disappeared without a trace (7 out of 8), and the majority (6 of 8) disappeared while still less than 11 days old. There were 45 eggs over the three seasons where it was not known whether loss occurred before or after hatching (i.e., the clutch disappeared, and chicks were never found). Of these eggs of unknown fate, if any chicks had hatched, they must have died at under 14 days old based on when the territories were checked.

Timing of the breeding season

The entire breeding period, from egg-laying to dispersal of fledglings, extended over at least six months from mid-October to April and probably into May (Figure 8). The nesting and chick periods, the main time when management activities to increase productivity normally occur, peaked from November through February. Fledglings were present from January to April, when data collection ceased. Dispersal or eviction of fledglings began in late January and continued into April.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Clutches	? - -	* * * *	* * * *	* * * *	- - - -	-	
Chicks		- -	* * * *	* * * *	* * * *	- - -	
Fledglings				= = = =	= = = =	= = = =	= ? ? ?
Dispersals				=	= = = =	= = = =	= ? ? ?
Checks	- - - -	- * * *	* * * *	* * * *	* * * *	* * * *	-

*Figure 8 Timeline of presence of clutches, chicks, fledglings and timing of dispersal of fledglings from parental territories on the north coast, Chatham Island, 1994-1997, and dates when territories were checked for breeding activity. * 90% of activity occurred within this time, - remaining 10% of activity, = indicates period fledglings were present and dispersals were occurring. ? - little or no data available for this time period.)*

Nesting and hatching dates

The estimated initiation date for the earliest clutches was 13 October, but could have been as early as 9 October. Clutch initiation varied by 4-6 weeks in 1995 (the only year with complete early season data), with earliest pairs nesting in mid-October, and later pairs not commencing first clutches until mid-November or early December.

Peak clutch initiation occurred from the last week of October to the second week of December (Figure 9). Second clutches were initiated from the last week in November, and third clutches from the first week in January. Clutches were initiated as late as the end of January. Two clutches laid as late as mid-January resulted in chicks surviving to fledging. The main period when eggs were present was from November to January (Figure 10). Eggs began hatching in mid-November and the last eggs hatched in mid-February.

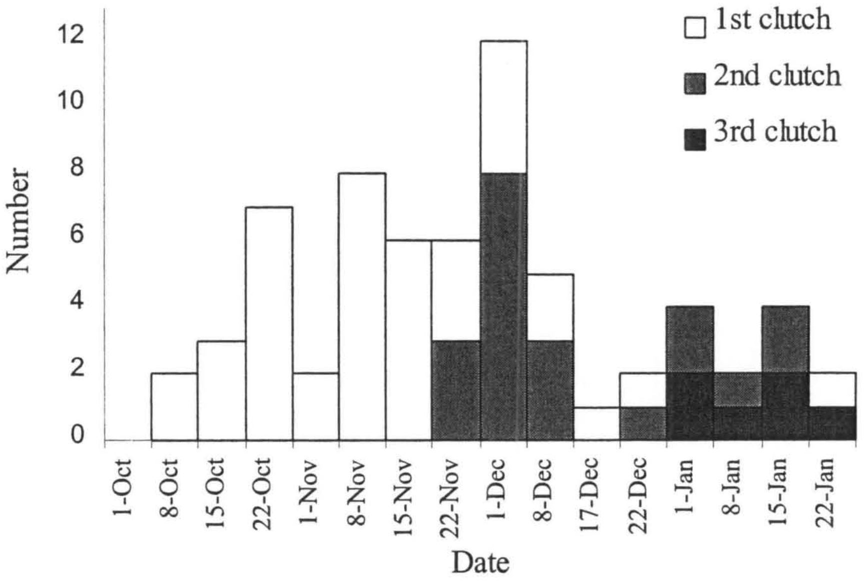

Figure 9 Clutch initiation dates, Chatham Island Oystercatcher 1994-1996.

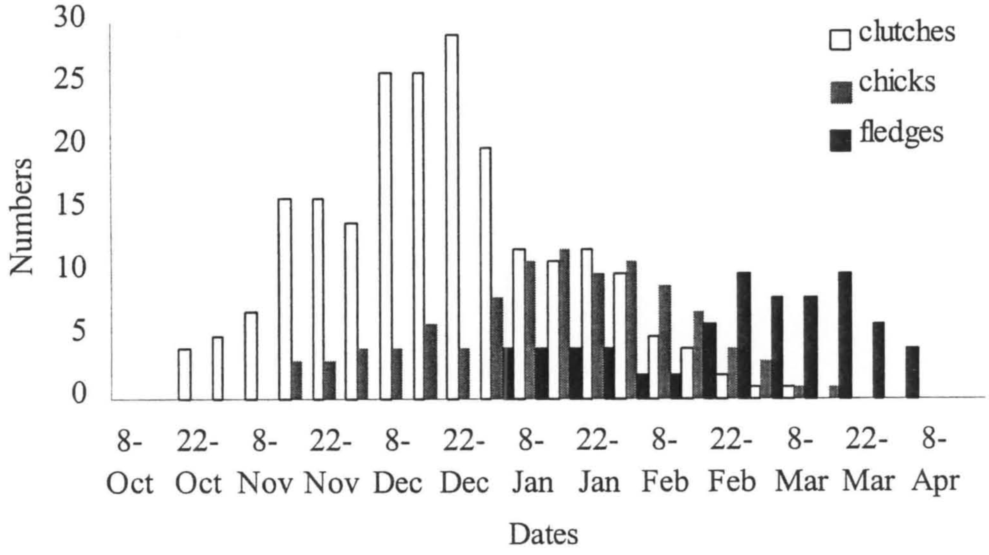

Figure 10 Abundance of clutches, chicks and fledglings in north coast Chatham Island Oystercatcher territories 1994-1996.

Laying, incubation, and hatching

Only one clutch yielded data on laying intervals. The first egg of the clutch was present for two days in a row before another egg was laid, suggesting a 24-48 hour laying interval. The clutch was eventually complete at three eggs.

Two clutches with known clutch completion and hatching dates (to within a day) had incubation periods of 27-29 days and 28-30 days. One other successful clutch had a minimum incubation period of 30 days. One unsuccessful clutch had a minimum incubation period of 37 days. This three-egg clutch was first sighted after completion on 23 November 1994; pipping was recorded 36 days later (28 December). The following day (29 December) the chick had almost hatched but appeared cold and lifeless. This hatching egg/chick had disappeared by the following day and the other two eggs never hatched. This pair was subject to disturbance (e.g., fence maintenance activity) due to conservation management activities (fence maintenance) on at least three days during incubation (29 November, 6 & 7 December or 8, 15, and 16 days after the estimated clutch completion dates) and were observed spending up to 1.25 hours continuously off the nest at a time.

Hatching started with tiny star-shaped fractures appearing in the egg and chick vocalisations about 2-3 days before hatching. Distinct holes were pipped one day or less before hatching. Newly hatched chicks were occasionally found in or adjacent to the nest just after hatching. Hatching was asynchronous by up to one day in some clutches and occurred over at least two days (Table 5).

Table 5 Hatching times for five Chatham Island Oystercatcher pairs, north coast, Chatham Island.

Pair	Day 1	Day 2	Day 3	Final outcomes
Cliff	2 pipping	2 chicks		2 chicks
Cape	2 pipping	1 chick, 1 pipping		1 chick, 1 unknown
Island	2 pipping	2 pipping		2 chicks
Waitangi West	2 pipping	1st chick, 1 pipping	2nd chick	2 chicks

Three nests were flooded by high or storm tides but incubation continued, with the eggs either in a new location, remaining in the nest, or being recovered by the pair. Two of these tidally flooded nests were unsuccessful (in one, the egg was probably inviable, the other nest was lost to a later storm tide), and one hatched a single chick. CIO will recover eggs dislodged from the nest by rolling them back in to the nest. One pair of CIO repeatedly retrieved a displaced egg (previously damaged but still being incubated) back into the nest scrape from as far as a metre away.

Re-nesting intervals

Pairs frequently re-nested after losing clutches and, in at least one case, a pair re-nested after losing a young chick (3-7 days old). Almost all first clutches were replaced if no damaged or inviable eggs were left in the nest scrape and the pair was intact. Of 21 first clutches lost, with no damaged or abandoned eggs left in the nest scrape, a minimum of 19 (90%) were replaced. Second clutches were replaced much less often; only 31% were replaced after loss (n = 16) (Table 6). No third clutches were replaced.

Table 6 Minimum replacement rates of clutches after loss (ie. clutch no longer viable) of first and second clutches, with and without damaged/inviable eggs left in nest scrape after loss.

	1994	1995	1996	total
1st clutch				
total loss of clutch				
percent replaced	100%	100%	80%	90%
total number (n)	3	8	10	21
damaged or abandoned eggs				
percent replaced	0%	50%	0%	12%
total number (n)	4	2	2	8
total 1st clutches lost	7	10	12	29
2nd clutch				
total loss of clutch				
percent replaced	0%	33%	37%	31%
total number (n)	2	6	8	16
damaged or abandoned eggs				
percent replaced	-	0%	-	0%
total number (n)	-	1	-	1
total 2nd clutches lost	2	7	8	17

If damaged eggs were left after the clutch was damaged (i.e., became inviable), replacement was delayed or precluded due to the pair attempting to incubate these eggs. Of eight first clutches with damaged eggs left in the clutch, only one was replaced. No damaged second clutches (n = 1) were replaced. The one pair which initiated a second clutch after having damaged eggs in its first clutch, did so quite late in the season (19 January 1996).

The mean time for a pair to re-nest after losing a clutch was 15 days (range 7.5-24 days, SD = 4.46, n = 23). Because nests were not checked daily, there was a range of possible days when the renesting could have occurred for any one clutch. The variation ranged from plus or minus 3-13 days, (mean = 4.39, SD = 3.17).

First clutches were replaced on average more quickly than second clutches. Midpoint estimates for first clutch replacements averaged 13.9 days (range 7.5-22 days, SD = 4.4, n = 18), and for second clutches 17.6 days, (range 15-24 days, SD = 3.76, n = 5).

Replacement intervals varied between pairs, year and clutch order as illustrated in Figure 11 (using a subsample of the data).

			Days to replace lost clutches																									
Pair	Yr	CO	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
WW	95	c1	|	-	-	-	-	X	-	-	-	|																
	96	c1											X															
	96	c2											|	-	X	-	|										
WOC	96	c1															X											
TW	96	c1													X													
	96	c2																		|	-	-	-	X	-	-	-	|
TE	96	c1							|	-	-	X	-	-	|												
OTF	94	c1							|	-	-	X	-	-	|												
	95	c1														|	-	-	-	-	-	X	-	-	-	-	-	|
	96	c1					|	-	X	-	|																
Creek	95	c1														|	-	-	X	-	-	|					
Pounamu	95	c1																|	-	X	-	|					
	96	c1					|	-	-	X	-	-	|														

Figure 11 Range of days from loss of clutch to initiation of replacement clutch for CIOs, north coast, Chatham Island where the range of dates were known to within five days. Yr - breeding season, CO - clutch order (i.e, first or second clutch being replaced), X - midpoint estimate, |----| possible range of replacement days. Arranged by territory in geographical order from west to east.

Fledging

Chicks were present from mid-November until late March. The earliest recorded chick was on 15 November, the latest 19 March. Numbers of chicks were highest from the first week in December until the last week in February (90% of observations). Fledglings were present from the first week of January into April and probably beyond. The earliest recorded fledgling was on 6 January (but the actual dates of fledging were probably earlier - sometime between 23 December and 6 January, the dates when the areas were checked). Fledglings were still present until observations ceased in the first week of April (1995 and 1997).

Chicks fledged, on average, 41 days after hatching (SD = 5.9, n = 15) (Appendix 4). One chick broods fledged more quickly, on average, than two chick broods (39 days, range 30-47 days, SD = 4.8, n = 10 and 44 days, range 36-54 days, SD = 6.9, n = 5 respectively); however, there was overlap with some two-chick broods fledging more quickly than one-chick broods. Within territories dominated by a particular habitat type (e.g., sandy beach, rocky platform, or mixed), differences in fledging time between one- and two-chick broods were greatest in the sandy beach territories (Table 7).

Table 7 Average fledging times (days) of one- and two-chick CIO broods within territories predominated by different habitat types. SB - sandy beach, RP - rocky platform, MX - mixed, n - sample size.

	Fledging time (days) by habitat types							
Brood size	SB	(n)	RP	(n)	MX	(n)	Total	(n)
One-chick	38	6	38	1	41	3	39	10
Two-chick	47	3	40	2		0	44	5
Overall average	41	9	39	3	41	3	41	15

Dispersal of fledglings

After fledging, juvenile CIO remained in their natal territories for varying times, but for eight fledglings monitored for six or more weeks, all were evicted from (or left) their natal territories. In one case where two sibling chicks fledged, one fledgling was driven out of the natal territory after 17-30 days. Although it was observed attempting to return to its natal territory, it was driven off by the adults and the remaining fledgling. The second fledgling was still present in the territory two days later when observations ceased. For five broods, where the dates were known to within 15 days, fledglings dispersed on average 33 days after fledging (range 24-42 days) (Table 8), beginning the third week of January.

Table 8 Dispersal periods and dates for five fledged Chatham Island Oystercatcher chicks, north coast, Chatham Island. Arranged from shortest to longest days after fledging.

Pair and season	Brood size	Days after fledging: Midpoint	Days after fledging: Possible range	Dispersal dates
WoC 1994	2	24	17 - 30	1st: 23 - 24.3.94
		unknown	32+	2nd: after 26.3.94
WoC 1995	1	28	18 - 39	23.1.96 - 2.2.96
WW 1995	1	32	30 - 35	18.3.96 - 21.3.96
Whanga 1995	1	41	37 - 46	6.2.96 - 12.2.96
TE 1995	1	42	37 - 49	1.2.96 - 21.2.96
Overall averages		33	28 - 40	

Measurements

Clutch size varied between one and three eggs with a mean size of 2.20 (n = 61). Over 95% of the clutches contained two or three eggs, with two-egg clutches the most common (70%) (Table 9). One-egg clutches were found only during the third season of monitoring. In 1994 there was a higher percentage of three-egg clutches (38%) than in the following two years (20-22%).

Table 9 Frequency of clutch sizes (e - egg) and clutch order for three breeding seasons in Chatham Island Oystercatcher, 1994 - 1996, north coast, Chatham Island.

	1994			1995			1996			Mean
Clutch	Clutch size			Clutch size			Clutch size			clutch
order	1 e	2 e	3 e	1 e	2 e	3 e	1 e	2 e	3 e	size
First	-	6	5	-	10	3	-	9	3	2.31
Second	-	2	-	-	7	2	1	5	2	2.16
Third	-	-	-	-	3	-	2	1	-	1.67
Total	0	8	5	0	20	5	3	15	5	2.20

Average clutch size tended to decrease with both advancement of the breeding season and with the number of replacement clutches. There was a significant relationship between clutch size and number ($F_{2,60} = 4.60$, $P = 0.014$)(Table 9). Third clutches were significantly smaller ($p < 0.05$) than first and second clutches (Fisher's pairwise comparison). A replacement clutch was always the same size or smaller than the previous clutch. Nearly all (88%) second clutches were the same size as the first clutch (n = 16); in contrast, many (66%) third clutches were smaller than the second clutch (n = 6). There was no significant difference in average clutch size between years.

Some pairs consistently laid larger clutches than others (Table 10). First and third clutches were more likely than second clutches to fledge at least one chick successfully (Table 11). This must be interpreted with caution, however, because if a clutch was lost before being found (e.g., was flooded in the days between initiation and a search for the nest), some second and third clutches could have been wrongly identified as first or second clutches. If time of year, rather than clutch order, is used in the analysis there is a similar pattern (Table 11). A much larger proportion of two-egg clutches were successful (28%) than three- or one-egg clutches (7% and 0% respectively) (Table 12). Egg measurements recorded in 1996 are shown in (Table 13).

Table 10 Percentage of 3-, 2-, and 1-egg clutches laid by Chatham Island Oystercatcher breeding pairs, north coast, Chatham Island and number of chicks fledged over three seasons from 1994-1997. Excluded - pairs checked less than 8 times/season, clutches of unknown final size, or less than 2 clutches total).

	Clutch size (percent)			Total no.	Total
Pair	3 egg	2 egg	1 egg	of clutches	fledglings
Island	80	20	0	5	4
OTF	80	20	0	5	0
Rock	40	60	0	5	1
Woolshed	33	67	0	6	1
Cape	25	75	0	4	0
Creek	25	75	0	4	0
Cliff	20	80	0	5	0
WW	0	100	0	5	2
WOC	0	100	0	4	3
Dune	0	100	0	3	0
TE	0	80	20	5	1
TW	0	80	20	5	3
Pounamu	0	67	33	3	0

Table 11 Effect of clutch order and season (nest period) on fledging success. Early - before 29 November, mid - 29 November - 3 January, late - after 3 January.

Clutch order	Proportion of clutches which were successful*	N	Nest period	Proportion of clutches which were successful	N
1st	25%	36	early	27%	30
2nd	11%	19	mid	15%	20
3rd	33%	6	late	18%	11
overall	21%	61	overall	21%	61

* fledged 1 or more chicks

Table 12 Effect of clutch size on fledging success in Chatham Island Oystercatcher, north coast, Chatham Island.

	Percent of clutches that were successful				
Clutch size	1994	1995	1996	Total	N
1 egg	-	-	0%	0%	3
2 egg	50%	30%	13%	28%	43
3 egg	20%	0%	0%	7%	15
all sizes	38%	21%	9%	20%	61

Table 13 Size and fresh weights of Chatham Island Oystercatcher eggs. Sources: a) this study, b) H.A. Robertson and M.D. Dennison, 1980, c) A. Davis, unpubl. data.

Parameter	Mean	SD	Range	No. eggs	No. clutches	Source
Length (mm)	56.9	2.7	50.3 - 62.7	48	22	a
	56.5	3.2	52.9 - 61.2	6	3	b
	56.0		55.5 - 56.4	22		c
Width (mm)	40.2	1.1	37.8 - 42.2	48	22	a
	40.5	1.6	37.6 - 42.2	6	3	b
	40.6		40.4 - 40.8	22		c
Weight (g)	47.9	4.1	40.0 - 52.5	7	4	a

Plumage and soft part colouration by age

Colour changes as CIO matured are summarised in Table 14. All individually marked CIO of known age that were less than 11 months old (from estimated hatching date) had brown eyes, brown bill tips and pale legs. They also tended to have 'cleaner' black/white demarcation lines on the breast and were more shy than older birds, i.e., they often ran or flew away more quickly than older birds when approached. From 11 months, the eye

Table 14 Colouration by age of Chatham Island Oystercatcher.

Age	Bill	Eyes	Legs	Other
2 - 10 months	brownish and/or brown tip	brown	grey to pale ('putty')	often clean black/white chest line, 'shy' behaviour
11 - 16 months	orange, may have brown tip	brown to brownish-orange to reddish-orange	pink, pale red, or pinkish-red	bolder behaviour - may approach model of Chatham Island Oystercatcher
22 - 25 months		reddish (but not scarlet), some with slightly more brown in centre	red	
mature adult	orange/red or red with yellowish tip	scarlet (iris and orbital ring, with dark pupil)	red	

colour began to change, but the timing of the colour change appeared to be variable between individuals. Birds 22 and 25 months (n = 3) had colouration like adults including plumage, bill colour and leg colour except for the eye colour. The eyes tended to be reddish rather than scarlet and to have more brown in the centre. These colour differences were subtle, however, and best confirmed in a mixed group of birds with mature birds as reference points.

DISCUSSION

Hatching and fledging success

Summary of breeding outcomes for pairs on the north coast, Chatham Island

Breeding effort was much higher during this study than that reported by Davis (1988). During this study only one pair (2%) apparently did not attempt to breed out of a total of 42 pair-seasons. This is in contrast to Davis (1988) who found that 27% of pairs did not breed in 1987 and 21% could not be confirmed, resulting in only 52% of pairs confirmed as attempting to breed. Methodology could affect reported non-breeding effort. Davis' (1988) definition of pairs included those that were sexually immature, which accounted for some, but not all, of the non-breeding effort. Clutches can be laid and lost quickly (Ens *et al.* 1996). As a result, frequent monitoring is needed over the nesting season to confirm lack of breeding effort. Due to the nature of the work in 1987 in which many sites were visited, but not frequently, the level of monitoring was possibly not sufficient to determine breeding effort, at least in some cases. As a result the number of pairs attempting to breed may have been under-estimated. (On Chatham and Pitt Islands a total of 34 territories were checked during 1987 on average 5.4 times, range 1-13. Twenty-two territories (65%) had no visits recorded between mid-December and late March). Alternatively breeding effort may have varied considerably between this study and the 1987 season due to differences in weather, the sites studied, other factors, or most likely some combination of methods plus conditions.

Hatching and fledging success rates

The average productivity of north coast pairs during this study was similar to the average for pairs monitored on Rangatira between 1974 and 1986 (Davis 1988), but much higher than in 1987 for the whole of the Chathams which is the only productivity estimate for the whole of their range (Table 15). The productivity for the 1987 season might have been unusually low due to storms or other factors. Over the three seasons of this study, fledging success during one of the seasons was especially low (0.14 fledglings/pair) compared with the other two seasons (0.50 and 0.73 fledglings/pair). Rangatira productivity shows a similar pattern with average productivity at 0.48 fledglings/pair/season, but during the worst season was only 0.22 fledglings/pair compared with 0.85 fledglings/pair during the best season.

Table 15 Hatching and fledging success of the Chatham Island Oystercatcher breeding at various locations and dates. Ranges of different year in parenthesis.

Location	Years	Pairs	Fledge/pr/yr (range)	Source
North coast, CI	1994 -1996	13 (11-14)	0.44 (0.14 - 0.73)	this study
Chathams group	1987	30	0.27	Davis 1988
Rangatira Island	1974 - 1986	10 (8 - 11)	0.48 (0.22 - 0.85)	Davis 1988

Breeding success reported for the 1987 season should also probably be considered a minimum, since eviction/dispersal times of juveniles were not known when this work was done and re-analysis of the data shows many pairs were not checked often enough to determine productivity accurately. During the 1987 season, breeding was assumed to be unsuccessful if no chicks or fledglings were found in territories during a single check in mid- to late March. This may not be accurate because fledglings could already have left their natal territories by mid-March. In addition, a single check may be insufficient to determine success, as evidenced by several accounts where a record of 'no chicks or fledglings found' was logged in territories that must have had chicks or fledglings present based on later sightings of fledglings in these areas.

CIO productivity on the north coast was low compared to that of most other oystercatcher species around the world (Table 16). Success for eggs surviving to fledging was as low or lower than most recorded averages except for a very small sample of Australian pied oystercatcher (*H. longirostris*). Hatching and fledging success of CIO eggs, though within the range of that for other species, is low, especially for hatching success. The success of clutches is reported less often than the success of individual eggs. Compared with one study of American black oystercatcher (*H. bachmani*), CIO clutches had better hatching and much better fledging rates. However, compared with Eurasian oystercatcher (*H. ostralegus*), overall success was very low (20% in CIO compared with 61-86% for Eurasian oystercatcher). Number of CIO fledglings/pair/season was towards the low end of the averages, but variation is quite wide from study to study and species to species.

If hatching success is low, management efforts can be concentrated on the nesting period; alternatively, if chick survival is low, management can be concentrated on this portion of the breeding phase. During this study, hatching rates were lower than fledging rates in two of the three seasons, with both being low during the third season (1994). On Rangatira Island from 1984-1987, loss of eggs was higher than loss of chicks in two seasons, but in the other two seasons losses of chicks were greater than losses of eggs (Davis 1988). In a review of oystercatcher species worldwide Hockey (1986) found that most mortality occurred during incubation, rather than chick-rearing, although higher hatching than fledging success has been reported for the Eurasian oystercatcher (Harris 1967; Heppleston 1972).

The estimates for hatching success were maximums because some nests might not have been found before disappearing. Hatching probabilities were calculated to correct for variable monitoring and the risk of inflated hatching success figures due to early undetected losses of clutches (Mayfield 1975). In 1994 and 1996 the calculated hatching probabilities and traditional hatching successes were similar (62%). In 1995, however, the traditional hatching probability was 31%, compared with a calculated 42% hatching success, suggesting some nests were missed.

Mayfield calculations assume mortality rates are constant (Mayfield 1975; Johnson and Shaffer 1990). This is not necessarily the case for CIO clutches that are lost due to flooding, which are often clustered in time and space. In the first season (1994), there would have been time for pairs (up to 10, but probably about 4-8 based on other seasons) to lay and lose a first clutch before monitoring started, especially if there had been a large storm in late October. As a result, both the hatching success estimate and the Mayfield estimate of daily survival rates may have been overestimates for the 1994 season. In addition there appears to be a higher risk of loss close to hatching from causes other than

Table 16 Comparison of CIO productivity from this study (both by eggs and by clutch) with that of other OC species. Ranges represent the high and low averages reported in the literature reviewed. Species: EO - European Oystercatcher (H. ostralegus), AO - American Oystercatcher (H. palliatus), BO - Black Oystercatcher (H. bachmani), PO - Australian Pied Oystercatcher (H. longirostris), SIPO - South Island Pied Oystercatcher (H. ostralegus finschi), VOC - Variable Oystercatcher (H. unicolor). E - eggs laid; C - chicks hatched; F - fledglings. Clutches % hatching - percent of nests that hatched at least one egg, clutches % fledging - percent hatched that fledged at least one chick, clutches % success - percent of nests that fledged at least one young. Sources: a) Harris 1967; b) Heppleston 1972; c) Kersten and Brenninkmeijer 1995, d) Newman 1992, e) N-T 1986, f) Andres and Falxa 1995; g) Hartwick 1974; h) Nol and Humphrey 1994; i) Groves 1984; j) Sagar et al. 2000; k) Goss-Custard 1995; l) this study, m) Paine 1990, n) Marchant and Higgins 1993, o) Newman 1983, p) Vermeer 1992.

	Species						
	EO	AO	BO	PO	SIPO	VOC	CIO
Breeding pair years	15 - 32		10 - 206	5	31	147	39
No. eggs (total)			57 - 614	23, 27	782		134
Hatching success (C/E)	44 - 94%	48 - 71%	25 - 70%	30%	49%		36%
Fledging success (F/C)	20 - 78%	34 - 80%			59%		43%
Overall success (F/E)	13 - 72%		12 - 39%	7 - 13%	29%		13%
No. clutches			81 - 114				60
Clutches % hatching			23 - 38%				41%
Clutches % fledging			12%				56%
Clutches % successful	61% - 86%						20%
Fledglings/pair/year	0.13 - 0.80	0.24 - 0.39	0.19 - 1.10	0.25 - 0.89	0.70 - 0.79	0.64	0.44
Sources	a,b,c,e,h,k	h	f,g,i,m,p	d,n,o	j, n	n	l

flooding, but the risk of the nests disappearing before being recorded is much less. The rate of clutch losses during laying may have been under-estimated. Because incubation probably does not commence until clutch completion, there may be high losses during laying. As a result, first egg(s) may be at higher risk from predators. In the Netherlands, survival rates of European oystercatcher eggs during laying were lower than in the incubation phase (Beintema and Muskens 1987). On Schiermonnikoog, 40% of first-laid eggs were lost before the second egg was laid (Ens *et al.* 1996). This could have resulted in clutches that would have been three-egg clutches being classified as only one- or two-egg clutches in the analysis. Daily monitoring during the laying period would be required to determine if there are high rates of losses during laying in CIO clutches.

Causes and timing of nest and chick loss

Weather appeared to be a major factor affecting productivity in some years, through flooding and possibly food availability. In this study about half of all egg losses were because of tidal flooding. This pattern is similar to that for other oystercatcher species where the main causes of egg loss are storms and predators (Table 17) (Hockey 1996b). A large percentage of eggs were also lost to causes unknown (26%). Normally little sign is left after a nest disappears due to winds and rain. In addition CIO, similar to other oystercatchers, remove shells if eggs are crushed or after hatching (pers. obs.) (Hartwick 1974; Nethersole-Thompson 1988; Nol and Humphrey 1994; Andres and Falxa 1995). The unknown losses may have been predators, since this cause is difficult to detect and many potential predators occur along the north coast. Disturbance may also be a significant factor in decreasing productivity or even lack of breeding attempts, but this is also difficult to determine. In other oystercatcher species, disturbance and/or habitat loss has led to significant declines or even local extinction (Jehl 1985; Nol and Humphrey 1994).

Virtually all the chicks disappeared without trace. Possible factors included predators, starvation, neighbouring pairs of CIO, and trampling (Table 17). In one case, a dead chick was found in its territory. This death was probably not due to predation since the chick had not been eaten or carried away. The most likely causes were the neighbouring CIO pair, sibling rivalry, starvation or disease. Oystercatchers will "viciously attack and sometimes kill chicks from other pairs that wander into their territories" (Ens et al. *1992). Table 17 Causes of nest and chick loss among OC species. Species: EO - European Oystercatcher (H. ostralegus), AO - American Oystercatcher (H. palliatus), BO - Black Oystercatcher (H. bachmani), PO - Australian Pied Oystercatcher (H. longirostris). Sources: a) Sagar et al., in press, b) Newman 1992, c) Lauro and Nol 1993, d) Harris 1967, e) Nethersole-Thompson 1988, f) Heppleston 1972, g) Hartwick 1974, h) Groves 1984, i) Andres and Falxa 1995, j) Nol 1989, k) Lauro and Burger 1989, l) Nol and Humphrey 1994, m) Johnsgard 1981, n) Marchant and Higgins 1993; o) Vermeer et al. 1992; p) Nol and Humphrey 1984; q) Hockey 1983; r) Ens et. al. 1992, s) Beintema 1987.*

	Causes of loss		
Species	Primary	Others	Source
SIPO	Stock, human activity, unknown	Predation, weather, infertility, died hatching	a
VOC	Storms & high spring tides	Human disturbance, predators	n
PO	High tides	Predation of adult & eggs, damage of eggs	b
PO	Storms, flooding (62 - 80%)		c
EO	Predation	Floods, infertile, dead embryos, human interference, desertion, livestock, disease	d
EO	Tides / flooding	Predation	e
EO	Predation (chicks), agriculture (eggs)	Flooding, infertile eggs, stock/humans, died hatching	f
EO	Starvation of chicks (leapfrog territories)		r
EO	Predation (42%), trampling (34%)	Agriculture, abandoned, unknown	s
ABO	Predation (76%)	Flooding, died hatching	q
BO	Tides (storms) (48%)	Predation	g
BO	Storms, avian predation		h
BO	Predation, waves	Damaged, abandoned, addled	o
BO	Predation (eggs/young chicks)	Disturbance	i
AO	Storms and high tides, predation, starvation	Human disturbance, disease, habitat loss, red tide poisoning	j,k,l,m,p

Known causes of chick loss at Schiermonnikoog, the Netherlands, included two species of gulls (*Larus* spp.), drowning during a flood, trampling by cattle, stabbing to death by neighbouring oystercatchers after venturing into their territory, starvation, and probably diseases (Ens *et al.* 1992).

Weather affecting food availability might explain why there are were more two-chick broods surviving to fledging compared with one-chick broods in some years. At Schiermonnikoog, food availability changed with weather conditions and, in poor years, decreased the fledging success of oystercatchers, in part because hungry chicks became more active and thereby more vulnerable to predators (Heg 1999).

On Rangatira Island, where there are no mammalian predators, the main factors affecting breeding success were losses of eggs and young to avian predators and failure of eggs to hatch. Causes of eggs failing to hatch included possible infertility, cracked shells, and chicks dying during hatching. Human disturbance may also have been a factor in the failure of some eggs to hatch (Davis 1988). Flooding has not historically been identified as a major cause of loss.

Flooding, as a significant cause of egg loss, is consistent with egg loss in other coastal nesting oystercatcher species (Table 17). In Virginia, of 20 pairs that failed to hatch any eggs in any one season (n = 3.1 mean number of seasons), 18 (90%) of these pairs lost nests to high tides (Nol 1989); 47% of American oystercatcher nests at salt marshes were flooded by spring tides over a two-year period (Lauro and Burger 1989); 48% of clutches of American black oystercatcher were lost to storms (Hartwick 1974); and with Eurasian oystercatcher, the main cause of loss is flooding (Nethersole-Thompson 1988).

On the Chatham Islands, nest sites on high ground may become the limiting factor for nesting. American oystercatcher nests on high ground are the most successful (Lauro and Burger 1989); in some locations, high elevation nest sites appear to be limited and the habitat saturated (Lauro *et al.* 1992). In general, oystercatchers exhibit high nest site fidelity from year to year. For the American oystercatcher this results in some pairs experiencing nest loss due to high tides nearly every year (Nol and Humphrey 1994). This could also be true for CIO, especially with any population expansion and the use of lower quality territories, or in areas exposed to prevailing winds.

The incidence of tidal flooding of CIO nests (and even chicks) along sandy beaches may have increased with the introduction of marram grass (*Ammophila arenaria*). Planted widely around the islands in the late 1800s and early 1900s to stabilise sand dunes, which had become denuded by livestock, marram changes the shape of dunes, capturing sand very effectively and creating much steeper dunes than the native pingao-dominated dunes (Esler 1970; Heyligers 1985). Marram grass is now well established and covers well over 90% of the sandy dune systems on Chatham and Pitt Islands (pers. obs.). This has had two possible effects: reduction of areas of sandy beach above the high tide line available for nesting, and creation of habitat for introduced predators such as weka, possum (*Trichosurus vulpecula*) and cat (*Felis domesticus*). Weka were observed at high densities within the marram grass dunes, foraging and nesting. Possum used the dunes for daytime denning, and both cat and possum tracks were often seen on the sandy beaches adjacent to the dunes (pers. obs.).

In Australia, the establishment of marram grass has negatively impacted closely related nesting shorebirds, the Australian pied oystercatcher and hooded plover (*Thinornis rubricollis*), which nest on terraced-shaped foredunes formed by native grasses. At Calverts Beach in southern Tasmania, hooded plover nested in the foredunes in the mid 1970s. The whole dune system has since been stabilised with marram and the birds no longer nest there (Park 1994). In Oregon, USA, Snowy Plover (*Charadrius alexandrinus*) nesting habitat has been lost due to establishment of marram grass. In areas where marram has been removed and predators excluded, nest success is 70% versus 6% in other areas (P. Moore, pers. comm.).

In attempting to determine the relative causes of nest loss, flooding as a source of nest failure is the easiest to identify and may appear over-represented relative to other causes that are more difficult to determine. The effects of flooding on productivity may vary more significantly from year to year and perhaps from place to place (see below) than do the effects of other causes. Three years is too short to estimate the long term significance of flooding on population levels. If correlations between weather patterns and nesting success could be established, long-term trends and the overall impact of stormy weather and the resultant flooding (both past and future) might be determined.

Likelihood of flooding may vary significantly between areas due to prevailing winds (Pugh 1987). In Australia, this influenced nesting success on Big Green and Flinders Islands with significantly less flooding of nests on leeward coasts. Losses due to floods, wind and rain on exposed Flinders Island were 62% and 80% in the 1988 and 1989 seasons respectively, compared with 10% for both seasons on sheltered Big Green Island (Lauro and Nol 1993). Longer term if, because of global climate change, ocean heights rise or storm frequencies or intensities increase, CIO could be especially susceptible to effects of tidal flooding. Between 1970 and 1978 gale force winds (28+ knots) on the Chathams during spring (Sept-Nov) and summer (Dec-Feb) were predominantly from the west and southwest (67%, n = 75). Very high swells (14+ metres) came primarily from the south and southwest (82%, n = 22) (Thompson 1983). Assuming these general weather patterns hold, the risk to CIO nests from storms on the coastline of the Chathams is greatest for those exposed to the south and to the west.

Predation is an important cause of breeding failure in birds worldwide (Nice 1957; Ricklefs 1969; O'Conner 1991; Martin 1993; Côté and Sutherland 1995). Predation of CIO was suspected as a cause of egg and/or chick losses. A number of known oystercatcher predators occur on Chatham Island (Table 18) and were trapped in the area where CIO was nesting (Table 19). Many of the 'unknown' cases of mortality noted in this study might have been caused by predation, which would have been more difficult to detect than flooding or some of the other causes.

Table 18 Potential predators which occur on the Chatham Islands of oystercatchers or other ground nesting birds specie. Sources: 1) Nol and Humphrey 1994, 2) Rebergen et al. 1998, 3) Sanders 1997, 4) Marchant and Higgins 1993, 5) Pierce 1986, 6) Atkinson 1978, 7) Brown et al. 1993, 8) James and Clout 1996, 9) Hutton and Sloan 1993, 10) Rönkä and Koivula 1997, 11) Nethersole-Thompson 1988, 12) Andres and Falxa 1995, 13) Nol and Humphrey 1994, 14) Harris 1967, 15) Groves 1984, 16) Ainley and Lewis 1974, 17) Oliver 1955, 18) Dowding, pers. comm.; 19)Dowding 1993;20) Dowding 1997b.

Species	Life stage depredated	Source
cat (*Felis catus*)	adult, chick	1,2,3,4
dog (*Canus familiaris*)	adult	1,4, 19
Norway rat (*Rattus norvegicus*)	adult	1, 5,6
ship rat (*Rattus rattus*)	adult	1,6
hedgehog (*Erinaceus europaeus*)	eggs	2,3,20
possum (*Trichosurus vulpecula*)	eggs	7,8
gulls (*Larus* spp.)	eggs, chicks, adults	1,4,9,10,11,12,13,14,15,16
weka (*Gallirallus australis*)	eggs	17
harrier (*Circus approximans*)	eggs, chicks	4,5
spur-winged plover (*Vanellus miles*)	eggs	18
turnstone (*Arenaria interpres*)	eggs	10

Table 19 Number of predators removed near Chatham Island Oystercatcher breeding areas, north coast, Chatham Island 1992, 1993, and 1998 (sources: Murman 1991, Sawyer 1993, 1994; P. Moore 2000). (Data for 1997 unavailable.)

Breeding seasons	Possum	Cat	Weka	Hedgehog	Rat	Gulls
1990		1	150			
1992	8	3	55	6	1	
1993	6	2	14	0	0	
1998	133	47	654	39	0	23
1999	61	51	719	41	44	53

Predation is often assumed to be a significant cause of breeding failure and population declines in threatened bird species; however, the actual losses are difficult to document. Because significant amounts of time and money are devoted to predator control this is often a topic of much debate and speculation. In addition, although losses of nests to predators may be high, predators in some cases may not be a major threat to populations because overall nesting success can still be high due to re-nesting (Beintema and Muskens 1987). However, predation is a significant factor affecting breeding success in at least some situations for oystercatcher. Throughout its range, the American oystercatcher tends to be more common and more successful in areas with few or no terrestrial predators (e.g., islands) (Nol and Humphrey 1994). Nests of American black oystercatcher are rare on accessible mainland sites, and those sites accessible to mammalian predators had higher predation rates than nests on offshore rocks (Nysewander 1977; Campbell *et al.* 1990; Vermeer *et al.* 1992). In South Africa, oystercatchers breeding on predator-free islands have much higher productivity than their mainland counterparts (Urban and Shugart 1986). On Marcus Island, South Africa, after terrestrial predators gained access via a causeway in 1976, 28 adult oystercatchers were killed (25%) and productivity was only 0.03 fl/pr/yr. After fencing and trapping eliminated predators, productivity increased 10-fold to 0.30 fl/pr/yr and was as high or higher in subsequent years (Cooper *et al.* 1985; Hockey 1996a). Adults may be especially susceptible to predation during incubation. At Marcus Island, mortality due to predation was significantly higher during the breeding season (Hockey 1985).

Cats have the potential to be especially problematic for oystercatcher populations due to their ability to kill adult birds, as well as chicks and eggs. Feral cats (*Felis catus*) are known to have killed adult oystercatchers of several species (Summers and Hockey 1977;

Heg 1999). They have been videotaped killing nesting adult banded dotterel (*Charadrius bicinctus*) (as well as killing chicks and eating eggs) in the Mackenzie Basin of New Zealand (Sanders and Wells 1999), and have been videoed attacking incubating CIO along the north coast (Peter Moore, pers. com.). Populations are often more sensitive to the loss of breeding adults than to other factors (Hamilton and Moller 1995; Reed *et al.* 1998). Populations may also exhibit threshold responses to changes in mortality rates. In Hawaiian Stilts (*Himantopus mexicanus knudseni*), population modeling suggested that a 10% change in adult mortality could result in a drop in persistence probability from 100% to 0% (Reed *et al.* 1998).

