

SYSTEMATICS AND AFFINITIES OF  
NEW ZEALAND OYSTERCATCHERS.

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by

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"..... the ability to prove that two populations are statistically different in one or several characters is only a measure of the persistence and patience of the systematist."

Lidicker (1962).

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## Chapter 1.

INTRODUCTORY.1.1 INTRODUCTION.

Systematic studies have three main objectives: firstly to determine the unique properties of taxa at and above the species level; secondly, to determine common properties of selected taxa and to suggest reasons for similarities and differences; and thirdly, to investigate variation within taxa (Mayr, 1969). Oystercatchers provide excellent material for such studies. Despite their distinctiveness and evolutionary conservatism, they have had a surprisingly unstable systematics. This has occurred mainly because Old and New World species are rarely sympatric, and thus the latter have commonly been regarded as only subspecies of the former. New Zealand is perhaps the only country where species of both Worlds overlap in their distributions, and thus afford opportunity for comparative study.

Further impetus for a systematics study of oystercatchers is provided by their relative homogeneity. They comprise a monogeneric family of shorebirds which has not undergone any major adaptive radiations into a diversity of ecological niches, but rather has dispersed from original centres of distribution to occupy identical niches in new geographical localities. The uniformity of structure and habit of this family has been attributed by Larson (1957) to extreme ecological specialization coupled with strong stabilizing selection.

Although Lack (1961) has pointed out that ecological divergence of closely related forms is not known to initiate species-formation, the inherent potential of such divergence to function as an isolating mechanism is well established (Mayr, 1963; Cain, 1966). Conversely, specialization is

likely to restrict speciation and result in evolutionary conservatism. This restriction is reflected in the taxonomy of oystercatchers, with a maximum of eight species being generally accepted at present.

## 1.2 TAXONOMY OF WORLD FORMS.

The Order Charadriiformes includes 13 families of wading birds. One of these, the Family Haematopodidae, is represented by a single genus Haematopus Linnaeus, 1758 to which the oystercatchers belong. Within this family, Peters (1934) recognized four species, but contemporary taxonomists describe six species as follows:-

- (1) Haematopus ostralegus Linnaeus, 1758 - World wide distribution.
- (2) Haematopus palliatus Temminck, 1820 - southern North America through to central South America.
- (3) Haematopus ater Vieillot and Oudart, 1825 - central and southern South America.
- (4) Haematopus leucopodus Garnot, 1826 - southern South America.
- (5) Haematopus bachmani Audubon, 1838 - west coast of North America from Alaska to California.
- (6) Haematopus unicolor Forster, 1844 - New Zealand.

The addition of up to three more species to the above list may now be warranted. In its fifth report, the South African Ornithological Society List Committee (1961, 78) reinstated the South African Black Oystercatcher as Haematopus moquini Bonaparte, 1865 (H. ostralegus moquini of Peters) on the basis of its obvious phenetic separation from H. ostralegus.

The Australian Sooty Oystercatcher possibly represents

a good species. Uncertainty exists as to whether it should be considered as conspecific with the New Zealand Black Oystercatcher Haematopus unicolor (R.A.O.U. Checklist, 1926), or as a separate species Haematopus fuliginosus Gould, 1845 (Peters, 1934; Serventy and Whittell, 1948).

The Chatham Islands Oystercatcher has recently been assigned species status Haematopus chathamensis Hartert, 1927 by the New Zealand Ornithological Society Checklist Committee (Kinsky, 1970), presumably because of morphological differences from its mainland congeners.

The limited speciation outlined above is mirrored by the small number of subspecies that have been described; Peters (1934) lists only 19. Although Murphy (1936) has suggested that the formation of continental subspecies is correlated with discontinuities in littoral distribution, it is not certain at this time whether or not many of these subspecies are simply products of geographic variation and are thus invalid.

### 1.3 TAXONOMY OF NEW ZEALAND FORMS.

#### A. History.

The nomenclature of the New Zealand species of oystercatcher has had a checkered history. Although the earliest reference is to a pied bird collected during one of Cook's expeditions (Latham, 1785, cited by Oliver, 1955), a melanistic specimen was the first to receive nomenclatural recognition. Forster described a bird collected at Dusky Sound in 1773 as Haematopus unicolor, but this description was not published until 1844. Pied oystercatchers observed breeding in Canterbury riverbeds were referred by Potts (1870) to Haematopus longirostris Vieillot which was originally described from New South Wales. Travers (1872) used this name for birds collected at the Chatham Islands, and Buller (1872, 1888, 1905) subsequently applied it to all New Zealand

oystercatchers. Rothschild (1899) gave the name reischeki to a specimen from Kaipara which was actually intermediate in plumage between black and pied.

Martens (1897) regarded a specimen from Saltwater Creek near Timaru sufficiently distinct to warrant species status, for which he proposed the name finschi. Mathews (1913) lumped all New Zealand pied birds under Haematopus ostralegus and retained finschi as a subspecies. He restricted longirostris as an Australian subspecies. This classification was accepted by Hartert (1921) who later (1927) ascribed the Chatham Islands Oystercatcher to Haematopus ostralegus chathamensis. Stresemann (1927) considered all black oystercatchers to be melanistic mutants of the pied Haematopus ostralegus, and submerged all the New Zealand oystercatchers except chathamensis under Haematopus ostralegus unicolor Forster. This synonymy was accepted by Peters (1934, 253). Falla's review (1939) retained finschi, reischeki and unicolor as full species and raised Hartert's chathamensis to species status. On the basis of plumage, voice and general habits Sibson (1945) referred finschi to a subspecies of Haematopus ostralegus. The first Checklist of New Zealand Birds (Fleming, 1953) accepted this reference and tentatively placed the other pied and black birds under a single species Haematopus unicolor Forster.

Oliver (1955) considered the 1953 Checklist's classification unacceptable as it constituted excessive lumping. He described four types of oystercatcher:

- (1) a smaller pied migratory species - Haematopus ostralegus finschi;
- (2) a larger pied non-migratory species - H. longirostris chathamensis;
- (3) a black non-migratory species - H. unicolor unicolor;
- (4) hybrids between (2) and (3).

Falla, Sibson and Turbott (1966) restored finschi, reischeki, unicolor and chathamensis to species status on the grounds that they were "strong" races. Finally, the second Checklist Committee (Kinsky, 1970) returned finschi to a subspecies of Haematopus ostralegus and deleted reischeki altogether, regarding Haematopus unicolor as an "apparently polymorphic" species.

#### B. Present Taxonomic Status.

Three species of oystercatcher are listed in the Annotated Checklist of the Birds of New Zealand (Kinsky, 1970) as follows:

- (1) Haematopus ostralegus finschi Martens, 1897 - South Island Pied Oystercatcher.
- (2) Haematopus unicolor Forster, 1844 - Variable Oystercatcher.
- (3) Haematopus chathamensis Hartert, 1927 - Chatham Islands Oystercatcher.

#### 1.4 THE SYSTEMATIC CONTROVERSY AND AIMS OF THE STUDY.

It is evident from the foregoing that the systematic status of New Zealand oystercatchers is uncertain. Major controversy is centred on the status of the Variable Oystercatcher, especially the inter-relationships of the southern black phase, the northern black phase and the pied phase. Three hypotheses have been put forward by Heather (1966) to explain this complexity:

##### (1) HYBRID HYPOTHESIS.

The black oystercatchers of New Zealand are specifically distinct from and tend to hybridize with a northern pied form.

##### (2) CLINE HYPOTHESIS.

Clinal variation of colour phases is occurring, ranging from entirely black populations in southern New Zealand to predominantly pied populations in the north.



## (3) MELANISM HYPOTHESIS.

The northern Variable Oystercatcher has strong melanistic tendencies and is specifically distinct from the southern Black Oystercatcher.

The status of either the South Island Pied Oystercatcher or the Chatham Islands Oystercatcher is not irrevocably determined. Doubt as to the correct rank of finschi and chathamensis has arisen through the allopatric distributions of these forms and from an inadequate assessment of their affinities.

The aim of this study, then, is to attempt to clarify the existing taxonomic confusion by evaluating the above hypotheses and by assessing the affinities of the New Zealand taxa.