Gulls are probably the best documented predator of oystercatchers and have been reported to take eggs, chicks and even adults for many species (Table 17). In South Africa, human disturbance of incubating birds caused them to leave their nests. Under these conditions predation of eggs by kelp gulls (*Larus dominicanus*) was observed once and suspected in three cases. Kelp gulls were also observed several times taking small chicks (Summers and Hockey 1977). Oystercatchers can defend their eggs and chicks from gulls, but eggs and chicks may be vulnerable if a breeding pair is disturbed by humans or other predators (pers. obs.) (Summers and Hockey 1977; Marchant and Higgins 1993). Super-abundance of gulls is a well documented and wide spread phenomenon around the world (Blokpoel and Scharf 1991; Blokpoel and Spaans 1991; Isenmann *et al.* 1991; Spaans *et al.* 1991; Vermeer and Irons 1991). Black-backed gulls (*Larus dominicanus*) are probably super-abundant on the Chathams due to human activities - feeding from fish factory offal, on livestock carcases, and at rubbish tips. Black-backed gull were often observed in large numbers (100 or more) feeding on offal at Waitangi West and Port Hut (pers. obs.).

Gulls may also compete with oystercatchers for food. Kleptoparasitism (food stealing) by gulls can be significant to oystercatchers in some situations (see Ens and Cayford 1996). Oystercatchers feeding on giant bloody cockles (*Anadara senilis*) on the Banc d'Arguin in Africa lost almost half their food to kleptoparasites, mainly to lesser black-backed gulls (*Larus fuscus*) (Swennen 1990). CIO was sometimes harassed by gulls attempting to steal food (pers. obs.), but the amount actually lost is unknown. Several events were observed over the course of three seasons, but did not appear to be common relative to overall feeding times.

Disturbance and trampling by vehicles or livestock were important potential causes of breeding failure and, on the Chathams may preclude use by CIO breeding pairs of otherwise suitable areas. Some beaches and coastline areas around Chatham, Pitt, and Rangatira Islands were frequently used by humans for a variety of activities including travelling, fishing, launching fishing boats, and mustering sheep (pers. obs.). The use could be prolonged (several hours in duration) and there were often dogs and vehicles associated with various activities.

Human-induced disturbance is the most important factor limiting population growth in blackish oystercatcher (*H. ater*) in some parts of its South American range (Andres and Falxa 1995). For American black oystercatcher human disturbance and feral cats on Channel Island, California, caused pairs to abandon nest sites. The density of birds on disturbed islands was only 3% of densities on undisturbed islands (Warheit *et al.* 1984). For 100 years, disturbance by humans and domestic animals precluded American black oystercatcher from breeding on South Fallaron Island, California. Twenty breeding pairs re-established within just five to seven years after removal of disturbances (i.e., relocation of four resident families and their domestic animals) (Ainley and Lewis 1974). On Destruction Island, Washington, USA, the number of pairs increased three-fold from 4 to 12 pairs within seven years of the lighthouse being automated (Nysewander 1977). Human disturbance was believed to be the cause of a rapid population decline of the American oystercatcher in Florida, and resulted in relatively low nesting success in traditional open sandy beach habitat compared with forested spoil islands (Toland 1992). In South Africa, there are apparently suitable areas that now contain few or no oystercatchers. This is thought to be due to human disturbance which may keep birds off their eggs for extended periods (Summers and Hockey 1977). Near Cape Agulhas, South Africa, there was a decline from 13 to 0 fledglings/annum over seven years due to increased human disturbance (vehicular traffic, egg removal, nest crushing and exposure) (Jeffery 1987).

Dogs frequently accompany humans in their various activities along the coastline of the Chathams (pers. obs.). The presence of dogs may increase the impact human disturbance has on breeding shorebirds. In the Mornington Peninsula National Park near Melbourne, Australia, a management scheme to reduce disturbance from humans and dogs along the coast during the breeding season led to a 158% increase in breeding success of hooded plover (a shorebird species with similar nesting habits to oystercatchers) from an average of less than three fledglings per year to over 10 (Dowling 1999). Dogs disturb shorebirds by running after them (Retallick and Bolitho 1993) and, in another wader species, the New Zealand dotterel (*Charadrius obscurus*), the presence of dogs caused birds to leave the nest much sooner than when humans alone approached (Lord 1996).

Livestock may trample nests and cause significant losses. In simulated trials with artificial nests in the USA and in the Netherlands, trampling caused over a third of all nest losses (Beintema and Muskens 1987; Paine *et al.* 1997). Sagar, *et al.* (2000) reported that 47% of losses of South Island pied oystercatcher nesting in paddocks were due to trampling by livestock. Both sheep and cattle were frequently observed on the Chatham's coastline, often eating kelp. In addition, sheep were occasionally mustered along the coast (pers. obs.). In one case, a chick disappeared after a flock of several hundred had been mustered through its territory.

Asynchronous hatching is common in many bird species, and may sometimes lead to the abandonment of the terminal egg, especially in species that use open nests at ground or water level and have precocial or semi-precocial chicks (Evans and Lee 1991). The eggs of American oystercatcher hatch in the order they are laid, the first two relatively synchronously. Newly hatched chicks may leaving the nest before the third has hatched. Parents will attend the hatched young, which may result in the third egg being abandon (Nol and Humphrey 1994). At Schiermonnikoog, the Netherlands, abandonment of pipping eggs occurred in 4.5% of the nests (Heg 1999). Abandonment of the last egg laid was thought to have occurred at least once in the north coast Chatham Island population during the 1994-1997 study. The causes of this behaviour are not clear (Heg 1999).

Incubation of damaged eggs by CIO reduced overall productivity since several pairs did not re-nest while incubating these eggs. These eggs were mostly intact and may have been damaged due to adults jumping off the nest quickly, livestock, flooding, weka (*Gallirallus australis*), or spur-winged plover (*Vanellus miles*). In variable oystercatcher (*H. unicolor*), the longest unsuccessful incubation lasted over 81 days (Fleming 1990). One pair of CIO incubated eggs that were not viable, probably infertile, through most of the season. The male of the pair was probably only two years old and possibly sexually immature, as most oystercatcher species do not begin breeding until at least three or four years old (Hockey 1986; Marchant and Higgins 1993).

Following to this study, video monitoring of CIO nests along the north coast, Chatham Island during the 1999 season recorded two nests lost to predators, one each to a cat and a weka. There were also several 'visits and interactions' (which did not result in loss of the clutch): four cats, six cattle, one sheep, two possum, one weka, one rodent (spp unknown), and one person (P. Moore, pers. comm., Feb 2000). Incubating adults experienced 'close calls' escaping attacks by cats.

The period of highest risk for CIO eggs and chicks was the week either side of the estimated hatch date. Some of this variation was due to uncertainty in hatching dates and the timing of nest checks. In most oystercatcher species, chick losses are highest during the first week or two after hatching. Kersten and Brenninkmeijer (1995) found that only 44% of 548 Eurasian oystercatcher chicks survived until they were 12 days old. Older chicks survived better, with 77% of 184 chicks still alive at an age of 21 days fledged. In American black oystercatcher, chicks were most vulnerable during the first two weeks after hatching (Groves 1984). For Eurasian oystercatcher and African black oystercatcher the first week after hatching was most perilous, over 60% and 87% respectively of chick mortality occurred during this time (Heppleston 1972; Hockey 1983).

In oystercatcher species around the world, the two most common factors in chick losses are either lack of food or predation (especially by gulls). Other causes of chick loss include sibling rivalry (which is related to food supplies), neighbouring oystercatchers, trampling, disease, and weather (Groves 1984; Hockey 1986; Ens 1992; Heg 1999). At Forvie, Scotland, the main factors influencing chick survival were the density of predators and other oystercatchers and the location of food supplies (Heppleston 1972).

Chick mortality in oystercatchers is apparently often due to starvation and has been recorded in Eurasian oystercatcher (Safriel *et al.* 1996), American oystercatcher (*H. palliatus*) (Nol 1985), American black oystercatcher (Groves 1984; Purdy 1985), and African black oystercatcher (*H. moquini*) (Hockey 1996a). In American black oystercatcher, all except one chick heavier than 200g at 20 days old fledged (n = 15), whereas only 5 of 10 chicks weighing less than 200 g at 20 days old survived to fly (Groves 1984). In years of stormy weather (and therefore more limited food supplies), some of this starvation may have been due to the establishment of a sibling hierarchy and death of the subordinate chick, due to the subordinate chick being more active due to hunger and therefore more vulnerable to predation (Groves 1984; Heg 1999).

Timing of food availability and bad weather can be critical. In periods of extended strong winds, or heavy swells, food may become a problem and long-legged shorebirds may stay all day on sheltered roosts without attempting to feed (Evans and Smith 1975; Davidson 1981; Evans and Pienkowski 1984). At Marcus Island, South Africa, numbers of African black oystercatcher during one such storm in 1975 more than trebled in numbers (to c. 600) and fed on stranded mussels - possibly due to a temporary food shortage elsewhere (Hockey 1984). Rain and chilling affected chick survival at Schiermonnikoog, the Netherlands and, during rain, parents stopped feeding (Heg 1999).

Good weather and more food availability may explain the high proportion of two-chick clutches (75%) in 1994 compared with the other two seasons (33% in 1995 and none in 1996). Good weather means fewer nests are lost to flooding and possibly fewer losses of chicks to drowning or starvation. After several days of high seas, if alternative foraging on rock platforms or beaches is not available, chicks might starve or become more active due to hunger, and so more susceptible to predation (Groves 1984). No data on growth curves of CIO chicks were available from this study to give an indication of the role of food supply in chick losses on the north coast, Chatham Island. However, two-chick broods took longer to fledge than one-chick broods suggesting food competition decreased growth rates and increased time to fledging. Food is more likely to be a limiting factor at higher population densities or in stormy years.

Causes of mortality in chicks may interact in complicated ways (Safriel 1981; Safriel 1982) so the most important causes remain unknown. Location of food within or around breeding territories, rather than the total amount of food available, may be a key factor in fledging success. In studies of Eurasian oystercatcher (Heppleston 1972) and American oystercatcher (Nol 1989), fledging success was related to location of food and adult attendance of chicks. The more time parents spent away from chicks collecting food the lower the fledging rates, because the chicks had less parental protection from predators.

Timing of the breeding season

Nesting (date of laying)

The first nesting dates (9-13 October) from this study were earlier than any previously recorded. Saywer (1993) reported first nesting attempts on 24 October 1991, and 23 October 1992. These differences were probably due to the intensity of the monitoring rather than to any differences between years in initial laying dates. CIO begins nesting later than South Island pied oystercatcher, which began nesting in early August on the

Canterbury Plains (later in Mackenzie Basin) or variable oystercatcher, which initiates nesting in mid-September (Baker 1969; Marchant and Higgins 1993; Heather *et al.* 1996; Maloney *et al.* 1999; Sagar *et al.* 2000). This may be due to Chatham Island's weather patterns affecting the availability of food and increased risk of nests being lost to storms and tidal flooding. In Tasmania, which is about the same latitude as the Chathams, Australian pied oystercatcher (*H. longirostris*) nested from early September to late December or early January. Sooty oystercatcher (*H. fuliginosus*) in South Australia nests at about the same time as CIO, incubating eggs from October to January and, rarely, February (Marchant and Higgins 1993). African black oystercatcher (*H. moquini*), nests with eggs have been found from 10 October to 1 May, with the most being found from mid-November to the end of February (Summers and Hockey 1977).

CIO clutch initiation times varied between pairs by at least four weeks. Early laying is well known to increase the chances of successfully fledging chicks in single-brooded bird species (reviewed in Dann, 1989). The causes for earlier laying in some pairs are difficult to determine. In Eurasian oystercatcher, the range of laying dates spanned more than 40 days (Ens 1992). Ens *et al.* (1993) found that with advancing age, females lay progressively earlier, but at the same time differences in laying between individual females remained consistent. They concluded that it was impossible to decide whether the laying date was due to differences in food availability in the territories, the female's foraging ability (which may improve with experience), or the extent to which she could abstain from assisting her mate in territorial defence. Heg (1999) found, in a follow-up study, that food and age were minor causes in advancing laying dates, but the main causes were pair bond duration and time spent defending the territory pre-laying. He concluded that, ultimately, territory quality and pair bond duration were probably the main factors. Newman (1992) reported up to six weeks of variation in the initiation of first clutches by pairs of Australian pied oystercatcher in Tasmania. He felt maturity did not adequately explain the variation, and hypothesised it was due to differences in the quality of the territories and of food supply.

Laying, incubation and hatching

A laying interval of 24-48 hours is similar to that reported for clutches laid on Rangatira Island (Davis 1988). Hemming (1987) also reported a CIO nest in which the first egg was seen on one day and the second egg the following day. In variable oystercatcher, the laying interval averaged 48 hours (range 36-52) with incubation commencing when the last egg is laid (Baker 1969). Laying intervals of about one to two days have also been recorded for Australian pied oystercatcher, Eurasian oystercatcher, and American oystercatcher (Keighley and Buxton 1948; Newman and Park 1992; Nol and Humphrey 1994). Cold and/or wet weather can delay egg laying in American oystercatcher (Nol and Humphrey 1994).

An average incubation time of 28-29 days is significantly longer than those reported by Davis (1988) and Marchant and Higgins (1993) of 25 ±1.2 days (n = 3 pairs). CIO eggs taken from the north coast, Chatham Island and kept in incubators began hatching on day 26 (26.75 ± 0.89, n = 8), with chicks taking between 48-72 hours to hatch (Sawyer 1993), giving a total incubation time (i.e., clutch completion to hatching completion, or the beginning of incubation of a particular egg to completion of hatching of that egg) of 28-29 days. Hemming (1987) reported a 30-day incubation period (including hatching) for one nest on Rangatira, which took about 2 days (eggs not pipping 20.12.86, pipping mid-day the 21st and 9:00 am the 22nd, both eggs hatched by 9:30 am the 23rd).

A 28-29 day incubation period for CIO is similar to that for variable oystercatcher (average 28 days, range 25-32 days). South Island pied oystercatcher has a shorter incubation period of 24-28 days (Marchant and Higgins 1993). Incubation periods of other oystercatcher species range from 23.5-39 days (reviewed in Hockey 1996). Occasionally, successful incubation periods can be unusually long - one pair of Australian pied oystercatcher hatched eggs after 44 day incubations (Newman 1992). (This pair hatched its eggs in the stump of a tree, an unique site. Regular visits by the researcher excluded the possibility that two clutches were involved. No other explanation for this long incubation period were offered.)

There is much evidence that chilling of eggs during incubation can retard hatching and extend the incubation period (Nysewander 1977; Webb 1987). In the present study, this may have been the cause of the extended incubation period for one clutch where one chick died while hatching after an incubation period of a minimum of 37 days. It may also explain the longer incubation period of 30 days plus for another pair. Disturbance and chilling, and the consequential delay in hatching, may increase the risk of terminal egg abandonment (Evans and Lee 1991).

CIO continued to incubate eggs after flooding by the tide. This behaviour has also been reported for several other oystercatcher species. Eggs in nests washed over by spring or storm tides have successfully hatched in American oystercatcher and American black oystercatcher. Of 31 American black oystercatcher eggs (12 nests) submerged 1-4 times in Glacier Bay, Alaska, 17 survived to hatch (Andres and Falxa 1995). American oystercatcher does not normally roll its eggs back into the nest (Nol and Humphrey 1994). American black oystercatcher eggs were either incubated where they were left by the receding tides or returned to the nest (Andres and Falxa 1995).

An asynchronous hatching period, with hatching lasting 1-2 days for CIO, was similar to that of other oystercatcher species. Hatching periods (from first pipping to hatching) are about 36 hours for variable oystercatcher (Baker 1969); and 53-67 hours for Eurasian oystercatcher (Nethersole-Thompson 1988).

Re-nesting (replacement clutches)

Re-nesting patterns on the north coast, Chatham Island are similar to those reported by Davis (1988), with the exception of pairs on Rangatira Island which are reported to have laid third replacement clutches (i.e., up to a total of four clutches in one season). Up to three replacement clutches have also been reported for Eurasian oystercatcher (Heg 1999).

Replacement rates of first clutches were high in CIO (80-100%), but declined for second clutches, which were replaced in only about one third of the cases (31% on average). Some replacement clutches may not have been found or identified as such, so these numbers are minimums. Quantitative information on re-nesting is scanty, but during the first weeks of the breeding season about 100% of all Eurasian oystercatcher nests lost were replaced. This probability of re-nesting decreased, but more research would be needed to quantify this (Beintema and Muskens 1987). There were only two cases during this study when first clutches were not replaced. In one case the pair acted oddly, and there may have been turnover in one or both of the pair members. The other pair was not monitored very closely in December and January. A scrape was found, but never any eggs. A re-nesting attempt may have been missed due to the low number of checks.

The replacement interval of about 10-20 days for the north coast, Chatham Island CIO was shorter than those reported by Davis (1988) and Marchant and Higgins (1993) of a minimum of 21 days for most pairs. They were similar to the replacement intervals reported for several other oystercatcher species: Australian pied oystercatcher in Tasmania, 11-25 days (Newman 1992), Eurasian oystercatcher, 11-19 days (Mercer 1968; Nethersole-Thompson 1986), and American oystercatcher, 14 days (Nol 1989). The differences between the results from this study and that of Davis may be due to differences in location, years, or methodology.

The interval between clutch loss and initiation of the next clutch may reflect the food resources available for egg production. The costs of egg production can strain a female's daily energy balance and slow down egg formation (Walsberg 1983). Evidence of food as a limiting factor in the breeding of oystercatchers is, however, inconclusive. In a study of American oystercatcher, food supplies and reproductive performance were examined, and no apparent correlation was found between food supply and interclutch intervals (Nol 1989). In contrast, Newman (1992) speculated that the shorter intervals between clutch replacement of different years for Australian pied oystercatcher in Tasmania were due to more favourable (e.g., less stormy) tides and weather, and therefore better food availability.

Chick rearing and fledging

The average time to fledging of approximately 39 days (range 30-47 for one-chick broods, 36-54 for two-chick broods) for chicks on the north coast was less than that reported by Davis (1988) for Rangatira Island of 47.8 ±1.5 days (n = 4 chicks). This is probably because of differences in chick growth due to food availability. Kersten and Brenninkmeijer (1995) reported fledging times ranging from 27 to 52 days in Eurasian oystercatcher. This wide range was due to chicks fledging at an early age displaying much faster growth rates than later fledging chicks. Differences in food availability could arise from differences between years (weather and its effect on food availability), territory quality and/or brood size.

Two-chick broods grow significantly more slowly than one chick broods in American black oystercatcher (Groves 1984). This same pattern appeared in CIO, with two-brood chicks always taking longer to fledge than one-chick broods (n = 7). Where days to fledging were known to within two weeks, two-chick broods on the north coast (n = 2) fledged in 42 to 47 days on average; one-chick broods (n = 5) from 30 to 40 days on average. The size of broods on Rangatira was not reported, but on average they took longer to fledge than all but the slowest growing two-chick broods on the north coast. Young (cited in Davis 1988) reported a single chick taking about 50 days to fledge on Rangatira in 1974. These data suggest that chicks on Rangatira grew slowly relative to north coast chicks due to either poor years when the data were collected, or poorer quality territories, rather than differences in brood size (i.e., all Rangatira broods were slow growing due to being from two-chick broods).

Dispersal of fledglings

The average time to eviction or dispersal after fledging for CIO juveniles on the north coast (33 days) is quite short relative to that for most other oystercatcher species and to juveniles on Rangatira. On Rangatira some fledglings remained with their parents for at least 27 days after fledging, with many fledglings apparently remaining in or near their natal territory until the following breeding season (Davis, 1988). In many oystercatcher species, movement to wintering areas away from breeding areas determines when young birds leave their natal territories (Nol and Humphrey 1994). Kersten (1995) reported that Eurasian oystercatcher fledglings remained dependent on their parents up to an age of 3 months and often longer. In American black oystercatcher, pairs evict offspring from territories about 5-6 months after fledging (Helbing 1977 in Andres and Falxa 1995). In variable oystercatcher, young often remain with the parents through the winter, but otherwise they join winter flocks 3-4 weeks after fledging and appear to be independent of their parents (Moon 1967; Baker 1969; Fleming 1990).

The type of food available within a territory may determine how long young depend on their parents for food. Oystercatchers are well known for their unique combination of precocious young which are fed by their parents (Hockey 1996a). If soft food is available, chicks may be able to feed themselves at an earlier age and therefore become independent of their parents at a younger age.

Clutch sizes

The decline in clutch size within the season and with each replacement clutch in CIO is similar to that found in many other oystercatcher species, including the closely related South Island pied oystercatcher (Baker 1969; Hockey 1996b; Sagar *et al.* 2000).

Variation in clutch size is affected by a variety of factors including genetic differences between individuals, age, food availability and season (Boag and Noordwijk 1987). Food shortages can reduce or stall egg production and thus affect clutch size (King 1973; Ricklefs 1974). Year-to-year variation in average clutch size in Great Tit (*Paris major*) and California gull (*Larus californicus*) are directly related to food abundance (Perrins

1965; Winkler and Walters 1983). In magpies (*Pica pica*), over 80% of the variation in clutch sizes within years is due to differences in territory quality (Högstedt 1980).

In oystercatchers, variations in clutch size has been related to age and food. In American oystercatcher no relationship was found between food and clutch size, but age appeared to be a significant factor. Older birds were more likely to lay three-egg replacement clutches than younger birds (Nol 1989). In contrast, reduced food availability was suggested as the reason for declining clutch size in South Island pied oystercatcher as declines occurred in both experienced and inexperienced pairs (Sagar *et al.*, 2000).

The tendency for two-egg clutches to be more successful in CIO than one-egg clutches is also seen in other oystercatcher species. In Eurasian oystercatcher, larger clutches (two - four eggs) were more successful than one-egg clutches (50-68% versus 33%) (Harris 1967). In American black oystercatcher, an average 0.75 chicks/clutch survived to fly from two-egg clutches compared with 0.50 chicks/clutch from one-egg clutches (Groves 1984). Oystercatchers may lay one more egg than the number of chicks they can normally fledge, a type of 'insurance' against egg loss. In Eurasian oystercatcher, 48% of clutches that hatched at least one chick lost one or more eggs (Heg 1999). The lower success of three-egg clutches (0.13 fledglings/clutch) compared with two-egg clutches (0.37 fledglings/clutch) in CIO is puzzling, but the sample size was small.

Third clutches were most successful with a third successful (Table 11), but the sample size was small (n = 6). When classified by season, rather than clutch order, early clutches were more successful than late clutches (27% and 18% respectively). This was due to the low success rate of five first and second clutches that were laid late in the season (i.e., clutches completed after 3 January). Three of these clutches may have been initiated late in the season because in every case the first clutch was initiated late (after 19 November) and then survived until hatching or near hatching so, by the time the pair replaced them, it was late in the season. Alternatively, some or all of these apparently second clutches might, in fact, have been third clutches, mis-identified as second clutches (due to the first clutch of the season being lost before I found it). The other two late clutches were unlikely to have been mis-identified. In one case, the pair was probably newly established (a conclusion based on events observed during the preceding season). They made nest scrapes all season, but did not finally lay until 31 January 1997. They were checked frequently (29 times over the season), so any earlier clutches would probably have been discovered. In the other case, a damaged egg from the first clutch was left in the nest, which delayed re-nesting by 29-38 days.

The initiation of up to three clutches may indicate good quality pairs (e.g., long pair bonds, experienced individuals) or perhaps good quality food within the territories. In Eurasian oystercatcher, females that initiate early clutches benefit because they are more likely to produce replacement clutches within the same season if all eggs or chicks are lost (Heg 1999).

SUMMARY AND MANAGEMENT RECOMMENDATIONS

In spite of high breeding effort by pairs over all seasons, productivity was relatively low along the north coast, Chatham Island. Weather appeared to be a major factor affecting productivity in some years, through flooding and possibly food availability. In the 1996 season storms destroyed most of the nests and only two fledglings were produced that season. Over all seasons flooding was the main cause of nest losses, but pairs re-nested up to three times, which compensated for some of this loss in less stormy years. Habitat modification on the Chathams, especially the establishment of marram grass, has probably increased losses of nests to tidal flooding and may also be providing suitable habitat for predators. A large proportion of nest losses were lost to causes unknown, which may have been due to predators, a cause more difficult to detect than flooding.

Chick losses are particularly difficult to establish, since most chicks disappear without trace; however, predation was probably a significant factor based on the high number of predators present. Weather, interacting with predation pressure may explain why there are were more two-chick broods surviving to fledging compared with one-chick broods in some years (i.e., hungry chicks became more active and thereby more vulnerable to predators (Heg 1999)). More data on food availability between territories/habitats and years would be needed to determine the role of weather and food availability and potential interactions with predators.

In some locations, such as Virginia, oystercatcher nests have been protected from flooding tidal during specific periods only when the risk was highest (E. Nol, pers. comm.). Flooding occurs during spring tides with on-shore winds. The spring tides were predictable and susceptible nest sites could be raised during the 3-4 hours of tidal surges. A similar technique may be useful for some nests on the Chathams, although long travel times to and between pairs, access difficulties during surge tides, and lack of resources may make this difficult for most nests.

The highest risk times for non-flooding losses (which may be primarily caused be predation) appear to be around hatching. This may be the best time to concentrate any management efforts aimed at minimising non-flooding losses. The laying period may also be high risk as has been shown for some other oystercatcher species, but more detailed monitoring would be needed to determine if this is so for CIO.

Removing damaged eggs could increase productivity by encouraging re-nesting. Because CIO parents continued to incubate damaged eggs that were inviable, rather than re-nest, these types of losses had more impact on overall productivity than the clean loss of a clutch where all eggs disappeared from the nest or were so clearly damaged that the pair re-nested. Over the three seasons of this study, 17% of breeding pair seasons (n = 7) were lost or shortened due to damaged eggs in the nest. In the most optimistic scenario, if all damaged eggs had been removed from nests in the study area and all pairs successful re-nested and fledged chicks, the overall breeding success for pairs would have been raised from 33-50% and an additional 14 chicks could have fledged. This is a relatively low cost and easy management option for raising CIO productivity, and could be combined with monitoring of productivity rates of CIO in other areas on the Chathams.

The fact that CIO fledglings along the Chatham Island north coast appear to be evicted or disperse of their own volition within four to six weeks of fledging has important implications for censuses and monitoring of productivity. Past monitoring has probably been to infrequent to detect all fledglings. Because nests can be difficult to detect unless territories are monitored frequently the behaviour of pairs when young are present is probably the best indicator of breeding activity for infrequently monitored territories. Even when chicks are present, observers may not always detect their presence (Davis 1988, Sawyer 1993, Schmechel pers. obs.). Chicks or fledglings are present in a territory for about 9 to 12 weeks. Therefore, for monitoring purposes, CIO territories should be checked at least every nine weeks between mid-December and mid-March for chicks or fledglings. If chicks are found, a follow-up visit within four weeks to determine if the chicks survived to fledging must be made to determine fledging success accurately. If monitoring visits are any less frequent, the chick(s) may fledge and disperse from the territory without being detected. There is still a possibility of chicks fledging successfully, but dying before detection, which could underestimate fledging success. Analytical methods (such as the Mayfield method (1975) to correct for these errors should be considered. If historic records of fledging success are used, they should be reviewed in light of these data to determine whether checks were made frequently enough to determine breeding success accurately.

Productivity varied considerably from year to year, and probably varies significantly from area to area. Therefore, caution should be used when considering productivity estimates from small non-randomly selected areas or seasons to estimate population trends or evaluate management effectiveness for other areas or seasons.

The number of breeding pairs in any given area can fluctuate with time and, as the numbers of breeding pairs increase, the productivity per pair may decrease (due to lower quality habitats being occupied, or other density-dependent factors coming into play). Productivity values can, therefore, be misleading. If there are few pairs in a given area, they may produce many fledglings per pair per decade for example; but if there are more breeding pairs, even though there may be less fledglings per pair, the total number of fledglings produced for that area may be higher. For this reason, the number of chicks fledging in specific areas should be monitored in addition to productivity per pair.

Lack of food may preclude two- or three-chick broods in some circumstances, such as in difficult years (low food availability due to weather), or in lower quality territories. If other species are competing for food with CIO, a secondary benefit of control of these species (e.g., weka, gulls) may be increased food availability through increased food supplies, as well as the reduced predation risk during foraging.

The number of CIO chicks that survive successfully in a brood has interesting implications for conservation management strategies. The same number of fledglings may be produced in various ways. For example, 10 fledglings could be produced either from 10 pairs each successfully raising one chick, or by five pairs each raising two chicks. It may be more effective to manage fewer pairs on higher quality territories than more pairs over a wider area.

Future research and monitoring recommendations

- Productivity probably varies considerably between different areas. Estimates of fledging success for various areas over several years could provide information essential for predicting population trends over time, and for determining levels of productivity needed to achieve population recovery goals.

- Correlations between weather patterns and breeding success could help determine how much weather determines productivity and fledging success. It could also help with predictions of fluctuations in productivity not attributable to the influence of management.
- Eviction/dispersal periods for fledglings needs to be confirmed because some of the data from this study were incomplete and some were inconclusive.
- Collection of growth curves for chicks, and of fledging times, would help provide an indication of the role of food supplies in productivity between years and between areas. However, this can be time consuming and potentially increase predation risk for chicks, especially if black-backed gulls are present. Therefore, the risks and benefits should be considered. Alternately, collecting data on parental feeding rates may provide an indication of relative food supply between areas and seasons, and their role in productivity.

The CIO in context with other oystercatcher species

Apparently unique to CIO on the north coast was the short time to juvenile eviction/dispersal (33 days, range 24-42). In most other species, the time is longer. For Eurasian oystercatcher the time is three months or longer, for American black oystercatcher five to six months, and for variable oystercatcher it is often through the winter (otherwise they join winter flocks three to four weeks after fledging).

Some breeding parameters are quite variable within oystercatcher species, probably because these are more influenced by external factors, such as habitat quality or age of the female. Average fledging time for CIO on the Chatham Island north coast was 39 days, on Southeast Island 48 days and for other species 25 to 49 days (Hockey 1996b). Within a single species (eg. Eurasian oystercatcher), fledging periods may range from 27 to 52 days depending on chick growth rates and food availability (Kersten and Brenninkmeijer 1995). For CIO on the north coast the length of the replacement interval, if a clutch were lost was similar to that of Australian pied oystercatcher, Eurasian oystercatcher, and American oystercatcher.

Laying dates for CIO was later than for either of the New Zealand mainland oystercatcher species (excepting South Island pied oystercatcher pairs in the Mackenzie basin). CIO initiated first clutches about a month later than variable oystercatcher, and over two months later than South Island pied oystercatcher. Compared to Australian pied oystercatcher in Tasmania (which nest at a similar latitude) CIO began laying about six weeks later; but at about the same time as sooty oystercatcher nesting in the south of Australia.

CIO was similar to other oystercatcher species in a variety of breeding parameters. An incubation period for CIO of 28-29 days is similar to that for variable oystercatcher (28 days), and just slightly longer than that for South Island pied oystercatcher (26 days, range 24-28), and was well within the range for other species (24-39 days). Laying intervals are similar for all oystercatcher species. CIO shared the habit, with other oystercatcher species, of incubating eggs after flooding and displacement. Asynchronous hatching of chicks is common in many oystercatcher species.

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APPENDICES

Appendix I

Monitoring effort (number of monitoring visits per pair per season and dates territories were checked for breeding activities). No. - number of checks for that pair. Numbers in italics - visits under 8, excluded from breeding success analyses.

		1994		1995		1996
Pair	No	Dates	No	Dates	No	Dates
Study area						
WW	*5*	*8.1.95 - 22.2.95*	18	8.11.95-22.3.96	23	18.10.96-19.3.97
WOC	18	24.11.94-24.3.95	18	8.11.95-22.3.96	39	8.10.96-19.3.97
TW	19	1.12.94-24.3.95	19	8.11.95-22.3.96	33	8.10.96-19.3.97
TE	19	30.11.94-24.3.95	17	8.11.95-22.3.96	33	8.10.96-19.3.97
OTF	18	7.11.94-22.3.95	14	9.11.95-22.3.96	28	18.10.96-19.3.97
Creek	18	23.11.94-24.3.95	16	9.11.95-22.3.96	29	18.10.96-19.3.97
Pounamu	14	9.11.94-24.3.95	14	9.11.95-22.3.96	24	18.10.96-19.3.97
Dune	9	25.11.94-24.3.95	15	9.11.95-22.3.96	27	18.10.96-19.3.97
Cliff	13	25.11.94-24.3.95	17	9.11.95-22.2.96	24	18.10.96-19.3.97
Cape	10	30.11.94-4.4.95	10	13.11.95-20.3.96	8	26.10.96-6.3.97
Mairangi	9	30.11.94-4.4.95	12	12.11.95-21.3.96	10	26.10.96-6.3.97
Woolshed	11	22.11.94-4.4.95	13	13.11.95-21.3.96	14	29.10.96-6.3.97
Rock	10	30.11.94-4.4.95	16	13.11.95-21.3.96	16	29.10.96-6.3.97
Island	10	30.11.94-4.4.95	17	13.11.95-21.3.96	12	27.10.96-6.3.97
Whanga	*3*	*12.12.94-26.1.95*	10	14.11.95-26.2.96	*7*	*29.10.96-5.2.97*
Other areas						
Okahu	4	30.11.94-2.4.95	4	6.3.96-23.3.96	5	28.11.96-6.2.97
Ohira Bay			4	18.1.96-19.2.96	4	27.11.96-9/1/97
Paritu E.					2	14.12.96-28.12.98
Paritu W.					1	28.12.96
Taupeka			2	1/2/96-20/3/96	1	24.1.97
Matarakau W.			1	21/3/96	2	7/1/97-28/1/97
Rangitai Pt.			2	19/2/96-21/3/96	2	7/1/97-28/1/97

Appendix 2

Breeding season effort, pair status, and outcomes, north coast, Chatham Island. Parenthesis - excluded from breeding success calculations due to low monitoring rates. Codes: s - successful (one or more chicks fledged), ie - infertile eggs, c - clutches, de - damaged eggs, a/pto - abandon/pair turnover, ch - hatched chicks (but lost before fledging), nnf - nest never found, ? - no nest found (breeding attempt unknown) but monitored infrequently, tp - territorial pair, sbp - suspected breeding pair, nkp - no known breeding or territorial pair, p - pair of unknown breeding status.

Territory	1994	1995	1996
Study area			
WW	(s)	s	s
WOC	s	s	2 c
TW	s	s	3 c
TE	ie	s	3 c
OTF	2 c	2 c, de	2 c
Creek	1 c, de	2 c	a/pto
Pounamu	a/pto	ch	2 c
Dune	nba	2 c	1 c, de
Cliff	1 c, de	3 c	1 c, de
Cape	2 c	1 c, de	2 c
Mairangi	p/pto?	s (nnf)	s
Woolshed	s	3 c	2 c
Rock	s	2 c, de	1 c
Island	s	s	1 c
Whanga	(?, ch?)*	s	(2 c, de)
Other			
Okahu	?, p?	?, tp	2c
Ohira Bay		s	loc
Paritu E.			1 c
Paritu W.			?, tp
Taupeka		nkp	?, sbp
Matarakau W.		?, p	?, sbp
Rangitai Pt.		s	?, p
Totals			
successful	6	9	2
pairs	14	19	22
successful	43%	47%	9%

* strong anti-predator behaviour 12/12/1994, suspected chick(s) were present, but later lost

Appendix 3

Number of chicks known to have fledged, northern Chatham Island 1994 - 1996. Numbers only for territories where pairs territorial, resident or suspected to have bred.

	No. of fledglings			
Territory	1994	1995	1996	Notes
Study area				
WW	2	1	1	
WOC	2	1	0	
TW	2	1	0	
TE	0	1	0	
OTF	0	0	0	
Creek	0	0	0	possible pair turnover
Pounamu	0	0	0	pair member disappeared during 1994 season; lost an older chick (over 2 weeks old) in 1995
Dune	0	0	0	1994 - territorial pair, but no known breeding attempt
Cliff	0	0	0	
Cape	0	0	0	
Mairangi	-	1	1	1994 - no known breeding attempt, pair not consistently in residence
Woolshed	1	0	0	
Rock	1	0	0	suspect pair turnover 1996 (?)
Island	2	2	0	
Whanga	0	1	0	
Other				
Okahu	-	0	0	1994 - pair not consistently in residence, 1995 - territorial pair
Ohira Bay		1	0	
Paritu E.			0	
Paritu W.			0	1996 - new pair, territorial, unknown if attempted to breed
Taupeka		-	0	1995 - no known pair, 1996 - suspected nesting
Matarakau W.		0	0	1995 and 1996 - pair of unknown status
Rangatai Pt.		1	0	1996 - pair of unknown status
Totals				
fledglings	10	10	2	
pairs	14	19	22	
fledglings/pair	0.71	0.53	0.09	

Appendix 4

Estimated fledging times (days) for Chatham Island Oystercatcher chicks, north coast, Chatham Island. In order from shortest to longest fledging periods by brood size. Plus/minus column is the possible range of days chicks may have fledged.

Territory	Year	Midpoint (days)	+/- (days)
One chick broods			
TW	95	30	8
Mairangi	95	35	11
TE	95	36	7
Rock	94	38	31
Woolshed	94	39	4
WW	95	39	2
Whanga	95	40	5
WW	96	40	6
WOC	95	45	10
Mairangi	96	47	16
Two chick broods			
Island	95	36	9
WW	94	40	11
Island	94	43	5
TW	94	47	1
WOC	94	54	16

CHAPTER 4

HABITAT SELECTION AND USE

ABSTRACT

Habitat selection at the general and territory level were examined for CIO on the Chathams Islands from the 1994 to 1996 breeding seasons. To determine general habitat use at the broadscale, the coastline of Chatham, Pitt, and Rangatira Islands and the Te Whanga lagoon shoreline were mapped, and sightings of CIO recorded. To explore use within breeding territories, time observations were conducted for a minimum of one-half hour for 15 breeding pairs along the north coast, Chatham Island for three seasons.

A total of 277 kms of coastline (92%) on Chatham, Pitt, and Rangatira Islands, and 93 km (100%) of the Te Whanga Lagoon shoreline, were visited and mapped. During mapping 115 CIO were sighted. Results from the mapping and a 1998 census were combined to determine habitat use. CIO were found around the entire coastline of all three islands, but in quite low densities on some types of coastline (e.g., cliff, narrow schist, and areas with no storm-zone) and the shoreline of Te Whanga Lagoon.

CIO selected general habitats that provided foraging habitat and breeding pairs, in addition, selected sites that provided nest-sites and chick-rearing habitat. Breeding territories were confined to coastal areas. Sections of coastline with wide storm-tide zones were preferred over similar narrow sections in all cases but one. Along the coastline, use (relative to availability) was highest for intertidal rock platform and areas with sandy beaches in the storm-tide zone. The high use of rock platform was similar to that reported by Davis (1988), but the extensive use of sandy beaches was either previously under-detected or is a recent development. Sandy beaches provided foraging habitat even when rock platforms were covered by the tides, and were often used for nesting. Paddock was selected less than available, especially by breeding pairs, but more than previously reported. Much of the paddock area (70%) was along sections of coastline with intertidal habitat types general avoided by CIO such as boulder/cliff, sand or schist.

The highest density of breeding pairs (4 pairs/km) were at Tioriori on the north coast, Chatham Island, an area with extensive intertidal rock platform. Territories along the north coast were of three basic types: 1) long stretches of sandy beach with a stream or creek mouth (with one exception), 2) sections of coastline with intertidal rock platform, or 3) a mix of sandy beach and boulder or rock outcrops. Within territories, sandy beach was the most used habitat type for all activities, but the amount of use varied considerably among pairs. In rocky platform territories, rock platform was used extensively for foraging (12-60%), whereas in sandy beach territories sand was used almost exclusively for foraging (76-95%). Paddock was used up to 22% of the time for foraging by some pairs.

INTRODUCTION

Understanding the factors which regulate or limit the CIO population on the Chathams is necessary for the most effective management and recovery of the species. If secure nest-sites are limiting, for example, providing additional secure nest-sites should result in an increase in breeding pairs and an increase in the total population; however, if foraging habitat is poor, additional nest-sites will probably not be effective in increasing the population size (Newton 1998). Many factors have been suggested as limiting bird populations including critical habitat resources, such as food or nest-sites, with food resources providing an upper theoretical limit to population levels; however, populations may equalise below this level due to predation pressures, limitations in nest-sites, or occasionally other factors such as diseases or parasites (reviewed in Newton 1998).

Measurable habitat features may provide, or be correlated with, critical resources that limit a population, e.g., resources such as nest-sites and food. By understanding the links between habitat types and population regulation/change it may be possible, for example, to measure foraging areas or nesting substrates and determine if particular habitat-related factors are limiting population growth (see for example, Goss-Custard *et al.* 1994; Goss-Custard *et al.* 1995a; Goss-Custard *et al.* 1995b, Newton 1998).

Habitat selection assumes that individuals can assess and choose among various options. CIO (and other animals) probably do prospect for, assess, and select habitat based on of several factors including direct sampling, cues from conspecifics during intrusions, instinct (i.e, a genetic predisposition for certain sites), or early experience. In Eurasian oystercatcher (*H. ostralegus*) floaters appeared to prospect for territories and were often drawn to disturbances and fights (Ens 1992; Heg 1999; Heg *et al.* 2000). Nonbreeders not already committed to obtaining a nesting territory in a particular location performed an estimated 400 intrusions per year (Ens 1992; Heg *et al.* 2000). Heg *et al.* (2000) suggested that the purpose of these intrusions from nonbreeders was to extract information on territory ownership, territory quality and the cost of territory establishment. Territory quality may be gauged from vegetation characteristics, feeding opportunities and presence of chicks. Clues to the cost of territory establishment may be gleaned from how often territory owners are absent from their territories and the degree of cooperation shown by pair members when defending territories. Early experience can also influence habitat choice in birds (Glück 1984), although this appears to be untested as yet in oystercatchers.

The CIO is an endangered shorebird species endemic to the Chatham Islands (Baker 1973; Davis 1988; Collar *et al.* 1994), with a population estimated at approximately 150 individuals and 50 pairs (Schmechel and O'Connor 1999, P. Moore, pers. com.). Historic numbers are unknown, but were probably higher and have declined due to the nature of the changes that have occurred on the Chathams. Based on densities of other oystercatcher species, the upper limit is likely to have been in the hundreds or low thousands because the island area is small. Efforts by the New Zealand Department of Conservation to increase numbers through management have been ongoing since the late 1980s. To understand what factors are limiting the population, and if management aimed at increasing productivity would be effective, research on habitat requirements and estimates of carrying capacity were identified in the recovery plan as high priority items (Grant 1993).

CIO were thought to occur primarily in association with rocky shoreline (Best 1987; Davis 1988), although historically were reported to use both rocky shoreline and sandy beaches (Travers and Travers 1872; Fleming 1939). Best (1987) searched only areas of rocky shoreline in one of the first systematic attempts to determine total numbers of CIO. Davis (1988), in a survey of the coastline of the four main Chatham islands, concluded that wide wavecut volcanic rock platforms were optimal habitat, but CIO were also found to use sandy beaches associated with rock platforms and around stream mouths. Historically they had also been reported using schist and sedimentary rock platform areas (in Davis 1988). Fossil records of CIO bones indicate CIO are not recent migrants to the Chathams responding to changes brought about by humans, and have probably been present for at least thousands of years (A. Tennyson, Te Papa/National Museum of New Zealand, pers. comm., and Holdaway *et al.* 2000).

CIO should prefer territories which provide abundant food adjacent to good nesting sites (e.g., those with low flooding risk and good visibility for predator avoidance in areas where ground predators occur). Areas with low predator pressure and disturbance levels should also be preferred over areas with higher predator densities and disturbance.

The aims of this study were to determine:

1) habitat selection by CIO at the broadscale and territory level during the breeding season,
2) habitat characteristics within breeding territories along the north coast, Chatham Island, and
3) use of micro-habitat types within territories.

I examined habitat use at three scales: general habitats (e.g., coastline or lagoon shoreline), territories, and nest-sites because birds may select habitats in this respective sequence (Burger 1985; Klopfer and Ganzhorn 1985; Sherry and Holmes 1985). This chapter is devoted to general and territorial habitat selection and use. Chapter 6 examines nest-site selection in more detail.

Definitions

Territory - defended areas with exclusive use ([Maher, 1995 #266]). In this study a territory is defined as an area used by a breeding pair of CIO for feeding and breeding (nesting and chick-rearing) and defended from other CIO.

Habitat selection - the process in which an animal chooses a resource/

Habitat preference - the chance a resource will be selected from a range of resources offered in equal proportions (Johnson 1980). Selection indices measure the use of habitat types in relation to their availability. In essence, when resources are used disproportionately to their availability in the environment, use is said to be selective.

Floater - nonterritorial, nonbreeding CIO.

METHODS AND LOCATION

CIO habitat use was studied on the Chatham Islands, which lie between latitudes 43° and 45° south, 870 km east of the New Zealand mainland. There are two larger islands, several small islands, and numerous stacks and islets. CIO are known to breed on four islands. The majority of pairs (85-90%) breed on Chatham (90,000 ha) and Pitt Islands (6300 ha) (Schmechel 1999; Moore *et al.* 2000), the two largest islands. Both Chatham and Pitt Islands are inhabited and farmed, with extensively modified vegetation, and introduced mammalian and introduced and native avian predators. The remaining 10-15% of CIO pairs breed on Mangere (113 ha) and Rangatira Islands (218 ha) (Schmechel 1999; Moore *et al.* 2000). Both of these were cleared for pastoral farming but, as protected nature reserves for the last three decades, are rapidly becoming re-forested, and are free of introduced mammalian predators and weka (*Gallirallus australis*).

The Chatham islands experience frequent strong winds and occasional high storm swells, especially from the south and west. The prevailing winds during spring (Sept-Nov) and summer (Dec-Feb) are predominantly from the west and southwest. Mean average wind speed is 25 km/hr with gale force winds (greater than 63 km/hr) occurring 14 times per year on average (Thompson 1983).

Chatham Island has a wide range of shore habitats, with an sheer cliff line along the entire south coast, and extensive sand beaches punctuated with rocky headlands elsewhere. There are also smaller areas of shell and boulder beaches in some areas. Schist rock areas are found only in the northern part of Chatham Island (Hay *et al.* 1970). Davis (1988) categorised the Chathams into 14 different shore types based on the combined intertidal and storm-tide zones. The primary categories were volcanic or schist platform (narrow or wide), sand and shingle beaches, boulders, and cliff. Under her classifications about 40% of the coastline of Chatham Island was classified as sandy beach, 29% as schist (narrow and wide), and 15% as cliff. Pitt Island was classified as 41% cliff, 28% volcanic platform (narrow and wide, backed by various habitat types), and the remainder as other types (e.g., sand, boulder). Rangatira was volcanic platform of some type (62%) and cliff (38%). Terrestrial areas adjacent to the coast include sand dunes covered in marram grass, paddocks, rough vegetation (e.g., bracken fern), occasional small patches of native vegetation in reserves, and cliff. The large, brackish Te Whanga Lagoon occupies a major proportion (16,000 ha) of the northern half of Chatham Island (Hay *et al.* 1970).

I studied habitat use within 15 breeding territories along the north coast of Chatham Island between Waitangi West and Okahu Point near Wharekauri, and between Whangamoe and Whangatete Bays (a total of about 28 kms of coastline). Names and locations of territories in the north coast of Chatham Island are given in Chapter 3, Figure 1. These sections of coastline are characterised by a mix of volcanic (or volcanic derived) intertidal rock platform, schist rock, sandy beaches, and small sections of shell or boulder beaches. Terrestrial areas along the coastline include long sections of marram dunes, paddock, forest patches, rough vegetation and cliffs (Table 1 and Appendix 2).

Coastline survey

To determine general habitat use at the broadscale, the coastline of Chatham, Pitt, and Rangatira Islands and the Te Whanga lagoon shoreline were mapped by walking the areas and marking habitat types on 1:50,000 maps (Chatham Islands, NZMS 260 series, 1&2). Distances were estimated by extrapolation from marked sections measured using an ipsometer (map wheel). Mangere Island and about 26 kms of the southern-most cliff coastlines of Chatham Island were excluded because they were inaccessible to me.

Habitat types were divided into three zones: intertidal, storm-tide, and terrestrial (i.e., those areas immediately adjacent to the coastline, directly behind the storm-tide zone). Within each zone, habitat categories were defined and delineated (Plate 1 and Appendix 3). A total of 351 sections of coastline and lagoon shoreline habitat types were

Table 1 Summary of habitat types by zone along the north coast study areas, Chatham Island. Within each zone categories arranged from most to least common by linear kilometre. See also Appendix 2.

Zone	Habitat categories within each zone	Percentage
Intertidal	sand	41%
	boulder/cliff/shell	20%
	schist	18%
	rock platform	11%
	rock or rock/sand mix	10%
Storm-tide	sand	61%
	rock or shell narrow	15%
	rock or shell	11%
	sand narrow	7%
	no storm zone	4%
	boulder/cliff	2%
Terrestrial	vegetation	70%
	paddock	21%
	cliff	9%

delineated in minimum 250 m sections, as these were the shortest sections that could be measured reasonably accurately on the maps. The storm-tide sections were defined as those not inundated daily, but washed by ocean tides only during storms (normally less than every 30 days on average during the breeding season). The upper portion of these areas were discernible based on the lack of vegetation, the lower boundary by the fresh debris or wrack line. In sections where two or more habitat types were intermixed (e.g., cliff and rock platform, or sand and shell) classifications were made using the following criteria: 1) by predominance of the habitat types (e.g., if a beach were 60% shell, 40% sand it would be classified as shell) or, 2) if the mix was fairly even, by habitats known to be used by CIO (e.g., if a 250 m section of intertidal area was about half rock platform and half cliff it would be classified as rock platform). Because CIO rarely used the lagoon shoreline, and because subtle differences in the habitats and other factors may have affected use, the lagoon shoreline figures were excluded from some habitat selection calculations.

To determine whether CIO selected habitat with respect to availability, the proportions of available habitat types were compared with the proportion of sightings of CIO found on these same substrates. Birds were divided into three groups: breeders, pairs of unknown status, and nonbreeders. Breeders included pairs known to have bred, those suspected of breeding, and pairs defending territories. Habitat selection by pairs of unknown status was similar to known breeders, so the two were combined.

Use of habitats by CIO was determined during extensive searches of the coast and shoreline of the islands and lagoon on two separate occasions. One census was done in conjunction with the mapping of habitat categories during the 1995/6 and 1996/7 seasons (hereafter seasons are given as the year in which breeding begins). The second census was conducted in December 1998 (Schmechel and O'Connor 1999). A small section of coastline (8.5 kms) covered by the habitat mapping was not covered during the 1998 census, and this area was excluded from both the use and availability calculations. To avoid very small denominators in the available columns which could inflate ratios, habitat categories were combined so that no single category comprised less than a total of 5% (except in one instant which is noted in the appropriate section). Results of habitat selection from both censuses were similar, and were therefore combined to give a clearer picture of general use over time, especially for nonbreeders which move around more than breeding pairs. Chi-squared tests were used to compare observed and expected values of habitat use.

To determine if storm-tide zone width influenced selection by CIO, the habitat types were classified into wide or narrow. Similarly, to determine if foraging substrate was important in the storm-tide and terrestrial zone, habitats were classified 'food' or 'no food' based on observations of habitats where oystercatchers have been seen to forage (Table 2). To check if coastline habitat types categorised as wide were more likely to provide foraging habitat than those classified as narrow, the percent of narrow and wide categories with foraging substrates (the 'food' or 'no food' groups) were calculated. The associations between paddocks and preferred intertidal and storm-tide zones were calculated to determine patterns of selection for paddocks by CIO. Ratios of use compared to availability were determined for habitat use and those where use was 50% more or less

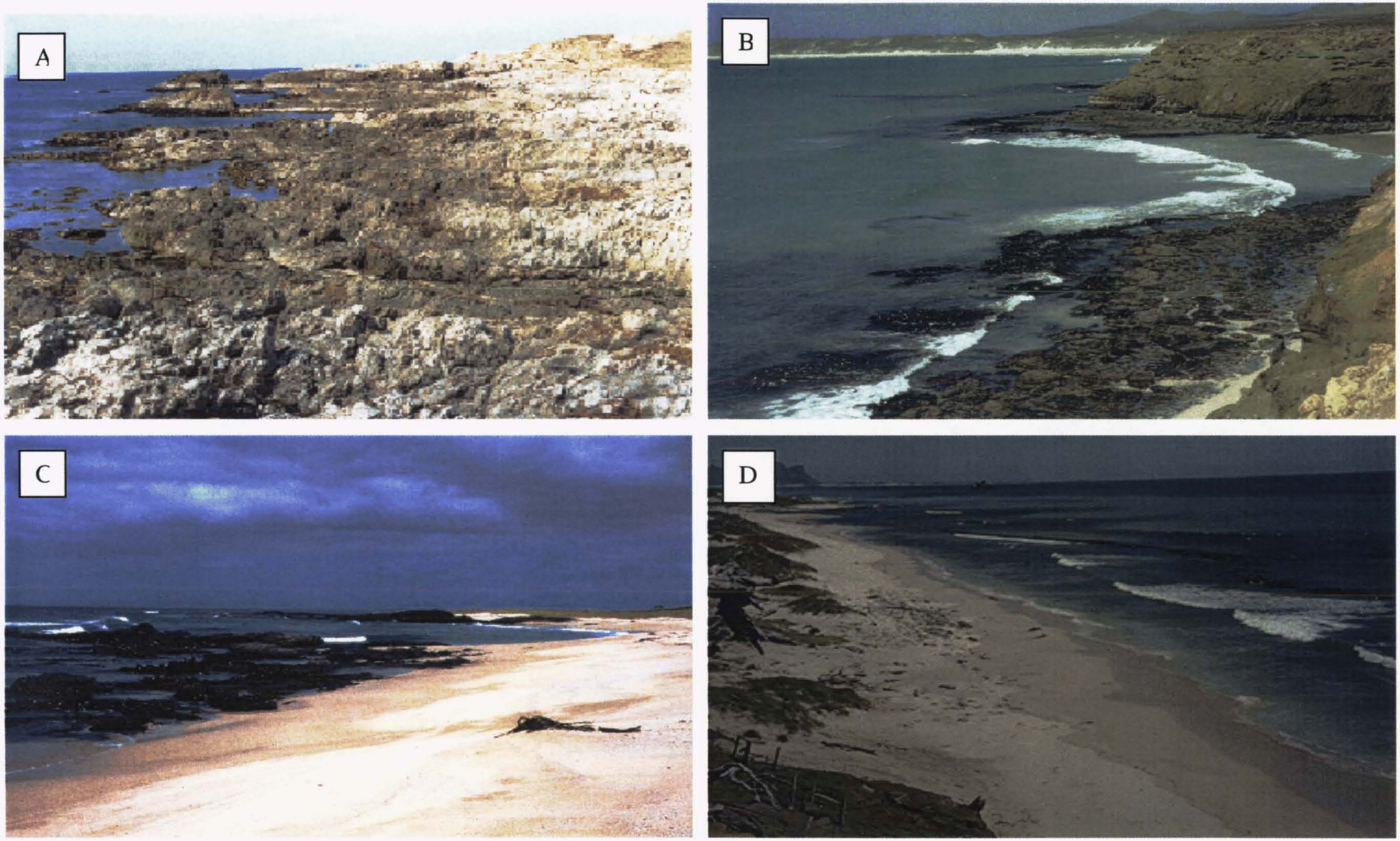


Plate 1. Examples of habitat types along the Chathams coastline: (A) schist rock; (B) exposed rock platform and cliff; (C) 'mixed' rock and sandy beach at Wharekauri; (D) intertidal rock platform, wide sandy beaches, and marram-covered dunes at Tioriori.

than available were considered higher or lower than might be expected (and usually shown in bold font in the tables).

Table 2 - Classifications of storm-tide and terrestrial zones into categories of 'food/no food' and 'narrow/wide'; where 'food' is suitable foraging habitat and 'no food' areas are those with no suitable foraging habitats.

Zone	food/no food	narrow/wide
Storm-tide		
boulder/cliff	no food	narrow
rock/shell	no food	wide
rock/shell narrow	no food	narrow
no storm zone	no food	narrow
sand/mix	food	wide
sand narrow	food	narrow
Terrestrial		
paddock	food	
cliff	no food	
vegetation	no food	

To determine if special features within general habitat types were used selectively they were classified into the following categories: 1) creeks, 2) bays, 3) areas with high amounts of kelp and wrack, and 4) 'corners' (areas where sandy beaches meet rock outcrops). The proportion of areas that contained bays, kelp/wrack, and corners were too infrequent to analyse individually, so these were combined.

Territory habitat description, selection and use

Territory boundaries were determined by a combination of watching birds defend boundaries against neighbouring pairs and intruders, observations of general use, and by using cardboard decoys (Chapter 7) which resident birds would often attack if placed within their territory boundaries.

Habitat use within 15 territories was studied during three successive breeding seasons from 1994-1996. During observations, the habitat type used and associated behaviours were noted at five minute intervals for at least one-half hour per observation. Behaviours were classified into six categories: foraging, resting, incubating, territory defence, preening, and other. Walking was often associated with either foraging or territory defence, but was noted as ‘other’. Preening included bathing. Resting included standing or sitting still, guarding behaviour and brooding. Micro-habitats within territories used during timed observations of CIO were classified into six categories: sand, rock platform, paddock, boulder/rock, freshwater, schist and shell. If a mix of habitat types were present (e.g., shell and sand) the predominant habitat type used was recorded. For some calculations the sandy beach and freshwater categories were combined because all the freshwater areas had sandy substrates; this was noted in the appropriate section.

For incubating pairs, the non-incubating bird was the focus of observations. When beginning a round of observations, a pair was chosen at random for the initial observation and all pairs then observed over several days. After a round of observations was completed, a new pair was randomly chosen from the 15 study pairs for beginning the next round and the process repeated. Observations were conducted only during daylight hours and no attempt was made to time observations for a particular tide cycle or time of day. Pairs were observed with 10-power binoculars from a distance (usually 30 or more metres depending on the topography) using hides or natural cover from vegetation and topography. If it appeared the pair was becoming overly influenced by the observer (e.g., alarm behaviours, false brooding, etc), observations were discontinued and a new location for observations sought with a period of time (a minimum of 20 minutes) out of sight of the birds to allow them to resume normal activities. If individuals moved out of sight during the observations this was noted and included as part of the calculations.

Breeding was classified into four stages: pre-breeding, incubating, chick-rearing and post-breeding. Pre-breeding was defined as the period before and between clutches. Chick-rearing included flying juveniles until they were evicted (or dispersed) from their natal territories (usually about 24-42 days). Post-breeding was defined as the period after the last known nesting attempt or after juveniles had been evicted or left the territory. If no nesting attempts were detected, but the date was prior to 1 January, pairs were assumed to be still breeding.

To determine use of habitat types within territories they were grouped into three types: sandy beach, rocky platform, and mixed. The third of territories which contained no rock platform and pairs used sandy beach (including the areas around fresh water) 85% of the time or more the territory was classified as 'sandy beach'; the third of territories where rock platform was available within the territory and was used over 25% of the time were classified as 'rock platform'; the other third of the territories, which contained a mix of habitat types, were classified as 'mixed' territories (Appendix 1).

RESULTS

Coastline surveys

A total of 277 kms of coastline (92%) on Chatham, Pitt, and Rangatira Islands, and 93 km (100%) of the Te Whanga Lagoon shoreline, were visited and mapped. During mapping 115 CIO were sighted. During the 1998 census (Schmechel 1999) 136 CIO were recorded in the mapped areas (of 142 total) (Table 3). CIO were found around the entire coastline of all three islands, but in quite low densities some types of coastline (e.g., cliff, narrow schist, and areas with no storm-zone) and the shoreline of Te Whanga Lagoon.

Table 3 - Numbers of CIO pairs (p) and floaters (f) along the coastline and lagoon shoreline from mapping and census data for the Chathams coastline (Chatham, Pitt, Rangatira and Mangere Islands) and Te Whanga lagoon edge.

	Coastline CIO Nos.			Lagoon CIO Nos.			Total CIO Nos.		
	p	f	total	p	f	total	p	f	total
Survey									
Mapping survey	41	31	113	0	2	2	41	33	115
1998 census	51	32	134	0	2	2	51	34	136
Combined average use	46	31.5	123.5	0	2	2	46	33.5	125.5

Along the coastline, some relatively abundant combinations of intertidal/storm-tide categories received very little use by CIO (Appendix 4). Intertidal sandy beaches with narrow sandy or no storm-tide zone comprised 19% of the coastline, and areas of intertidal schist with narrow rock in the storm-tide zone 10%, yet each received only about 1% of the recorded use. One intertidal/storm-tide combination which was common, and used in higher proportions than available, was coastline with sand in both zones (18% use:12% availability). Most combinations of intertidal plus their related storm-tide zones were too infrequent (less than 5% availability) to determine selection accurately (because of the small denominators and potentially resultant inflated ratios).

When analysed by individual zone, some habitats were selected in much greater proportions than available (e.g., ratios of 1.50 or greater); these preferred habitats were those with sand (or sand/rock mix) in the storm-tide zone and areas with rock platform in the intertidal areas (Table 4 and Appendix 5). The differences in use of habitat types within zones was significant for all but floaters in the terrestrial zone (Table 5). Pairs and floaters used sections of coastline with no storm-tide zone, or sections of narrow rock or shell in the storm-tide zone, and areas with cliff/boulder/shell in the intertidal zone less

Table 4 Proportions of use and availability of habitat types for CIO pairs and floaters along the coastline of Chatham, Pitt, and Rangatira Islands, (lagoon excluded). Ratios of use/availability - those greater than 1.00 indicate use of habitat types by CIOs in higher proportions than available. Ratios in bold (above 1.50 or below 0.50) indicate use that is much higher or lower (i.e., at least 50% more or less) than would be expected based on the availability of the habitat. + indicates selection for and - selection against use of habitat. (See also Appendix 5a). Ratios calculated to 4 digits.

	Floaters			Pairs		
Habitat types by zone	use	avail	ratios	use	avail	ratios
Terrestrial						
cliff/boulder	0.13	0.17	0.73	0.12	0.17	0.70
paddock	0.32	0.26	1.24	0.11	0.26	**0.43** -
vegetation	0.56	0.57	0.98	0.77	0.57	1.35
Storm-tide						
cliff/boulder	0.10	0.13	0.72	0.09	0.13	0.66
no storm zone	0.02	0.06	**0.28** -	0.01	0.06	**0.19** -
sand narrow	0.08	0.22	**0.37** -	0.16	0.22	0.76
rock/shell	0.41	0.28	1.47	0.29	0.28	1.02
rock/shell narrow	0.05	0.13	**0.35** -	0.03	0.13	**0.24** -
sand/mix	0.35	0.18	**1.97** +	0.42	0.18	**2.35** +
Intertidal						
cliff/boulder/shell	0.02	0.10	**0.16** -	0.01	0.10	**0.11** -
rock/mix	0.24	0.17	1.41	0.15	0.17	0.91
rock platform	0.33	0.13	**2.57** +	0.54	0.13	**4.14** +
sand	0.21	0.36	0.57	0.20	0.36	0.55
schist	0.21	0.24	0.86	0.10	0.24	**0.41** -
N	31.5	267.5 kms		45.5	267.5 kms	

Table 5 Chi-squared values for habitat use by zone for CIO pairs and floaters along the coastline of Chatham, Pitt, and Rangatira Islands.

	Floaters				Pairs			
Zone	χ^2	df	p		χ^2	df	p	
Terrestrial	4.90	2	0.086	ns	7.77	2	0.021	*
Storm-tide	13.27	5	0.021	*	21.20	5	<0.001	***
Intertidal	14.95	4	0.005	**	69.27	4	<0.001	***

than was available. Pairs seldom used areas with schist in the intertidal zone, or paddock in the terrestrial zone. Floaters avoided using narrow sand beaches.

When the storm-tide zones associated with particular habitat types were categorised into 'narrow' or 'wide', CIO select wide over narrow for every habitat type but one (Table 6). The exception was the boulder/cliff/shell category of habitat types.

Table 6 Proportions of use and availability of narrow (n) or wide (w) storm-tide zones. Ratios over 1.00 indicate use in greater proportion than is available. Ratios in bold indicate where the difference in selection is greater than 25% between wide or narrow storm-tide zone within a habitat category.

Intertidal	Use		Available		Ratios	
habitat type	n	w	n	w	n	w
Pairs						
boulder/cliff/shell	0.01	0.00	0.08	0.02	0.14	0.00
rock/mix	0.03	0.12	0.06	0.11	0.59	**1.07**
rock platform	0.23	0.31	0.07	0.06	3.09	**5.58**
sand	0.01	0.19	0.23	0.13	0.05	**1.42**
schist	0.01	0.09	0.10	0.14	0.11	**0.63**
Floaters						
boulder/cliff/shell	0.02	0.00	0.08	0.02	0.20	0.00
rock/mix	0.05	0.19	0.06	0.11	0.85	**1.68**
rock platform	0.14	0.19	0.07	0.06	1.91	**3.45**
sand	0.02	0.19	0.23	0.13	0.07	**1.45**
schist	0.02	0.19	0.10	0.14	0.16	**1.37**

Similarly, if the terrestrial and storm-tide zones were classified as either providing, or not providing, foraging substrate ('food' or 'no food'), CIO selected sections of coastline with 'food' regardless of the intertidal zone in all but two cases (Table 7). The two exceptions were sections of coastline with intertidal schist or rock platform. In these two habitat types, the presence of foraging substrate in the storm or terrestrial zones did not increase the amount of use over those with 'no food'.

Table 7 No food (nf) versus food (f) in the storm and terrestrial zones. Combined ratios over 1.00 indicate use in greater proportion than is available. Ratios in bold indicate where the difference in selection is greater than 25% between wide or narrow storm-tide zone within a habitat category.

Intertidal	Use		Available		Ratios	
habitat type	nf	f	nf	f	nf	f
Pairs						
boulder/cliff/shell	0.00	0.01	0.09	0.01	0.00	**0.73**
rock/mix	0.05	0.10	0.08	0.09	0.55	**1.15**
rock platform	0.23	0.31	0.09	0.04	2.66	**7.16**
sand	0.00	0.20	0.04	0.32	0.00	**0.61**
schist	0.05	0.04	0.08	0.16	**0.65**	0.28
Floaters						
boulder/cliff/shell	0.02	0.00	0.09	0.01	0.19	0.00
rock/mix	0.05	0.19	0.08	0.09	0.57	**2.22**
rock platform	0.21	0.13	0.09	0.04	2.37	2.95
sand	0.00	0.21	0.04	0.32	0.00	**0.64**
schist	0.05	0.17	0.08	0.16	0.57	**1.01**

In the comparison of food availability in narrow and wide storm-tide zones, wide storm-tide zones were more likely to include foraging substrates than narrow storm-tide zones in all cases but one (Table 8). The exception was the storm-tide zones associated with intertidal rock platform; these sections, whether narrow or wide, had similar percentages of habitat types which provided foraging substrates (e.g. sand or sand mix).

Table 8 Food availability in narrow and wide storm zone. Arranged by intertidal zone.

	Storm-tide zone						
Intertidal	Narrow (kms)		Wide (kms)		Total	Food availability	
habitat type	no food	food	no food	food	(kms)	narrow	wide
cliff/boulder	20.25	1.25	2.50	2.75	26.75	6%	52%
rock/mix	10.50	4.50	10.75	19.50	45.25	30%	64%
rock platform	13.00	7.00	10.25	4.50	34.75	35%	31%
sand	9.00	52.00	0.50	34.75	96.25	85%	99%
schist	13.00	14.25	9.50	27.75	64.50	52%	74%
Grand Total	65.75	79.00	33.50	89.25	267.50	55%	73%

Paddocks were often located in areas that were otherwise not used by CIO, that is they were often inland from the storm-tide or intertidal zones that CIO avoided, such as cliff and boulder areas (Table 9).

Table 9 Percentages of intertidal and storm tide areas with paddocks, Chatham and Pitt Island and selection of these areas by CIO. CIO selection: + positive, 0 neutral, - negative. Habitat types: rp - rock platform, r/l - rock/shell, s - sand, t - schist, b/c/l - boulder/cliff/shell, s/mx - sand/mix of sand and rock, b/c - boulder/cliff, nsz - no storm zone, rn/ln - rock/shell narrow, sn - sand narrow.

Zone	CIO selection	Percent areas with paddocks	Habitat types
intertidal	+	13%	rp
	0	17%	r/l
	-	70%	s,t,b/c/l
storm-tide	+	18%	s/mx
	0	28%	r/l
	-	54%	b/c,nsz,rn/ln,sn

Creeks alone were not used more than available (Table 10). However, if the creeks or streams were in areas with other special features, these areas were used over twice as often as would be expected according to their availability. ‘Corners’, bays or areas with abundant kelp/wrack were also favoured.

Table 10 Use by CIO and availability of special features on the Chathams. 'Other' includes areas with 'corners', bays, or beaches with an abundance of kelp and/or wrack. Corners are areas where sandy beaches meet rock outcrops. Ratios in bold (above 1.50) indicate use that is much higher (i.e., at least 50% more) than would be expected based on the availability of the habitat.

	Floaters			Pairs		
	use	available	ratio	use	available	ratio
no special feature	0.40	0.64	0.62	0.36	0.64	0.57
creek	0.24	0.18	1.36	0.18	0.18	1.00
corner, bay or kelp/wrack	0.19	0.11	**1.71**	0.18	0.11	**1.58**
creek plus ‘other’	0.17	0.07	**2.35**	0.29	0.07	**3.84**

Lagoon shoreline use

Along the entire 93 kilometres of shoreline of the lagoon, only two individual CIO, both nonterritorial nonbreeders (floaters) were seen in each survey. Selection by CIO of coastline (by linear kms) was 98% use:74% availability, in contrast with the lagoon shoreline with only 2% use:26% availability. One of these sightings was near the lagoon mouth which has habitat more similar to that of the coastline than the majority of lagoon shoreline.

During the 1996 season CIO were incidentally sighted along the lagoon shoreline a total of four times. In every case they were immature birds. Twice two birds were seen together (a banded two year old and an unbanded first-year bird), and twice a single first-year bird was seen. Observations of foraging were collected on two occasions. During 30 minutes of observations in November 1996 two immature CIO feeding on bivalves (commonly referred to as pipis, *Ammphidesm spp*?) which they consumed at an average rate of 5.25 per minute (range 3 to 8). Possibly the same pair were also observed foraging on cockles (*Chione stutchbury*) and mussels (*Aulacomya ater* or *Mytilus edulis*) on 20 December 1996.

Territories

The highest density of breeding territories was located at Tioriori, with four territories in a single kilometre of coastline. This section of coastline was characterised by its extensive rock platform, backed by marram dunes and paddock. From Washout Creek to Tutuiri Creek (including Tioriori) the density of breeding pairs was just over one per kilometre. This section includes long stretches of sandy beach and stream mouths backed by extensive marram dunes and some paddocks. Wharekauri also had a high density of pairs. Between Cape Young and Okahu Point there was just under one pair per kilometre of coastline. This area was a mix of sandy beaches and rocky platforms, or outcrops of rock and boulders backed by either paddock or marram dunes. The other northern area with high densities of CIO territories was around Whangamoe (four pairs along about seven kilometres of coastline, 1.7 pairs/km). The Whangamoe area was characterised by a mix of schist rock interspersed with sand and shell beaches, with a small volcanic rock area. The storm-tide zone was backed by paddock and rough vegetation.

Territories used by CIO along the north coast, Chatham Island, varied in length along the coastline from 170 to 1540 m, and the width of the coastline sections varied from 1 to 70 m (Appendix 6). Of fifteen territories, ten had paddocks within their territory boundaries, and an additional three had paddocks within short flying distances. In these latter three instances, use of paddocks by these pairs was suspected (based on reports by land owners or movements of birds), but never confirmed.

Within the 15 study territories habitats tended to either be predominantly sandy beach, and contain a large creek or be adjacent to rock platform, but not both. All of the territories composed primarily of sandy beach had major streams except Woolshed, which had a minor creek (Appendix 6). Pairs from Tioriori probably visited Tutuiri Creek. CIO were often seen flying from Tioriori in that direction and visa versa, and CIO were often in the Tutuiri Creek area. CIO used streams for foraging, drinking and bathing. Eleven of the territories contained either intertidal rock platform or intertidal sections of boulder/rock coastline. One territory (TE) had a small section of boulders/rock that was exposed intermittently, depending on sand movements.

Fifteen CIO pairs along the north coast were observed for a total of 83 hours over three seasons. During a total of 155 half-hour sets of observations 1,992 individual behavioural and habitat use records were noted. Sandy beach habitat was used far more than any other habitat type (Table 11 and Figure 1), followed by rocky platform habitat. Fresh water areas (which in every case had sandy substrates), sandy areas interspersed with boulders and paddock were used less. Shell and schist were used very little.

Use of habitats varied considerably between pairs in different territories. Sandy beach (including the areas around streams) was used from 10-96% of the time for all activities, and rocky platform from 14-55% of the time where present (Table 11). Pairs used anywhere from two to six different habitat types, with the majority (12 of the 15 pairs) using between two and four different habitat types within their territories.

Table 11 Use of habitats by territory for all activities by CIO, north coast, CI. SB - sandy beach, RP - rock platform, B - boulder, PAD - paddock, FW - fresh water, SHL - shell, T - schist rock platform, UNK - unknown. N = the number of half-hour observation sets. Total = the total number of habitat types used. 0% indicates habitat available, but not used during observation sets.

Territory	SB	RP	B	PAD	FW	SHL	T	UNK	N	Total
Whanga	10%		11%	7%		31%	38%	3%	7	6
WW	89%				7%			4%	8	2
WoC	85%				8%	0%		6%	15	2
TW	76%			8%	10%			6%	13	3
TE	78%		6%	6%	6%			3%	13	4
OTF	76%		22%					2%	11	2
Creek	77%	17%			5%			2%	12	3
Pounamu	73%	14%		8%				5%	12	3
Dune	47%	29%	6%	14%				4%	14	4
Cliff	60%	28%	2%	2%				7%	11	4
Cape	59%	32%						9%	7	2
Mairangi	66%	14%	12%	4%	0%			5%	10	4
Woolshed	96%		2%		0%			2%	9	2
Rock	26%	55%	14%					6%	7	3
Island	47%	50%			0%			3%	6	2
Mean	67%	30%	9%	7%	5%	15%	38%	4%	155	3.07

For foraging, all pairs used sandy beaches, some pairs almost exclusively, but use varied widely from 15-95% of the total time spent foraging by pairs (Table 12). For pairs with creeks within their territories, sandy substrates near and in fresh water were used up to 16% of the time. All pairs used rock platform for foraging if it was available within their territories, some quite extensively (up to 60% of the time). A total of seven pairs foraged in paddocks, 4-22% of the time. Schist rock platform, boulder, and shell were only used in a couple of territories.

Pairs spent 30-49% of their time feeding, depending on breeding activity (Table 13). Pairs with chicks spent the most time foraging, and incubating pairs the least. Resting was the most common non-foraging behaviour among pairs (33-34% of the observations) unless they were incubating a clutch, which took 46% of their time. Territory defence was observed from 3-7% of the time for non-incubating pairs, whereas incubating pairs were not recorded in territory defence.

Table 12 Habitats used for foraging by territory. SB - sandy beach, RP - rock platform, B - boulder, PAD - paddock, FW - fresh water, SHL - shell, T - schist rock platform. N = the number of observation sets. Total = the total number of habitat types used. In order by geographic distribution from southwest to northeast.

Territory	SB	PAD	RP	T	B	FW	SHL	(N)
Whanga	15%	22%		48%			14%	6
WW	92%					8%		8
WoC	84%					16%		13
TW	85%	4%				11%		11
TE	76%	8%			11%	5%		11
OTF	58%				42%			9
Creek	75%		18%		2%	5%		10
Pounamu	71%	8%	21%					9
Dune	31%	10%	48%		12%			10
Cliff	31%	7%	60%		1%			9
Cape	48%		52%					5
Mairangi	63%	10%	12%		15%			10
Woolshed	95%				5%			7
Rock	36%		57%		7%			7
Island	71%		29%					5
Mean	64%	10%	37%	48%	12%	9%	14%	130
All territories	64%	5%	18%	2%	7%	4%	1%	

Table 13 Percent of time spent by CIO in various behaviours by breeding stage, north coast, Chatham Island. PN - prenesting, I - incubating, CH - chick-rearing, O - other.

	Breeding stages				
Behaviour	PN	I	CH	O	Total
foraging	38%	30%	49%	33%	36%
resting	34%	9%	33%	33%	26%
preening	9%	6%	7%	14%	9%
territory defence	5%	3%	0%	7%	4%
incubating	0%	46%	0%	0%	14%
other	15%	7%	11%	13%	11%
total nonforaging	62%	70%	51%	67%	64%
(n)	39	46	26	44	155

The type of habitats used for foraging varied by territory type. Pairs in territories composed primarily as sandy beach spent 94% of their time on average foraging in sand (including fresh water areas) (Figure 1). In contrast, pairs in rocky platform territories spent only 40% of their time foraging in sand, instead using rock platform over half the time observed (51%) for foraging. Pairs in mixed type territories foraged on rock platform 12% of the time on average, on sandy substrates 61% of the time, and in boulders, paddock, and schist from 7-13% of the time. Shell received little use, only 2% by pairs in mixed type territories.

DISCUSSION

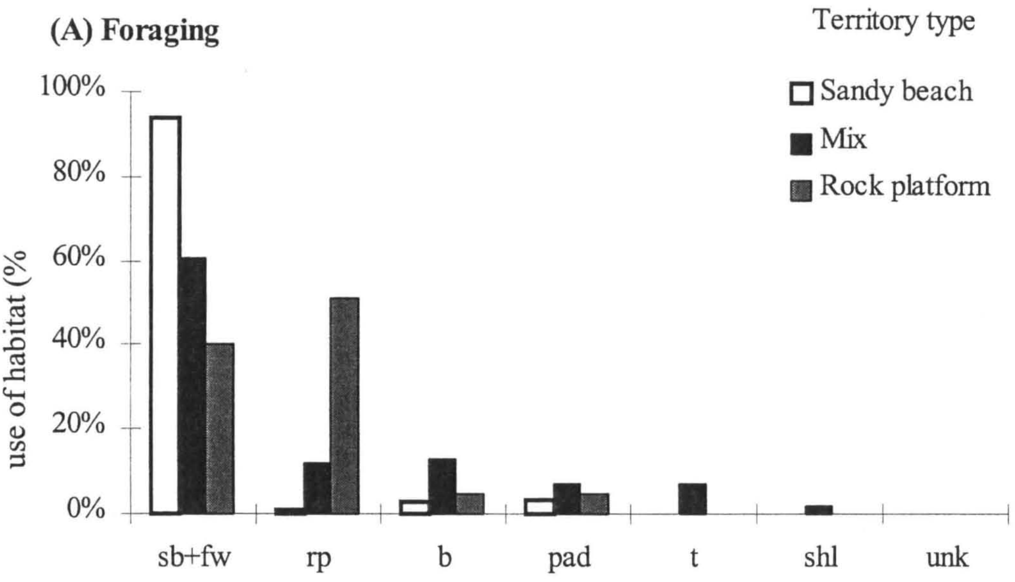
General habitat use

The following habitat types should be preferred because they provide critical resources such as food, nest-sites, and safe roosting areas include, described by coastline zone:

1) Paddocks in the terrestrial zone (i.e., areas never flooded by high tides) because these provide potential feeding areas, including during high or storm-tides. If directly backing the storm-tide zone they provide less cover for predators than marram-grass covered dunes.