1.5 IDENTIFICATION OF NEW ZEALAND OYSTERCATCHERS.(1) South Island Pied Oystercatcher - Haematopus ostralegus finschi.

The South Island Pied Oystercatcher has very stable plumage characters which serve as distinguishing features. Williams (1963) lists three main ways of positively identifying this subspecies:

- (a) when in flight, broad white bands (alar bars) may be seen along the upper wings which appear almost continuous with a white rump patch extending in a bright wedge into the middle of the back;
- (b) boundaries between black and white areas are sharply defined; and
- (c) the white recess on the shoulder in front of the wing is unique to the species.

These three features are illustrated in Plate 1.

Plate 7.

The South Island Pied Oystercatcher (Haematopus ostralegus finschi). Key to letters:

- A. Bird approaching nest. Note the white bay in front of the wing and the sharp boundary between black and white plumage on the breast.
- B. Distraction display in defence of young. Note the extensive alar bar, and the rump patch which extends high on the back between the wings.



A



B

(2) Variable Oystercatcher - Haematopus unicolor.

The plumage of the Variable Oystercatcher is extremely variable, ranging from pied to wholly black phases (Plate 2). Between these two extreme phases, a great number of intermediates exist, which do not appear to have any fixed plumage patterns. Pied birds can be distinguished from H. ostralegus finschi by:

- (a) the alar bar and the rump patch being restricted and not so conspicuously white;
- (b) the boundaries between black and white areas being blurred with smudgy markings, especially on the breast; and,
- (c) the absence of a white recess on the shoulder in front of the wing.

Entirely black forms of this species appear to vary geographically in plumage pigmentation. Falla et al. (1966) note that the northern black phase may be a brownish black and lack the purple gloss of the southern black phase, but add "this needs verification".

(3) Chatham Islands Oystercatcher - Haematopus chathamensis.

The Chatham Islands Oystercatcher is exclusively pied. (Plate 3). According to Oliver (1955) its affinities are with the pied phase of the Variable Oystercatcher, differing mainly in its stouter short bill and disproportionately large feet. This species is distinguished from finschi as follows:

- (a) the alar bar is less extensive than that of finschi;
- (b) the boundary between black and white areas on the chest is indistinct; and,
- (c) the area of white on the rump and lower back is reduced.

The New Zealand species of oystercatcher can thus be distinguished on plumage characters.

Plate 2.

The Variable Oystercatcher (H. unicolor).

Key to letters:

- A. Black phase. (Photo: J.A. Mills)
- B. Field phase. Note the mottling on the breast at the boundary of black and white plumage, and the absence of a white bay in front of the wing.



A



B

Plate 2:

The Chatham Islands Oystercatcher (*H. chathamensis*).

Key to letters:

- A. Ventral view of breast, showing faint mottling near the boundary of black and white plumage.
- B. Dorsal view showing the alar bar on the wing and the rump patch. Neither of these white areas is as extensive as those on the South Island Pied Oystercatcher.



A



B



## Chapter 2.

DISTRIBUTION AND NUMBERS OF NEW ZEALAND OYSTERCATCHERS.2.1 INTRODUCTION.

In any systematics study it is necessary to establish clearly the ranges of the taxa involved, and if possible, to analyse the distribution and numbers of animals within these ranges. Although the ranges of these taxa may overlap or coincide, differential distribution within the ranges can result in spatial or temporal isolation in the breeding season, and thus indicate separate species status.

New Zealand oystercatchers gather into easily located coastal flocks or small groups which are especially suitable for census purposes. Although many population counts have accumulated in recent literature, no attempt to synthesize them into a coherent whole has yet been published. This chapter presents an analysis of censuses made throughout New Zealand, and compares the distribution and numbers of the three species of oystercatcher.

2.2 METHODS.

Records of distribution and estimates of abundance were extracted from several sources: (i) the early literature of ornithological discovery in New Zealand; (ii) Classified Summarized Notes (in New Zealand Bird Notes and Notornis); (iii) the Recording Scheme of the Ornithological Society of New Zealand; and, (iv) personal records and communications. Whenever possible all population estimates were based on figures for 1970-71. When these were not available the next most recent data were used. To minimize discrepancies in counts due to seasonal fluctuations in populations, most figures for South Island Pied Oystercatchers were taken from censuses made in the winter months

Figure 1.

World distribution of oystercatchers (Adapted from Larsen, 1957).

Key to species:

1. Haematopus bachmani
2. H. palliatus strasari
3. H. p. palliatus
4. H. p. pretti
5. H. p. salomonensis
6. H. p. pitmanii
7. H. ater
8. H. p. sumfordi
9. H. leucopodus
10. H. ostralegus ostralegus
11. H. o. malaccensis
12. H. o. occidentalis
13. H. o. longipes
14. H. o. esculans
15. H. nequini mende-valdoi
16. H. n. nequini
17. H. o. longirostris
18. H. fuliginosus fuliginosus
19. H. f. schultzei
20. H. unicolor
21. H. p. tinianus
22. H. chathamensis

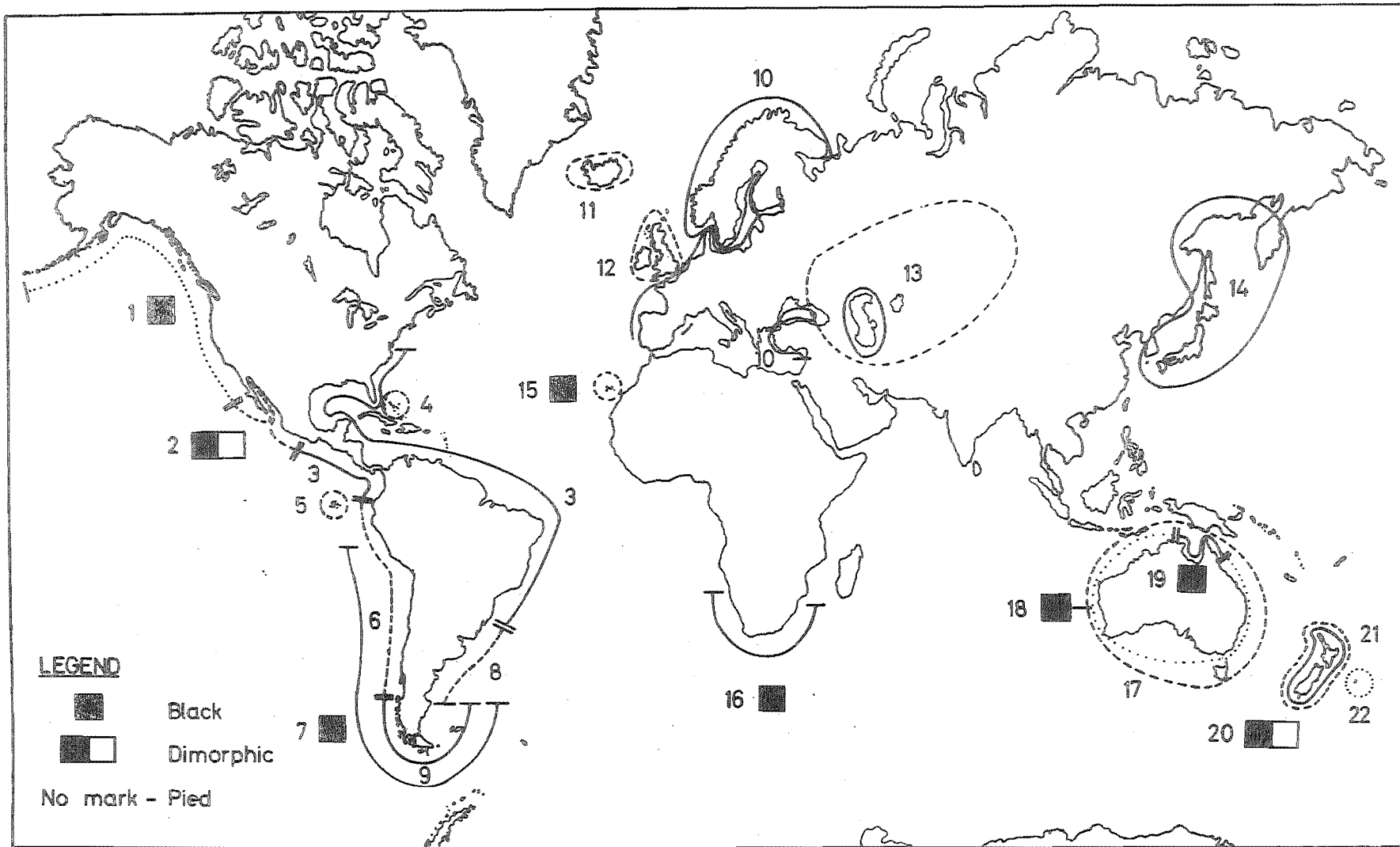


Figure 2.