2) Wide sandy beaches (especially those with kelp and wide or high rock areas) and wide or high rock areas with low mat-forming vegetation in the storm-tide zone. These habitats types should provide safe (high visibility), low flood-risk nesting sites. Kelp and wrack on sandy beaches should provide additional foraging substrate during mid and high tides, and may also help provide a more complex visual patterns, making nests and chicks more difficult for predators to locate (Heppleston 1971; Hockey 1982; Lauro and Nol 1995).

3) Wide, flat rocky platforms; wide sandy beaches; wide areas with rock and sand in the intertidal zone. These areas would provide good foraging habitat during low tide. The best areas would be flat and accessible to young chicks (Hazlitt 1999).


(A) Foraging

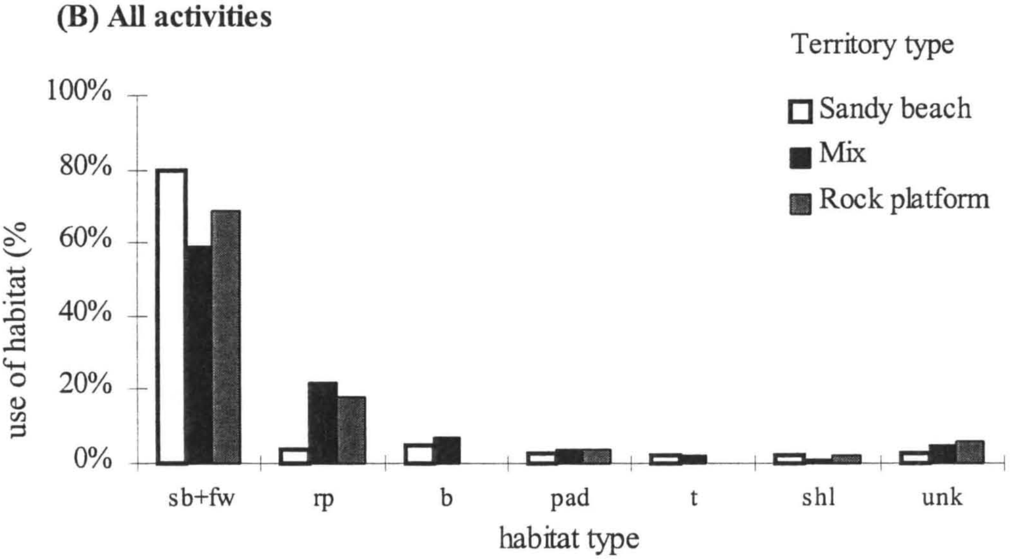

(B) All activities

Figure 1 Habitats used for (A) foraging and (B) all activities within territories by territory type. Habitat types: sb+fw - sandy beach and fresh water (sand substrate), rp - rock platform, b - boulder, pad - paddock, t - schist rock, shl - shell, unk - unknown (birds out of sight).

Habitat use by CIO around the islands on a broadest scale is probably influenced by a combination of the general geology of the islands and prevailing wind patterns. The southern half of Chatham Island, and portions of Pitt and Rangatira, are volcanic rock with steep cliff areas and little storm-tide zone, and with prevailing southerly or southwesterly winds, probably limit nesting areas for CIO. Aspect and prevailing winds have been shown to affect likelihood of flooding, lowering productivity (Pugh 1987). In Australia, losses due to floods, wind and rain was much higher for oystercatchers on exposed Flinders Island (62% and 80% in 1988 and 1989 respectively) than on sheltered Big Green Island (10% for both seasons) (Lauro and Nol 1993). Additionally, food availability may be less during prolonged high winds or storms (Evans and Smith 1975; Davidson 1981; Evans and Pienkowski 1984), making these exposed areas unsuitable for chick-rearing.

Along the coastline, use by zone (relative to availability) was highest for intertidal rock platform and areas with sandy beaches in the storm-tide zone. CIO probably select rock platform and wide sandy beaches because they provide good foraging habitat and, for breeding pairs, good nesting habitat. The high use of rock platform was similar to that reported by Davis (1988), but the extensive use of sandy beaches was either previously under-detected or is a recent development. Sandy beaches provided foraging habitat even when rock platforms are covered by the tides, and were often used for nesting (Chapter 6).

Use was lowest for intertidal boulder/cliff; intertidal sandy beach backed by narrow or no storm-tide zone; and intertidal schist back by narrow rock in the storm-tide zone. Any area with narrow rock or shell storm-tide zones, or which had no storm-tide zones, were used very little relative to their availability. These areas probably provided little in the way of foraging habitat and no good nesting sites.

All of the intertidal areas except cliff/boulder were used more if backed by wide, compared to narrow, storm-tide zones and were almost always used more if backed by areas that provided foraging substrates. However, higher use of wide storm-tide zones may have been because wider sections of coastline were more available (i.e., there was more surface area in total than narrow ones), and the use of linear measurements did not accurately reflect this greater availability.

Schist was used less than available by both pairs (ratio 0.41) and nonterritorial nonbreeders (ratio 0.86) (Table 4). The topography of schist varies considerably; some sections are flat and wide with pools and good foraging areas, others are more narrow or uplifted, with less substrate for marine vertebrates (Davis 1988, pers. obs.). Although pairs had historically been reported to use wide schist platform at Taupeka Point, Okawa Point, Cape Pattisson and Te Raki Bay (see map Chapter 3, p. 35), use of schist was thought to have decreased in the late 1980s (Davis 1988). In the most recent counts CIO were found using these areas (Schmechel and O'Connor 1999; Moore *et al.* 2000). Schist use may vary with the total population of CIO, decreasing when numbers are lower. It may also be that monitoring has been historically insufficient to accurately detect use on schist coastlines, especially for floaters which move around more frequently than pairs. Much of the schist coastline is more difficult to access, and it would be easier for birds to remain undetected if they crouch down and are silent, which they sometimes do, than along sandy beaches.

Pairs also used paddocks in lower proportions than available even though they were often used for foraging along the north coast. Much of the paddock area (70%) was along sections of coastline with intertidal habitat types general avoided by CIO such as boulder/cliff, sand or schist. Floaters used paddocks in proportions greater than available, suggesting that, although paddocks are selectively used for foraging, they are less important than the intertidal and storm-tide areas for breeding pairs. Use of paddocks probably varies depending on the season and the wetness of the paddocks. In lapwings (*Vanellus vanellus*), wetness was suggested as the most important factor in habitat selection, because earthworms were probably an important food item for lapwings early in the season (Klomp 1954 cited in Berg 1993). Earthworms were more difficult to catch when the soil dried up, when they move deeper into the soil (Gerard 1967). In mid-Canterbury earthworms were abundant on farmland during July when the soil was wet (Lobb and Wood 1971). CIO were observed foraging on earthworms during this study, but may also have taken other invertebrates. Other oystercatcher species are also known to feed on earthworms (Heppleston 1972). On the New Zealand mainland oystercatchers on wet coastal fields ate grass grub beetle larvae (Baker 1974).

Special features such as creeks, areas with kelp and wrack, bays and 'corners' (i.e., areas where long sandy beaches meet rocky points) were used in higher proportions than available. Creeks, when in areas with one or more special features, were selected more than twice as often as predicted from their availability. Creeks were frequently used for foraging and bathing, and kelp and wrack for foraging. Corners may be selected because of the variety of foraging substrates (i.e., sand and rock) and because they are sheltered and provide both nesting and foraging habitats.

Differences in use of habitats by floaters compared with breeders may be because they have different habitat requirements. Floaters probably seek out food, safe roost sites, other floaters and, during stormy weather, possibly shelter. Breeders, in contrast, seek areas with nest-sites adjacent to foraging and chick-rearing habitat. Floaters are therefore more free than breeding pairs to move around and use a broader range of habitat types. Use of habitat by floaters was also probably influenced by breeding pairs excluding them from their territories, thereby forcing floaters into potentially less desirable habitat types.

CIO used Te Whanga lagoon shoreline infrequently relative to its availability, and it was used only by nonterritorial nonbreeders. This may be because the lagoon does not provide critical resources such as good foraging habitat (either quality or quantity); or alternatively, non-habitat factors such as predator pressure, disturbance, or social factors (such as prospecting for mates and territories) may have affected use. Food supplies appeared, from limited observations, to be good for CIO based on feeding success rates for molluscs. However, Murray and Sanders (2000) found molluscs occurred only rarely and in low numbers in the five sites they sampled. Amphipods, oligochaete worms and fly larvae were the main invertebrates present, all potential food for CIO (Baker 1969; Davis 1988, pers. obs). Food supplies around the lagoon are probably quite patchy and more extensive sampling would be needed to determine foraging quality and availability for CIO. Winds and the water levels within the lagoon may also change food availability significantly from day to day, potentially rendering the lagoon shoreline unsuitable for chick-rearing due to changes in food availability. Changes in water levels because of winds often dramatically change the amount of mudflat exposed along the northern lagoon edges over short periods of time (Murray and Sanders 2000, p. 3; pers. obs.). Moreover, the lagoon blocks and unblocks irregularly, therefore food supplies over years is likely to be unreliable due to changing salinities and water levels. Predator pressure or disturbance around the lagoon shorelines are unquantified.

Breeding territories

CIO showed a preference for foraging in sandy beach and rock platform habitats and most territories were established in this kind of habitat as well. Thus, CIO seem to select territories with a high proportion of foraging habitats, which included sites for nesting and possibly chick-rearing. Although use of sandy beach and rock platform was high, pairs also used a wide variety of other habitat types including paddock, schist, boulder, and shell.

Contrary to expectations for CIO habitat use, five of the territories were predominantly sandy beach. These territories had several common features: all but one had a large stream running through it (the one exception had a small creek); all had wide sections that were not inundated by daily tides; and all had regular deposits of kelp and other wrack along the tide-line. CIO were regularly seen foraging along the wrack line on items such as mussels (*Aulacomya ater* and *Mytilus edulis*), sea tulips (*Pyura pachydermatina*), sand hoppers (Amphipoda: *Talorchestia maorianus?*) or, in one case, on kelp fly (Diptera: *Coelopidae & Helcomyzidae*) larvae.

The highest densities recorded for CIO, of four pairs per kilometre, was less than half that reported for Australian pied (*H. longirostris*) and sooty oystercatchers (*H. fuliginous*) on Big Green Island, Australia, in their most preferred habitats. On Big Green Island the number of breeding pairs at sandy, mixed beach, rock beach and overall was: 4.8, 8.8, 1.4 and 3.1 per km respectively. Sooty oystercatchers per km at rock beach, mixed beach and overall was 4.6, 7.5 and 4.9 pairs respectively (Lauro and Nol 1995). The average of between 1.0 and 1.7 CIO pairs/km in other areas of high density were lower or similar to densities of variable oystercatcher (*H. unicolor*) on Mana Island (2.5 pairs/km) (Colin Miskelli, pers. comm.) and black oystercatcher (*H. bachmani*) at Skidegate Inlet, B.C., Canada (1.6 pairs/km of shoreline) (Vermeer *et al.* 1992). The density of pairs per km for the Chatham Islands was 0.4 on Chatham Island, 0.6 on Pitt and Mangere, and 1.2 on Rangatira (Chapter 2, Table 1). If food supplies are similar on the Chathams to other areas around the world, this suggests that CIO densities could increase significantly if other limiting factors were reduced or removed in preferred areas.

The length of territories in this study of 170-1540 m are similar to those reported by Davis (1988) of 200-760 m, but the longest territory was over twice as long as the longest one she reported. New territories in this study, as compared to those reported by Davis (1988), were WOC, WW, TE and TW which were three of the four longest territories measured. The four longest territories were those composed primarily of sandy beach and no rock platform (OTF, TE, WW, WOC). These territories may be longer because of the more linear nature of the foraging area, the distribution of streams and wide sandy beach areas, a more patchy distribution of foraging areas than the rock platform territories, or the habitat is not yet at carrying capacity and the current pairs have expanded their territories to cover the space present.

Territory size was probably a compromise between the area birds need to feed their young and the area they can defend (Harris 1970; Davies and Houston 1984). Sutherland (1996) further expands this concept to show that there is little reason to expect a simple relationship between territory size and reproductive success or the quality of individuals, because territory size is a tradeoff between the costs of defending a territory and the benefits gained from a larger territory and these change depending on population size.

Nevertheless, food was probably a significant factor in determining territory size and there is often a negative correlation between territory size and food abundance and experimentally increasing food abundance often reduces territory size (Myers *et al.* 1979; Enoksson and Nilsson 1983; Gauthier 1987a; Newton 1989; Watson *et al.* 1992), but not always (see Yom-Tov 1974; Franzblau and Collins 1980; Moss and Watson 1985; Gauthier 1987b; Enoksson 1988).

Habitat use within territories

Although CIO have been considered only one of two pied coloured oystercatcher species to specialise on rocky shore habitat (Hockey 1996b), most pairs along the north coast, Chatham Island, used sandy beaches extensively, and several pairs used sandy beaches almost exclusively for foraging and other activities. In territories with rocky platform, it was used extensively for foraging (12-60%), and in territories composed primarily of sandy beach, it was used almost exclusively for foraging (76-95%). Paddock was used up to 22% of the time for foraging by some pairs, but not at all by others.

Within their territories, pairs used intertidal boulder areas less often than most other habitat types, and those that were used for foraging tended to be interspersed with sand. The birds foraged on both the boulders, primarily for limpets (*Patelloidea corticata* or *Cellana strigilis*) and chitons (*Sypharochiton pelliserpens*), and also in the sand around the boulders (often on marine worms, probably Polychaeta and/or Nermertea). Boulder areas were used mainly for foraging in the intertidal zone. In one territory (TE) the boulder platform was only exposed some parts of the year, depending on sand movements. The shell areas that were used for foraging were a mix of sand and shell (with more shell than sand). All of the foraging observed occurred in the sandy portions of the substrate. No foraging was recorded in areas composed predominantly of shell.

CIO pairs spent from 5-16% of their diurnal time using fresh water. Oystercatchers have well developed salt glands (Hockey 1996a), so fresh water may not be required for drinking, but was perhaps preferred if available. The stream areas were associated with, and may help create, the wider beach areas. Streams seem to provide a mix of resources including water, a good foraging substrate, bathing, and wider areas for nesting and roosting. However, there were at least two areas with streams (Ngatikitiki and Okahu) that, although often used by CIO, have not been occupied by successful pairs for much of the 1990s. This may be because of a lack of suitable nest-sites, as both areas are backed by large dunes and have little high ground clear of marram grass.

Paddocks were used for foraging between 4% and 22% of the time by about half the pairs. During this study pairs never attempted to nest in paddock; however, Moore et. al (2000) did report one instance of CIO nesting in paddock more recently. Davis (1988) reported only one occasion of CIO using paddock which was for foraging. Reasons for these differences in use of paddocks by CIO between the two studies could be because of changes in paddock availability, differences in weather, changing behaviour by CIO as they learn to use paddock for foraging, or, mostly likely, differences in observation methods (e.g., observations during different times of the year or in different locations). A combination of any of these factors was also possible. Davis found no pairs during the 1987 seasons in the areas between WW and OTF (see Figure 1, Chapter 3). The pairs in the Tioriori area were observed twice a month from mid-October until mid-December and once a month until March. These were the pairs which were observed using paddocks most extensively during this study. Possibly the observations during 1987 were not frequent enough or extensive enough to detect use of paddocks by the Tioriori pairs, or it was an especially dry or cold year making the paddocks less suitable for foraging. Extensive use of paddocks have been a relatively recent adaptation by some other oystercatcher species (reviewed in Hockey 1996a), and this may also be the case for CIO.

Limitations

Observations of foraging behaviour in CIO were only made during the day. Night foraging is very widespread in waders and in other species of oystercatcher (Evans 1976; Dugan 1981; Zwarts *et al.* 1990; McNeil *et al.* 1992; Kersten and W. 1996; Rohweder and Baverstock 1996), and almost certainly occurs in CIO. If so, they may use different habitats at night, or for different amounts of time. In those Eurasian oystercatchers which breed near tidal areas, feeding activity was as high at night as during the day. Radio-tracking indicated similar ranges were used day and night, and that food intake rates were similar. South Island pied oystercatcher are also active at night (R. Maloney, pers. comm.). In contrast, activity patterns of inland-breeding oystercatchers seemed to be determined by the light-dark cycle with no activity occurring at night (Exo 1998). Feeding at night may occur only when food availability during day-time is restricted. In CIO, night-time foraging activities may depend on how much they depend on intertidal areas for feeding, with those in the rock platform territories feeding the most at night, and those in mixed or sandy beach type habitats or that use paddocks extensively needing to feed less at night.

The potential to over- or underestimate habitat use and selection was minimised as much as possible but some habitats were more difficult to observe CIO in, such as broken boulders and rocky areas. Therefore, these habitat types may be slightly under-represented in the use figures. Pairs with chicks were more difficult to observe as they were very alert, and changed behaviours at a greater distance as I approached than pairs without chicks. Pairs in some territories were especially difficult to approach and/or observe, such as in the Island territory which could only be observed during low tides or with difficulty from off the island at high tide. At least one pair (WOC) was observed foraging in paddock at times other than during the observations. If pairs were away from their territories during high tides, or observations of particular pairs happened to occur by chance primarily during low tides, this would overestimate time spent using intertidal habitats, which could be the case with, for example, the Rock territory.

Although the time observations of habitat use were from a significant percentage of the total CIO territories on the Chathams (about a third), they were not from a random sample of territories, as they included only north coast territories, and therefore the results may not be representative of other areas.

During this study territory defence was never recorded during incubation (even though it was commonly seen at other times), but it has been observed during the incubation period in other oystercatcher species (e.g., Nol and Humphrey 1994). The behavioural recording method used for this study (instantaneous sampling) is better for estimating common, longer-duration, behaviours rather than uncommon, shorter-duration, behaviours (Martin and Bateson 1986). The sampling intervals were 5 minutes, and although territory defence behaviours usually lasted at least this long, occasionally bouts were shorter than this (pers. obs.). Also, the way behaviours were classified, only the more intensive behaviours were classified as territory defence and not the behaviours that were often associated with them like walking or standing.

The impacts of excluding the southern cliffs and Mangere Island in the calculations for habitat use may result in the amount of cliff and some rock or rock platform habitat available (and possibly used) to be under- or overestimated, as occasionally a few CIO have been sighted along the southern cliffs, and two to three pairs of CIO breed on Mangere. However, the number of CIO using these areas and the amount of coastline excluded was a small percent of the total. There was some error because of rounding or measurement methods, but totals were within 11 kms (4%) for Chatham Island, 5 kms

(5%) for the lagoon, 6 (13%) for Pitt, and 0.7 (8%) for Rangatira of estimates obtained from the 1998 CIO census and those calculated by A. Davis (pers. comm.).

The use of broad classifications of habitat types has several limitations. Most habitats are a mix of features. The classification simplifies this, and CIO may be using small patches of one habitat type within a section of habitat that has been classified as another type. In the analysis of habitat use by zone, some habitat types may seem to be favoured, but this could be because some habitat types are often association with each other. For example, marram dunes (classified as 'vegetation') were almost alway associated with wide sandy beaches. CIO often used these beaches; in the analysis it appears they preferred vegetation when it was the beaches they were selecting. CIO do much of their foraging at mid- to low tides on marine invertebrates (Davis 1988; pers. obs). The use/availability calculations probably tend to underestimate the selection for these intertidal areas because they are only available for a few hours per day, further confirming the trend that they are highly selected for, and used in relation to, their availability, possibly up to two or three times as much as my data indicated.

Care must be made in interpreting habitat selection information. Habitats may appear suitable for CIO, but are not, because of predation or disturbance, and short term limitations of habitat suitability may be difficult to detect. For example, food may be unavailable because of storms and wind for a couple of days which could be fatal for young chicks. Large storm events, which flood nests, may only occur in some years, and some areas may be more susceptible than others, but may not be easily measured or assessed.

Non habitat factors may influence habitat selection, factors such as social cues, predator pressure, or disturbance (Stamps 1987; Stamps 1988; Smith and Peacock 1990; Reed and Dobson 1993; Baptista and Gaunt 1997; Newton 1998; see also Chapter 3). Therefore, areas with good habitat for CIO may be unoccupied and individuals may be found only in less preferred habitats because of predator pressure. For example, Takahe were thought to prefer high altitude tussock grassland, but they may be found only in these areas because of predator pressures elsewhere in their more preferred habitats (Newton 1998).

Birds may avoid nesting in areas when predators or disturbance are present, or may select different types of nesting habitat depending on the type of predator present (i.e., aerial versus ground). Several experiments have shown when predators are reduced or eliminated from areas, breeding pair densities may quickly increase from new immigration and settlement (reviewed in Newton 1998). Terrestrial predator pressure and disturbance on Chatham and Pitt Island may have discouraged CIO from settling in what were otherwise suitable or preferred habitats, and skua or disturbance may influence habitat use on Rangatira. Predators may also influence the choice of habitat used.

Disturbance may cause otherwise suitable habitat to be abandoned or avoided (reviewed in Newton 1988, see also Chapter 3). Livestock have been video-taped harassing nesting birds (Moore *et al.* 2000), and some CIO territories are subject to periodic high levels of human use (e.g., Ohira Bay and Te Awanui Island) (see map Chapter 3, p 35) (pers. obs). Areas such as around Waitangi, Owenga and possibly Kaingaroa may receive little or no use from CIO because of disturbance from humans rather than from a lack of suitable physical habitat.

This study provides some understanding of habitat selection by CIO, that is which habitats are used under current conditions, but not preference. This is because the least dominant floater might prefer an area with intertidal rock platform and wide sandy beaches, for example, but it may select other areas because territorial pairs exclude it from using its most preferred areas. Density is also not necessarily a better indicator of habitat preference or quality for a variety of reasons (Fretwell 1972; Van Horne 1983). Sequential filling of habitats is a good indication of preference. Ideally, to determine preference, all the CIO would be removed and reintroduced one at a time. Obviously this is impractical. Some indication of preference might be gained by determining which habitats are most consistently occupied, over seasons and over years.

Summary

CIO selected habitats along the entire coastline which provided critical resources, such as food and nest-sites. CIO use and have territories at high densities in areas of rock platform (e.g., Tioriori), mixed sand/rock (e.g., Wharekauri), and wide schist platform (e.g., Whangamoe); and also some sections of sandy beach, especially around river mouths, were high (e.g., Washout Creek to Tutuiri Creek). Breeding pairs tended to select breeding territories which included rock platform and wide sandy beaches. Floaters selected habitats in somewhat different ratios than breeders, probably in part because they were more free to move around, they were excluded from breeding territories, and they can use areas which are have good foraging habitat but are not good for breeding. Use of the lagoon shoreline by CIO was low and restricted to floaters. This may be because availability of food supplies are unpredictable due to fluctuating water and salinity levels within the lagoon. Paddocks tended to be in sections of coastline that were avoided by CIO, such as cliff areas, which may explain why they were used less than expected as the intertidal and storm-tide zones may be contain more critical habitats, especially for breeding pairs.

The highest density of territories (4 pairs/km) was at Tioriori, along the north coast, Chatham Island. The 15 territories within the north coast study area tended to be of three main types: primarily sandy beach, territories with rock platform, or those which were a mix of habitat types. The longest territories were those composed primarily of sandy beach, with no rock platform within their boundaries.

Although CIO have been considered only one of two pied coloured oystercatcher species to specialise on rocky shore habitat (Hockey 1996b), most pairs along the north coast, Chatham Island, used sandy beaches extensively, and several pairs used sandy beaches almost exclusively for foraging and other activities. The extensive use of sandy beaches was either previously under-detected or is a recent development. Sandy beaches provided foraging habitat even when rock platforms are covered by the tides, and were often used for nesting. Streams seem to be a preferred feature, especially along sections of sandy beach. Some pairs used paddocks for foraging quite extensively (up to 22%). Paddock and sandy beaches provided forage even during high tides for many pairs.

Some caution must be used in interpreting habitat use data as birds may be avoiding preferred habitat areas because of factors such as disturbance or predation pressure. Predicting future use from current use is difficult because as populations increase, less preferred habitats may be used which are not used at lower densities.

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APPENDICES

Appendix 1

North coast territory categories and characteristics. Categories: MX - mixed, SB - sandy beach, RP - rock platform. Habitat types: SB - sandy beach, FW - fresh water RP - rock platform, OTH - other, UNK - unknown. Numbers in bold - habitats used for a high percentage (top third) of the time by the CIO breeding pair in residence. N = number of observation sets. In order by geographic distribution from southwest to northeast.

Territory	Category	SB+FW	RP	OTH	UNK	(n)
Whanga	MX	10%	6%	81%	3%	7
WW	SB	**96%**		0%	4%	8
WoC	SB	**94%**		0%	6%	15
TW	SB	**86%**		8%	6%	13
TE	SB	**85%**		12%	3%	13
OTF	MX	76%		22%	2%	11
Creek	MX	82%	17%	0%	2%	12
Pounamu	MX	73%	14%	8%	5%	12
Dune	RP	47%	**29%**	21%	4%	14
Cliff	RP	60%	**28%**	4%	7%	11
Cape	RP	59%	**32%**	0%	9%	7
Mairangi	MX	66%	14%	16%	5%	10
Woolshed	SB	**96%**		2%	2%	9
Rock	RP	26%	**55%**	14%	6%	7
Island	RP	47%	**50%**	0%	3%	6
Mean		70%	27%	11%	4%	155

Appendix 2

Combinations of habitat types that occur along the north coast study areas (Waitangi West to Okahu Point, and Whangamoe to Whangatete Bays).

Intertidal	Storm-tide	Terrestrial	Kms
boulder/cliff/shell	boulder/cliff	vegetation	0.25
	rock or shell narrow	vegetation	3.50
	sand or sand mix	vegetation	1.75
total			5.50
rock or rock/sand mix	sand or sand mix	cliff	2.50
	sand or sand mix	paddock	0.25
	sand narrow	vegetation	0.25
total			3.00
rock platform	boulder/cliff	paddock	0.25
	rock or shell narrow	paddock	0.25
	sand or sand mix	vegetation	1.25
	sand narrow	vegetation	1.75
total			3.50
sand	no storm zone	paddock	1.25
	sand or sand mix	vegetation	10.50
total			11.75
schist	rock or shell	paddock	3.00
	rock or shell narrow	paddock	0.75
		vegetation	0.75
	sand or sand mix	vegetation	0.75
total			5.25
Grand total			28.00

Appendix 3

Habitat categories by zone. Wide or narrow categories (e.g. rock platform) were those section greater or less than 30 metres wide.

Zone	Habitat categories within each zone	Total kms	Total no. of sections
terrestrial	cliff	46.50	69
	paddock	68.75	76
	vegetation	152.25	151
storm-tide	boulder/cliff	35.50	64
	no storm zone	15.25	16
	rock/shell	75.25	96
	rock/shell narrow	36.00	41
	sand	47.50	54
	sand narrow	58.00	25
intertidal	boulder/cliff/shell	26.75	38
	rock/mix	45.25	70
	rock platform	34.75	69
	sand	96.25	50
	schist	64.5	69

Appendix 4

Ratios of use versus availability for combinations of intertidal plus storm-tide zones for all CIO (pairs and floaters combined). Bold print - habitat types with 5% or more availability and with ratios above or below 1.5 or 0.5 (indicating selection at least 50% higher or lower than would be expected based on availability), plus or minus signs indicate the nature of the selection. For habitat types with availability below 5% caution in interpretation is needed because of the small denominator, which may inflate the ratios.

Intertidal	Stormtide	Use	Available	Ratio
b/c/l	b/c	0.01	**0.06**	**0.19 -**
	l	0.00	0.00	0.00
	ln	0.00	0.01	0.00
	nsz	0.00	0.00	0.00
	r	0.00	0.01	0.00
	s	0.00	0.01	0.00
b/c/l total		0.01	**0.10**	**0.12 -**
r/mx	b/c	0.02	0.03	0.55
	l	0.01	0.00	2.91
	ln	0.00	0.00	0.00
	mx	0.00	0.00	1.09
	nsz	0.01	0.01	1.19
	r	0.07	0.09	0.74
	rn	0.01	0.01	1.25
	s	0.06	0.01	4.70
	sn	0.00	0.01	0.00
r/mx total		0.18	0.17	1.04
rp	b/c	0.06	0.04	1.64
	l	0.01	0.00	8.73
	ln	0.00	0.00	0.00
	mx	0.02	0.01	4.37
	nsz	0.00	0.01	0.00
	r	0.17	0.04	3.81
	rn	0.02	0.01	1.46
	s	0.08	0.00	16.60
	sn	0.13	0.01	8.73
rp total		0.49	**0.13**	**3.74 +**
s	b/c	0.00	0.00	0.00
	l	0.00	0.00	0.00
	mx	0.01	0.01	0.58
	nsz	0.00	0.03	0.00
	s	0.18	**0.12**	**1.55 +**
	sn	0.01	**0.19**	**0.06 -**
s total		0.20	0.36	0.56
t	l	0.00	0.00	0.87
	mx	0.03	0.01	4.37
	r	0.06	0.12	0.50
	rn	0.01	**0.10**	**0.12 -**
	s	0.02	0.01	3.12
t total		0.13	0.24	0.52

Appendix 5a

Habitat ratios by zone for the combination of mapping and census, mapping alone, and census alone. (See also Table 4.)

MAPPING & CENSUS	**Floaters**					**Pairs**				
	Use		Available			Use		Available		
	No.	Prop.	Kms	Prop.	Ratio	No.	Prop.	Kms	Prop.	Ratio
terrestrial										
c	4.00	0.13	46.50	0.17	0.73	5.50	0.12	46.50	0.17	0.70
p	10.00	0.32	68.75	0.26	1.24	5.00	0.11	68.75	0.26	**0.43 -**
v	17.50	0.56	152.25	0.57	0.98	35.00	0.77	152.25	0.57	1.35
total	31.50	1.00	267.50	1.00		45.50	1.00	267.50	1.00	
stormtide										
b/c	3.00	0.10	35.50	0.13	0.72	4.00	0.09	35.50	0.13	0.66
nsz	0.50	0.02	15.25	0.06	**0.28 -**	0.50	0.01	15.25	0.06	**0.19 -**
sn	2.50	0.08	58.00	0.22	**0.37 -**	7.50	0.16	58.00	0.22	0.76
r/l	13.00	0.41	75.25	0.28	1.47	13.00	0.29	75.25	0.28	1.02
m/ln	1.50	0.05	36.00	0.13	**0.35 -**	1.50	0.03	36.00	0.13	**0.24 -**
s/mx	11.00	0.35	47.50	0.18	**1.97 +**	19.00	0.42	47.50	0.18	**2.35 +**
total	31.50	1.00	267.50	1.00		45.50	1.00	267.50	1.00	
intertidal										
b/c/l	0.50	0.02	26.75	0.10	**0.16 -**	0.50	0.01	26.75	0.10	**0.11 -**
r/mx	7.50	0.24	45.25	0.17	1.41	7.00	0.15	45.25	0.17	0.91
rp	10.50	0.33	34.75	0.13	**2.57 +**	24.50	0.54	34.75	0.13	**4.14 +**
s	6.50	0.21	96.25	0.36	0.57	9.00	0.20	96.25	0.36	0.55
t	6.50	0.21	64.50	0.24	0.86	4.50	0.10	64.50	0.24	**0.41 -**
total	31.50	1.00	267.50	1.00		45.50	1.00	267.50	1.00	

Appendix 5b

MAPPING ONLY	**Floaters**					**Pairs**				
	Use		Available			Use		Available		
	No.	Prop.	Kms	Prop.	Ratio	No.	Prop.	Kms	Prop.	Ratio
terrestrial										
c	2.00	0.06	55.00	0.20	**0.32 -**	7.00	0.17	55.00	0.20	0.86
p	12.00	0.39	69.25	0.25	**1.55 +**	4.00	0.10	69.25	0.25	**0.39 -**
v	17.00	0.55	152.25	0.55	1.00	30.00	0.73	152.25	0.55	1.33
total	31.00	1.00	276.50	1.00		41.00	1.00	276.50	1.00	
stormtide										
b/c	1.00	0.03	37.00	0.13	**0.24 -**	6.00	0.15	37.00	0.13	1.09
nsz	0.00	0.00	15.25	0.06	**0.00 -**	0.00	0.00	15.25	0.06	**0.00 -**
sn	1.00	0.03	58.00	0.21	**0.15 -**	5.00	0.12	58.00	0.21	0.58
r/l	15.00	0.48	80.75	0.29	**1.66 +**	13.00	0.32	80.75	0.29	1.09
rn/ln	1.00	0.03	38.00	0.14	**0.23 -**	1.00	0.02	38.00	0.14	**0.18 -**
s/mx	13.00	0.42	47.50	0.17	**2.44 +**	16.00	0.39	47.50	0.17	**2.27 +**
total	31.00	1.00	276.50	1.00		41.00	1.00	276.50	1.00	
intertidal										
b/c/l	0.00	0.00	29.75	0.11	**0.00 -**	0.00	0.00	29.75	0.11	**0.00 -**
r/mx	9.00	0.29	47.00	0.17	**1.71 +**	6.00	0.15	47.00	0.17	0.88
rp	9.00	0.29	39.00	0.14	**2.06 +**	25.00	0.61	39.00	0.14	**4.32 +**
s	4.00	0.13	96.25	0.35	**0.37 -**	6.00	0.15	96.25	0.35	**0.42 -**
t	9.00	0.29	64.50	0.23	1.24	4.00	0.10	64.50	0.23	**0.42 -**
total	31.00	1.00	276.50	1.00		41.00	1.00	276.50	1.00	

Appendix 5c

CENSUS		**Floaters**					**Pairs**			
ONLY	Use		Available			Use		Available		
	No.	Prop.	Kms	Prop.	Ratio	No.	Prop.	Kms	Prop.	Ratio
terrestrial										
c	6.00	0.19	46.50	0.17	1.08	5.00	0.10	46.50	0.17	0.56
p	8.00	0.25	68.75	0.26	0.97	6.00	0.12	68.75	0.26	**0.46 -**
v	18.00	0.56	152.25	0.57	0.99	40.00	0.78	152.25	0.57	1.38
total	32.00	1.00	267.50	1.00		51.00	1.00	267.50	1.00	
stormtide										
b/c	5.00	0.16	35.50	0.13	1.18	2.00	0.04	35.50	0.13	**0.30 -**
nsz	1.00	0.03	15.25	0.06	0.55	1.00	0.02	15.25	0.06	**0.34 -**
sn	4.00	0.13	58.00	0.22	0.58	10.00	0.20	58.00	0.22	0.90
r/l	11.00	0.34	75.25	0.28	1.22	13.00	0.25	75.25	0.28	0.91
rn/ln	2.00	0.06	36.00	0.13	**0.46 -**	3.00	0.06	36.00	0.13	**0.44 -**
s/mx	9.00	0.28	47.50	0.18	**1.58** +	22.00	0.43	47.50	0.18	**2.43** +
total	32.00	1.00	267.50	1.00		51.00	1.00	267.50	1.00	
intertidal										
b/c/l	1.00	0.03	26.75	0.10	**0.31 -**	1.00	0.02	26.75	0.10	**0.20 -**
r/mx	6.00	0.19	45.25	0.17	1.11	8.00	0.16	45.25	0.17	0.93
rp	12.00	0.38	34.75	0.13	**2.89** +	25.00	0.49	34.75	0.13	**3.77** +
s	9.00	0.28	96.25	0.36	0.78	12.00	0.24	96.25	0.36	0.65
t	4.00	0.13	64.50	0.24	0.52	5.00	0.10	64.50	0.24	**0.41 -**
total	32.00	1.00	267.50	1.00		51.00	1.00	267.50	1.00	

Appendix 6

Features and dimensions of CIO breeding territories, north coast, Chatham Island. X indicates the presence of the feature. Items in parenthesis indicate feature is outside territory boundaries but nearby.

	Coastline			Rock	Boulder/rock	
Territory	Length (m)	Widths (m)	Paddock	platform	sand mix	Stream
Whanga	350	10 - 30	x	x		
WW	1000	13 - 67				x
WOC	990	3 - 28	x			x
TW	700	4 - 25	x			x
TE	1310	30 - 64	x		x	x
OTF	1540	10 - 16	x		x	
Creek	180	15 - 37	x	x		x
Pounamu	170	4 - 8	x	x		
Dune	200	6 - 15	x	x		
Cliff	200	18 - 24	x	x		
Cape	450	1 - 9	(x)*	x		
Mairangi	490	5 - 15	x		x	x
Woolshed	700	5 - 70			x	(x)**
Rock	560	1 - 3	(x)	x		
Island	360	2 - 4	(x)	x		(x)
mean / count	610		10	8	4	8

* paddock use nearby and suspected use

** minor creeks, rather than larger streams

CHAPTER 5

TERRITORY QUALITY AND POPULATION LIMITATIONS IN CHATHAM ISLAND OYSTERCATCHER

ABSTRACT

To determine which limiting factors (e.g., nest-sites, foraging habitat, predators) were most likely to critical for the endangered Chatham Island oystercatcher (CIO), and during which season (breeding or nonbreeding), a study of several aspects of survival and breeding were examined in 15 pairs (about 25-33% of the estimated population) along the north coast, Chatham Island. In order to determine if lack of foraging habitat during the nonbreeding season was potentially a critically limiting factor to the population, over-winter survival of first-year birds was monitored during the 1994/5 and 1995/6 breeding seasons. To examine the role of territory quality in the population dynamics of the species during the breeding season, productivity and habitat characteristic within the territories were compared from the 1994/5 to 1996/7 breeding seasons. Additional comparisons were made with three seasons of past and recent data from this same area in which management occurred (primarily in the form of predator control) to assess the effects of predator pressure and habitat quality on productivity in CIO. To determine the role of habitat in productivity, territories were classified according the predominant habitats present and used by the resident pairs, and productivity by territory type compared.

Over-winter survival of first-year CIO was high (83% and 71% of 6 and 7 fledglings in 1994/5 and 1995/6 respectively), suggesting that the main regulating factors within the population are more likely to be operating during the breeding season, rather than over winter.

Several pairs in territories had breeding parameters predicted to reflect good quality habitat (e.g., large, early clutches; short clutch replacement intervals) but productivity was low or nil during the three seasons of this study. Some pairs in territories that produced

few or no fledglings during the three seasons of this study were highly productive in the three seasons before and after this study. The high number of multi-chick broods produced during nine seasons of monitoring suggests that quality and availability of food within territories along the north coast was very good, at least in some years. Hatching failure from tidal flooding was a major cause of breeding failure in some territories. Eight of fifteen pairs lost 50% or more of their clutches to flooding over three seasons, with one pair losing 83% (5/6) clutches to tidal flooding.

Sandy beach type territories were by far the most productive (0.80 fledglings/pair/season), followed by mixed and rocky platform type territories (0.33 and 0.22 fledglings/pair/season respectively). The differences between territory types were especially pronounced during the seasons of this study when there was little or no management. During periods of management, especially intensive predator control, these differences in productivity between territory types decreased. Under unmanaged conditions on the north coast of Chatham Islands, CIO may have to choose between good quality foraging habitat and low quality nest-sites; the areas with better nesting sites, and higher hatching success, may have less optimal foraging habitat as reflected in the breeding parameters examined.

INTRODUCTION

Two key questions need to be answered to effectively understand the population dynamics of CIO. What are the factors limiting the population and when do they occur (e.g., during the breeding or nonbreeding season)? To understand limiting factors and their effect on populations requires understanding recruitment and mortality rates. Factors that change either recruitment or mortality rates, and are not compensatory, will affect the total population size. The probable limiting factors include food availability, nest-sites, predation and disturbance. These factors probably interact to limit the CIO population and may vary from season to season and location to location.

It is important to understand the effect of season when limiting factors are operating. Often the main density dependent regulatory influences may occur mostly or completely during one season ([Fretwell, 1972 #39]). This has important implications for conservation management and also determining when habitat quality may be limiting.

For example, in oystercatchers, over-winter survival rates are the lowest among first-year birds because of their lower dominance rank relative to the older birds (Goss-Custard *et al.* 1982; Goss-Custard 1985; Goss-Custard and Durell 1988; Hulscher 1989; Hulscher 1990; Goss-Custard *et al.* 1994b; Nol and Humphrey 1994; Andres and Falxa 1995; Ens and Cayford 1996; Goss-Custard *et al.* 1996; Hockey 1996). If over-winter survival is low and density dependent, this may be the main factor regulating the population and no amount of management to increase productivity during the breeding season will succeed in increasing the breeding population. However, if the main limiting factors are operating during the breeding season, it would then be crucial to target research and conservation management during this period.

During the breeding season, limiting factors which have been found to affect productivity and survival of breeding oystercatchers include: 1) food - amount, availability, and location - especially proximity and access for chicks, 2) nest-sites - availability of sites which are free from flooding and provide good visibility, 3) predator pressures, and 4) disturbance factors. The best quality breeding territories for CIO would therefore be predicted to have the following characteristics: 1) high quality and density of food which is easily accessible to both adults and chicks, 2) nesting areas that are safe from flooding and allow good visibility to allow for detection and escape from predators, 3) islands or areas with low predator pressure and/or little cover for predators, and 4) little or no disturbance from humans or livestock.

Background

Vegetation, predators, and disturbance factors have changed significantly on the Chathams since humans arrived, possibly changing habitat use patterns by CIO. In dune areas, grazing by stock, and competition with marram grass (*Ammophila arenaria*) has largely eliminated the original, more open dune community of pingao (*Desmoschoenus spiralis*) and endemic herbs (Atkinson 1996). Marram typically changes dune structure causing steeper dunes and thick vegetative cover (Heyligers 1985), reducing the availability of habitat for CIO (Best 1987; Park 1994).

Many predator species have been introduced to Chatham and Pitt Islands, the most significant being cats (*Felis catus*) as they are known predators of eggs, chicks and adult shorebirds including oystercatchers (see Table 18, Chapter 3). Other introduced predators include weka (*Gallirallus australis*) (a flightless rail endemic to the New Zealand mainland), possum (*Trichosurus vulpecula*), hedgehog (*Erinaceus eruopaeus*), rats (*Rattus norvegicus, R. rattus*), and dogs (*Canus familiaris*). High numbers of cats, weka, rats, and possum have been documented during recent control operations along the north coast of Chatham Island (see Chapter 3, Moore *et al.* 2000). All of these species, except rats, are known to attack CIO nests and disturb, or attack, incubating adults (Moore *et al.* 2000).

Habitat changes and human activities have probably resulted in establishment of spur-winged plover (*Vanellus miles*), a potential predator/competitor, and higher densities of aerial predators such as black-backed gulls (*Larus dominicanus*) and harriers (*Circus approximans*). Harriers may attack oystercatchers with young chicks, and black-backed gulls are well documented predators of other species of oystercatcher chicks (Table 18, Chapter 3).

Livestock, and other forms of non-historical disturbance (e.g. vehicles, dogs, humans) are frequent and widespread along portions of the coastline of the two main islands (pers. obs.). Conversely some forms of predation and disturbance may now be less because of human occupation of the islands, especially that from brown skua (*Catharacta skua*), which have been extirpated from Chatham Island where they were once common (E. Young, pers. comm.).

Management to increase CIO productivity occurred in the three breeding seasons before and after this study (Murman 1991; Sawyer 1993; Sawyer 1994; Bell 1998; O'Connor 1999; Moore *et al.* 2000). The intensity of the management varied, being lower in the 1991/2-1993/4 breeding seasons (referred to hereafter as seasons), and higher during the 1997/8-1999/0 breeding seasons (hereafter seasons are given as the year in which breeding begins). The primary management action was control of predators in both periods. Artificial incubation of eggs occurred during the 1991-1993 seasons, and exclusion of livestock in some areas in the 1997-1999 seasons. Two pairs, WW and Whanga, were outside the management areas in all seasons. See Chapter 3, Table 19 for details of predator control.

Objectives

Ideally territory quality would be assessed by finding measures that accurately predict fitness of pairs within the territories (i.e., productivity and survival of the pair, and subsequent survival and productivity of their young) which is independent of the confounding factors of individual bird quality; and by understanding the critical resource(s) that are provided by these territories such as visibility to allow escape from predators, nest-sites, or food supplies. This is difficult however, and reviews by Cluton-Brock (1988) and Newton (1989) yielded only three studies that reported critical resource(s) determining territory quality, and even then understanding was still incomplete. In this study, territory quality is inferred from habitat selection, preference, and breeding parameters.

In the best quality breeding territories, the following responses might be predicted in breeding parameters: 1) high hatching success (few clutches flooded or lost to other causes); 2) large, early clutches (because of good food availability); 3) similar egg masses within a clutch; 4) high adult survival and 'high quality' pairs (i.e., older birds and a long pair bond); 5) a relatively high proportion of two or three-chick broods; 6) high survival rates of chicks to fledging; 7) short fledging times for equal-size broods; and 8) short clutch replacement times (Ens 1992; Hockey 1996; Newton 1998; Hazlitt 1999; Heg 1999). High quality territories should be preferred by CIO if they follow the same patterns as many other birds and, therefore, the highest quality territories would be predicted to have the following characteristics: 1) high rates of occupancy from year to year, 2) low pair turnover, and 3) be defended for as much of the year as conditions allow (Baeyens 1981; Møller 1982; Matthysen 1987; Nilsson 1987; Andrén 1990; Winker *et al.* 1995).

The aims of this study were:

1) to determine if over-winter habitat was a potentially critically limiting factor during the non-breeding season by estimating over-winter survival of first-year birds (these are the cohort most likely to starve if over-winter foraging habitat is limited, therefore, if first year survival was low and density dependent, it may be a critically limiting factor),

2) to determine characteristics of territory quality by comparing breeding parameters between 15 pairs of CIO,
3) to determine correlations between habitat features of territories and breeding success, and
4) to compare productivity of the study territories under three periods of varying management intensity to determine the effects of predator control (and other management) on breeding success in different territory types and thereby identify probable limiting factors.

It would have been desirable to determine the role of storm patterns over the periods when management intervention was occurring (i.e, 1991-1993 and 1997-1999), compared to the seasons of this research would have been desirable, but was outside the scope of this study.

Definitions

Breeding success, unless otherwise defined, refers to successfully raising at least one chick to fledging.

Floaters - nonterritorial, nonbreeders.

METHODS AND LOCATION

I studied habitat use within 15 breeding territories along the north coast of Chatham Island between Waitangi West and Okahu Point near Wharekauri, and between Whangamoe and Whangatete Bays (a total of about 28 kms of coastline). Names and locations of territories in the north coast of Chatham Island are given in Chapter 3, Figure 1. These sections of coastline are characterised by a mix of volcanic (or volcanic derived) intertidal rock platform, schist rock, sandy beaches, and small sections of shell or boulder beaches. Terrestrial areas along the coastline include long sections of marram dunes, paddock, forest patches, rough vegetation and cliffs (Chapter 4, Table 1 and Appendix 1).

In order to gather evidence on if the main factors limiting the population were occurring during the breeding season, or over winter, some juveniles were colour banded with powder-coated metal bands the first two seasons and records of any resightings kept in the following seasons. Minimum survival rates of first-year birds were then calculated from these sightings. Unfortunately the colours on the bands wore off to the point where resighting information was unreliable after the first year of wear on these bands.

To determine breeding success within territories over longer time periods and under different management scenarios, productivity was compared over nine seasons for the territories within the north coast study area.

To determine if differences in breeding success were because of the type of habitats predominantly available and used by pairs, territories were categorised into three types: sandy beach, rocky platform, and mixed. The third of territories which contained no rock platform and pairs used sandy beach (including the areas around fresh water) 85% of the time or more the territory was classified as 'sandy beach'; the third of territories where rock platform was available within the territory and was used over 25% of the time were classified as 'rock platform'; the other third of the territories, which contained a mix of habitat types, were classified as 'mixed' territories (Appendix 1). To determine if any of the territory types were more productive than the others, productivity was compared between the three major habitat types. Hatching success and losses to flooding were also calculated by territory type to determine variations in these parameters between habitats. A repeated measures ANOVA was used to test for significant differences between territory types, management level and productivity.

To compare territory quality several breeding parameters were tabulated including: early clutch initiation dates, absences of pair members from territories during the breeding season, clutch replacement intervals, fledging times, suspected pair turnover, hatching success and losses to flooding. Because monitoring began late in the 1994 season, early clutch initiation was compared for only the 1995 and 1996 seasons. Data on presence or absent of pair members from their territories were collected for the last two seasons only. When unusual behaviours were seen that might indicate pair turnover, these were noted; for example an unusual amount of calling, chasing, and interactions between the two birds seen within the territory boundaries. For clutch replacement intervals and fledging times the mid-point of possible dates was used.

To determine if territories were defended during the nonbreeding season, territories were checked for pair occupancy in late winter (August). Unfortunately, due to logistic constraints, other areas could not be checked for comparison. To estimate potential pair turnover, notes on pair behaviour was noted if pair turnover was suspected. Adult birds were not allowed to be individually marked by the banding office during this study due to past problems with colour bands.

Pairs monitored less than seven times per season were excluded from all hatching success and flood loss calculations. Some clutches excluded from hatching success and flooding calculations in Chapter 3 were included in this chapter to give a better indication of differences between territories. Clutches of unknown final size (i.e., clutches only seen once) were included in hatch success calculations, but excluded from clutch size calculations.

When calculating hatching success, the fate of some clutches was unknown because they may have been lost either before or after hatching. For those that were unknown, the likelihood of hatching was divided into three groups: high, low and unknown based on the available information about the clutch including estimated hatch date, dates of disappearance, and events which occurred around the time the clutch disappeared (e.g., eggs pipping and flooding events). Those with a high or low likelihood of having hatched were assumed to have hatched, or not, based on the likelihood assigned. For those assessed as having an equal probability of being lost before or after hatching were subdivided into two groups, with half being assumed to have hatched and half as not. Some nests were suspected, but not known, to have been lost to flooding. When calculating losses to flooding for these clutches, they were divided evenly into the two categories: flooded and non-flooded.

Egg volume was calculated by using the volume formulae from Davis (1988): volume = $0.507*(l*b^2)$, where l = length (mm) and b = breadth (mm).

RESULTS

Over-winter survival of first-year birds

Over-winter survival rates were high for the two years data were available. From the 1994 season 5 of 6 fledglings were seen the next season (minimum 83% survival rate), and from the 1995 seasons 5 of 7 fledglings were seen the following season (minimum 71% survival rate).

Territory quality

Breeding parameters predicted to be associated with high quality territories for 15 territories occupied along the north coast, Chatham Island from 1994 to 1996 were collated by territory and are reported below and summarised in Table 1.

Breeding attempts were high over the three seasons along the north coast (Table 1). All pairs attempted to breed in all breeding seasons except for the Dune pair during the first season. One territory, TE, was newly established in 1994 with a pair 'squeezing in' between the TW and OTF territories, primarily next to the TW territory. This pair did attempt to breed, but the male of this pair was probably only two years old (which may have resulted infertile eggs) (see Chapter 3).

Pairs either initiated clutches early, or had large clutches, but not both, except for the Cape pair. Pairs in five territories (Whanga, WOC, TW, TE, and Cape) initiated clutches early in both seasons monitored (Table 1). Seven territories had large first clutches (i.e., 2.33 eggs or more); of which three averaged 2.67 eggs/first clutch or more (Island, OTF, and Rock). In a few territories, pairs maintained relatively large clutch sizes for first, second, and third clutches (Island and Woolshed). Five territories (TW, TE, WW, Pounamu, and Dune) had pairs with consistently small first and second clutches (2.0 eggs/clutch or less).

Differences in intraclutch egg volumes varied by clutch order, territory, and the number of eggs within the clutch. Of two-egg first clutches (n = 8) TW, TE, and Woolshed had the least differences between eggs respectively (1.00-1.60 cm^3). However, eggs in the second two-egg clutches of TE and TW had the largest differences (3.44 cm^3 and 4.90 cm^3),

Table 1 *Summary of breeding parameters by territory. Bold numbers are those in the top third or more for parameters associated with high territory quality. Numbers in italics are those in the bottom third or less. +/- for clutch replacement intervals and fledging periods indicates range of possible dates events could have occurred (certainty measure).*

Territory	no. of seasons initiated clutches early*	mean clutch size**						1996/7 intraclutch egg volume differences (cm^3)					replacement intervals for first lost clutches (days)						hatching success***			
								2-egg clutch			3-egg clutch								flooded	hatched		
		1st	(n)	2nd	(n)	3rd	(n)	1st	2nd	3rd	1st	2nd	94	(+/-)	95	(+/-)	96	(+/-)	%	%	(+/-)	(n)
Whanga	**2**	2.00	1					2.35											**0%**	*33%*	0	3
WW	0	2.00	2	2.00	2	**2.00**	1	2.18		2.13					**8**	4	13	7	40%	40%	0	5
WoC	**2**	2.00	3	2.00	1												17	9	50%	**50%**	0	4
TW	**2**	2.00	3	2.00	1	1.00	1	**1.00**	*4.90*								15	8	30%	**60%**	0	5
TE	**2**	2.00	3	2.00	1	1.00	1	**1.23**	*3.44*								**12**	6	**0%**	40%	0	5
OTF	1	**3.00**	3	**2.50**	2						**0.56**	*5.80*	**12**	6	*22*	11	**10**	5	*83%*	*17%*	0	6
Creek	0	**2.33**	3	2.00	1			*2.91*							*19*	10			**25%**	38%	1.5	4
Pounamu	0	2.00	1	*1.50*	2										*20*	10	**11**	5	**20%**	40%	0	5
Dune	0	2.00	2	2.00	1			*2.84*							15	8			50%	*33%*	1	3
Cliff	1	**2.33**	3	2.00	1	**2.00**	1								*20*	10			*60%*	*30%*	0.5	5
Cape	**2**	**2.33**	3	**2.50**	2							5.05	**9**	5					50%	*30%*	1.5	5
Mairangi	1	2.00	1					2.32											**0%**	**100%**	0	2
Woolshed	1	**2.33**	3	**2.50**	2	**2.00**	1	**1.60**	**1.22**						**12**	6			50%	**42%**	0.5	6
Rock	0	**2.67**	3	2.00	2						3.71		**12**	6	17	9			50%	*20%*	0.5	5
Island	0	**3.00**	3	**3.00**	1	**2.00**	1				3.00				**11**	6			50%	**42%**	0.5	6
mean/total		2.31	37	2.16	19	1.67	6	2.05	3.19	2.13	2.42	5.43	11	5	16	8	13	7	41%	38%	4.5	69
(n)	15	15		13		6		8	3	1	3	2	3		9		6					

* two seasons only monitored

** clutches of uncertain size excluded

*** clutches of uncertain size included

(Continue overleaf)

Table 1 (cont...) *Summary of breeding parameters by territory. Bold numbers are those in the top third or more for parameters associated with high territory quality. Numbers in italics are those in the bottom third or less. +/- for clutch replacement intervals and fledging periods indicates range of possible dates events could have occurred (certainty measure).*

	fledglings		multi-chick broods		successful seasons		time to fledge (days)										absences by CIO pair members from their breeding territories			no. of checks	pair turn-over	new pair	brding attmpts
	mean		% of all				1-chick broods						2-chick broods										
Territory	per yr	(n)	broods	(n)	%	(n)	94	(+/-)	95	(+/-)	96	(+/-)	94	(+/-)	95	(+/-)	mean	95/6	96/7	(n)	over	pair	attmpts
Whanga	0.33	1	0%	0	33%	1			41	5							**0%**	0%	0%	17	?		100%
WW	**1.33**	4	**33%**	1	**100%**	3			39	2	39+*	6+	**42**	11			**0%**	0%	0%	41			100%
WoC	**1.00**	3	**50%**	1	**67%**	2			*47*	10			*53*	16			4%	6%	3%	57			100%
TW	**1.00**	3	**50%**	1	**67%**	2			**30**	8			47	1			2%	0%	3%	52			100%
TE	0.33	1	0%	0	33%	1			36	7							**0%**	0%	0%	50		y	100%
OTF	0.00	0	0%	0	0%	0											*10%*	0%	*14%*	42	?		100%
Creek	0.00	0	0%	0	0%	0											**0%**	0%	0%	45	y?		100%
Pounamu	0.00	0	0%	0	0%	0											3%	0%	4%	38	y		100%
Dune	0.00	0	0%	0	0%	0											7%	0%	11%	42			*67%*
Cliff	0.00	0	0%	0	0%	0											*20%*	*29%*	*13%*	41	y?		100%
Cape	0.00	0	0%	0	0%	0											*11%*	*10%*	*13%*	18			100%
Mairangi	**0.67**	2	0%	0	**67%**	2			**35**	11	46	16					**0%**	0%	0%	22	y?		100%
Woolshed	0.33	1	0%	0	33%	1	39	4									4%	8%	0%	27			100%
Rock	0.33	1	0%	0	33%	1	33	31									*13%*	*13%*	*13%*	32	y?		100%
Island	**1.33**	4	**100%**	2	**67%**	2							**43**	5	**36**	9	3%	0%	8%	29			100%
mean/total	0.44	20	33%	5	33%	15	36		37		43		46		36		7%	7%	8%	553			98%
(n)							2		6		2		4		1						7	1	

* fledged sometime after last monitoring check, when it estimated to be close to flying based on size and plumage

which was in contrast with the Woolshed pair, where differences in egg volume decreased slightly (1.22 cm^3, n = 3). Egg volume differences within three-egg clutches (n = 5) tended to be greater than those within two-egg clutches, with one notable exception. The volume difference between the largest and smallest egg within OTF's first three-egg clutch was a mere 0.56 cm^3, the smallest recorded of any clutch. After losing this clutch, the pair laid another three-egg clutch. In contrast to the previous clutch, the volume difference in this clutch was the largest recorded for the season of any clutch (5.80 cm^3).

Hatching success varied widely between territories, ranging from 17-100% (n = 69 clutches). Three territories had hatching success rates of 50% or more: Mairangi (100%), TW (60%), and WOC (50%); four had rates of 30% or less: OTF (17%), Rock (20%), Cliff and Cape (30% each). Losses to flooding varied from 0-83% (Table 1). The OTF territory pair lost five of its six clutches (83%) to flooding over the three seasons of the study. Three territories experienced no known losses to flooding (Whanga, TE, and Mairangi). In one territory (Pounamu) the pair attempted to nest behind a small set of dunes at the beginning of two seasons on bare sand and pebbles, but were unsuccessful both times because of trampling and disturbance. If hatching rates were below 40% on average, fledging success tended to be low (0-0.33 fledgling/pair/season).

Overall success rates ranged from 0-1.33 fledglings/territory/season and 0-4 fledglings in total over the three seasons. The two most productive territories were Island and WW (four fledglings each). The percentage of successful breeding seasons (at least one chick raised to flying) varied from 0-100%. One territory (WW) was successful every season. Almost half of all pairs fledged no chicks during the three seasons (all those at Tioriori plus OTF and Cape). Pairs from only four territories had multi-chick broods, and no pair raised a three-chick brood to fledging.

No single territory had consistently shorter replacement intervals than the others. The shortest replacement intervals were 8-12 days, the longest between 20-22 days. For the single pair with data for all three years (OTF), in two seasons the replacement intervals were short (12 and 10 days), but in the other season it had the longest replacement interval recorded (22 days).

Two-chick broods took longer to fledge than single-chick broods. Single-chick broods fledged in an estimated 30 to 47 days (mean 38.5, SD = 5.3) and two-chick broods took from 36 to 53 days to fly (mean 44.2, SD = 6.3). The shortest one-chick fledging times (n = 10) were in the TW and Mairangi territories (30 and 35 days respectively), and the shortest two-chick brood fledging times (n = 5) were in the Island (36 and 43 days) and WW (42 days) territories.

In summary, five territories were the most successful in many breeding parameters over the three seasons of this study, including chicks fledged per season: WW, Island, WOC, TW and Mairangi. Six territories had no breeding success at all; and of these, two (Pounamu and Dune) were among the lower third of most clutch parameters. OTF, Cliff and Cape were notable for their large, early and numerous clutches, as well as their rapid replacement intervals (except OTF in one season), but very low hatching success in all three cases.

Pair turnover was suspected in a number of territories (i.e., one or both members of a pair leaving or disappearing from the territory), but was mostly unconfirmed because of lack of individually marked birds. On one territory a banded bird disappeared during the first season and was replaced with a metal banded bird, and turnover was suspected (based on behaviours) for almost half of the others (7 of the 15 territories).

When the 15 north coast territories were checked during the non breeding season in late winter (between 8 and 23 August 1995), pairs were found in all of them on almost all occasions that the territories were checked. The soft part colourations all appeared as bright as during the summer breeding season. Numerous pairs were seen to either evict neighbouring pairs, or floaters, that came into their territories, or defend territory boundaries with neighbouring pairs. In one case the TE and TW pairs spent over 20 minutes in vigorous territory defence behaviours against one another. Flocks or individual floaters were occasionally tolerated for limited amounts of time within the territory boundaries. Mating by one pair was also observed, in spite of the fact that the earliest known nesting did not commence until mid-October.

During the 1995 and 1996 seasons, absences of CIO breeding pair members from their territories were recorded. One, or both, members of a pair were absent over 10% of the time in four territories (Table 1). Five territories recorded no absences. There was a difference of 10% or more between years for three pairs. One of these (Cliff) was probably due to the discovery in the 1996 season of the use by this pair of an adjacent cove which I had not been aware of in 1995. Most of the absences (82%) were after 1 January, rather than during the peak breeding period (October to December).

Productivity of territories over nine seasons

Breeding success for the 14-17 territories over nine seasons from 1991 to 1999 varied widely between seasons and also between territories. Three new territories were established along the north coast between 1991 and 1999 (TE in 1994, and WOCe and Ngatikitiki after 1996). Some territories were not monitored, newly established, or only intermittently occupied during the 1991 to 1993 seasons (Whanga, WW, WoC and Rock). Successful pairs tended to either be successful over many seasons, or have a high proportion of multi-chick broods, but not both (the Island territory being the only exception). Three pairs had successful seasons over 70% of the time: WOC, WOCe, and TW (Table 2).

Four territories were notable for the large number of multi-chick broods, successfully raising three or four such broods to fledging over nine breeding seasons (TW, OTF, Island, and Woolshed) (Table 2). Some territories consistently had a high percentage (67-100%) of multi-chick broods (Ngatikitiki, Dune, OTF, Woolshed, Rock and Island). Three-chick broods were extremely rare, but two territories had pairs which successfully raised three-chick broods to flying, Ngatikitiki and Woolshed, both in the 1999 season (Appendix 2).

Overall, some territories were very productive. Two territories sustained especially high productivity rates over the nine seasons: TW (1.33 fledgling/season) and Island (1.11 fledgling/season). WOCe averaged 1.50 fledgling/season over the two seasons the pair was in residence. Several other territories had an average of 1.00 fledgling/season over the nine seasons: WOC, TE, and OTF. Ngatikitiki also averaged 1.00 fledgling/season over the three seasons that a pair was in residence in this territory.

Table 2 Breeding success of CIO by territory over nine seasons, north coast Chatham Island. Successful seasons - the number of seasons a pair raised at least one chick to fledging.

Territory	seasons territory known occupied	seasons attempt to breed	successful seasons %	successful seasons (n)	multi-chick broods % of all broods	multi-chick broods total (n)	fledglings mean per yr	fledglings total (n)
Whanga	7	100%	33%	2	50%	1	0.43	3
WW	8	100%	67%	4	25%	1	0.63	5
WoC	8	100%	75%	6	33%	2	1.00	8
WoC e	2	100%	100%	2	50%	1	1.50	3
TW	9	100%	89%	8	50%	4	1.33	12
TE	6	100%	67%	4	50%	2	1.00	6
Ngatikitiki	3	100%	33%	1	100%	1	1.00	3
OTF	9	100%	56%	5	80%	4	1.00	9
Creek	9	100%	44%	4	25%	1	0.56	5
Pounamu	9	89%	11%	1	0%	0	0.11	1
Dune	9	89%	22%	2	100%	2	0.44	4
Cliff	9	100%	33%	3	33%	1	0.44	4
Cape	9	89%	11%	1	0%	0	0.11	1
Mairangi	9	100%	67%	6	0%	0	0.67	6
Woolshed	9	100%	44%	4	75%	3	0.89	8
Rock	8	88%	38%	3	67%	2	0.63	5
Island	9	100%	67%	6	67%	4	1.11	10
totals	132	97%	48%	62	47%	29	0.70	93

Many more territories reached high levels of productivity (i.e., 1.00 or more fledglings/season on average) during the periods with intensive management than in periods without management (Table 3). Five and four territories reached this level during the 1991-1993 and 1994-1996 periods respectively, compared with 11 during the most intensive management period (1997-1999). The very highest levels of productivity (1.67 fledglings/pair/season) were achieved only during periods with management. A total of four pairs (TW, TE, OTF, and Island) reached this level in at least one season, three during the more intensive period of management (1997-1999).

Some territories which were unsuccessful at producing fledglings during the three year study, were very successful in the seasons either before and/or after this study. If territories are ranked relative to one another, several pairs had higher rankings (i.e., top third versus bottom third) only in periods with some level of management (OTF, Dune, and Cliff). Across all years, regardless of management, only one territory (TW) was consistently in the top third (Appendix 3). Two were consistently in the bottom third,

Table 3 Average productivity of territories by three-season periods, north coast study area, in geographical order from western to eastern territories. Dashed lines (--) indicates no pair in residence. Management effort: 1991-1993 - low, 1994-1996-none, and 1997-1999 - intensive; management included predator control, nest manipulation, and livestock control. Numbers in bold, where productivity was 0.67 fledglings/pair/season more in the managed seasons compared with the unmanaged seasons. Pairs in bold - those with higher rates of productivity during both periods with management; pairs in bold italics - higher rates in one period. Two territories were never managed: Whanga and WW. Numbers in parenthesis - number of seasons monitored (if less than 3).

	Average fledglings/pair/season		
	1991-93	*1994-96*	*1997-99*
Territory			
Whanga	***2.00 (1)***	*0.33*	*0.00*
WW	*0.50 (2)*	*1.33*	*0.00*
WoC	*1.00 (2)*	*1.00*	*1.00*
WoC e	--	--	*0.50 (2)*
TW	*1.33*	*1.00*	***1.67***
TE	--	*0.33*	***1.67***
Ngatikitiki	--	--	*1.00*
OTF	***1.67***	*0.00*	***1.33***
Creek	***0.67***	*0.00*	***1.00***
Pounamu	*0.00*	*0.00*	*0.33*
Dune	*0.00*	*0.00*	***1.33***
Cliff	***1.33***	*0.00*	*0.00*
Cape	*0.00*	*0.00*	*0.33*
Mairangi	*0.33*	*0.67*	*1.00*
Woolshed	***1.33***	*0.33*	***1.00***
Rock	*0.00 (2)*	*0.33*	***1.33***
Island	*0.33*	*1.33*	*1.67*
Totals/means			
fledglings	*26*	*20*	*47*
no. pairs	*14*	*15*	*17*
fl/pr/yr	*0.62*	*0.44*	*0.92*

Pounamu and Cape. Three pairs were in the top third only in the seasons with no management (Mairangi, Island, and WW).

Habitat types and productivity

Productivity in all three periods, and overall, was higher in the sandy beach territories than the mixed or rock platform territories (Figure 1), but not significantly so at the 0.05 level (Table 4). Overall the sandy beach territories were almost twice as productive as the other two types, but the differences between habitat types was much less pronounced during the last period (1996-1999) of intensive management.

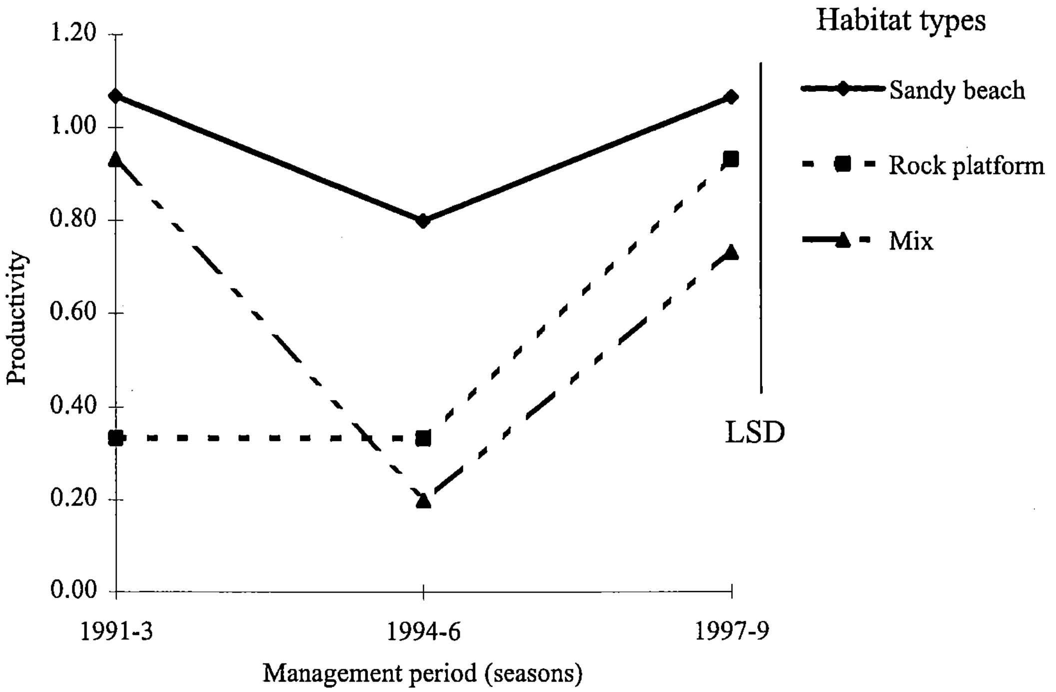

Figure 1 Average productivity (fledgling/pair/season) of CIO by territory type and by management period (each three breeding seasons long). Management intensity: 1991-3 - low, 1994-6 - none, 1997-9 - high. N = 5 for each habitat type each period. Two territories were included in all three periods, but were outside the management areas. Error bar is the LSD (= 0.754).

Table 4 Repeated measures ANOVA for territory types and season on productivity of CIO. (See also Figure 1).

Source	DF	SS	MS	F	P
Territory type	2	1.7387	0.8693	2.52	0.095
Period	2	1.6634	0.8317	2.41	0.104
Territory type * Period	4	1.1402	0.2850	0.82	0.518
Error	36	12.4395	0.3455		
Total	44				

In the comparison of hatching success and losses to flooding by territory type for 1994-1996, hatching success was higher in the sandy beach territories (46%, n = 5), compared with the mixed and rock platform territories (38%, n = 5 and 31%, n = 5 respectively). Flooding losses were higher for the territories classified as rock platform (52%, n = 5), and similar for mixed and sandy beach territories (38%, n = 5 and 34%, n = 5 respectively).

DISCUSSION

Seasons and limiting factors

The critical limiting factors for the northern population of CIO are almost certainly operating primarily during the breeding season, rather than over-winter, at least in most seasons. If over-winter habitat were a significant limiting factor, survival of first-year birds should be low; however, minimum survival rates of first-year birds were high (71-83%). The 1998 cohort had a similarly high survival rate of 72% (O'Connor, pers. comm.). This suggests that foraging habitat for floaters over-winter is adequate for high survival rates of immature CIO, as they are the portion of the population most vulnerable to starvation if food is limited because of their low dominance ranks and inexperience (reviewed in Goss-Custard *et al.* 1996; see also Goss-Custard *et al.* 1994a; Ens and Cayford 1996; Durell *et al.* 2000). If this is the case, at current densities the main factors limiting the population are operating during the breeding season through either low productivity and/or high mortality of breeding birds.

Territory quality

The most productive pairs over the three seasons were those in the Island and WW territories (1.33 fledgling/season), followed by WOC and TW (1.00 fledgling/season) (see Appendix 5 for detailed descriptions of each territory). All of the most productive pairs raised at least one multi-chick brood to fledging. Only one territory (WW) had a pair that was successful all three seasons (i.e., raised at least one chick to fledging per year). Pairs in six territories failed to fledge any chicks in the three seasons of the study (all the Tioriori pairs, OTF, and Cape). The most successful territories tended to be those with the highest average hatching success over the three seasons (40% or better), although some successful pairs had lower hatching success than unsuccessful pairs. In territories with moderately high hatching success (40% or better) but no successful seasons, predators or other factors (e.g., food availability, disturbance) were probably more significant than flooding.

Not attempting to breed was rare, only one pair in one season (Dune) did not nest. Possible causes for not attempting to breed include pair turnover, a combination of a low quality territory and poor year (i.e., bad weather), or monitoring frequencies which were too low to detect breeding attempts. Neither insufficient monitoring effort nor pair turnover can be ruled out for this territory. During the first season of the study monitoring was less frequent than other years, which was the season that the no breeding attempt was recorded. The pair was noted as acting suspicious (as if breeding) during one visit, but a nest was never found. It was also possible that this was a newly established pair or one of the pair members was too young to breed. The Dune territory may be one of the lower quality territories when there is no management intervention, but there is no reason to assume that 1994 was a poor year. On the contrary, it seemed to be an especially good year for other pairs as there were several two-chick broods produced and clutch replacement intervals were generally short.

The best territories were predicted to have pairs which initiated first clutches early in the season, had large clutches, low volume differences between eggs within a clutch, and short replacement intervals between clutches. No territory had all the predicted clutch characteristics of high quality territories relative to the others. Four pairs had both early and large clutches, but unexpectedly only one of these territories were ever successful at producing fledglings during the study period. The three unsuccessful territories (OTF, Cliff, Cape) may be good quality territories except for factors influencing hatching success. All of these territories had low hatching success (33% or less) and high losses to tidal flooding (50% or more).

Several pairs laid small, early first and second clutches, and if these were lost, they laid third clutches. Most of these pairs were successful. Early clutch initiation was associated with higher breeding success in Eurasian Oystercatchers, primarily because it allowed for more repeat breeding attempts if a nest or young chicks were lost (Heg 1999). Several factors were associated with earlier laying dates in Eurasian Oystercatchers including (in order of importance): length of the pair bond, food, females not spending time during the prelaying period in territory defence, and age of females (Heg 1999). Some of these factors are probably related. For example, with increasing age females may become more efficient feeders, and so may in effect have a better food supply. Older females may also be more likely to be in a well established pair. Pairs with long pair bonds may know their neighbours well and, therefore, need to spend less time defending the territory. This may in turn translate into less energy spent by the female in territory defence and more in feeding and egg production. On the Chathams, several of the territories with early clutch initiation were those without adjacent territories, or the territory had only one set of neighbours which may have decreased time spent in territory defence. Alternatively, many of these were sandy beach territories, and perhaps had better food supplies, or better habitat for escaping predators and therefore pairs with longer pair bonds (due to lower pair turnover).

Clutch characteristics may be influenced by a number of factors (turnover of pairs, differences in conditions between years, and interactions between factors), so no one set of breeding parameters alone may be accurate for assessing habitat quality. For example, based on the small, late clutches of the pairs in the Dune territory, low quality foraging habitat might have been assumed, yet the pair raised two multi-chick broods during the 1998 and 1999 seasons. However, it is also possible that the clutch characteristics were an accurate indicator of foraging quality during those years, and differences in weather and/or reduction of predators (especially weka) affected food availability.

Pairs can have relatively low hatching success and still be successful if they replace lost clutches, or if chicks have high survival rates after hatching. However, if hatching success is too low it can create a bottleneck, reducing or precluding breeding success regardless of how the quality of the territory and pair in other respects (e.g., excellent foraging habitat, or low predator pressure). Of the five territories with the highest average hatching success, four of these were the most successful at producing fledglings. Low hatching success appeared to impact one pair particularly during the period of this study, creating a bottleneck. The OTF pair only hatched 17% of its six clutches. Most of the clutches (83%) were lost to tidal flooding during storms. In the years before and after the study this pair had very high success raising fledglings (Table 2). In the three years before the study it was the most successful pair averaging 1.67 fledgling/season, and was among the most in the three year period after this study (1.33 fledgling/season). Much of this success was because the pair produced a high proportion of two-chick broods (4 out of 5), indicating this was probably a very high quality territory lacking only in good nesting sites, at least in years of stormy weather. (However, length of the pair bond or quality of the individuals as the reason for the differences in productivity can not be ruled out as an alternative explanation.)

Time to fledge is indicative of food availability. Four territories had short fledging periods (Island, WW, TW and Mairangi), indicating food availability was good. WOC had a long fledging period which, combined with the moderately high clutch replacement interval in 1996, suggests this territory may have lower quality foraging habitat than some of the other territories. Fledging periods might have been influenced by season as well as territory. The Mairangi territory, for example, had one of the shortest fledging times for one-chick broods during one season (35 days), but a relatively long one the next (46 days). Food availability may be influenced by predator or disturbance pressures. If these are high, chicks may not be able to spend as much time foraging as they would otherwise (Groves 1984).

Two territories, Pounamu and Dune, had breeding parameters indicative of poor quality territories for most clutch parameters (i.e., small, late clutches, and large intraclutch egg volume difference). Possible causes include high pair turnover, low food availability, and/or high predator pressure. In the seasons before and after this study, pairs within the Pounamu territory were never very successful; although the Dune territory produced 1.33 fledgling/season during the 1997-1999 seasons and, in both successful seasons, they raised multi-chick broods. This suggests food was abundant; as food abundance, rather than pair bond duration, is the best predictor of survival of multi-chick broods in oystercatchers (Groves 1984; Ens 1992; Hazlitt 1999; Heg 1999). Therefore, predator pressure and/or pair turnover were probably the prime limiting factors.

The TE territory may be of higher quality than the breeding success rates indicate because this was a new pair, and the male was probably only two years old, possibly too young to breed. (There was a metal banded male in this territory in 1994 and 1995, but a method for reading the band number was not discovered until 1995 which involved drawing birds with a metal band in close enough to use binoculars to read the number. If it was the same bird both seasons, then it was only two years old during in 1994.) This pair 'squeezed' in between the TW and OTF pairs.

The frequency of pair turnover during the three seasons of the study was potentially high, about 16% per season, but unfortunately data were limited because of lack of individually marked birds. Only one case of pair turnover was confirmed, which was in the Pounamu territory where a bird colour-banded on Rangatira Island in 1978 was in residence. If all the suspected or potential turnovers were accurately identified, this rate of turnover was high relative to other oystercatcher species, which is normally from about 8-15% from year to year (Hartwick 1974; Harris *et al.* 1987; Davis 1988; Ens 1992; Hockey 1996; Hazlitt 1999; Heg 1999). Populations are often more sensitive to the loss of breeding adults than to other factors (Hamilton and Moller 1995; Reed *et al.* 1998). Populations may also exhibit threshold responses to changes in mortality rates. In Hawaiian Stilts (*Himantopus mexicanus knudseni*), population modeling demonstrated that a 10% change in adult mortality could result in a drop in persistence probability from 100% to 0% (Reed *et al.* 1998). Population modeling could be used to explore these dynamics (but was outside the scope of this study).

Consequences of pair turnover are potentially serious for breeding success, especially if the main cause of turnover was death of pair members. Loss of a breeding pair member often results in loss of the any productivity for that breeding season, and always loss of the pair bond. Loss of the pair bond decreases productivity because pairs that have been together for longer are more successful than pairs that are newly established, with the highest success rates reached after seven years of association (Heg 1999). Causes of pair turnover can include either death of a pair member or divorce. Either of these may reflect poorer quality habitat within territories, either because pairs exposed to higher predation pressure were experiencing lower breeding success and therefore abandoning the territory, which is more common in unsuccessful than successful pairs (Hartwick 1974; Gavin and Bollinger 1978; Harvey *et al.* 1979; Roth and Johnson 1993; Winker *et al.* 1995; Ens *et al.* 1996) or incubating adults were being killed by predators.

Some pairs apparently spent time outside their core territories, especially when they were not nesting or raising chicks suggesting resources within the territory were not optimal. One or both members of a pair were absent from four territories over 10% of the time. In the Cliff territory some of the absences may have been because of pair turnover during the last season and/or the use of a nearby bay just east of the nesting territory which I did not discover the use of until the 1996 season. There was no significant source of fresh water in several territories so the Cliff pair (as well as other Tioriori birds) might have occasionally visited the mouth of Tutuiri Creek about 1 to 2 kms away to bath, drink and perhaps forage. Although CIO have well developed salt glands (Hockey 1996) and therefore probably do not require fresh water, they seem to use it frequently when available. CIO were often seen at the mouth of Tutuiri Creek, including some birds known to be from the Tioriori territories. Unsuccessful pairs were found less often than successful pairs, but since most of the absences were outside the main breeding season it seems unlikely that the absences were a prime cause of breeding failure. Possibly some factor affecting both breeding success and occupancy was common to unsuccessful territories, such as food availability.