Winter distribution and numbers of South  
Island Pied Oystercatchers in New Zealand.

NEW ZEALAND

LEGEND

- > 5000
- 3000 - 5000
- 1000 - 2999
- 200 - 999
- 10 - 199
- < 10

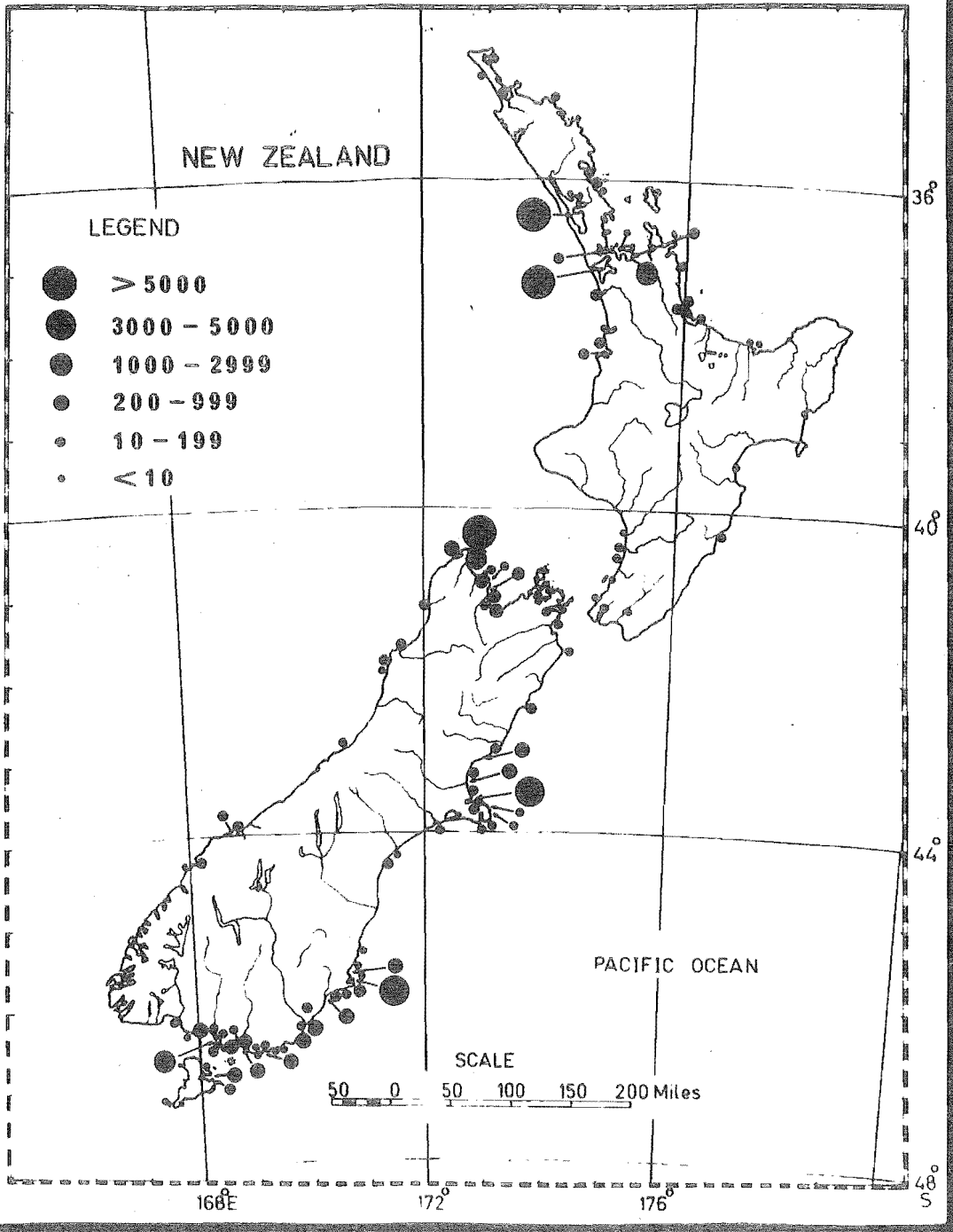


Figure 3.

Distribution and numbers of black phase Variable Oystercatchers in New Zealand. To facilitate the plotting of numbers in areas where dense concentrations of census figures occurred, the figures were pooled and plotted as single locality values. See Appendix II for separate locality figures.

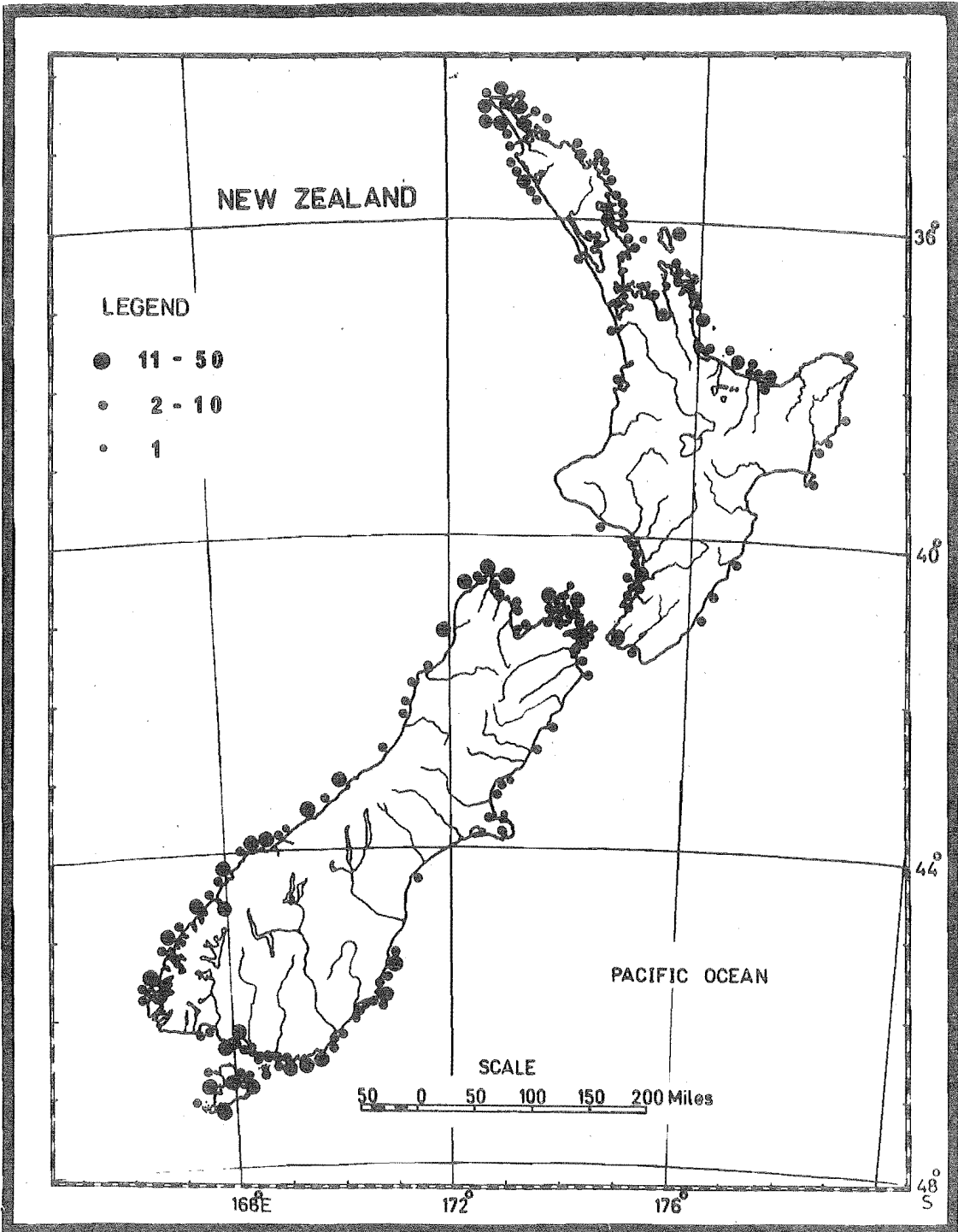


Figure 4.