Pairs along the north coast, Chatham Island, appeared to defend territories at least nine months of the year (from August to April). Higher quality habitats and territories should be preferred over, and also occupied during more of the year, than lower quality ones (reviewed in Newton 1998, p 54-59). Davis (1988) reported that the majority of pairs occupied the same territory throughout the year, although defence of the territory was lessened in the non-breeding season and there may be some movements between islands, e.g., from Rangatira to Pitt and visa versa. Strength of territory defence and occupancy throughout the year may be good indicators of preference in CIO if variations between areas exist, but more detailed monitoring would be needed to detect these differences.

Habitat types and productivity

Sandy beaches were by far the most productive type of territory, especially during this study, possibly because of differences in management intensity between the different periods (see introduction for description). During periods of management, especially intensive predator control, these differences in productivity between territory types decreased. With conditions of no management, wide sandy beaches may offer better escape from predators for adults and/or chicks than the other two territory types, or predator pressure may be higher in the mixed and rock platform type habitats.

Alternatively, the study period may have been an especially stormy one relative to the other two periods and sandy beaches offered better nesting habitat on average than the other two types. There is some evidence to support this hypothesis, in that hatching success was highest, and losses to flooding lowest, on sandy beach territories compared with rock platform territories during the study period. Hatching success was higher on sandy beaches than mixed territories, but the losses to flooding were about the same for both the sandy beach and mixed territories. Therefore, losses of clutches were occurring in the mixed territories in addition to flooding losses, compared with the sandy beach territories. Future research should include examination of past storm patterns and comparing them to breeding success by territory.

Limitations

In determining territory quality, conditions may change from year to year and there may be large variation between years. Three years and 15 territories was a relatively small sample, especially if there is large variation within sets, or interactions between factors. Ultimately, it is lifetime reproductive success that is of interest and CIO are long lived, so even several years with no breeding success could be insignificant if other years were very successful. However, over the nine total seasons, there were large differences between the most and least productive territories (1 versus 12 fledglings), and it is difficult to imagine that all of these differences would be erased, even over an additional five or ten years.

Some differences between territories may not have been detected because of large ranges for some of the parameters (especially clutch replacement intervals and fledging periods), and because for some parameters data were only available for one or two of the seasons. Some of the differences in the parameters could be because of various factors or a combination of them such as differences between territories, pairs, or years. Some factors may interact, for example, in the Netherlands lower quality territories had average productivity in good years, but had very low productivity in poor years (Heg 1999).

Caution must be used in interpreting habitat use data. Future, or even past habitat use is difficult to predict from current use. Determining habitat quality is best done from preference studies rather than selection or density data. The areas with the highest density of pairs may often be, but are not always necessarily, the best quality habitat (Pienkowski and Evans 1982; Van Horne 1983). High densities in some areas may be due to availability of habitats or other factors (e.g., predator pressure, disturbance, social cues), rather than the quality of habitat. Additionally, young birds may select the best areas available, changes in conditions occur, but due to strong site fidelity the birds stay in the same territories. To better determine preferences (as opposed to selection) a study of occupancy over time, including over-winter occupancy, would be needed. Even then it is difficult to predict preferences from current use - individuals may be using remnants of habitat that are less preferred because that is the only refuge from predators left available.

In the portion of this study looking at correlations between breeding success and habitat characteristics of territories some of the parameters that may reveal high quality habitat in territories, such as adult survival, were not determined, and some parameters were measured only broadly. Many of the sample sizes were small, so for some parameters the patterns are not clear and some of the results are not necessarily representative of other areas. However, the overall trends and results for the north coast population, which is significant proportion of the population (about 25-33% of the breeding population of CIO), are useful for understanding the population dynamics and social organisation potential needed to identify, and ultimately alleviate, the limiting factors affecting CIO on the Chatham Islands.

Productivity and management

Pairs in some territories such as WW, WOC, TW, Island and Mairangi were relatively productive regardless of management intervention, or in the absence of any management. Territories that were successful in the seasons with little or no management tended to be those with nesting sites available some distance from extensive vegetation cover. All these areas had large amounts of sandy beach for nesting, or in the case of the Island territory, they were well away from the main dune vegetation. The characteristics of these territories may have increased breeding success in several ways. The most likely is that pairs may were at less risk of predation during incubation and they may have had more options for nesting in areas of lower flood risk.

Pairs in some territories appear to respond especially well to management (e.g., OTF, Creek, Dune, Cliff, Woolshed, and Rock). The territories where pairs seemed to respond best were, in general, in areas with higher densities of CIO and which used rock platform for foraging to a greater degree than other territories. They also all had limited areas for nesting far from thick dune vegetation.

The very highest levels of productivity were only reached when there was at least some level of management. Four territories produced 1.67 fledglings/season on average with management, compared with the period without management where the highest level reached was 1.33 fledglings/season by two pairs. This suggests management was highly effective at increasing breeding success. In other bird species predator control is often highly successful. In a meta-analysis of 20 published studies of predator removal programs, removing predators had a large, positive effect on hatching success, with removal areas showing higher hatching success, on average, than 75% of control areas. Similarly, predator removal increased significantly post-breeding population sizes (Côté and Sutherland 1995). However, it is possibly that the differences were not due to management but to differences between years (e.g., storms), and/or a combination of year and management or other factors. Because management included several different techniques (e.g., predator trapping, moving nests, etc.), there is no way to know if it was any particular technique, or a combination of them, caused these higher productivity rates. The role of stormy years was also unknown. Flooding can be a very significant cause of egg loss (this chapter and Chapter 3), and some of the variability in nesting success may be related to direction and intensity of prevailing storms during a particular season. For pairs such as OTF which lost most clutches to flooding over the three seasons, predator control may do little to increase productivity during stormy years.

SUMMARY AND CONCLUSIONS

The main limiting factors for the population of CIO on the Chatham Islands were almost certainly operating primarily during the breeding season, rather than over winter. This could change in the future if the population increased. Based on the number of multi-chick broods and other breeding parameters, it does not appear food was a critical limiting factor for CIO during the breeding season along the north coast. Lack of high quality nest-sites, predator pressure, or disturbance were more likely causes of low productivity (and possibly high mortality among breeding adults).

Sandy beach territories were the most productive under all management scenarios, but especially in periods when there was little or no management. Many of the most recently established territories along the northern coastline of Chatham Island (i.e., established within the last 10-15 years) were in sections of coastline that were predominantly sandy beach (e.g. WW, WOC, TE, TW, Ngatikitiki). Many of the differences in habitat use reported in Davis (1988) and this study may be because of these newly established territories. Possibly CIO are expanding or changing their habitat preferences in response to changes on the Chathams.

Six pairs failed to raise any chicks to fledging during the entire three seasons of the study. In spite of loosing up to 50% of clutches, pairs were often successful at fledging chicks, but the more successful pairs tended to be those with higher hatching success. Among the 15 breeding territories studied in detail, it appeared that different factors may have been the primary cause of breeding failures. It is also likely that factors are interacting. In at least one territory (OTF) the main limiting factor was probably the lack of good quality nest-sites as evidenced by its very low hatching success due to high flooding losses (83% of clutches). Other territories had reasonably high hatching success (40% or better), but no chicks surviving to fledging (Creek, Pounamu, and Cape). In these territories the most critical limiting factors were probably predator pressure, disturbance, or other factors, rather than lack of suitable nest-sites.

All but three territories produced multi-chick broods, and some territories had multi-chick broods in up to four seasons of the nine. The ability of territories on the north coast to produce two- and even three-chick broods that survive to fledging suggests that food availability, at least in some years, was very good.

Productivity tended to increased significantly with management intervention, especially in the rock and mixed type territories. The highest levels of productivity (1.67 fledglings/pair/season) were reached only during periods of intensive management (including predator control, livestock exclusion, and nest manipulation), and overall fledging production was much higher (over twice as high per pair per year during the seasons with intensive management).

Habitat characteristics that make for high quality territories may change with circumstances or area. When ground predators are present, especially in high densities, then good visibility and open areas far from vegetation to avoid predators may be important. If ground predators are not present, or are in low densities, other habitat features may be more critical. Therefore, the most productive territories along the north coast may change depending on the management regime in place.

Adult turnover or mortality could be an important factor in limiting the CIO population, but lack of individually marked birds prevented determining pair turnover conclusively. The role of stormy weather in affecting productivity for the periods before and after this study was outside the scope of this study.

In summary - foraging habitat in either season is probably not a critical limiting factor, but predator pressure, lack of suitable nest-sites, disturbance, or a combination of these probably are critical factors limiting productivity and/or adult survival during the breeding season. Intensive management appears to be very successful at increasing productivity, especially in rock and mixed type territories. However, why this is the case is less clear, as is the role of stormy weather. Reasons for the success of intensive management could include: 1) reduced predator pressure resulting in less adult mortality and/or increased egg and chick survival, 2) reduced disturbance due to livestock and/or humans, 3) reduced food competition due to removal of weka and gulls, 4) inconsistencies in data collect/biased estimates or some combination of these factors. Many areas that currently have high quality foraging habitat may currently be unoccupied due to lack of good quality nesting-sites and/or due to low CIO population densities.

Management implications

The results of this study suggest that limiting factors on productivity may vary between areas and also between years. For example, some territories may suffer most from lack of suitable nesting habitat than from losses to predators, whereas others may have more problems with predators. The main cause of losses may also vary from year to year within the same territories because of storm patterns. It is possible that some of the predators of CIO (e.g., weka, gulls) are also competitors for food, so that controlling their numbers may increase food supplies as well as lower the predation risks.

Many of these factors probably interact with one another. For example, predators such as weka and black-backed gulls may also be food competitors. Marram grass may simultaneously decrease nesting sites and provide habitat for predators. If food availability is low in some years chicks may become more vulnerable to predators because, compared with well-fed chicks, hungry ones become more active and therefore more visible (Groves 1984; Ens *et al.* 1995; Heg 1999). As a result of these changing interactions, what is effective one year, may be less so in another year. For example, a low food year may lead to higher predation rates even though predator densities are kept the same.

Although predator control appears to be very effective for increasing breeding success and breeding pair densities, it is expensive and only effective as long as control continues. Because predator control is labour intensive and expensive, and resources have been limited on the Chathams, there may be more gains per unit of effort from controlling predators around high quality habitats (i.e., those with the best food and nesting resources) than around lower quality ones. This is because there would be a better chance of eggs hatching, clutches would typically be larger and earlier, and there would be more chicks per brood, resulting in an overall higher numbers of chicks fledged/pair. If good nest-sites are lacking, creating a bottleneck in productivity, providing high ground for nesting may be more effective than predator control.

The same results may be possible through habitat management, which is longer term and may be more cost effective in the long term (Côté and Sutherland 1997; Newton 1998). Removing marram grass may be an effective management option as marram may provide cover, and foraging and breeding habitat, for predators. Loss of nesting space because of changes in dune structure has occurred in other shore nesting species such as pied oystercatchers (*H. longirostris*) and hooded plover (*Thinornis runbricollis*) in Australia. Both species nest on terrace shaped foredunes formed by native grasses. At Calverts Beach in southern Tasmania, both species historically nested in the foredunes into the 1970s, but ceased nesting in the area after the dune system was stabilised with marram (Park 1994).

Future research

Areas of future research that would provide information for more effective conservation management and a better understanding of the relationships between habitat characteristics and limiting factors of CIO are suggested as follows:

- Determine the role of stormy weather in past productivity by comparing storm patterns with productivity by territory type.
- Monitor mortality and turnover of breeding pairs in different areas and under different types of management, attempt to determine if predation is a significant factor and, if so, the type of predation.
- Measure some of the breeding parameters more precisely, such as fledging times and clutch replacement intervals, and measure them for other areas.
- Use population modeling to estimate which breeding and survival parameters are most likely to affect the population size and to determine where management and research could be most effectively targeted.
- Determine habitat preferences (rather than just selection) by determining which areas are occupied every year and which territories are occupied over-winter.
- Identify and confirm 'leapfrog' territories, and the movements of adults outside of core territory boundaries. When adults use areas outside core territories, determine what resources they are seeking.
- Determine if food is limiting at any life stage, and if weka or other species are significant food competitors of CIO.
- Determine if removal of Marram grass improves breeding success of CIO.
- Analyse cat stomach contents to determine their main food items.

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APPENDICES

Appendix 1

North coast territory categories and time spent by pairs (all activities) in combined habitat types. Categories: MX - mixed, SB - sandy beach, RP - rock platform. Habitat types: SB - sandy beach, FW - fresh water RP - rock platform, OTH - other, UNK - unknown. Numbers in bold - habitats used for a high percentage (top third) of the time by the CIO breeding pair in residence. N = number of observation sets. In order by geographic distribution from southwest to northeast. (See also Table 11, Chapter 4).

Territory	Category	SB+FW	RP	OTH	UNK	(n)
Whanga	MX	10%		87%	3%	7
WW	SB	**96%**		0%	4%	8
WoC	SB	**94%**		0%	6%	15
TW	SB	**86%**		8%	6%	13
TE	SB	**85%**		12%	3%	13
OTF	MX	76%		22%	2%	11
Creek	MX	82%	17%	0%	2%	12
Pounamu	MX	73%	14%	8%	5%	12
Dune	RP	47%	**29%**	21%	4%	14
Cliff	RP	60%	**28%**	4%	7%	11
Cape	RP	59%	**32%**	0%	9%	7
Mairangi	MX	66%	14%	16%	5%	10
Woolshed	SB	**96%**		2%	2%	9
Rock	RP	26%	**55%**	14%	6%	7
Island	RP	47%	**50%**	0%	3%	6
Mean		70%	30%	11%	4%	155

Appendix 2

Number of fledglings for each territory, north coast, by breeding season from 1991 to 1999. Codes: nba - no known breeding attempt, dashed line (--) - no pair in residence, ? - not monitored and/or not reported. Sources: a) G. Murman, b) S. Sawyer c) this study, d) M. Bell, e) P. Moore et al. Assumption - if pair present season before and after, assumed present in intervening year.

	Breeding season								
	1991	1992	1993	1994	1995	1996	1997	1998	1999
Territory									
Whanga	?	?	2 **	0	1	0	0	0 (?)	0
WW	?	1	0 (?)	2	1	1	0	0 (?)	0
WoC	?	2	0	2	1	0	1	1	1
WoC e	--	--	--	--	--	--	--	1	2
TW	1	1	2	2	1	0	2	2	1
TE	--	--	--	0	1	0	2	1	2
Ngatikitiki	--	--	--	--	--	--	0 (?)	0	3
OTF	1	2	2	0	0	0	0	2	2
Creek	1	0	1	0	0	0	0	1	2
Pounamu	0	0	nba	0	0	0	0	1	0
Dune	0	0	0	nba	0	0	0	2	2
Cliff	1	2 *	1	0	0	0	0	0	0
Cape	0	nba	0	0	0	0	0	1	0
Mairangi	0	1	0	0	1	1	1	1	1
Woolshed	2	2	0	1	0	0	0	0	3
Rock	--	nba	0	1	0	0	0	2	2
Island	0	1	0	2	2	0	1	2	2
Totals									
fledglings	6	12	8	10	8	2	7	17	23
pairs	10	13	14	15	15	15	16	17	17
fledges/pair	0.60	0.92	0.57	0.67	0.53	0.13	0.44	1.00	1.35
nba		2	1	1					
?	3	1							
Source	a	b	b	c	c	c	d	d	e

* Unknown if chicks belonged to C4 or C5 (Dune or Cliff)

** Reported by Tuanui family

Appendix 3

*Relative rankings of territories for productivity by management effort for three-season periods. *** - top third productivity in that period, ** - middle third, * bottom third.*

Territory name	Overall average	By season			Number of periods in	
		1991-3	1994-6	1997-9	top third	bottom third
management effort		**low**	**none**	**high**		
WoC	***	**	***	***	**2**	0
WoC e	***	--	--	**	0	0
TE	***	--	**	***	1	0
TW	***	***	***	***	**3**	0
Ngatikitiki	***	--	--	**	0	0
OTF	***	***	*	***	**2**	1
Creek	**	**	*	**	0	1
Pounamu	*	*	*	*	0	**3**
Dune	*	*	*	***	1	**2**
Cliff	*	***	*	*	1	**2**
Cape	*	*	*	*	0	**3**
Mairangi	**	**	***	**	1	0
Woolshed	**	***	**	*	1	1
Rock	**	*	**	***	1	1
Island	**	**	***	**	1	0
Whanga	**	***	**	*	0	1
WW	**	**	***	*	1	1

management effort	fl/pr/yr	symbol	management effort	fl/pr/yr	symbol
none	0.67-1.33	***	high	1.33-1.67	***
1994-6	0.33	**	1997-9	0.67-1.00	**
	0.00	*		0.00-0.33	*
low	1.33 - 1.67	***	Overall	1.00.-1.33	***
1991-3	0.33-0.67	**	1991-9	0.44-0.89	**
	0.00	*		0.11-0.33	*

Appendix 4 - Descriptions of high quality territories

The Island territory had one of the highest breeding success rates under the conditions present during this study (1.33 fledglings/season). The pair in this territory had a high percentage of multi-chick broods (100%) and the chicks fledged in a short period of time (Tables 13). Habitat factors which may have contributed to the success of this pair include the fact that the nest site, and most of the foraging area, was on a small island which was accessible only at low tides and had a rocky cliff face of about three metres had to be scaled to access the island, which would have discouraged cats and wekas, and decreased some of the disturbance pressures. Foraging habitat within this territory was varied, with a combination of intertidal rock platform, sandy beach and two small creeks within the territory boundaries. The dark, broken rock within the territory provided very good camouflage for the chicks to hide among. There were some factors which may have reduced the productivity of this territory. At times levels of disturbance were high around this area because of boat launching and recreational fishing activities. During the final season hatching success was nil for this pair because of unknown causes.

The pair within the WW territory was the other most productive over the three seasons (also averaging 1.33 fledglings/season). This pair had few multi-chicks broods, but was successful fledging chicks every season. This pair's territory was composed only of sandy beach with no paddocks adjacent to it. There was a large river that was used frequently by the pair. The area near the river mouth included the widest section of beach and was the region where the pair consistently nested. This section of beach had a westerly aspect and extensive offshore reefs, and frequently had large amounts of kelp and wrack, especially after storms. The foraging quality in this territory may have varied from year to year depending on storm patterns and kelp/wrack deposits. The chicks in this territory had a short fledging time in 1994 (Table 13), which would indicate good foraging, at least during that season. There was a family resident near here, which may have meant lower weka numbers due to the presence of dogs along this stretch of dunes.

Pairs in the TW and WOC territories both produced an average of one chick per season. Both pairs were successful in two of the three seasons, and each had one two-chick brood. TW had chicks that fledged in one of the shortest fledges periods, whereas chicks in the WOC territory with one of the longest fledging periods. Both territories were sandy beach (with no rock platform) and had large streams running through them. The TW pair used paddock adjacent to the river extensively, especially during the early chick-rearing periods. Although the WOC pair were seen to use the paddocks within their territory frequently for foraging, they were never seen using the paddocks during chick-rearing. The river and some broken dunes lay between the coast and paddocks, possibly making access difficult for the chicks.

The pair in the Mairangi territory had no multi-chick broods but was successful two of the three seasons. In this territory both foraging and good nest-sites may be somewhat limiting. During one season this territory appeared to be unoccupied, or there was turnover of pair members. In the second season the pair was first seen with a very young chick, and the nest never found. The pair probably nested about halfway along the beach towards the Woolshed territory, as that was where the birds had been seen previously and near where the very young chick was first seen. Within a few days the pair and young chick had moved about a kilometre to the corner where they remained for the rest of the season. During the third season the pair in this territory nested in the corner near a stream and was one of only two pairs to successfully raise a chick to fledging. This corner area was frequently and completely inundated by high tides and the nest-site was flooded only a few days after hatching. There was a paddock near the territory which the pair had been observed to use for foraging, but marram grass between the coastline and paddock areas probably makes access difficult and potentially risky for young chicks. Time to fledging was short during one season, but not the other. There was probably good foraging in the 'corner' where sandy beach, a creek mouth and rock all converged, but nest sites were limited due to the marram grass.

CHAPTER 6

BETWEEN THE DEVIL AND THE DEEP BLUE SEA: NEST-SITE SELECTION IN THE CHATHAM ISLAND OYSTERCATCHER (*HAEMATOPUS CHATHAMENSIS*)

ABSTRACT

The endangered Chatham Island oystercatcher (CIO) is a coastal nesting species that loses a high percentage of clutches to tidal flooding (40-50% over three breeding seasons). This reduced productivity due to flooding appears to sometimes be a significant limiting factor within the population (Chapter 4), which raises the question: 'Why do CIO choose nest-sites so vulnerable to tidal flooding?'

Nest-site selection of 15 pairs of CIO (25-33% of the total breeding population) was studied during the 1994-1996 breeding seasons along the north coast, Chatham Island. Data were collected for nest and random sites on distances from vegetation and the mean high tide line, elevation above the high tide line, substrate type and objects near nest-sites.

CIO appeared to select sites to minimise predation and flooding risks within the constraints of their territories. They avoided nesting less than five metres from the high tide line or significant vegetation. Most pairs nested on sandy beaches (77% of nests), usually in the widest section available within the territory. However, they showed flexibility in their nest-site selection, with two pairs using rock outcrops where wide sandy beaches were not available within their territories. All nests were in relatively open areas that provided good visibility for the incubating bird to see approaching danger and/or conspecifics. CIO often nested near objects such as logs, kelp or rocks, which probably made the nest more cryptic to predators.

Major changes have occurred on the Chathams over the last 200 years, especially on the main two breeding islands where 85-90% of the CIO population occurs. These changes include introduction of predators, such as cats and weka, and widespread establishment of marram grass (*Ammophila arenaria*), with subsequent changes in dune structure, i.e., increased risk of flooding and providing habitat for predators. CIO must balance trade-offs between nesting too close to the high tide line with the risks of losing clutches to tidal

flooding, and nesting too close to marram-covered dunes with the increased risk of predation of incubating adults. Evolutionary selection pressures should favour losing clutches rather than adult predation, because clutches can be replaced quickly. Additionally, short-term selective pressures, such as flooding, can oscillate unpredictably so that nest-site selection may reflect long-term optima that are neutral or maladaptive in the short term.

INTRODUCTION

Tidal flooding is a major cause of nest loss of the Chatham Island oystercatcher (CIO). During a three-year study along the north coast of Chatham Island, at least 40-50% of clutches were lost when flooded; in one year almost all clutches were lost to storm tides (Chapters 3 and 4). Evidence suggests that productivity within the territories during the breeding season is one of the main factors currently limiting the CIO population, and that foraging and chick-rearing habitat is good to excellent for 25-33% of the breeding population located along the north coast (Chapter 4). This raises the question: Why CIO select the risky sites that it does?

Studies of various oystercatcher species have shown that the main factors that determine breeding success and influence nest-site selection appear to be flooding of nests, predation of nesting adults, and quality of chick-rearing habitat (e.g., foraging sites adjacent to or within the territories, plus food quality and abundance) (Hartwick 1974; Ens 1992; Vermeer *et al.* 1992; Lauro and Nol 1995; Hockey 1996; Hazlitt 1999; Heg 1999). CIO is highly territorial and strictly coastal nester (Chapters 3 and 4). Within the constraints of their territories, CIO pairs must balance the above factors when choosing nest-sites.

Proximity of nest-sites to food is desirable, but not essential for oystercatchers because adults can carry food to their precocious young. Territories where food is not adjacent have been coined 'leapfrog territories' but, compared with pairs in territories containing chick-reading habitat, leapfrog territories tend to have poor reproductive success in most cases where they occur (reviewed in Ens *et al.* 1992). In Schiermonnikoog, The Netherlands, adults on leapfrog territories often do not provide enough food so their chicks sometimes starved (ibid). On the Chathams, this type of territory is rare (fewer than 8) and occurs only on Rangatira (Davis 1988).

Since the arrival of humans on the Chathams, nesting habitat, as well as predators and disturbance levels, have changed dramatically along the coastline, especially on Chatham and Pitt Islands where 85-90% of CIO breed (Schmechel and O'Connor 1999; Moore *et al.* 2000). Marram grass (*Ammophila arenaria*), a European sand binding species, was introduced to the Chathams in the late 1800s. Marram competes successfully with natives such as pingao (*Desmoschoenus spiralis*) (Partridge 1995), and now occupies about 95% of the sand dunes on Chatham and Pitt Islands (A. Baird and D. Given pers. comm.; pers obs). In contrast to the more open, less steep dunes created by pingao and other vegetation, marram effectively catches and binds sand, causing the dunes to become much steeper, at times almost cliff-like, with less or no open sand above the high tide line (Heyligers 1985) (Plate 1).

Numerous predators have been introduced to Chatham and Pitt Islands (see Table 18, Chapter 3), the most significant for CIO are cats (*Felis catus*) because they are known predators of eggs, chicks and adult shorebirds including many species of oystercatchers. On the Chathams, cats have been video-taped almost catching incubating CIO, and eating eggs (Moore *et al.* 2000). Other introduced predators include weka (*Gallirallus australis*) (a flightless rail endemic to the New Zealand mainland), brush-tailed possum (*Trichosurus vulpecula*), and rats (*Rattus norvegicus, R. rattus*), all of which, except rats, are known to attack CIO incubating adults, eggs and young (Moore *et al.* 2000). High numbers of these predators have been documented in CIO territories during recent control operations along the north coast of Chatham Island (Chapter 3, Moore *et al.* 2000).

Marram dunes provide habitat for many of these predatory species. Marram dunes are used by weka for breeding, foraging, and roosting and by possum for denning (pers. obs.). Cat tracks were often seen along the edges of the dunes, and the dunes probably provide good hunting cover. Marram-covered dunes possibly also provide good habitat for rats which, by being an important prey item for cats (S. O'Connor and J. Dowding, pers. comm.), may enable cats to inhabit dunes in higher densities.

These changes to the Chatham Islands have reduced the available nesting habitat for CIO (Best 1987) and increased the risk of predation, especially for incubating adults. Are CIO pairs now trapped between the devil and the deep blue sea? Nest too close to the ocean and increase the risk of clutches being flooded, or nest close to vegetation and increase the risk of predation of incubating adults (especially by cats).

Management to increase CIO productivity occurred before and after this study (Murman 1991; Sawyer 1993; Sawyer 1994; Bell 1998; O'Connor 1999; Moore *et al.* 2000). Management during this study was minimal, limited to some predator control the first season. No control of marram grass was achieved before or during the course of this study.

The objectives of this study were to:

1) describe the characteristics of CIO nests and nest-sites along the north coast Chatham Island and compare them with other oystercatcher species,
2) determine nest-site habitat selection in this portion of the CIO population, and
3) attempt to explain the reasons for nest-site selection in CIO.

METHODS AND LOCATION

Nest-sites were located and assessed over three seasons for pairs in the study area along the north coast, Chatham Island (see Figure 1, Chapter 3). Distance to the mean high tide line (hereafter referred to as high tide line) and the nearest significant vegetation (defined as clumps of vegetation a minimum of 10 metres diameter and a minimum of a metre high), elevation above the high tide line, and the composition of the substrate within a metre around the nest scrape were recorded. Substrates within a metre of the nest-site were classified into sand, rock, vegetation, and other (kelp, wood, shell, etc.), and amounts estimated to the nearest 5%. A grid was used to improve consistency between estimates. Any objects such as a log, kelp base, clump of vegetation or rock immediately adjacent to each nest-site were noted. In 1996, the total beach width from the high tide to the vegetation line was measured to the nearest metre.

To compare with the nest-sites, random sites within the territories were also measured for the same parameters as nest-sites in two of the three seasons (1994 and 1996). The random sites were chosen by starting at the nest-site, then using a random numbers table to determine distance and direction, up to 20 metres away, from the nest-site. These random sites were then measured for all the same parameters as the nest-sites. If the habitat in a site was clearly unsuitable (e.g., underwater), a new site was chosen to provide realistic comparisons.

Differences between distances of nest-sites and random sites from vegetation and high tide line, and elevation above the high tide line were tested using the Wilcoxon signed Rank Test for paired data. This test was also used to look for differences in amount of different substrate (vegetation, sand, rock, other) around nest-sites. A McNemar's chi-squared test was used to test if nest-sites were located near objects compared with random sites.

For details on location and description of habitats within the territories see Chapters 3 and 4.

RESULTS

A total of 45 nest-sites and 26 random sites were measured. All nests were located either on sand (77%) or rock (23%) (see Plate 1 and 2). Nests in sandy beach territories and in mixed sandy beach/rock outcrop territories tended to be in the widest sections of the territories; that is, in the storm-tide zone in the widest areas free of vegetation (i.e., no marram grass, but sometimes other fast growing, low mat species were present). The average width of beaches where nests were located was 40 metres (SD = 17 m, range = 14-67 m, n = 11).

Compared with random sites, CIO nests (1994 and 1996) were located further from vegetation (median = 13m) than random sites (median = 9 meters) ($p < 0.05$). There was no significant difference between nest-sites and random sites in distance to, or elevation above, the tide line. CIO, however, never nested within 5 m of vegetation or the high tide line, the majority of nests being 5-30 m away from significant vegetation, and 5-25 m from the high tide line (Figure 1 and 2); and more random sites were located at less than 0.50 m above the tide line and more nest-sites were located at 1.00-1.49 m above the tide line (Figure 3). The distributions of all three measures were clearly skewed.

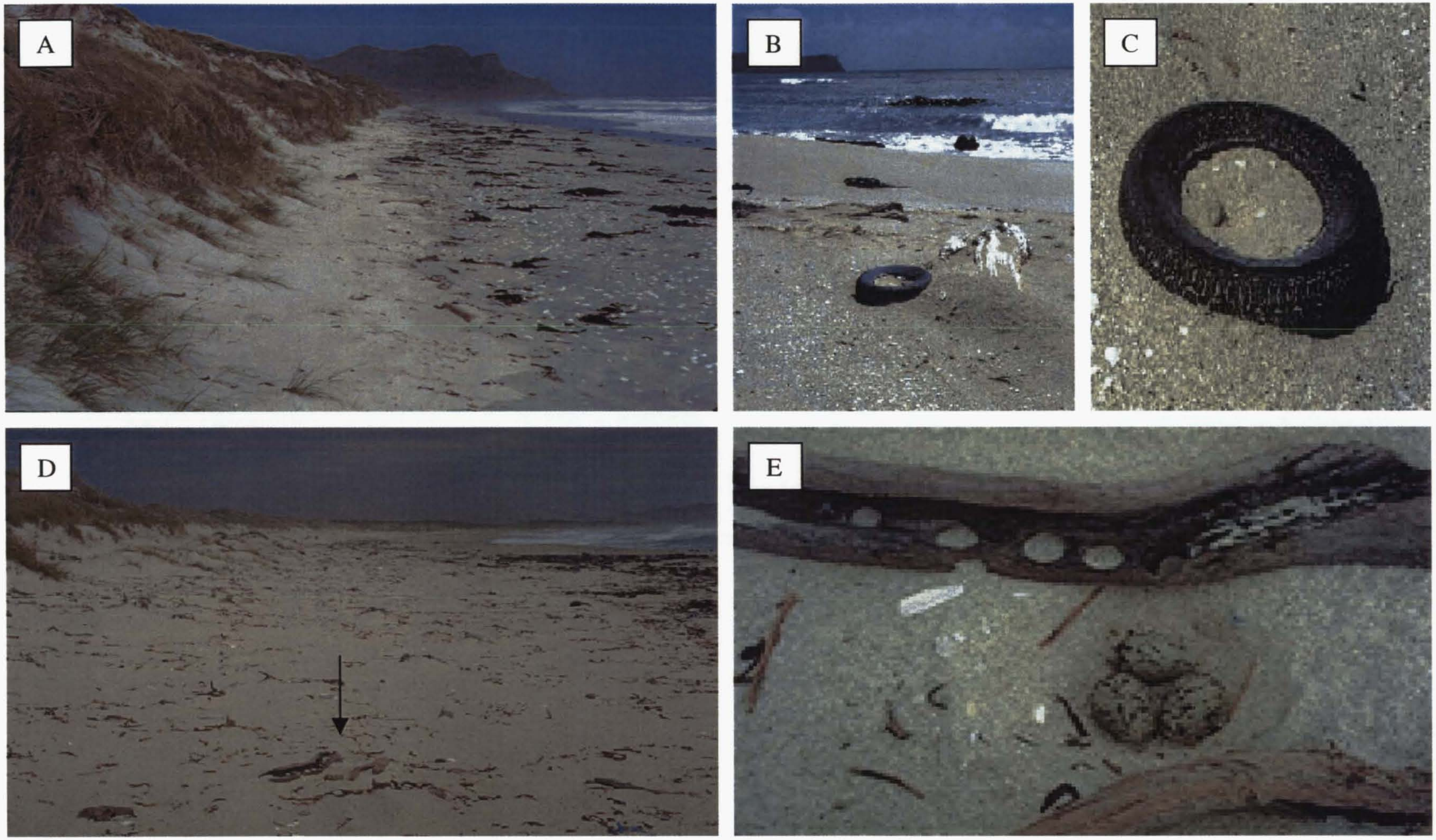

Plate 1. (A) Steep maram-covered dunes which leave little space for CIO nests (north coast); (B) & (C) use of an elevated site in a tyre by CIO at Wharekauri; (D) & (E) a typical sandy beach nest-site near Tioriori.

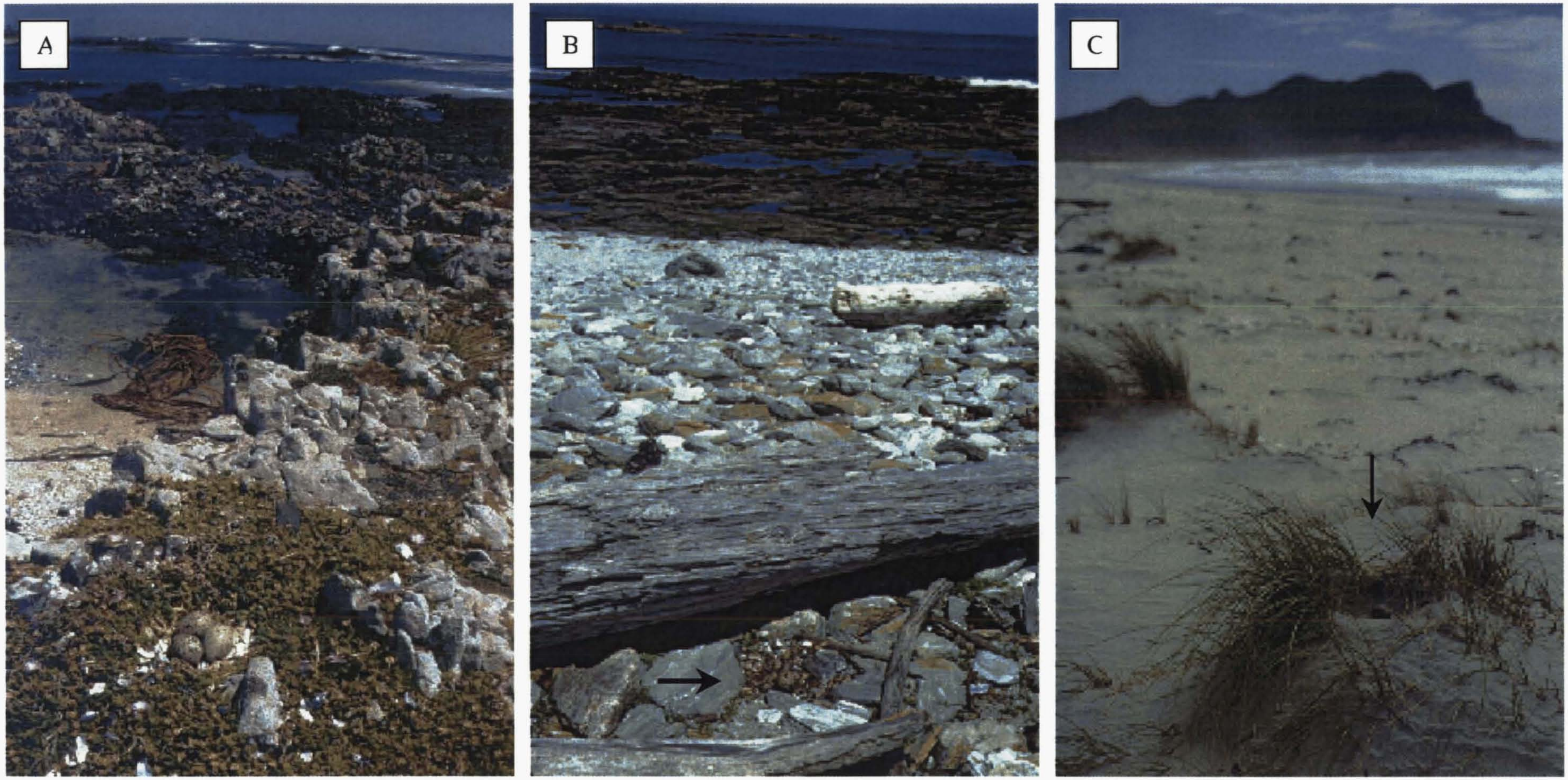

Plate 2. Examples of CIO nests: (A) on a rock outcrop (Island territory, Wharekauri); (B) along a section of schist coast line (Whanga territory); and (C) on a small sand hill (Maunganui Beach near Takehanga Stream).

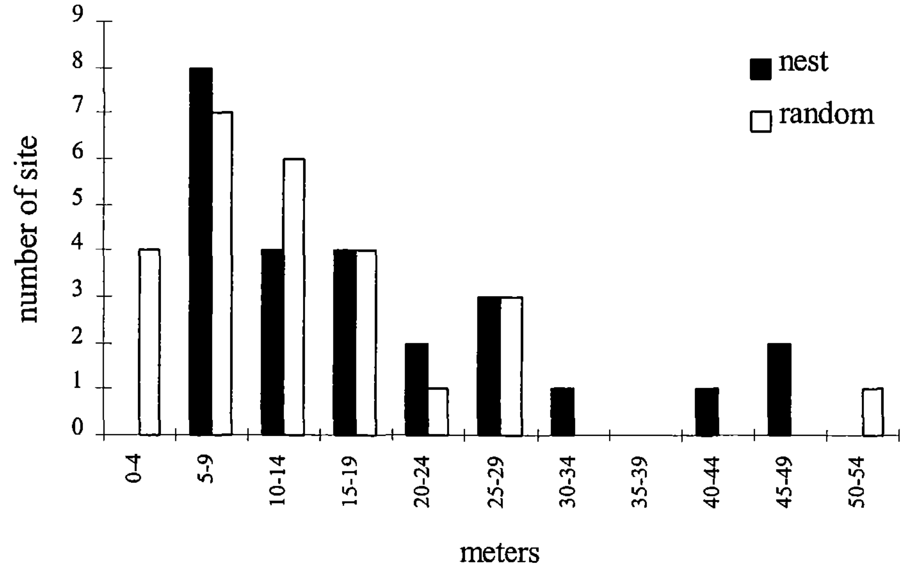

Figure 1 Distance from vegetation of CIO nests and random sites.

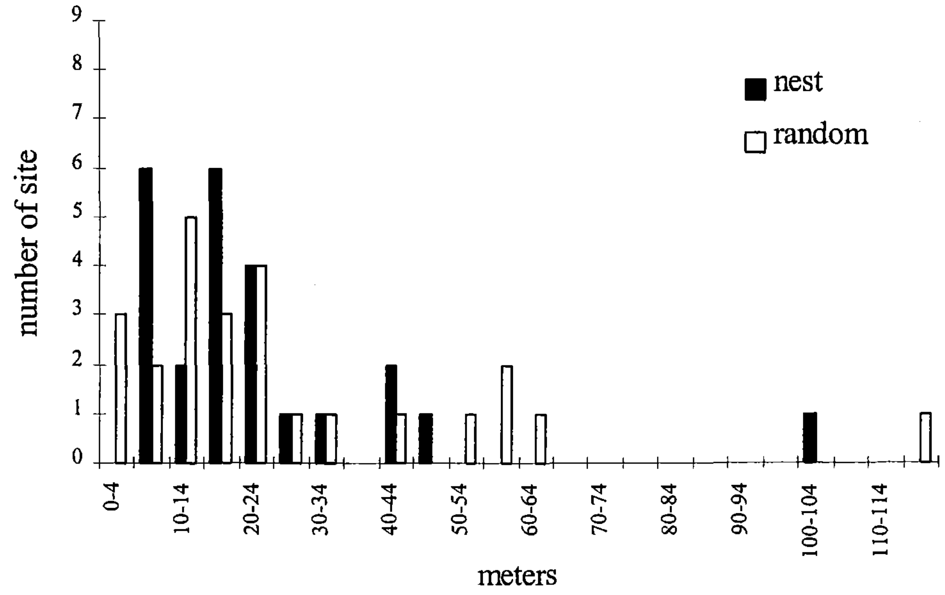

Figure 2 Distance from the high tide line of CIO nests and random sites.