Distribution and numbers of pied phase Variable Oystercatchers in New Zealand. In some localities pooled census figures were plotted as in Figure 3. See Appendix III for separate locality figures.



NEW ZEALAND

LEGEND

- 11 - 50
- 2 - 10
- 1

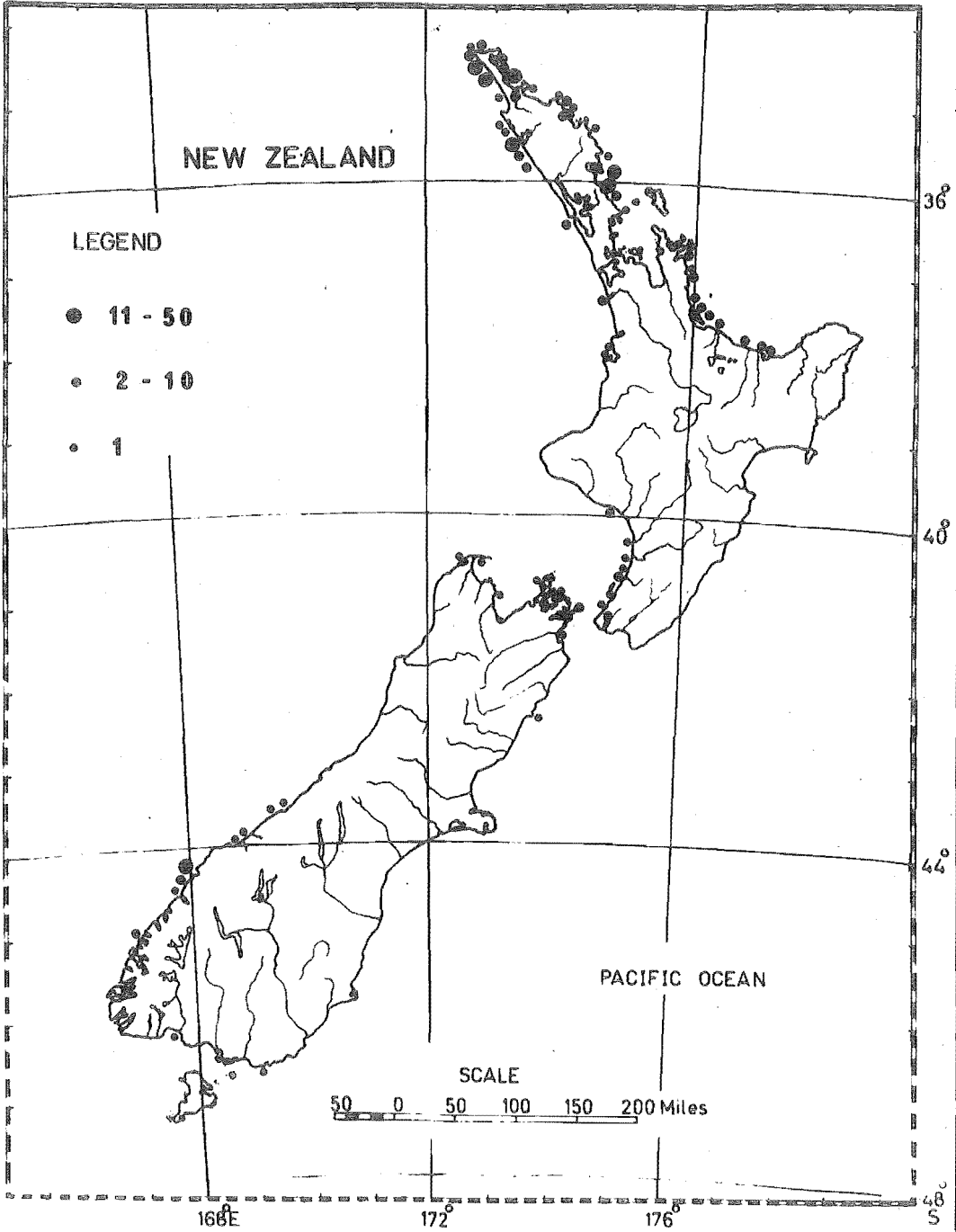
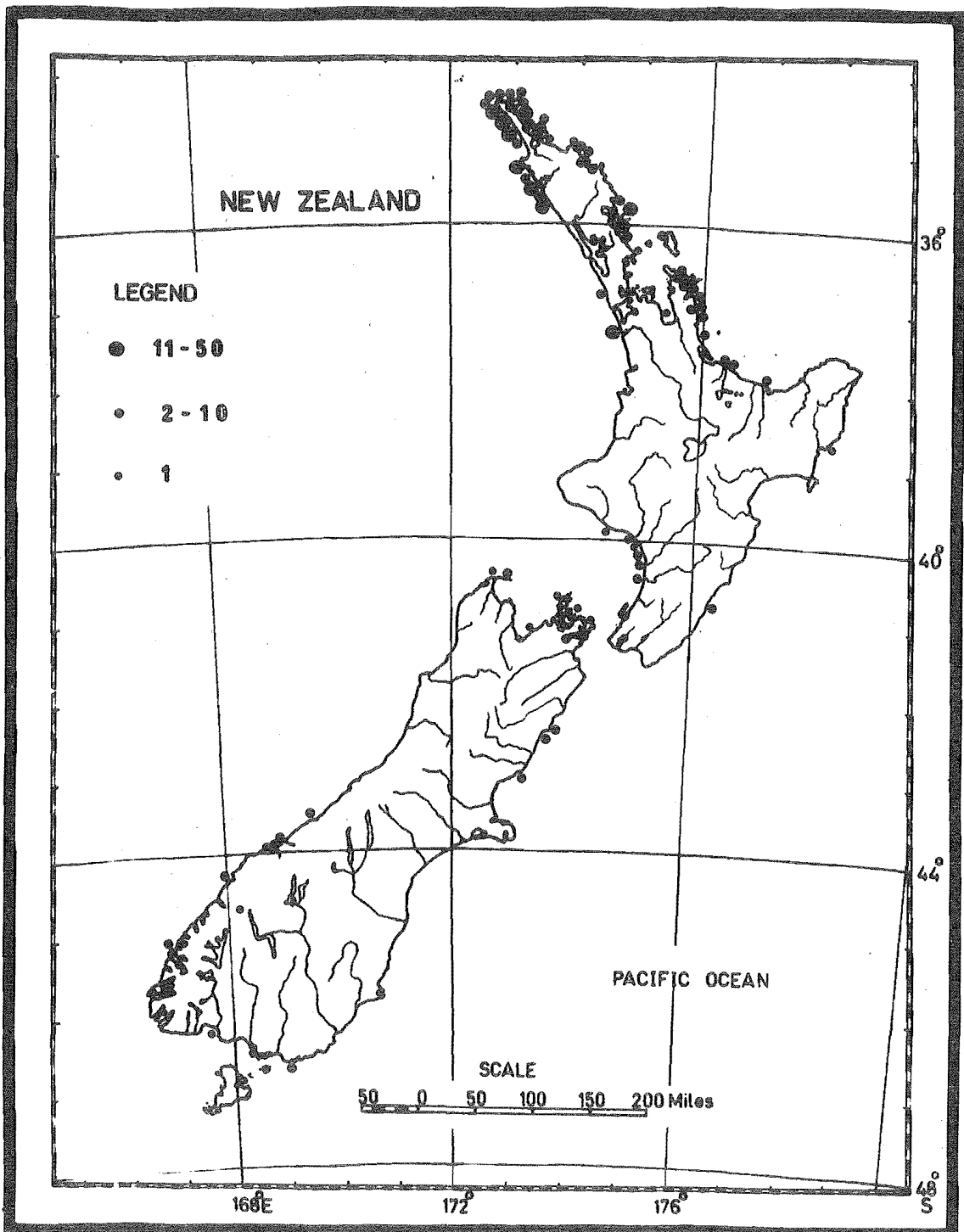


Figure 5.

Distribution and numbers of intermediate phase  
Variable Oystercatchers in New Zealand.



of May, June and July, by which time post-breeding dispersal and migration had ceased. Unfortunately winter counts were not available from some locations, so summer records had to be used in lieu of them. Since Variable and Chatham Islands Oystercatchers are non-migratory and tend to remain paired in their territories or localised in small flocks, census figures for these species have lessened seasonal bias. Hence both winter and summer census data were used, but in general, censuses were restricted to a particular season for discrete localities. In this way, errors due to local movements of birds between two census localities were reduced.

Personal records were obtained by counting individual birds in flocks at high water roosts. Large flocks were counted several times and mean figures accepted only if the error between successive counts was less than 5% of the total.

### 2.3 DISTRIBUTION AND NUMBERS.

#### A. Distribution Related to World Pattern.

Oystercatchers are widely distributed throughout the world, being present on most continental sea coasts. They are absent from the polar regions and remote oceanic islands excepting the Galapagos and Chatham Islands. Their range is most extensive in the breeding season, when they occur from northern Russia in the north to Cape Horn in the south. Although the majority of species are confined to a littoral distribution, some Old World forms have moved inland up the valleys of great river systems. The world distribution of oystercatcher species is shown in Fig. 1.

#### B. Ranges of New Zealand Species.

The winter ranges of the two mainland species of oystercatcher broadly overlap (see Figs. 2, 3, 4 and 5).

Figure 6.

Breeding distribution of South Island  
Pied Oystercatchers.

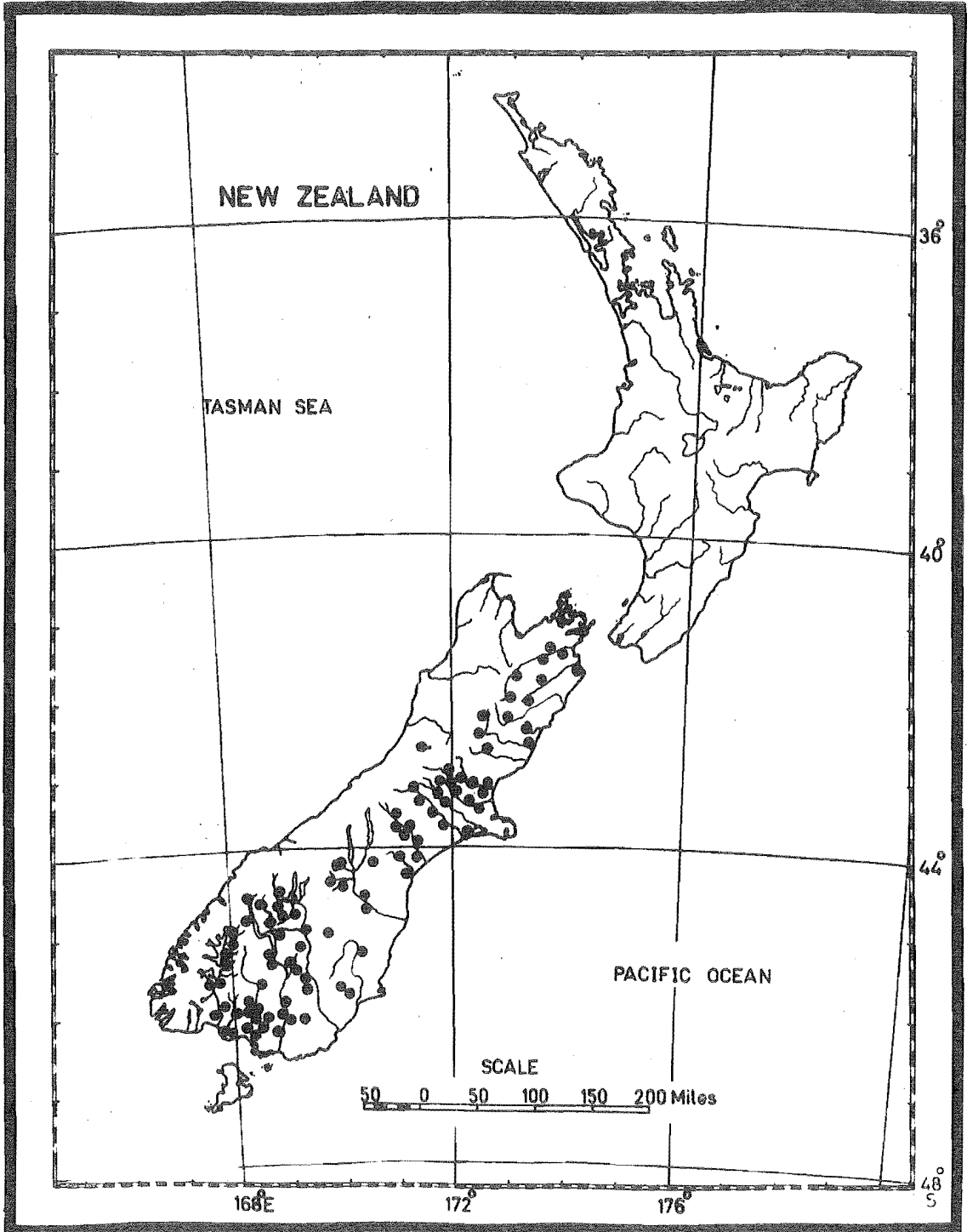


Figure 7.

Distribution and numbers of Clathromorphum  
Inlands Cysterentchers.

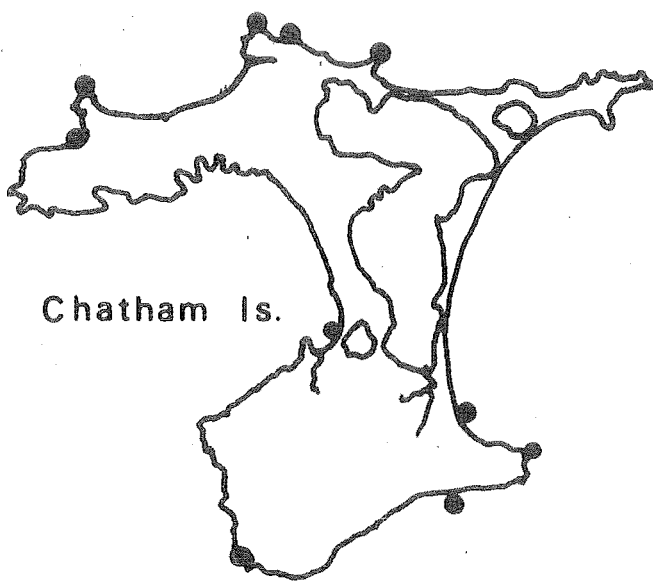
177°00'

176°40'

176°20'W

176°00'

43°40'

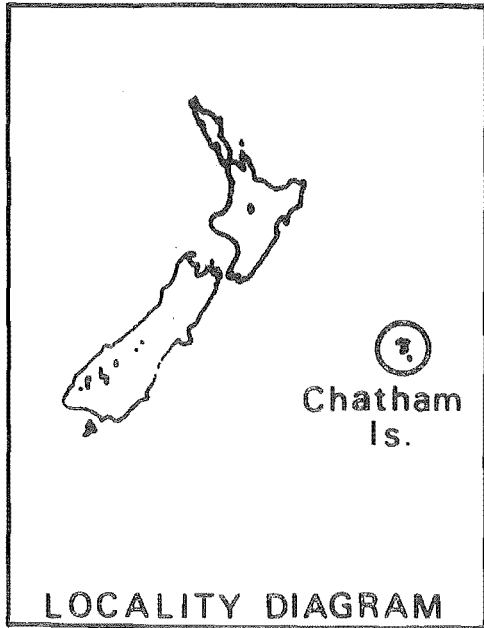


Chatham Is.

44°00'S

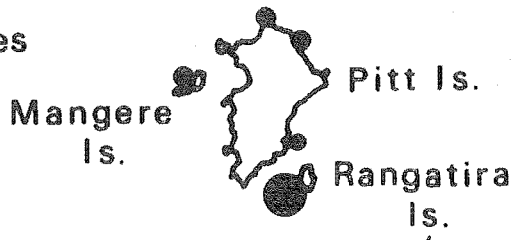
SCALE

0 10 20 Miles



Chatham Is.