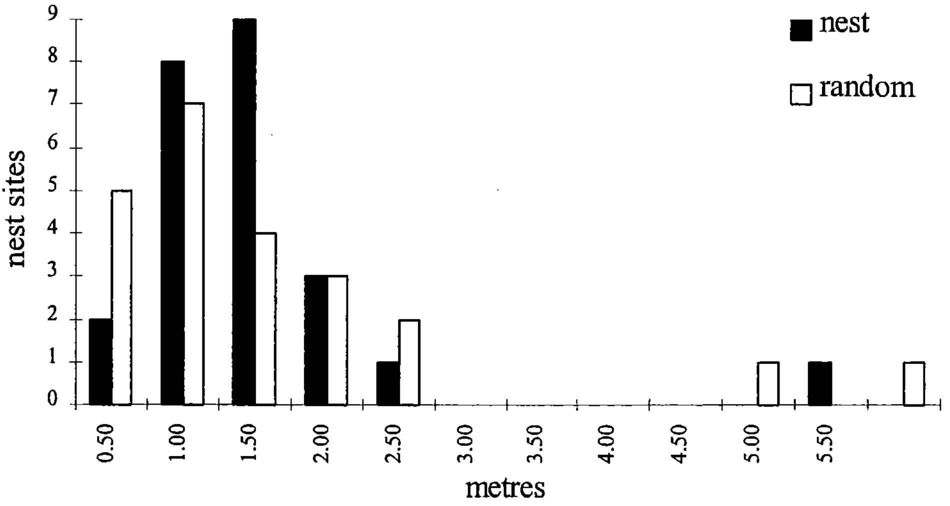

Figure 3 Elevation above the high tide line of CIO nests and random sites.

Nests on sand or rock were surrounded primarily by such substrates (Table 1). The amount of vegetation within 1 m of sandy beach and rock nest-sites was 28% and 37% respectively. Nests on rock were typically located in cracks or depressions with the nest on a soft substrate, such as low matt vegetation (either alive or dead), usually glasswort (*Salicornia australis*) or sand daphne (*Pimelea arenaria*), which cushioned the eggs. In the microhabitats immediately surrounding nests-sites, there was were no significant differences detected between nest-sites and random sites in the other parameters measured (i.e., rock, vegetation, and other); although the amount of vegetation near nest sites did approach significance (p = 0.59).

Table 1 Habitat composition within one metre around CIO nests, north coast, Chatham Island.

microhabitat type	sandy beach nests (n = 35)		rock nests (n = 10)	
	%	SD	%	SD
sand	76	20	3	0
vegetation	28	16	37	28
rock	9	4	66	16
other	18	23	4	6

CIO often nested near three-dimensional objects such as logs, kelp or kelp bases, rocks, marram grass clumps, and boards. A higher percentage of nest-sites (66% of 45 nest-sites) were located near an object (within one metre) compared with the random sites (15% of 26 sites). Sandy beach nests were more likely to be located near objects than nests located on rocks, 74% and 40% respectively.

All nests were scrapes in the sand or slight depressions in vegetation or shells if the nest was on rock. All but one replacement clutches were in nests located in new nest-sites. When available, pairs would sometimes use elevated sites within its territories for nesting. One pair (Woolshed territory) in 1996 laid two clutches, a first and a replacement clutch, on a raised platform of sand inside a tyre placed within their territory (Plate 2). Another pair nested on top of a small hill (about a metre high) created by a clump of marram grass (Plate 2).

DISCUSSION

Where do CIO nest?

Since survival and reproductive performance can depend on nest-site choices by birds (Burger 1985; Dow and Fredga 1985; Martin 1992; Badyaev 1995), this should create a basis for evolution of nest-site preferences. Since nest-site preferences are heritable (Klopfer 1963; Hilden 1965; Cink 1975; Sonerud 1985), natural selection should contribute to a species' current pattern of nest-site distribution. Short-term selection pressures, such as flooding, can oscillate unpredictably, both temporally and spatially (Wiens 1985; Burger 1987; Crabtree *et al.* 1989; Filliater *et al.* 1994; Hogstad 1995) affecting clutch survival. Therefore characteristics of successful nest-sites may vary in time and space (Austin 1975; Van Riper 1984), and nest-site selection may reflect long-term optima that are neutral or maladaptive in the short term (Clark and Shutler 1999). The risk of predation of adults should create stronger selection pressure than the risk of losing clutches to flooding, if clutches are replaceable and the species is long-lived.

It is believed that birds select habitats at three scales: general, territories, and nest-sites, in this order sequentially (Burger 1985; Klopfer and Ganzhorn 1985; Sherry and Holmes 1985). Because CIO pairs are highly territorial, once they have established territories they are then constrained to choose a site within their territory. This should be a site that maximises protection from predators, floods, and exposure to weather. Many factors may influence nest-site selection in oystercatchers such as vegetation, visibility, distance from the tide line, substrate, and objects (e.g.; Heppleston 1972; Hockey 1982; Lauro and Burger 1989; Andres and Falxa 1995; Lauro and Nol 1995; Hockey 1996).

CIO along the north coast, Chatham Island, showed patterns of nest-site selection that were very similar to other species of coastal breeding oystercatcher. They tended to nest predominantly on sand in open, high-visibility areas in the widest sections of beach within their territories, or on a soft substrate on rock outcrops if wide sandy beaches were unavailable. They avoided nesting close (< 5 m) to either vegetation or the high tide line. They did not appear to select sites based on elevation, although they sometimes nested on high objects like rocks, sand-filled tyres, or small sand hills if there was a depression in which they could hide themselves. Nests, especially those on sandy beaches, were often sited near objects, such as logs, kelp, rocks, or clumps of vegetation.

The habit of nesting in open coastal habitats above the high tide line is common to most oystercatcher species (Harris 1967; Heppleston 1972; Hartwick 1974; Nysewander 1977; Summers and Hockey 1977; Lauro and Burger 1989; Vermeer *et al.* 1992; Andres and Falxa 1995; Lauro and Nol 1995). Oystercatcher nests are often located close to high tide lines or on the shore side of vegetation lines, even though the risk of flooding is higher in these sites (Hartwick 1974; Hockey 1982; Lauro and Nol 1993; Andres and Falxa 1995).

The predominance of CIO nests on sandy beaches fits well with the general pattern of pied species of oystercatcher usually nesting on sandy beaches that are light in colour, and black species usually nesting where beaches are dark and rocky (reviewed in Lauro and Nol 1995, p 926). Also, CIO, like many oystercatcher species, chose nest-sites located near objects or clumps of vegetation (Vermeer *et al.* 1987; Andres and Falxa 1995; Lauro and Nol 1995; Hockey 1996).

All nests in sand were simple scrape, those on rock were a slight depression in soft vegetation. This contrasts with nest-sites recorded on Rangatira Island. In 1997, three nests were on soil and the birds had collected leaves and other material to create a substantial nest (pers. obs). Another scrape was located among boulders, and was constructed of hundreds of pieces of small shingle collected and arranged into a small hollow nest bowl. There are no sandy beaches on Rangatira; however, some CIO nests were located on rock and rock outcrops, often under overhangs or in areas with rock overhangs (pers. obs; E. Young, pers. comm.; Davis 1988).

Re-use of nest-sites in the same or different seasons was rare in CIO, only one pair in one season re-used the same site (2%). This may be due, in part, to the dynamic nature of sandy beaches. It is unusual for shorebirds to re-use the same nest scrape, though a number of wader species in New Zealand have been recorded using the same site in two consecutive seasons (reviewed in Crossland and Simamora 2000). American black oystercatchers (*H. bachmani*) may create substantial nests on rock outcrops, and these nests are re-used in subsequent years (Andres and Falxa 1995), with pairs in the Strait of Georgia, British Columbia, re-using nest scrapes 50% of the time (Hazlitt 1999).

Like CIO, there was no difference in elevation between nest-site and random sites for pied oystercatchers (*H. longirostris*) in Australia (Lauro and Nol 1993). This was because birds chose to nest near the shoreline and elevation rose inland. In contrast, American oystercatcher (*H. palliatus*) nesting in salt marshes chose nest-sites that were significantly higher in elevation and farther away from a water body than random sites. This apparent selectivity in elevation was related to topography since preferred sandy sites on salt marsh were higher in elevation than the surrounding spartina grass (*Spartina* spp.) habitats (Lauro and Burger 1989).

The differences found between CIO nests and random sites may have been less than that which would have been found if an alternative method for selecting random sites had been used. This is because random sites chosen in this study were selected by using the nest-site as the starting point for logistical reasons, and therefore random sites may sometimes at distances not far from the nest-site, and could have been more similar than sites located farther away from the nest-site. A better method may have been to create a grid of potential nesting habitat within the territory and select random points within those areas, potentially resulting in a more even scattering of random sites throughout the entire territory, rather than clustered around the nest-site. If this method had been used, there might have been more differences between nest and random sites in the variables studied (e.g., substrate, distances to vegetation and high tide lines, and elevation).

Why CIO nest where they do?

CIO pairs along the north coast nested primarily on sandy beaches. They may select nest-sites on sandy beaches because they are pied, or they may be pied because they nest on sandy beaches, or are most closely related to species that nest on sandy beaches. Most pied species of oystercatcher nest on sandy beaches (Lauro and Nol 1995; Hockey 1996), which could be advantageous to avoiding predators. Pied oystercatchers may be more cryptic on light coloured sand than black species due to the visual effects of countershading (Lauro and Nol 1995 and references therein), especially when they are standing or moving to and from the nest. Jehl (1985) observed American black oystercatcher (a black species) and American oystercatchers (a pied species) both appear very cryptic in their nest habitats: dark rocky shores and light sandy beaches respectively. He suggested that this pattern of habitat use for the two species may have been a result of predator pressure. An experiment using oystercatcher models, conducted by Lauro (1994), found that on open, sand beaches of light colour, a black standing model was detected by human observers at a greater distance than the pied model. As a result of current predator pressures, CIO may be using sandy beaches more, or rock sites less, than they would in the absence of predators.

The average distances of nests from the tide line and vegetation were similar, and CIO often nested in the widest sections of coastline. This suggests they may be balancing the risks of nesting near the tide line (risk of nest being flooded), with the risk of nesting near dune vegetation (increased risk of predation). CIO may avoid nesting too close to vegetation in order to reduce the risk of predators using dune vegetation as cover to approach incubating birds closely before attacking.

Dune vegetation has been documented as providing shelter for mammalian predators. For example, Burger (1987) found that vegetated sand dunes provided shelter and concealment while stalking for mammalian predators of piping plover (*Charadrius melodus*), and in another study of the same species, predated nests were significantly closer to vegetation than successful ones (Espie *et al.* 1996). At Brigantine, New Jersey, predation was the primary cause of nest failure in least tern (*Sterna antillarum*) and distance from the dunes was the significant factor in egg and chick survival. Cats and foxes lived in the dunes and entered the colonies from there, preying heavily on the nests closest to the dunes (Burger and Gochfeld 1990). Lauro and Nol (1993) found that pied

(*H. longirostris*) and sooty oystercatchers (*H. fuliginosus*) in Australia selected high visibility sites, arguing that it was most probably to provide birds with the opportunity to detect and avoid predators. Alternatively, high visibility sites may have allowed the pair to detect other oystercatcher intruders or predators. These two alternative explanations are not mutually exclusive. However, the selective pressure by predation should be stronger since it may involve the death of a breeding adult and immediate cessation on any genetic contribution to future generations.

Predator pressure may strongly influence nest-site selection in birds and is the most important selection force affecting nest success (reviewed in Newton 1998, see also Ricklefs 1969; Martin 1995). Many coastal birds and ground-nesting ducks commonly nest at higher densities on island, compared with mainland, sites and two important factors that may contribute to this pattern are reduced predation risk and lower human disturbance (Buckley and Buckley 1980; Williamson 1981; Blondel 1985; Nilsson *et al.* 1985; George 1987; Erwin *et al.* 1995; Clark and Shutler 1999).

The trade-off hypothesis assumes that CIO pairs are able to recognise and respond to mammalian predator pressure, which has been present on these islands for only about the last 100 years, and that the risk of predation is real. CIO recognise humans and dogs as potential threats and show very strong anti-predator behaviours towards both, especially when chicks are present, displaying the full range of anti-predator strategies described for other oystercatcher species (pers. obs.). Indeed, humans have been predators of CIO eggs within the last 40 years on the Chathams (L. Tuanui, pers. comm.). Whether they recognise and respond similarly, the presence of cats or other mammalian predators is less obvious, but they have been videoed escaping from two attempted cat attacks (Moore *et al.* 2000). Presumably a strong anti-predator response either never disappeared, or has evolved very quickly, which seems feasible given that CIO would have inherited latent anti-predator behaviours from its ancestors and predation is a very strong selective force. The historical predators that would have been present on the Chathams were the New Zealand falcon (*Falco novaeseelandiae*) and brown skua (*Catharacta skua*) (Holdaway *et al.* 2000).

Most of the evidence for predator pressure is circumstantial because actual losses to, or pressures from, introduced mammalian predators are difficult to determine. Evidence to suggest the risk is significant includes the two videoed cat attacks on incubating CIO during the 1999 season (Moore *et al.* 2000), and documentation of cat predation of other oystercatcher species around the world (see Chapter 3, and Table 18 Chapter 3). This information, combined with the historically high number of cats along the north coast based on trapping records of 47 and 51 cats trapped in 1998 and 1999 respectively (4.2 x 10^{-4} cats/trap night/km for 1999) (Moore *et al.* 2000), would suggest that the predation risk to CIO has been a real danger.

The risks of nesting too close to the tide line are clear, and many CIO nests were lost to tidal flooding (see Chapters 3 and 4); however, predation pressure may force CIO to nest close to the high tide line. Harwick (1974) suggested that American black oystercatchers nested close to the water's edge even though nests were commonly flooded, because these sites were less susceptible to predation by nesting gulls. Very similar trade-offs between nesting close to vegetation with associated predator risks and the coastline have been proposed for piping plover (Burger 1987; Espie *et al.* 1996).

In addition to providing habitat to predators, the establishment of marram grass has almost certainly resulted in reduced nesting habitat for CIO on the Chathams (Best 1987). Loss of nesting space due to changes in dune structure has occurred for other shore nesting species such as Australian pied oystercatchers and hooded plover (*Thinornis runbricollis*) in Australia. Both species nest on terrace-shaped foredunes formed by native grasses. At Calverts Beach in southern Tasmania, both species historically nested in the foredunes into the 1970s, but ceased nesting in the area after the dune system was stabilised with marram (Park 1994).

CIO nests and random sites did not differ significantly in elevation. This may be because suitable higher elevation sites were not available, CIO could not assess elevated areas very effectively, other factors (such as vegetation and distance to water) may have been more important for nest-site selection, or differences were not detected due to methodology (including sample sizes). In at least one other oystercatcher species, a lack of difference between nest-sites and random sites has been reported, suggesting that this lack of difference may be real. This lack of selection for elevated sites appears paradoxical since choosing open, high elevation sites would seem advantageous because of the decreased risk of flooding and depending on the site, increased visibility, which would allow CIO to see approaching danger or conspecifics. For example, Burger (1990) found that least terns, a coastal ground-nesting species, preferred ridges and slopes, and argued this was probably because they could more easily detect approaching predators. This was supported by the fact that at least 18 adult terns were killed by predators, so this visibility was likely to be an important factor in nest-site selection. An additional advantage in these elevated sites for the terns was that they were less prone to flooding during storm tides (ibid).

For CIO pairs to choose between sites at various elevations, they would have to be able to assess them. The beach areas tend to be relatively flat, so detection of elevation may be difficult. If CIO cannot assess elevation directly they may, however, be able to assess flooding risk, and thereby elevation, indirectly through their habit of building multiple nest scrapes. CIO and other oystercatcher species often make several scrapes for days or even weeks before choosing one to lay in (Hockey 1982; Andres and Falxa 1995). Scrapes that disappear through tidal flooding may then be eliminated as a choice for the final nesting site. In many of the CIO territories, higher sites were closer to dune vegetation because the elevation of the land increased inland. CIO probably choose nest-sites based primarily on other criteria, such as distance from vegetation and the coastline, rather than elevation. However, if open, elevated sites were available, they were sometimes selected. CIO pairs often nested on higher ground or rock so long as the nests were in a slight depression. One pair nested in a sand-filled tyre placed on the beach, which provided a site that was less likely to flood. Another pair nested on a small sand hill created by a clump of marram. Two pairs nested on rocks in a crack or depression. These rocky sites probably provide a good substrate for the eggs because they usually had some vegetation in them, and sufficient elevation to allow the birds to be hidden while also having a good view of approaching predators.

Many species of oystercatcher and other shorebirds nest near objects, including small clumps of vegetation (summarised in Hockey 1996, see also (Hockey 1982). Several reasons have been offered for this including protection from weather, as a cue to nest location, and concealment from predators (see for example Page *et al.* 1985; Vermeer *et al.* 1987; Espie *et al.* 1996). The reasons and effectiveness probably vary from location to location and from species to species. Few data are available on the effectiveness of objects as cues to nest location, but Maclean and Moran (1965) concluded that white-fronted sandplovers (*C. marginatus*) did not need objects to find their nests. They watched birds return as directly and quickly to nests when an object was adjacent and when it had been moved. Many authors considered, from other studies, that objects were too small to provide much protection from the elements for various species of nesting shorebird (e.g., Purdue 1976; Page *et al.* 1985; Vermeer *et al.* 1989). However, Hockey (1982) found that the aspect of the majority (76%) of African black oystercatcher nests fell in the 180° arc facing away from prevailing winds and they preferred to nest in sheltered sites. Bergstrom (1982 in Page *et al.* 1985) suggested that microclimate was an important factor in the selection of nest-sites by Wilson's plover (*C. wilsonia*) in a hot Texas environment. Most authors, however, have suggested concealment as the main reason for oystercatchers and other shorebirds often nesting near objects (Bunni 1959; Graul 1975; Hockey 1982; Vermeer *et al.* 1987; Vermeer and Smith 1989; but see Page *et al.* 1985).

How flexible are CIO when choosing a nest-site?

As Lauro and Burger (1989) convincingly argued, flexibility in habitat selection is important to the success of species because biological constraints like food availability, predation and competition, as well as the abiotic limitations of the physical environment (e.g. weather, space, physiognomy of habitat). When nesting habitat is limited, birds can forego breeding, or adapt to new habitats, expand into similar habitats elsewhere, if available, or adapt to a new habitat in other areas. Flexibility is an important aspect of adapting to new environments. Flexibility in nest-site choice can also minimise costs of tidal flooding or predation, thereby increasing reproductive success.

Oystercatchers as a family are surprisingly versatile in their nest-site selection and have been reported nesting on roof tops, logs or other unusual substrates (Cramp and Simmons 1983; Newman 1992; Andres and Falxa 1995). Due to their flexibility in nest-site selection, South Island pied oystercatcher and Eurasian oystercatcher now nest in paddocks and ploughed fields, expanding their numbers and range (Buxton 1961; Dobbs 1970; Heppleston 1971; Baker 1973). Another indication of flexibility in nesting habitat selection has been the recent range expansion of American oystercatchers (Post and Raynor 1964; Zarudsky 1985), and American black oystercatchers (Eley 1976). Flexibility in nesting habitat has been critical to the reproductive success of American oystercatchers because they have had to adapt to differences in habitat physiognomy across their breeding range (Nol 1984).

CIO pairs show flexibility in their choice of nest-sites, although they are probably constrained by the presence of predators. Along the north coast, Chatham Island, in 1998 one CIO pair nested on a large rotten log located among tall grass (pers. obs). During the 1994 to 1996 seasons, none of the CIO pairs along the north coast nested in paddock areas, but in 1999 one pair nested in a paddock (P. Moore, pers. comm.). Pairs on Rangatira often select very different habitat for nesting in compared with CIO on Chatham and Pitt Islands. In January 1997, the three nests found were located near the coast, all underneath vegetation such as small trees or shrubs; all had good visibility of the coastline.

Differences in habitat availability or predator avoidance may account for birds on Rangatira nesting in overhanging vegetation (i.e., shrubs and trees) when this has never been observed among CIOs on Chatham or Pitt Islands. On Rangatira, there are no terrestrial mammalian predators such as cats, possum, or pig. This could lessen the predation risk to CIO incubating near or under vegetation. Newton (1998) found that most avian species accepted a fairly narrow range of nest-sites but, in some species, this can change under altered predation pressure; less safe sites become acceptable where mammalian predators are absent, which enables pairs to occupy areas that would otherwise be unsuitable.

Another factor which may account for the differences in choice of nest-site habitat used by CIO is the presence of breeding brown skua on Rangatira. Skua might prey on nest contents more easily in open locations (E.C.Young, pers. comm.). Several other birds that normally nest in the open (e.g., red-billed gulls, white-fronted terns, and shore plover) also nest underneath vegetation on Rangatira (Davis 1994). From 1987 to 1990, Davis (pers. comm.) found CIO nest-sites sited among boulders or shingle, usually under the cover of rock overhangs or drift wood, although some were built in the open.

Differences both in habitat type and in the predator suite between Rangatira and Chatham and Pitt Islands make it difficult to determine the causes of the differences in nest-site selection in CIO. There are no sandy beaches or marram grass on Rangatira, and much of the area adjacent to the wave-cut rock platform is vegetated with bush or trees. This vegetation, which CIO nested under on Rangatira, was open underneath, allowing good visibility and access. This is not the case with marram dunes, the most common vegetation near CIO nesting areas on the main islands. There is less open area above the high tide available for nesting on Rangatira than on wide sandy beaches on the main islands. If these habitats were available on Rangatira, perhaps they would be the most preferred for nesting. Conversely, the currently used sites in the areas just under the vegetation behind the rock platforms offer many potential advantages: elevation for visibility, camouflage, some protection from skua predation, and no cats are present to compromise this choice (R. Powlesland, pers. comm.). The most likely explanation is a combination of which habitats are available and the types of predator pressures present which accounts for the differences in nesting habitats of CIO on Rangatira and the two main islands.

The ideal nest-site

The ideal nest-sites for CIO would include areas with low predator pressure and with topography that allows birds to escape predators, plus habitat that would allow nesting in areas that are safe from flooding of their clutches. These areas would be adjacent to good chick-rearing habitat and have low levels of disturbance.

Lack of quality nest-sites can have profound ramifications for populations. Nest-site availability can clearly constrain breeding numbers and output in a density-dependent manner (Newton 1994; Rodenhouse *et al.* 1997; Newton 1998). Moreover, where shortages of nest-sites limit breeding density, they must also limit total population size; where the output of young is limited, no population can increase beyond a certain level (Rodenhouse *et al.* 1997; Newton 1998). Nest-site availability can be a much more significant limiting factor than others. Providing food or removing predators in experiments of factors limiting bird populations led, in extreme cases, to a doubling of breeding density compared with control areas, but provision of extra nest-sites often led to much bigger increases, up to 20-fold in the most extreme examples (Newton 1998).

Predators are frequently a clear threat, but limiting factors often interact and, in grey partridge (*Perdix perdix*) in Europe, for example, a combination of habitat restoration to increase food for chicks and providing better nest cover combined with predator control to reduce egg and hen predation allowed for a 10-fold increase in nesting densities. Controlling predators without habitat improvement increased partridge numbers from 4.7 to 13.4 pairs per km^2, compared with an increase from 16.3 to 51.6 after habitat improvement (Aebishcer 1997). In both cases, the increase was approximately three-fold, but while predator control added only 9 pairs per km^2, habitat improvement followed by predator control added 35 pairs (described in Newton 1998, p 355.).

SUMMARY/CONCLUSIONS

Evidence suggests that the main limiting factors operating on the CIO population occur during the breeding season, rather than over winter, and foraging/chick-rearing habitat is good to excellent for 25-33% of the breeding population located along the north coast, Chatham Island. The main factors that appear to be limiting the population at this locality are the lack of high quality nesting sites and high predator pressure. Good nest-sites include areas that allow birds to escape predators and avoid flooding of their clutches, preferably adjacent to foraging areas for the chicks. Good nest-sites for CIO appeared to be very limited. This limitation probably imposes a significant constraint on productivity, and may also decrease survival of breeding CIO.

When choosing where to nest, CIO balances the need to survive predator attacks with the risk of nest losses due to tidal flooding. If pairs nest too close to marram grass dunes to avoid loss of clutches to tidal flooding they increase their risk of being killed by predators, especially cats. If they nest too close to the high tide line, they risk losing clutches to tidal flooding. Selection pressures to avoid predation should be stronger than selection pressures to avoid losses of clutches because lost clutches can be quickly replaced and CIO are long-lived (at least 28 years old) allowing them the opportunity to attempt breeding over many years, maximising life-time reproductive success.

Due to the changes brought about by human settlement, CIO may be caught “between the devil and the deep blue sea”. Before human settlement, dunes were more open and the slopes more gradual with no mammalian predators and, consequently, CIO would have been able to nest at points above all but the worst storm tides. Now, lack of quality nest-sites can be a strong density-dependent limiting factor in populations, and conservation management attempts to increase the CIO population should consider the factors which affect nesting success and the survival of incubating adults. Management recommendations include: 1) continued intense predator control, and 2) removal of marram and restoration of native dune communities so there is a wider beach with a gradual elevation so that CIO pairs have more opportunity to avoid tidal flooding of their clutches.

If marram grass is removed from some areas in the future it would be useful to determine if nest site selection changes (i.e., do CIO then nest further from the tide line). Also it would be beneficial to examine the relationship between height above the high tide and probability of flooding, and distance to vegetation and probability of loss to predators. These habitat variables, if predictive, would provide support for management issues (e.g,, if nests are significantly more likely to be lost to predators if close to marram grass than removal is warranted).

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APPENDIX

Distances from vegetation and high tide line of CIO nest sites and random sites and elevations of CIO nest sites and random sites along the north coast, Chatham Island. (Paired sites only used for statistical analysis.)

	Nest sites (m)				Random sites (m)			
	average	range	SD	N	average	range	SD	N
1994/5 & 1996/7								
vegetation	21	5 - 92	19	26	14	0 - 54	11	26
high tide line	23	6 - 102	20	24	27	1 - 114	26	25
elevation	1.26	0.30 - 5.15	0.93	24	1.32	0.10 - 5.96	1.40	24
All years								
vegetation	19	3 - 92	16	40				
high tide line	20	2 - 102	17	42				
elevation	1.18	0.30 - 5.15	0.75	42				

CHAPTER 7

SPLITTING THE DUMMY: TERRITORIAL RESPONSES TO CARDBOARD MODELS IN THE CHATHAM ISLAND OYSTERCATCHER (*HAEMATOPUS CHATHAMENSIS*)

ABSTRACT

Territoriality is almost ubiquitous in monogamous bird species and, by excluding other pairs from breeding or forcing them to breed in lower quality habitat, almost certainly regulates the population of many species, including Chatham Island oystercatcher (CIO). CIO pairs are highly territorial during the breeding season, and responded to cardboard models placed within their territories. Cardboard models of oystercatchers of varying colour patterns and size were used to study the cues CIO were responding to when defending their territories early in the breeding season (October to December, 1996), on the north coast, Chatham Island.

I argue that the strength and nature of the territorial response to the models was related to the perceived threat the models represented to the breeding pair, the quality of the territory, and the risks of defence. With only two exceptions, all oystercatcher-shaped models were approached to within one metre within three minutes of presentation (n = 40 trials), suggesting shape is an important cue to species recognition in CIO. Models with the same colour patterns as breeding CIO were approached most quickly (range 1-2 minutes) and physically attacked by the all the pairs (n = 7 pairs), suggesting that these CIO-coloured models represented a high risk to the pairs. Of the three CIO-coloured models, the time to attack was shortest for the smallest model, probably because it was perceived as the least risky to attack.

Although the total proportion of time spent in attacking all the models was not significantly different (control excluded), the amount of time spent in warning behaviour was. The model that most closely represented a CIO in colour, shape and size elicited the most warning behaviours, suggesting that warning displays and calls may be very species-specific and serve to minimise the risks of intra-specific fights, especially among closely

matched competitors, and where asymmetries in fighting ability are not obvious. Pairs in the lower quality territories (i.e., those with the lowest breeding success) were the least aggressive, suggesting that the pair members were less willing to invest in the costs of territory defence if the benefits were low.

INTRODUCTION

Territoriality in birds is almost ubiquitous in monogamous bird species (Lack 1968; Davies 1978; Moss and Watson 1985; Gauthier 1987). Reasons for, and benefits of, defending territories include exclusive access to resources (e.g., food and nest sites), mate guarding, access to chick rearing habitat, and lower predation risks (Davies 1978; Davies and Houston 1984; Carpenter 1987a; Carpenter 1987b; Møller 1987; Davies 1991; Sutherland 1996; Newton 1998). Territory establishment and defence is essential for successful breeding in oystercatchers, and defence behaviours are very strong in oystercatchers, often including piping displays, ground and aerial chases, fights, and hovering flight ceremonies (Harris 1970; Davis 1988; Ens 1992; Heg 1999). CIO pair members will spend up to 20 minutes in continuous intense interactions which includes piping and fighting (pers. obs.).

The main reasons proposed for territory defence in oystercatchers are access to and exclusive use of resources such as food, nest sites, and chick rearing habitat (Ens 1992; Banks 1998). Mate guarding in American oystercatchers has been suggested (Nol 1985); however, the evidence against mate guarding as a reason for territory defence in Eurasian oystercatcher (*H. o. ostralegus*) and South Island pied oystercatcher (*H. o. finschi*) is convincing (Banks 1998; Heg 1999). Heg (1999) found that male Eurasian oystercatchers in the Netherlands whose mate was absent sometimes evicted soliciting female intruders instantly, suggesting that extra-pair copulations (EPCs) were not necessarily beneficial, even when there was no apparent risk of a penalty by the mate. Banks (1998), in a study investigating why South Island oystercatchers defend territories found that a mount was equally likely to elicit a territorial response from a breeding pair at all stages of the breeding season, suggesting mate guarding was not the reason for territoriality. He also found males initiated a similar number of responses at all stages of the breeding season and that both males and females spent similar amounts of time at the mount before striking it, including at the pre-egg laying stage, which is the critical stage for protecting females from other males.

There are costs of defending territories (Brown 1969; Heppleston 1972; Safriel *et al.* 1984) and the implications of territorial behaviour are important for conservation management. Territorial behaviour or more specifically, site-dependent regulation as proposed by Rodenhouse (1997), is probably the key population regulating factor for many birds, including oystercatchers (Harris 1970; Ens 1992; Goss-Custard *et al.* 1995; Newton 1998; Heg 1999). Some bird species may defend territories larger than required, creating a purely behavioural limitation on population density and size (Davies 1978; Beletsky 1992). Territory defence tends to be stronger in the middle, and may be weaker at the boundaries depending on the density of territories and pressures by conspecifics (Vines 1979; Beletsky 1992). This information may be used to determine how compressed territories are, and therefore how close to carrying capacity (Vines 1979).

Territory defence may be aided by plumage and soft part colouration in oystercatchers. Similar male and female appearance (monomorphism) may aid in territory defence, and the plumage and colour patterns may be for signalling and warning, especially the brightly coloured eyes, bill and legs and the white of the plumage. The reasoning offered is that if females did not need to assist in territory defence and did most of the incubating her plumage would be more cryptic like that of chicks and eggs, similar to females of other wader species that do not assist in territory defence (Ens 1992). Alternative explanations for pied versus all-black plumage have been offered, suggesting that pied plumage is very cryptic on light sandy beaches where many oystercatcher species breed, and that all black plumage is cryptic on rocky shorelines (Lauro 1994; Lauro and Nol 1995). These theories are not mutually exclusive. For juvenile oystercatchers, their colouration (e.g., dark bill and eyes, less coloured legs) has been suggested as a means to allow them access to territories with less risk of attack because they are not a direct threat to the current inhabitants, giving them the opportunity to assess these territories for future settlement (Zack and Stutchbury 1992).

Models, stuffed dummies, and decoys have often been used to study behaviour in various species because the stimulus can be systematically varied, and behaviours can be elicited, instead of waiting for them to occur spontaneously. The terminology in this paper follows Lehner (1996): 'models' are items constructed to mimic animals or parts of animals and 'mounts' as stuffed skins of animals. The term 'decoy' is used for live animals (e.g., Vines 1979). Most avian literature follows this usage (e.g., Beletsky 1992), although model is sometimes used to include mounts (e.g., Strausberger and Horning 1998).

Oystercatchers often respond well to models. Two and three dimensional models have been used to test responses to varying colour patterns in Eurasian oystercatcher in Russia, with stronger responses elicited by three-dimensional models (L. Stepanova, pers. comm.). South Island pied oystercatcher in Canterbury did not respond to a two dimensional model, but did to a stuffed mount (Banks 1998). Vines (1979) found a live decoy was needed to obtain a sufficient response from Eurasian oystercatcher to study the strength of territory defence at different locations within territories. Two dimensional models were useful for determining the breeding status of CIO (Schmechel and O'Connor 1999), territory boundaries in CIO (e.g., Chapter 4), and for luring territorial CIO into noose mats for capture (pers. obs) (Plate 1).

Since CIO responded to two dimensional cardboard models as if they were other CIO (pers. obs.), and did not respond in the same way to other bird species, the models must represent a threat to which they react. We, and perhaps the CIO, can see that the models are not oystercatchers, which raises the question what cues cause them to react. Is it the colour, pattern, size or shape? The objectives of this study were to determine which cues elicit territorial defence behaviours in CIO and examine differences in responses to the models as predicted by the threat/risk hypothesis.

METHODS AND LOCATION

The pairs used in this study bred along the north coast, Chatham Island (see Chapters 2, 3 and 4 for details).

To test the responses of CIO to models of different sizes and colour patterns, six two-dimensional models and one control were made from cardboard (Table 1 and Plate 1). The purpose of the control was to determine if CIO were responding to any foreign object placed in their territories that was a similar shape and size to the models, and if not, what a neutral response by them was. The models were placed in the core portions of the territories (those areas that were near the nest sites and where the birds spent the majority of their time). The CIO were approached closely enough to ensure they had seen the model, but not so closely that it caused them to move away in alarm. The model was often waved for a few seconds and the reaction of the birds noted to see if they were aware of the model. When moving away from the model, it was kept between me and the CIO pair. A low profile was maintained (body near the ground) to minimise alarming the birds. I moved far enough away (usually about 20 metres) to ensure the birds were not reacting unduly to my presence.

Table 1 Models used to test responses of CIO, north coast, Chatham Island. (See also Plate 1).

Model	Description
CIO duplicate	Size and colour like CIO
Half size	Half normal size, CIO colours
Double size	Double normal size, CIO colours
Black body	Plumage all black; normal size; red bill, eyes and legs
Black bill	Bill, eyes, and legs all black, pied plumage, normal size
All-black (silhouette)	Entire model black, normal size
Control	Irregular shaped cardboard shape

The tests were conducted early in the 1996 breeding season (October to December). The total test time for each trial was 16 minutes or until the model was knocked over (KO), whichever occurred first. A Latin-square design was used in presenting models (Appendix 1) to minimise any order effect (i.e., all pairs were presented all models, all in a different order). Non-adjacent pairs were selected for the trials to minimise interactions between pairs. There was at least one day between trials. All behaviours for both birds were recorded continuously, and the time when the behaviours occurred. When pairs did not respond (i.e., the model was not approached), a latent period of 16 minutes was assigned to the trial (the maximum length of each test). Responses of either bird of the pair, or both, were recorded. The most aggressive responses of either bird at any particular point in time were used for analysis (e.g., if one bird was attacking the model

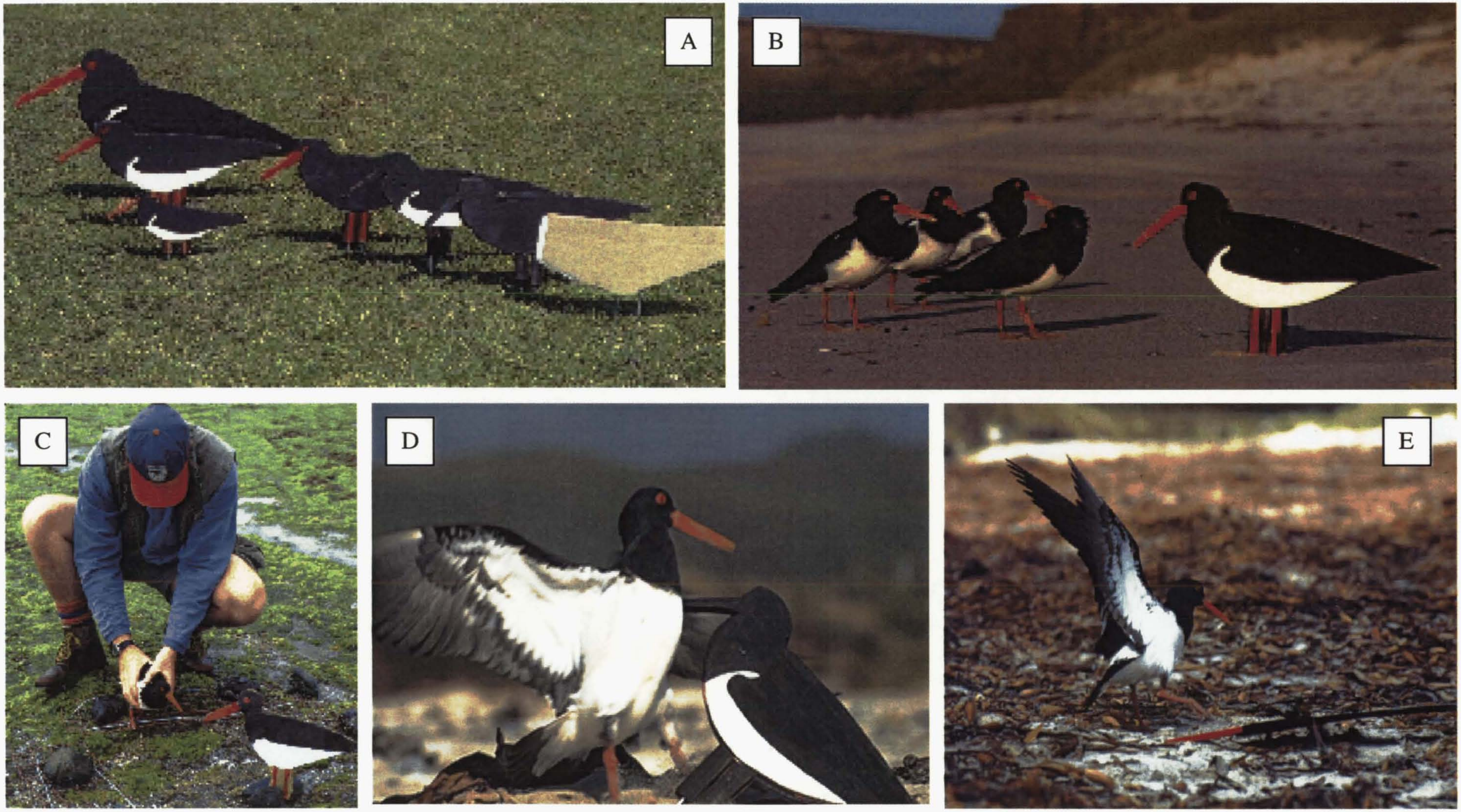

Plate 1. (A) Models used to test cues for territory defence behaviours; (B) CIO responding to the double-sized model; (C) a CIO which has been lured into a noosemat by a model; (D) CIO attacking the pied model; (E) a CIO and model after the model has been knocked over.

and the other bird standing back, the attacking behaviour was the one used for the analyses). Birds were not individually marked, and genders were unknown.

Behaviours were interpreted and coded into six levels of aggressiveness (see Appendix 2 for a detailed list). The behaviours were coded into the following categories: (a1) the highest category of aggressiveness involving direct, physical attacks that risked injury; (a2) 'warning' behaviours, which often immediately preceded attacks; (a3) a threat at a lower level, often seen before or after territorial displays between pairs, (a4) alert or alarmed, (a5) curiosity or awareness, and (a6) 'no approach' or lack of any indication of interest in the model.

Behaviours were interpreted using a combination of information from the literature, and data collected during this study. I reviewed behaviours described as antagonistic for CIO as well as for several oystercatcher species (Davis 1988; Ens 1992; Marchant and Higgins 1993; Nol and Humphrey 1994; Andres and Falxa 1995; Heg 1999). I also examined data collected during this study, which included observations of territorial disputes between pairs, attacks by pairs on intruding floaters, and attacks on models placed within territories.

For each model the following was analysed: 1) time to initial approach of model (to within one metre) (latency), 2) top level of aggression (TLA) displayed (intensity) towards the model, 3) time to reach the TLA, 4) total percent of time spent in each behaviour category, 5) total times KOed and piped at. Pairs were analysed to determine if they varied in their overall responses. The following were analysed for each pair: 1) TLA reached, 2) time to TLA, 3) number of KOs and piping displays, and 4) percent of time spent in each behaviour category (including a summary index). As a summation of the total proportion of time spent in various aggressiveness levels, an 'aggression index' was calculated by multiplying the percent of minutes CIO pair members spent in the different aggression levels by 1.00. This results in a possible range of scores from 1.00 - 6.00. For example, if a pair spent 50% of its time in the a1 level, and 50% at the a4 level it would have a score of 2.50 (1 x 50% + 4 x 50%), compared with a pair that spent 50% of its time in the a1 level and 50% at the a2 level which would receive a score of 1.50 (1 x 50% = 2 x 50%).

I analysed the data using nonparametric statistics because the data were not normally distributed. For the models, the initial time to approach, time to first reach the top level of aggression (TLA), and the aggression index were compared using a Friedman's two-way ANOVA. When a significant difference ($p < 0.05$) was found, post hoc paired comparisons (Zar 1984) of each response between models were performed to identify the models that elicited significantly different responses (using an experiment-wise alpha = 0.05).

RESULTS

The models were approached by at least one member of each pair in 94% of the trials (46/49) (see Plate 1). Only three times were the models not approached during the trials: the control twice, and the black bill once (Table 2). Almost all the models were approached within the first three minutes of presentation (44 of 49), but two (the control and the all-black silhouette) were not approach until after 10 and 13 minutes respectively. Those with oystercatcher type colouration and the silhouette were approached most quickly (all within 2 minutes) (Table 2).

*Table 2 Top level of aggression (TLA) and time for CIOs to reach top level of aggression during interactions with models. In order from most to least aggression displayed towards the model, (as summarised in the aggression index, see Table 3). Behaviour categories: **a1** - physical attack; **a2** - warning; high level threat preceding attacks; **a3** - lower level threats (not always followed by physical attacks, always directed at conspecifics); **a4** - alert or alarmed; **a5** - interest, aware; **a6** - no approach to within one metre of model. See appendix I for detailed description and ranking of aggression levels. Median time and range of times to first reach the TLA displayed. Time to initially approach the model upon presentation to within one metre.*

	Top TLAs reached (no. of pairs)				Time to TLA (minutes)			Time to approach (minutes)			
Model	a1	a3	a5	a6	Med.	Min	Max	Med.	Min	Max	N
Half	7	0	0	0	2	1	9	1.0	1	2	7
CIO duplicate	7	0	0	0	5	2	8	1.0	1	2	7
Double	7	0	0	0	4	1	12	1.0	1	2	7
Black bill	6	0	0	1	3	1	16	1.0	1	16	7
Black plumage	6	0	1	0	3	1	13	1.0	1	13	7
All black	5	1	1	0	1	1	5	1.0	1	2	7
Control	0	2	3	2	12	1	16	1.0	1	16	7

Responses, once the model was approached, varied from apparent curiosity and walking away, to an almost immediate flight towards and physical attack of the model, resulting in the model being knocked-over (KO) (see Plate 1). (The full range of behaviours displayed, descriptions of these behaviours and interpretations are listed in Appendix 2.) Trials lasted from 1 to 16 minutes. Over half the trials (57%) were terminated by a KO of the model (28/49) (Table 3), the remainder ran the entire 16 minutes.

Table 3 Summary of aggressiveness displayed towards models in order of most to least aggression elicited. Aggression (agro) index - a summation of aggression displayed (categories a1 to a6), with possible ranges from 1.00 (100% of time spent in top level of aggression, a1) to 6.00 (100% of time spent in a6 category - no approach or interest shown in model). See methods section for details. Percent of time CIO pair members reached various aggression categories. Number of times models were KOed or elicited piping displays. Behaviour categories: a1 - physical attack; a2 - warning; high level threat preceding attacks; a3 - lower level threats (not always followed by physical attacks, always directed at conspecifics); a4 - alert or alarmed; a5 - interest, aware; a6 - no approach to within one metre of model. Letters after results indicate results of post hoc comparisons, groupings with the same letters are not significantly different.

	Agro		Aggression categories (n = 7 all models								
Model	index		a1		a2-3	(a2)		a4-5	a6	KO	Piping
Half	1.71	a	60%	a	30%	(29%)	b,c	10%	0%	5	5
CIO duplicate	1.99	a	41%	a	46%	(44%)	b	13%	0%	5	5
Double	2.40	a,b	45%	a	32%	(22%)	b,c,d	17%	6%	4	6
Black bill	2.41	a,b	47%	a	32%	(23%)	b,c,d	8%	14%	5	5
Black plumage	2.47	a,b	46%	a	31%	(18%)	c,d	14%	10%	5	4
All black	2.83	a,b	54%	a	10%	(7%)	a,d	12%	25%	4	2
Control	5.59	b	0%	b	2%	(0%)	a,d	34%	64%	0	0

Almost two-thirds of the time (61%) both birds participated in defence behaviours together (i.e., both displayed the same top level of aggression) (30/49), but nearly a third of the time (31% of the trials) only one bird responded (15/49). Behaviours were often synchronised between pair members, especially for piping displays. Of 27 piping displays, only two were performed by a single member of the pair, in all others both members participated. Two pairs were notable in the lack of participation by both members (Creek and Rock) (Table 4).

Table 4 Aggressiveness displayed by pairs and the number of pair members participating in the displays. Pairs listed in order of most to least aggression displayed overall. The aggressiveness (agro) index - a summary of aggression displayed (categories a1 to 16), possible range from 1.00 (100% of time spent in top level of aggression, a1) to 6.00 (100% of time spent in a6 category - no approach or interest shown in model). Percent of time CIO pair members reached various aggression categories. Behaviour categories: ***a1*** *- physical attack;* ***a2*** *- warning; high level threat preceding attacks;* ***a3*** *- lower level threats (not always followed by physical attacks, always directed at conspecifics);* ***a4*** *- alert or alarmed;* ***a5*** *- interest, aware;* ***a6*** *- no approach to within one metre of model. See appendix I for detailed description and ranking of aggression levels.*

	Agro	Behaviour category				No. defending			
Pair	index	a1-a3	(a1)	a4-5	a6	both	one	n/a	N
WOC	1.96	85%	(60%)	15%	0%	6	1	0	7
TW	2.04	87%	(50%)	0%	13%	6	1	0	7
WW	2.06	82%	(62%)	4%	13%	6	1	0	7
Woolshed	2.59	75%	(34%)	11%	14%	5	1	1	7
Creek	2.69	69%	(43%)	16%	15%	2	4	1	7
Dune	3.42	55%	(24%)	28%	17%	5	2	0	7
Rock	4.64	23%	(17%)	33%	45%	0	5	2	7

The difference in the aggression index (overall proportion of time CIO spent in aggressive behaviours) (Table 2) was significantly different between models (S = 13.81, d.f. = 6, p = 0.033). The most overall aggressiveness was displayed towards the three CIO-like models, with the order from most to least proportion of time in higher levels of aggression being half, CIO-duplicate, then double. The lowest was for the all-black silhouette (and control).

Although differences in overall aggression (the aggression index) varied between models, there was no significant difference in the proportion of time spent in physically attacking (i.e., a1 category) the various models (control excepted). If the control is included, then the difference was significant (S = 14.75, d.f. = 6, p = 0.023).

There was a significant difference in the proportion of time CIO spent in warning behaviours (a2) between models (including the control) (S = 17.45, d.f. = 6, p = 0.008). In spite of high levels of aggression towards the silhouette (54% of the time spent attacking it), only 7% of time was spent in warning it (Table 2), which was significantly different from all other models (control excluded). (The differences in warning time between the control and silhouette were not significant.) This contrasts with the CIO-duplicate, which received the highest levels of warning; 44% of the time spent interacting was in warning (a2) behaviours towards it. There was no significant difference in proportion of time spent warning the four pied plumage models. This lack of warning behaviour towards the silhouette was also reflected in the number of pairs performing a piping display against it. Only two warned it this way, compared with four to five for all the other models (excluding the control).

There was a significant difference for the top level of aggression (TLA) displayed towards the models (the significance was due to the control) ($S = 21.51$, d.f. $= 6$, $p < 0.001$). The highest levels of aggression (i.e., physical attacks) were displayed by every pair ($n = 7$) towards the CIO coloured models, followed by black body and black bill (6 of the 7 times), and lastly the silhouette (5 or the 7 times) (Table 2). Only interest or alarm was displayed when the control was presented, and occasionally it was 'nibbled', but never aggressively attacked or 'warned' via pipping displays or other a2 warning behaviours.

There were patterns in the responses to the other variables, but none were statistically significant ($p > 0.5$). The median time to reach the TLA (which varied by model and pair) was reached most quickly for the silhouette (1 min.) and half sized model (2 min.) and most slowly for the CIO-duplicate (5 min.) (Table 2). The minimum times to reach TLA were about the same for all models (1-2 min.), but the maximums varied from 5 to 16 minutes, with all-black silhouette having the shortest maximum (5 min.). Although the TLA was reached most quickly with the silhouette, only five pairs or members of pairs attacked it, and virtually none 'warned' it.

There were marked differences in the level of aggression displayed by various pairs. This was accounted for in the statistics (blocked by pairs), but it is nevertheless interesting to note. Some pairs were more cooperative (both members participated in defence of territory) (Table 4). Five pair members attacked all of the models (control excepted), and KOed five or all six models (Table 5). In contrast, two pairs (Dune and Rock) were much less aggressive than the others. The Dune pair attacked five models and KOed only one, and the Rock pair attacked only three models and KOed none. The proportion of time spent in a1 or a2 levels of aggression (attacking or warning) also reflected these differences.

Table 5 Number of times particular levels of aggression were reached, median time to reach top level of aggression (TLA), number of KOs and number of times pipping displays occurred during presentation of six models and one control. Ordered by TLA and median times to reach TLA. Behaviour categories: ***a1*** *- physical attack;* ***a3*** *- lower level threats (not always followed by physical attacks, always directed at conspecifics);* ***a5*** *- interest, aware;* ***a6*** *- no approach to within one metre of model. See appendix I for detailed description and ranking of aggression levels.*

	Top TLAs reached for 7 models				Median time			
Pair	a1	a3	a5	a6	to TLA (min)	KOs	Piping	N
TW	6	1	0	0	2	6	6	7
Creek	6	0	0	1	3	5	2	7
WOC	6	1	0	0	3	6	4	7
Woolshed	6	0	0	0	4	5	5	7
WW	6	0	1	0	4	5	5	7
Dune	5	1	1	0	5	1	4	7
Rock	3	0	2	2	12	0	0	7

DISCUSSION

CIO approached the three CIO-like models and the silhouette most quickly, but tended to be less aggressive towards the silhouette (only five physically attacked the silhouette, versus seven for the CIO-like models). The control, although not shaped like an oystercatcher, was also approached by five pair members, and two of those pairs briefly displayed behaviours often associated with low levels of aggression towards it (2% of the time). This might be because they associated it with the other models, or it was a strange unknown object and they were curious and/or alarmed.

The three CIO-like models were the only models physically attacked by every pair. These models may represent the highest threat to the pairs due to their colouration, representing mature adults of the same species and therefore potentially competing for resources and/or a mate and even potentially displacing the pair members from the territory. That CIO pairs attacked the CIO-like models is perhaps not surprising, but that they attacked the other models as well (albeit with slightly less vigour) is interesting. The shape must play an important role in both recognition and as a cue to their response. Colour and size may then be secondary to the level of threat and risk posed. The black body and black bill models may appear to be less of a threat because they represent a different species (black body) or lack white signalling plumage, and a juvenile (black bill). In these cases, the threat may be only temporarily food resources, rather than something as serious as potential displacement.

The time to reach TLA might depend on the balance between the threat posed by the intruder and the risk involved in a fight. For models representing a high threat (i.e., all those with CIO-like colours), the model representing the lowest risk was attacked most quickly (e.g., the half-sized model), in contrast to the other two models, which represented a higher risk, and were therefore attacked after a longer time period (median times twice as long as the half size model).

Direct physical attacks or fights entail the risk of injuries, therefore warning systems such as calls and displays are often used, presumably to minimise the risks of physical confrontations, especially with closely matched conspecifics (Harper 1991). Some of the warning behaviours in oystercatchers are quite distinctive and well described, such as the piping display (Harris 1970; Marchant and Higgins 1993). In song birds, calls were found to be effective in deterring conspecifics from attempting to settle in occupied territories (Davies 1978).

The TLA never included the group of warning behaviours coded as a2 - those usually preceding an attack (Table 2). These warnings appeared to be 'in earnest' and were followed up with an attack. Although the silhouette was quickly approached and frequently attacked (five of 7 pairs) it was almost never warned (a2) (only 7% compared with 22-44% for the other pied plumage models). The all-black silhouette also received fewer a2 warnings (18%). However, if a2 and a3 are combined (the highly aggressive warnings plus the generally antagonistic behaviours), the differences between all the models except the all-black and control almost disappear, except for the CIO-duplicate model.

The CIO-duplicate elicited a higher proportion of time spent in warning behaviours ("a2") than all the other models (although not significant at the $p = 0.05$ level), and a significantly higher proportion of time spent in warning behaviours ("a2") than the silhouette and all-black plumage models. Perhaps these warning displays are very species specific and, even further than that, very specific to closely matched conspecifics. If the purposes of warning is to prevent injury, one might expect more warning towards the double size model. However, if the asymmetry between individuals is high, and the warning displays serve primarily as communication about asymmetry (Harper 1991), then when these asymmetries are obvious the warning behaviours may become redundant and therefore reduced or eliminated.

Some pairs were much less aggressive than others. Dune and Rock were lower than other pairs for most measures of aggression (Tables 3 & 4). The Rock pair was especially low. There are several possible reasons including low quality territories, pair turnover, impending divorce (Heg 1999), incubation, or some combination of these factors. The Rock pair was incubating during two trials. However, other pairs were also incubating during trials and still KOed all models presented except the control (n = 9). For four of the CIO pairs that were incubating and lost clutches, a repeat test was conducted and the responses were similar, or the response more aggressive, when incubating than when not incubating. In South Island pied oystercatcher, Banks (1998) found that response rate to a decoy were the same in all three different stages of the breeding cycles he tested (pre-egg, egg, and chick). Therefore it seems unlikely that incubation was the main reason for this lack of response in the Rock pair.

If the quality of the territory, and therefore the benefits, are low then the costs invested in defence should also be lower. If territory quality is reflected by reproductive success, then these were lower quality territories. Compared with 13 other territories along the north coast during the nine breeding seasons from 1991 to 1999, both the Dune and Rock territories were in the bottom third in terms of reproductive success and breeding effort (i.e., season's pair attempted to breed, number of successful breeding seasons, and mean number of fledglings per year) (Chapter 4). There may also have been some turnover of pair members in the Rock territory because it was not occupied during one of the breeding seasons. If one of the pair members was considering divorce, it would probably be less likely to assist in territory defence (Heg 1999) but there is no way to confirm this for these pairs, and this would not prevent the other pair member from vigorously defending the territory unassisted.

Zack and Stutchbury (1992) argued that subadult plumage is a reliable signal used for gaining access to high quality sites as a nonbreeder for the purpose of assessing territories, and establishing site dominance at high quality territories. This involves frequent interactions with older territory owners, and avoiding aggression from them via subadult plumage would presumably facilitate the maintenance of an 'assessment sphere'. This argument appears to be weakly supported by the results of this study. If the models with no adult colouration on the soft parts were perceived by the territory owners as juveniles, then the slightly lower level of aggression displayed towards them compared with the CIO-duplicate would allow them more access to the territories. However, since mate guarding is probably not a key function of territory defence in oystercatchers (Ens 1992; Banks 1998; Heg 1999), the main threats imposed by intruders are probably displacement and competition for food resources. An immature CIO would represent slightly less risk in terms of displacement than a mature CIO, but the same as an adult for food competition. An immature probably represents a lower risk in terms of fighting ability as well as a lower willingness to risk a physical fight. Therefore, in total, an immature intruder probably represents both a lower risk and a lower threat, resulting in a response similar to that of models with adult colouration which represent a higher threat, but also a higher risk.

Both black plumage models tended to incur slightly less wrath from the territorial pairs, but only the all-black silhouette significantly less. Perhaps, as Ens (1992) suggested, the white plumage patterns play a role in territory defence, but most effectively in combination with the bright colouration of eyes, bill and legs. Alternatively, the slightly lower levels of aggression may be similar to how CIO would respond to a different species of oystercatcher. The cues may be similar enough to represent a threat to resources, but less of a threat than a mature CIO, and therefore attacked slightly less vigorously.

Models, mounts and decoys have been helpful for testing theories of social stability, territory acquisition, strength of territory defence, changes in territorial behaviour across the breeding season, gender roles in territory defence, and many other behaviours in birds (see for example Beletsky 1992; Lehner 1996; Banks 1998). In oystercatchers, Vines (1979) suggested that the strength of defence near the perimeters of territories could provide clues of how close a local population is to carrying capacity. Strength of territory defence may also provide clues to the quality of territories. Lauro (1992) found communally nesting oystercatchers all responded by piping at models, confirming that all the members nesting together participated and cooperated in territory defence.

In this study, models were also useful for drawing birds to noosemats for capture. This meant that, compared with other commonly used methods, birds that were not incubating could be captured, and work could be done during the day (as opposed to using spot-lights at night or drop-traps over the nest). The strongest responses, and the most warning behaviours, were directed at the CIO-duplicate model, which made it the most useful of the models for a capture lure. The warning behaviours lasted longer, with more walking around, and were therefore more likely to draw in both pair members and allowed more chance of capture. Indeed, the CIO-like model was so antagonising that the same individuals were sometimes caught several times in succession while attempting to capture their mates.

If future research were undertaken into aspects of cue response, using territories that are similar as possible, and using fewer models and more pairs to increase the sample size, would increase the likelihood of detecting differences and make for a more powerful experiment. Eliminating differences in breeding stage would also be advisable. Examining gender differences in future research may also prove fruitful as well.

SUMMARY/CONCLUSIONS

Territoriality has important implications for the population dynamics of CIO. CIO pairs are fiercely territorial and, like other oystercatchers, holding a territory is essential for breeding. I argue that the response to the various models presented was a result of CIO members' assessment of the relative threat and risk these models represented. The CIO-coloured models, with the same colour patterns as mature adults of the same species, represented the greatest threat to the pairs, potentially even displacing them from their territories. The normal and largest sized model represented the greatest risk, and the smallest model the least risk. All CIO-like models were physically attacked by all pairs (due to the high level of perceived threat), but the normal and double-sized models were attacked after the longest time, probably due to the higher risk of injury in a fight that it represented. The main cues to recognition seemed to be shape (silhouette) and colour patterns; therefore, these models were approached most quickly. The all-black silhouette and black plumage models were warned very little, perhaps because they represented a different species, and warning behaviours are very species specific. Of all the models, the

CIO-duplicate model received the largest proportion of time in warnings, suggesting one function of warning behaviour is to avoid physical fights when asymmetry is minimal.

The pied plumage patterns of oystercatchers that use sandy beaches have been suggested as evolving to assist in defence and threats against intruding conspecifics in females or, alternatively, to maximise camouflage (especially for incubating birds), although these need not be mutually exclusive. In immature birds differences in colouration have been suggested as a signal of non-breeding status to allow for easier access to territories for assessment. The more aggressive responses of CIO pairs to models with pied plumage and colored soft parts, over those with no colour or all black plumage, lends some support to these arguments.

Models are very useful tools in studying a variety of behaviours because stimuli can be varied systematically and behaviours elicited, rather than having to wait for them to occur spontaneously. Models have also proved to be useful tools as a capture aid in CIO and for determining territory boundaries. With further research, the response of territorial pairs to models may also be able to provide clues to the quality of territories and how close a population is to carrying capacity.

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APPENDICES

Appendix 1

Latin square design used for model experiment. Codes: OC - CIO duplicate, HS - half size, DS - double size, BD - black body, BL - black bill, AB - all-black (silhouette), and CT - control. (See Table 1 for descriptions and Plate 1 for a photo of the models).

	Models						
Territory	OC	HS	DS	BD	BL	AB	CT
WW	4	5	1	3	6	2	7
WoC	5	1	6	4	7	3	2
TW	2	4	3	6	5	7	1
Creek	3	2	5	7	4	1	6
Dune	6	3	7	2	1	5	4
Woolshed	1	7	4	5	2	6	3
Rock	7	6	2	1	3	4	5

Appendix 2

Behaviours and aggression categories assigned.

Level	Behaviour	Description
a1	flying at	Direct flying attack
a1	feint at	Move suddenly at from close range
a1	ground attack	Attacking the model on the ground after a KO
a1	knock over (KO)	Physical attack which knocks model over
a1	peck	Direct peck at model
a1	pecking/lunging	A quick lunge with bill from close range
a1	wing beating	Attacking with wings
a2	aggressive approach	Very direct approach with wings held out ('carpel flexure')
a2	piping display, stand or walk	Distinct rapid calling and zig-zag walk with bills pointed downwards, usually by both members of a pair
a2	sidle	Moving sideways to within striking distance
a2	stand tall	Standing up erect, often with feathers on back of head erect
a3	body rocking	Rocking body back and forth
a3	bill tuck	Bill tucked under scapulars, eyes open
a3	carpel flex	Wings held out from body
a3	ground peck	Pecking at the ground, different motions than foraging
a3	head bobbing	Head bobbing up and down
a3	object toss	Picking up objects and tossing them to the side
a4	forage	Normal foraging behaviours
a4	false brooding	Sitting down as if brooding or incubating
a5	approach model	Or re-approach model
a5	nibble	Gentle nibbles (as apposed to pecking)
a5	standing near the model	Within one metre
a6	away from model	More than one metre
a6	no approach	Never approached model to within one metre
a6	walk away from model	To further than one metre

CHAPTER 8

CONCLUSIONS

The original questions

Several key questions were posed at the beginning of this thesis including:

- What are the factors limiting the population of Chatham Island Oystercatcher (CIO) on the Chathams?
- What is the abundance and distribution of the population and is it increasing, decreasing or stable?
- What are the recruitment and mortality rates, and within which segments of the population are they acting and during which season(s)?
- What habitats are CIO selecting at the general, territory and nest-site level?
- What are the links between productivity and habitat characteristics (what is high quality habitat?)

Specific management related questions from recovery planning ((Davis 1988a, Grant 1993)) which inspired these questions included:

- If management intervention increased productivity, would the breeding/total population increase? (Is there enough habitat to support increased productivity, especially over-winter?)
- What are the primary causes of clutch and chick losses?
- What recovery goal should be set, (when will the habitat on the Chathams be 'full', i.e., have reached carrying capacity?)
- How can breeding habitat be improved and/or increased?

To answer these questions, objectives for this study were set to collect and interpret data for CIO on: 1) population size, trends, and distribution across the Chathams, 2) basic breeding parameters for 15 pairs along the north coast, 3) recruitment and mortality rates, 4) habitat selection at the general, territorial and nest-site levels, 5) habitat factors that are correlated with territory quality as reflected in breeding success, and 6) cues that elicit territorial behaviour in CIO.

The findings

Abundance and distribution

Chatham Island (CI), and to a lesser degree Pitt Island, are essential to CIO conservation as about 85% of breeding pairs occur on these two islands. It appears that the population has increased by about 20-40 individuals (20-39%) since the late 1980s, probably due in part to management intervention along the north coast. The total population was estimated at 140-150 adults in 1998, with all of the increase having occurred on the two main islands (Chatham and Pitt Islands). Comparisons with past counts were difficult due to differences in methodology. The numbers of breeding pairs on Rangatira appears to be slowly declining. On the surface this is surprising since Rangatira is free from introduced mammalian and avian predators, although the native, predatory skua breeds on the island; however, Rangatira may not be preferred habitat for CIO, and relative use is probably dependent on overall predator pressure and other factors around the whole of the Chathams archipelago. Future counts of CIO should be conducted so comparisons can be made over time and changes in the population determined.

Recruitment and breeding parameters

Flooding was a major cause of clutch loss (40-50% of clutches) among the 15 pairs of CIO monitored over the three seasons of this study, but may only significantly decrease productivity in some pairs or in some years because pairs have the capacity to lay up to two replacement clutches. In one season (1996) tidal flooding destroyed most of the clutches. Damaged but whole eggs left in nests caused delayed or failed breeding in 17% of the pair-seasons (n = 42 pair-seasons). Productivity was variable between seasons, but overall was low compared to many other oystercatcher species. Overall breeding effort was high (98% of pair-seasons). Risk of losses for eggs and chicks, especially non-flooding losses, were highest the week just before and after hatching. If chicks survived their first two weeks they had good chance of fledging: 75% of losses occurred within the first 11 days after hatching. Eviction of juveniles was about 33 days after fledging.

Habitat selection

CIO used the coastline almost exclusively. The shoreline of the lagoon received only 2% use, compared with 26% availability and only by floaters (nonterritorial nonbreeders). Intertidal rock platform was selected by CIO over four times more than would have been predicted by their availability, and sandy beaches were selected over twice as often. Sections of coastline with wide storm-tide zones were selected more often than narrow zones in all cases except one (the little used boulder/cliff/shell sections of coastline).

Contrary to past findings, paddocks and sandy beaches were used extensively by some pairs for foraging along the north coast, Chatham Island. Among the 15 study pairs, sandy beach territories (those territories with no rock platforms or boulders) were the most productive, especially during periods of no management. There were some indirect indications that pair turnover may be high. High quality nest-sites appear to be limiting due to the establishment of marram grass and high predator pressure, especially in some territories. CIO pairs on Chatham and Pitt Islands may be trapped 'between the devil and the deep blue sea', forced to balance the risks of losing clutches to flooding with the risks of predation if they nest near the marram grass covered dunes.

Territorial cues

CIO responded well to two-dimensional models, and can be lured by them into noose-mats for capture and to study territory boundaries. The most CIO-like models were attacked most vigorously, probably because they represented the highest threat and risk. Warning behaviours were displayed the most to the model that was the most similar in shape, size and colour to CIO. CIO seem to use shape first for recognition, then colour and size for threat/risk assessment. There appeared to be a positive correlation between aggression and territory quality; pairs seemed reluctant to invest high amounts of effort defending lower quality territories (as reflected by productivity).

What regulates or limits the population?

A key objective of this study was to determine if habitat during one season was critically limiting and, if productivity was increased through management intervention, would it result in an increase in the total population. The high survival of first-year birds over winter from this study suggests that foraging habitat is not critically limiting at the current population densities. Survival of immature first-year CIO is likely to be density dependent (see for example (Goss-Custard et al. 1994, Goss-Custard et al. 1995, Goss-Custard and Durell 1988, Goss-Custard et al. 1982)), and at higher densities might become a critically limiting factor. Population modelling could be used to explore this further, but was outside the scope of this study.

Potential limiting factors on the CIO population include food, predators, competitors, weather, disturbance and pathogens. During the breeding season, foraging habitat did not appear to be critically limiting at current densities along the north coast, Chatham Island. Several territories had foraging habitat of high enough quality to support three-chick broods, and many territories (9 of 15 along the north coast, Chatham Island) were able to produce 1.33 or more fledglings/pair/season on average over one or more three-season periods.

It appears that high quality nest-sites and areas with low predator pressure (or good habitat for escaping predators) were the main limiting factors. These factors may vary from territory to territory. Some territories appeared to lack high quality nest-sites, resulting in significant losses to flooding. Other territories had good hatching success, but low chick survival, possibly due to predator pressure. Adult mortality rates, especially among the breeding population, may be a sensitive parameter, but could not be determined during this study.

Limiting factors may also vary from season to season. Productivity varied considerably because of weather patterns for some territories. In one case the pair in the OTF territory lost all but one clutch to tidal flooding over three seasons (n = 6), but in the three year periods before and after this study fledged 1.67 and 1.33 fledglings/pair/season respectively. In other territories variations in predator pressure may be the main factoring limiting breeding success in some seasons.

CIO in context

As a small worldwide family, with only a single genus, the oystercatchers tend to share many similarities. Therefore, much of information from other oystercatcher species may potentially be transferred to CIO, particularly from South Island pied oystercatcher and variable oystercatcher to which they are thought to be most closely related ((Baker 1972, Hayman et al. 1986, Hockey 1996a, Sibley and Monroe 1993)). Most of the comparative information in this section is drawn from two reviews of the oystercatcher family (Haematopodidae) by Hockey ((1986, 1996a)), plus work by Baker ((1972, 1975)) on the New Zealand oystercatchers.

Habitat use by CIO shared similarities with both South Island pied oystercatcher and variable oystercatcher, but was more similar to variable oystercatcher. The CIO, like variable oystercatcher was restricted to the coast with rare exceptions. However, CIO share the trait with South Island pied oystercatcher of foraging in paddocks, and subsequent to this study one pair was documented nesting in paddock adjacent to the coastline ((Moore et al. 2000)). Similar to other pied oystercatcher species, CIO made extensive use of sandy beaches.

In all oystercatchers fidelity to mate and breeding site tends to be strong ((Hockey 1996b)). This appears to be the case for CIO on Rangatira ((Davis 1988b)), but is unknown for those in other parts of their territory. Some CIO pairs defended territories throughout the year, which is a trait also found in a couple of other oystercatcher species, the Australian pied (*H. longirostris*) and African black (*H. moquini*) oystercatchers.

CIO along the north coast, Chatham Island, showed patterns of nest-site selection that were very similar to other species of coastal breeding oystercatcher. They tended to nest predominantly on sand in open, high visibility areas in the widest sections of beach within their territories, or on a soft substrate on rock outcrops if wide sandy beaches were unavailable.

Modal clutch size of oystercatchers in the Northern Hemisphere is three, but in the southern hemisphere is two except for variable oystercatcher and South Island pied oystercatcher, which are also three. Interestingly the CIO modal clutch size is two, rather than three, as would be expected by systematic affinities. The incubation period for CIO of 28-29 days is in the modal range for most spp of 27-30 days, and is similar to that for variable oystercatcher (28 days), and just slightly longer than that for South Island pied oystercatcher (26 days). All oystercatchers are single-brooded, but lay replacement clutches if the first clutch lost. Productivity of CIO was low compared to most other species. Causes of loss appeared to be similar, especially loss of eggs to flooding, which is common among many species of oystercatcher. CIO shared the habit, with other oystercatcher species, of incubating eggs after flooding and displacement.

Average time to fledging ranges from 33-49 in oystercatchers. For CIO on the north coast, average fledging times were 39 days, and on Rangatira 48 days ((Davis 1988b)). Within a single species (e.g., Eurasian oystercatcher), fledging periods may range from 27-52 days depending on brood size, chick growth rates, and food availability. Apparently unique to CIO on the north coast was the short time to juvenile eviction/dispersal (33 days, range 24-42). In most other species, the time is longer. For Eurasian oystercatcher the time is three months or longer, for American black oystercatcher (*H. bachmani*) five to six months, and for variable oystercatcher it is often through the winter (otherwise they join winter flocks three to four weeks after fledging). This may be because there is enough soft food (e.g., marine worms, sandhoppers) available that young CIO can feed themselves successfully.

The piping call seems to have a similar function in all species, that of territory defense. In some species it is also used as a greeting call when one member of pair returns from being away. This was found in CIO as well. CIO responded vigorously to two-dimensional oystercatcher-like models, attacking them within a minute or two of presentation and often knocking them down. Responses to models seem to vary among species. In South Island pied oystercatcher, a three-dimensional dummy was needed to elicit a vigorous response ((Banks 1998)). In Eurasian oystercatchers in Europe a live bird was used, as a dummy did not elicit the desired response ((Vines 1979)). However the same species in Russia responded to two- and three-dimensional models (A. Mosalov, pers. comm.). Unfortunately none of these communications described the response of oystercatchers to the various types of models tested in detail, making comparisons difficult, as different types of response may have been sought in different studies.

Management implications

.....of site-dependent regulation

Site-dependent regulation ((Rodenhouse et al. 1997)) has important implications for conservation management. If there is a significant difference in the quality of different territories, some pairs will be very productive, while those in marginal habitats may only just replace themselves. There may even be population sinks where mortality rates are higher than recruitment rates ((Pulliam 1988)), especially in areas with high adult mortality or where conditions change after the territory has been settled ((Newton 1998)). Normally higher quality sites, with higher rates of productivity, should be occupied first, followed by lower quality sites as the population increases (see for example (Ens 1992, Heg 1999); and the review by (Newton 1998)). If only high quality territories are monitored, changes in the breeding population may be missed. Overall estimates of productivity could also be significantly affected depending on which pairs are monitored.

If productivity increases through management, there should be a corresponding increase in the total number of breeding pairs over time. However, these additional pairs may be forced to settle in lower quality habitat because the higher quality territories are already occupied, resulting in lower productivity for the pair and on average for the population. As a result the overall productivity per pair will probably decline. Monitoring and reporting the total number of fledges for specific areas (or per unit area) would reflect more accurately a total increase in breeding pairs. Otherwise, depending on which areas are monitored, a decline in average productivity per pair may be interpreted as a negative outcome, in spite of increased numbers of breeding pairs and an absolute increase in the population.

Monitoring the composition of the nonbreeders may give indications as to the overall health of the population. Often mature birds, including oystercatchers, choose to delay breeding rather than settle in lower quality territories ((Ens et al. 1995, Heg et al. 2000, Zack and Stutchbury 1992)). Floaters can provide a buffer to the population so that if breeders are lost the mature floaters can recruit into the breeding territories. At higher levels of productivity the numbers of floaters should increase, and the age structure of the floating population should change as well, with a higher proportion of mature individuals. In order to detect changes in the population it is important to monitoring the floater populations, as well as lower quality territories, as these are the ones that should respond first to changes in the overall numbers.

The strong density dependent nature of site-dependent regulation means that increased population will not be self sustaining if there are no long term changes in limiting factors. In order for the increased numbers to be self sustaining there would need to be either increased numbers of territories, or increased productivity within existing territories, or some combination of the two. However, it may be more cost effective to temporarily increase productivity within existing territories through predator control, or other shorter-term management techniques, rather than implement more extensive long-term measures such as habitat restoration. Some combination may also be quite effective. Modelling various scenarios could be useful for exploring the options and cost/benefits of various strategies.

In summary, as productivity and the CIO population increases the following changes would be predicted: lower quality territories would be occupied, average productivity across the entire population would decrease as the newer pairs fledge fewer chicks, the proportion of floaters should increase, the average age of the floater population should increase and, eventually, first-year survival may decline. Many of these changes may be subtle and only detectable over long periods of time. Accurate assessment of territory quality by CIO is also essential for site-dependent regulation to occur. These responses in the population have implications for monitoring. To detect where critical limiting factors are operating, monitoring of first-year survival is important, as is monitoring the proportion and composition of the floater population. As populations increase, average productivity per pair may be lower, but the total number of fledglings produced will be higher due to the additional breeding pairs. Therefore, reporting fledglings per unit area rather than (or in addition to) per pair may be more accurate.

.....of limiting factors and bottlenecks

Limiting factors vary from area to area on the Chathams, with predation and nest-site habitat more important on the north coast; foraging habitat quality and possibly disturbance more important on Rangatira; and storms and nest-sites a major limitation along the exposed south and southeast coastline. Lack of nest-sites and disturbance, plus predator pressure may be significant on Pitt Island, especially around sandy beach areas. Disturbance alone, or in combination with other factors, may preclude CIO from using otherwise high quality habitat in areas such as around Owenga and Waitangi.

Many variables contribute to recruitment including hatching success, fledging success, and brood size. Removing limiting factors which affect these recruitment variables should result in higher productivity or survival, and an increase in overall numbers. However, if any of these factors is creating a bottleneck, changing the other limiting factors will have no effect on overall recruitment. For example, if tidal flooding consistently destroys all the nests in an area, no amount of predator control to decrease chick losses will be effective. Conversely if predators remove all the young chicks in an area, no level of nesting effort or success will result in increased recruitment.

If turnover of breeding pairs is high due to adult mortality, the impacts would probably be especially significant because it affects both recruitment and mortality. In addition to the death of an adult breeder, breeding effort for the season is often lost. The negative effects on recruitment may last over many seasons because the breeding pair bond is lost and fledging success is positively correlated with longer pair bonds in oystercatchers (Heg 1999).

.....of various management options

There are many options for recovery management as the path to recovery of a population need not be a reversal of the path leading to decline ((Green 1994)). Ideally management should result in the most fledglings and highest survival rates with the least cost and effort. Among the alternatives are the scale of management which might fall along a spectrum from very intensive management of just a few pairs to less intensive management of most pairs and variations thereof.

Because it appears that limiting factors may vary between areas, it may be more effective to manipulate different factors in different territories depending on the main factors limiting productivity. In some territories providing high quality nest-sites which reduce flooding and predation risk (e.g., by adding elevated areas for nesting or moving nests) may be most effective, whereas in others predator control might be more effective. Habitat restoration, and removal of marram grass, may simultaneous affect several factors (i.e., reduce flooding risk and decrease predator pressure) and over the long term could be more cost effective than predator control alone. It may be possible to refine predator control by removing just some predators or their prey species. For example, removal of rats, which in turn might reduce cat numbers, if rats are a main prey item of cats. Removing damaged eggs is probably an inexpensive and effective method to increase productivity over large areas by encouraging pairs to re-nest rather than incubate eggs that are not viable.

If management refinements are made systematically, and carefully monitored, it may be possible to understand the various mechanisms driving the system and over time to target management more specifically and effectively. Modelling and a cost/benefit analysis could be helpful in analysing the options to determine the potential magnitude of various limiting factors, which management would be most effective, the range of possible responses of population to different types/amounts of management, and targeting of future research and monitoring.

.....of responsiveness to two-dimensional cardboard models

Models proved to be useful for luring birds into noosemats for capture. This allows for capture of non-incubating birds during the daytime. The response of birds may vary with the season and quality of the territory. Sometimes one bird may respond more often or vigorously than an other. The CIO-like models also allow for determining approximate territory boundaries. With further research it may be possible to use responses of CIO to determine territory quality and how close an area is to carrying capacity.

Future directions

The following are suggested as some of the most important future research and management needs arising from the results of this study. Other management and research suggestions are listed at the end of each chapter.

- Use population modelling to explore the magnitude of various limiting factors, and to determine which management strategies are most likely to be effective, to predict potential responses of population to different types/amounts of management, and to test various cost/benefit scenarios.

- Determine mortality rates for breeding adults and pair turnover in both managed and unmanaged areas.

- Monitor first-year overwinter survival of CIO for several seasons and then periodically over the longer term.

- Monitor the floater population and marginal habitats, and determine the age structure of the floater population.

The encouraging response of CIO productivity to recent predator control suggests that with sufficient resources this species' future can be ensured. With thoughtful coordination between research and management, much can be learned from the results of ongoing management and activities refined to be more effective. Insights into the mechanisms driving the system can also be gleaned, allowing for predictions to be made and tested, which can be a powerful tool, and the knowledge gleaned from the CIO used for conservation work with other species as well.

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