LOCALITY DIAGRAM



Mangere Is.

Pitt Is.

Rangatira Is.

44°20'

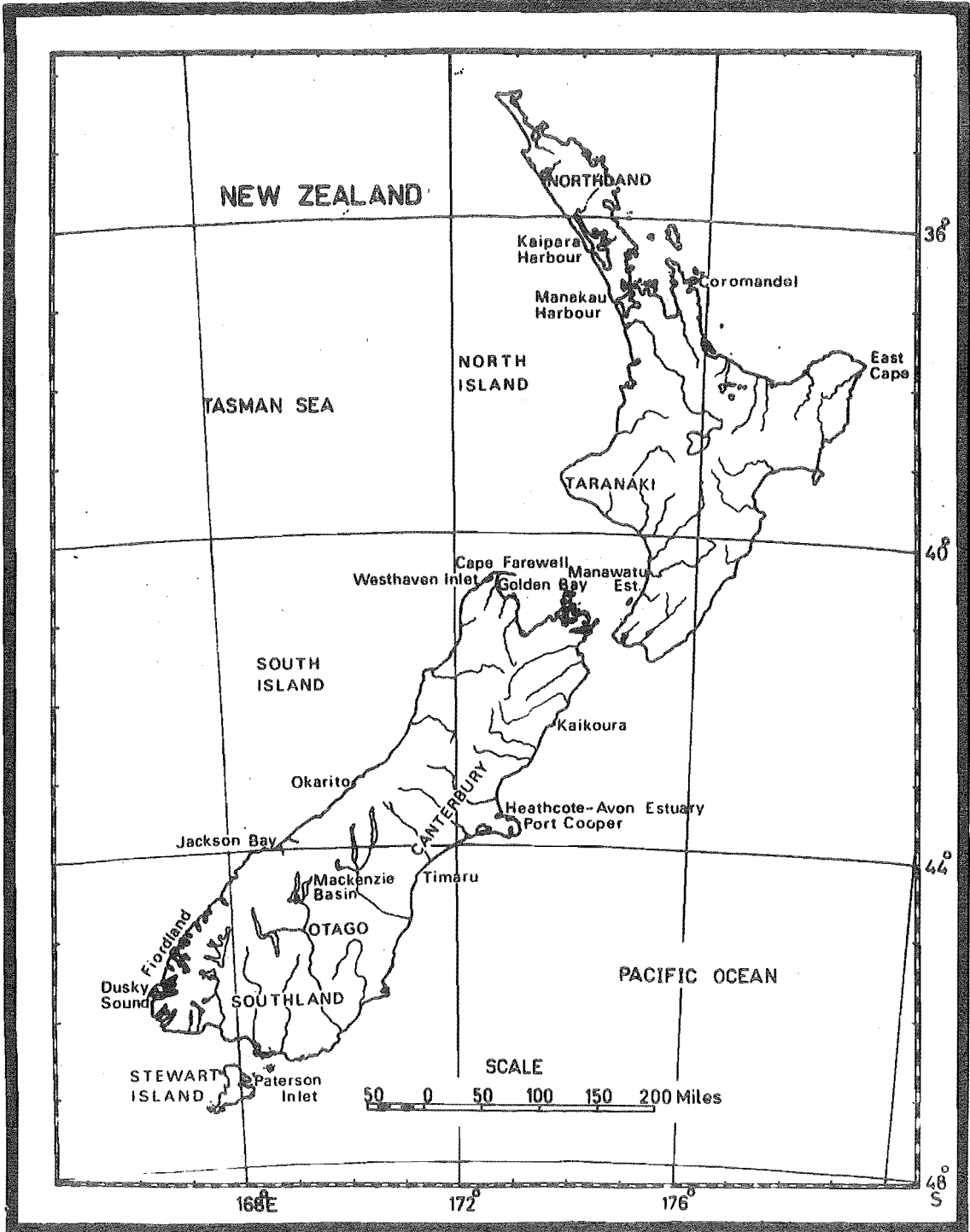
LEGEND

- 11 - 50
- 2 - 10
- 1



Figure 8.

Provinces and localities mentioned in the text.



In the breeding season, however, they occupy mutually exclusive ranges, as South Island Pied Oystercatchers (H. ostralegus finschi) move inland to breed whereas Variable Oystercatchers (H. unicolor) breed at or near their wintering haunts (see Fig. 6). The Chatham Islands Oystercatcher (H. chathamensis) is geographically isolated from the mainland species, being restricted to the Chatham Islands approximately 800Km east of New Zealand (see Fig. 7).

C. Distribution and Numbers of New Zealand Species.

The distribution patterns of the New Zealand species of oystercatcher are quite different. Although both mainland species are widely distributed throughout the country, South Island Pied Oystercatchers occur at fewer localities. A feature of the winter distribution of South Island Pied Oystercatchers is the occurrence of large flocks of birds at major harbours, bays and estuaries. These flocks result from the well developed gregarious behaviour in this species, and such flocks can only exist at localities where adequate food supplies are present. Smaller flocks occur around the coast, usually where rivers discharge into the sea, forming small estuaries in which bivalve molluscs are locally abundant (Fig. 2). South Island Pied Oystercatchers are notably absent or scarce in regions where rocks predominate in the littoral zone, e.g. Coromandel Peninsula, the east coast of the North Island from East Cape south, and Fiordland (see Fig. 8).

Variable Oystercatchers have a much more scattered distribution than their smaller pied congener. Larger flocks of these birds, nowhere exceeding 150 individuals, occur in the parts of their range where they are either allopatric with or numerically dominant to South Island Pied Oystercatchers. Small widely dispersed flocks occur in regions where the littoral zone is characterized by rock

platforms. Variable Oystercatchers exclusively occupy parts of Northland, Coromandel Peninsula, and Fiordland. Where the two mainland species coexist, variable birds occur only in small numbers. The marked disjunctions which occur in the distribution of the species are directly attributable to unsuitable feeding habitat in the littoral zone e.g. the scarcity of records from the Taranaki coast is due to the barren gravel beaches of this region.

The colour phases of the Variable Oystercatcher are not uniformly distributed throughout their range, their frequency of occurrence varying considerably with latitude as shown in Table 1.

TABLE 1. VARIATION IN FREQUENCY OF COLOUR PHASES OF THE VARIABLE OYSTERCATCHER WITH LATITUDE.

Latitude Grouping	Colour Phase					
	Black		Intermediate		Pied	
	N	%	N	%	N	%
34° - 39°S.	413	42.89	330	34.27	220	22.84
39° - 44°S.	364	84.85	37	8.63	28	6.52
44° - 48°S.	494	93.92	6	1.14	26	4.94

Black oystercatchers predominate in the southern part of the South Island although small numbers of pied and intermediate-plumaged birds also exist at these latitudes. On transition northwards black phases decrease in frequency, whereas intermediates and pied phase birds increase. However, even in the far north, the black phase is still the most abundant. This type of colour phase gradient in which black phases decrease in frequency on transition from colder higher latitudes to warmer lower latitudes is paralleled on

the coast of southern California. Black oystercatchers alone occur from Alaska south to southern California, they then merge and interbreed with pied and intermediate birds, and finally on the Mexican coast of the Gulf of California pied birds reach a frequency of 100%. The greater extent of the North American continent has allowed a clearer pattern to emerge, and possibly if the New Zealand mainland extended into lower latitudes nearer the Equator, the pied phase of H. unicolor would reach an exclusive frequency.

As Larsen (1957) has pointed out, these two colour phase gradients occur at approximately the same latitudes, representing the northern and southern limits of the palms. He suggested that the distribution of the various colour phases may be correlated with temperature. Hamilton and Heppner (1967) hypothesised that melanistic colouration of homeotherms could serve the function of reducing the metabolic cost of homeothermy by maximizing the absorption of radiant solar energy. They found that white Zebra Finches (Poephila castanotis) which were dyed black had a 23% metabolic economy over undyed birds when both were exposed to artificial sunlight at 10°C.

Heppner (1970) demonstrated that the metabolic differences noted above were accounted for by differential radiant energy absorption of blackened and white plumages. Since it is established that the emissivity (emittance of radiant energy) of black integuments does not differ significantly from that of white ones (Kelly, Bond and Heitman, 1954; Hammel, 1956), it follows that black homeotherms will experience greater heat stress at higher temperatures than will non-black homeotherms. This may explain why black oystercatchers are absent from the vicinity of the Equator, and also why black phases of dimorphic species predominate in colder parts of the range. However it is

doubtful whether temperature alone accounts for the distribution of black oystercatchers. All black oystercatchers occur either in rocky habitats or in habitats where rocks and sand alternate, suggesting that habitat selection is a potent factor influencing distribution.

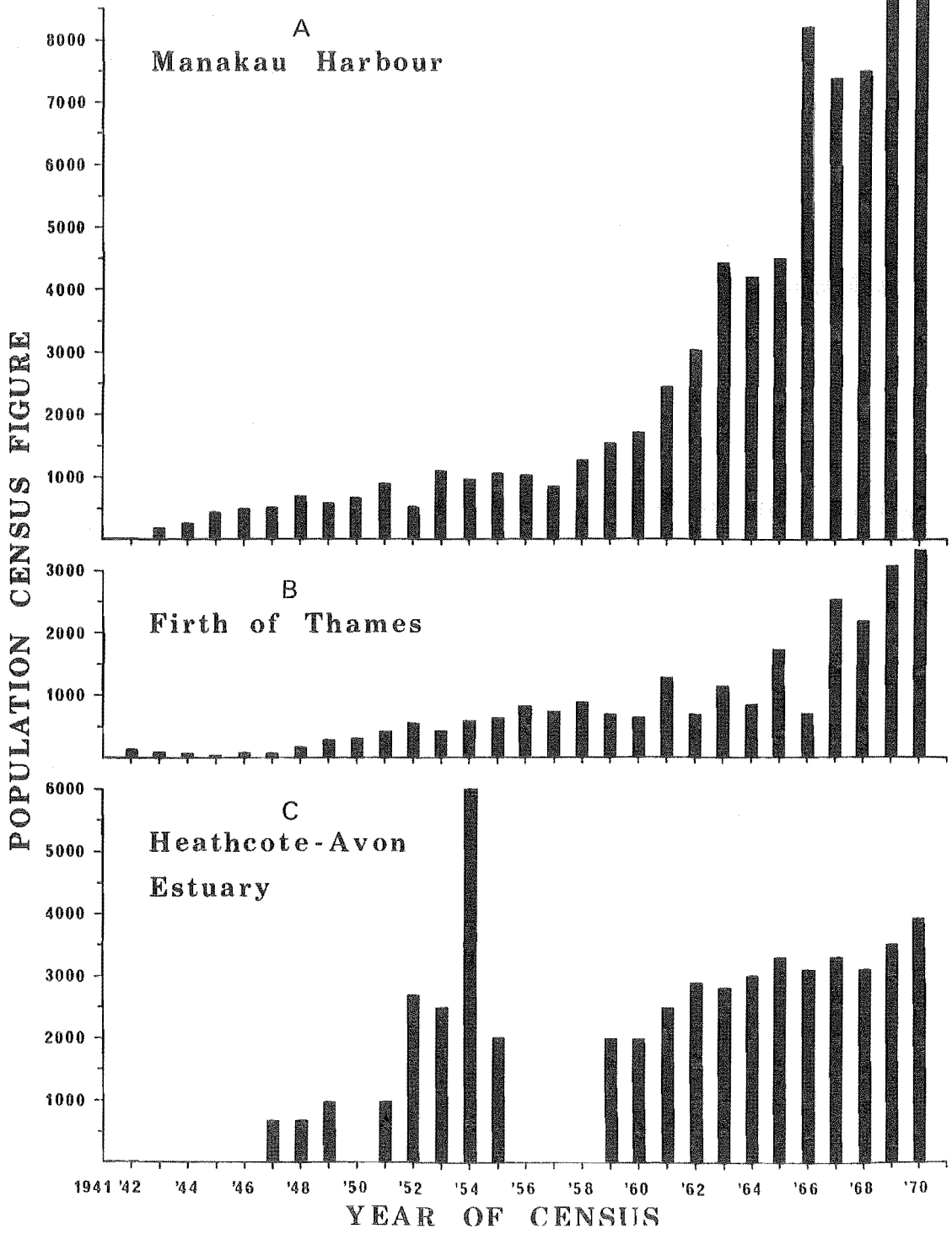
Variable Oystercatchers with plumage intermediate between black and pied phases have an interesting distribution. In all but two instances they occur where black and pied phases are sympatric, and in the two remaining cases they occur well within dispersal range of regions where mixed matings were known to occur (cf. Figs. 3 and 4). Intermediate-plumaged oystercatchers are nowhere abundant, the maximum number at any one locality never exceeding 50 birds.

The Chatham Islands Oystercatcher is not distributed evenly over the Chathams, but rather is concentrated on the smaller more isolated islands, Rangatira and Mangere (see Fig. 7). They tend to inhabit rocky habitats, but they do feed on some sandy beaches on Chatham and Pitt Islands.

Of the three New Zealand species of oystercatcher, the smaller South Island pied bird is by far the most abundant. Census figures (see Appendices I-V) indicate that the total population of this species approaches 49,000 birds. Black phase Variable Oystercatchers are less numerous (approximately 1300 birds), and pied and intermediate phase birds are scarce (approximately 300 and 400 birds respectively). The Chatham Islands Oystercatcher is rare enough to warrant Red Book listing, as the population totals only about 50 birds. The above census figures are probably conservative estimates of the true population levels, as figures are not available for some localities where oystercatchers are known to occur, and because old records were the only ones available from some localities where population increases have probably occurred.

Figure 9.

Peak winter census data for South Island  
Fled Oystercatchers at three major  
New Zealand water humms since 1942.





#### D. Recent Trends in Distribution and Numbers.

South Island Pied Oystercatchers have been abundant in New Zealand for at least the last 100 years. Potts (1869) recorded large flocks of pied birds on estuarine mudflats. He later (1885) recalled having seen a flock of "several thousands" of birds at the Heathcote-Avon estuary in 1858, and recorded a large flock at Port Cooper in 1871. Potts (1885) noted a decline in the abundance of South Island Pied Oystercatchers at that time, and attributed it to increasing human disturbance. Oystercatchers were then subject to considerable shooting pressure, as they were considered by many to be a choice table bird (Douglas, in Pascoe, 1969). Buller (1888 and 1905) confirmed that both pied and black oystercatchers were widely distributed but nowhere abundant. Travers and Travers (1872) recorded oystercatchers of pied plumage on the Chatham Islands as "not common".

The recession in numbers of oystercatchers continued until approximately 1940, when wintering populations of the South Island Pied Oystercatcher began a spectacular irruption, especially in northern New Zealand wintering haunts (see Fig. 9A and 9B). This population increase has been attributed by Sibson (1966) to the passing of legislation in 1940 prohibiting the shooting of shorebirds. Population levels at major wintering areas in the South Island have shown smaller increases in comparison with their northern counterparts (see Fig. 9C).

The differential population expansion within wintering haunts can be ascribed to three main factors:

- (1) before 1940, northern harbours and estuaries, containing vast supplies of food, were not extensively utilized by shorebirds;
- (2) also before 1940, southern harbours and estuaries were able to adequately support the smaller

- populations of birds inhabiting them; and
- (3) ecological pressure from population expansion since 1940 has forced birds to migrate northwards in search of new feeding areas.

As the migratory instinct is best developed in juvenile first-year H. ostralegus (Buxton, 1957), birds of this age tended to colonize northern New Zealand (Sibson, 1945; Falla, Sibson and Turbott, 1966). With population levels of South Island Pied Oystercatchers still rising, saturation of the littoral habitat appears imminent in the next few decades.

In Great Britain, following recent major irruptions of pied oystercatchers (H. ostralegus), increasing numbers of birds have moved inland to breed, exploiting terrestrial habitats as they did so (Buxton, 1961; Dare, 1966). They have recently begun to utilize coastal terrestrial habitats in certain parts of Britain (Dare, 1966; Heppleston, 1968), probably in response to increased intraspecific competition for littoral food supplies. South Island Pied Oystercatchers have also responded to increasing population densities by seeking food in coastal fields, and in some instances have become wholly terrestrial. Several pairs have remained at their breeding sites in North Canterbury over the past two years. It seems likely that this habit will increase in future if numbers keep on rising at their present rate.

#### 2.4 SUMMARY.

The mainland New Zealand species of oystercatcher have overlapping winter ranges, but their distribution within these ranges is very different. South Island Pied Oystercatchers are concentrated on large harbours and estuaries in the North and South Islands. Black birds are the dominant phase of H. unicolor in the South Island, but the frequency of pied and intermediate phases increase on transition

northwards. However, black is still the dominant phase in northern New Zealand. Variable Oystercatchers have a scattered distribution with flocks never exceeding 150 birds. Intermediate-plumaged birds occur where black and pied phases are sympatric. The two mainland species H. ostralegus finschi and H. unicolor are largely separated in their winter ranges. Where they do coexist, one or the other is numerically reduced, often occurring only as an odd pair.

In the breeding season, South Island Pied Oystercatchers migrate inland to locations in the South Island, whereas Variable Oystercatchers breed at or near their wintering haunts. Thus the mainland species are reproductively isolated in the breeding season due to their mutually exclusive breeding ranges. The Chatham Islands Oystercatcher (H. chathamensis) is geographically isolated from the mainland species. It is a comparatively rare form restricted to the islands.

Variable and Chatham Islands Oystercatchers have probably maintained their present numbers over the past years. South Island Pied Oystercatchers, once very abundant, declined in numbers over the period 1870-1940. Since 1940, however, when the shooting of shorebirds was prohibited, they have irrupted spectacularly. Increasing numbers of birds have migrated to harbours and estuaries in northern New Zealand in search of new feeding grounds. At the present rate of increase, this species will probably reach a population level in the next few decades where it will come under density-dependent control. This density effect may be alleviated for some time if the species continues to expand its tendency to remain inland at breeding localities throughout the year, and adopt a terrestrial mode of feeding.

## Chapter 3.

ECOLOGY AND BEHAVIOUR OF NEW ZEALAND OYSTERCATCHERS.3.1 INTRODUCTION.

The use of ecological characters in systematic research at all levels of classification is now widespread (Selander, 1969). So important are these characters that Mayr, Linsley and Usinger (1953) suggested they were requisite for complete species description. Modern studies frequently adopt a biologically integrated approach to systematics, involving synthesis of pertinent morphological, ecological and ethological information. However, as Selander (1969) has pointed out, systematists working at the species level must be very careful in selecting ecological characters for comparative study, since at this level characters are of value only if they reflect mechanisms of genetic isolation.

Behaviour also provides valuable characters for systematic studies of animals. In the higher vertebrates especially, ethological differences between species commonly function as reproductive isolating mechanisms. Comparative studies of closely related species of genera have led to significant improvements in the classifications of some groups of birds e.g. Moynihan (1959) and Smith (1966) on gulls, Johnsgard (1965) on ducks.

This chapter presents a comparison of some aspects of the ecology and behaviour of New Zealand oystercatchers relevant to elucidating their taxonomic status.

3.2 METHODS.A. Habitat Selection.

Many localities with contrasting substrates were visited during the course of this study. At each locality, the

extent and nature of the various substrates were recorded, and preference of feeding birds for particular substrates in heterogeneous habitats were noted.

B. Niche Utilization.

Prey-specific feeding behaviour was investigated over the period January 1967 to January 1968. Observations were made at several localities where different prey species were taken. The feeding habits of South Island Pied Oystercatchers were studied in detail at the Heathcote-Avon estuary, and comparative observations were made at Jackson Bay, Golden Bay and Kaikoura. Similar studies were made on Variable Oystercatchers at Westhaven Inlet, Cape Farewell, Kaikoura and Jackson Bay. The winter diet of New Zealand oystercatchers was determined by watching feeding birds taking food, by examining gut contents of birds collected from netted samples, and by examining faecal smears prepared on glass slides.

C. Food Requirements.

Comparative food intake observations of the mainland oystercatcher species were made at Jackson Bay and Kaikoura Peninsula in mid-winter, 1967. The rate of food intake was determined by direct observation. Recordings were confined to one bird at a time because of the difficulty of keeping more than one bird in the field of view of the fieldglasses. Each bird was observed for a 10 minute period during which the number of probes in search of food were recorded, the number of successful probes marked, and food taken identified where possible. To minimize observer fatigue, each observation period was followed by a 10 min rest period, and then the process was repeated until a tidal cycle was completed. Whenever possible, observations were taken in areas where a particular prey, which the birds were preferentially taking, was locally abundant. This enabled the

anomalous effects of differential feeding rates resulting from variation in diet to be eliminated (Hartley, 1948).

The daily food requirements of oystercatchers were determined by calculating the mean feeding rate per bird and multiplying by the mean time spent feeding each day. The mean weight of the prey taken was calculated from the sizes of the molluscan shells left at feeding areas. Dry weights of the food species were determined by drying samples of 30 animals of each species in a vacuum oven to constant weight at 65°C. Calorific values of these foods were determined by grinding the dry tissues into a homogeneous mixture, compacting a sample into a pellet, and then burning this sample in a Parr oxygen-bomb calorimeter. Five samples only were burnt for each food as even the most divergent calorific values obtained for samples of the same food differed by less than 1%.

#### D. Breeding Biology.

General breeding data on the duration of the breeding season, the time of breeding, dispersal to and from breeding areas, and breeding dispersion were gathered from the literature, and from the Recording Scheme and nest record cards of the Ornithological Society of New Zealand. In both the 1969-70 and 1970-71 breeding seasons a survey of major breeding localities was made from Stewart Island to Northland, and in early November 1970 a fortnight was spent in the Chatham Islands. Many breeding birds were trapped on the nest during these surveys. They were all colour-banded and their eggs weighed and measured.

The incidence of breeding behaviour over the period May to November 1967 was recorded by weekly visits to the Heathcote-Avon estuary. During each visit the types and numbers of breeding displays were noted over one hour observation periods. Comparative observations were made of Variable Oystercatchers at Jackson Bay, Okarito and Northland,

ranging over the period May to August 1970.

#### E. Parasites.

Mallophaga were collected from live-trapped birds of all three New Zealand species of oystercatcher. Helminth parasites were obtained from the guts of birds collected from netted samples for studies of seasonal variation in mensural characters.

#### F. Vocalizations.

Vocalizations of courting birds were recorded in the field using a FI-CORD 202 tape recorder with a frequency response of 40-20,000 Hz. Recordings were made through a low impedance DP<sup>4</sup>/L Grampian microphone of similar frequency response fitted to a parabolic reflector of radius 60.96 cm (24 in.). Several courting pairs were recorded, but only the highest quality recording for each species was selected for analysis on a KAY 6061 B Sonagraph.

### 3.3 HABITAT SELECTION.

Oystercatchers are essentially birds of the sea coast. They show strong selection for marine littoral feeding habitats, with only two continental subspecies of Haematopus ostralegus moving inland to utilize terrestrial habitats (see Fig. 2). In winter, New Zealand oystercatchers preferentially feed in the littoral zone of marine habitats, though in the last decade there has been an increasing tendency to feed in coastal terrestrial habitats.

South Island Pied Oystercatchers (H. o. finschi) show a marked selection for feeding habitats with soft substrates, such as estuaries, mudflats and sandy beaches. In contrast, the black phase of the Variable Oystercatcher (H. unicolor) is a characteristic inhabitant of rocky shores, especially in the South Island. Black, pied and intermediate colour phases in the North Island are most often found in habitats

where sandy beaches intermingle with rock platforms. The decreasing use of rocky areas here probably does not indicate a change in habitat selection, but rather reflects a lessening of interspecific competition with South Island Pied Oystercatchers for sandy habitats together with a change in habitat availability. In Northland, rocky areas are restricted, and H. o. finschi relatively scarce compared with other areas of New Zealand. It is therefore common to see Variable Oystercatchers feeding on estuaries and beaches there.

Wherever South Island Pied Oystercatchers are locally abundant in areas of species overlap, Variable Oystercatchers tend to retreat to the rocky parts of the coast. The exclusion of Variable Oystercatchers from habitats with soft substrates has been documented in at least two instances. Early in this century, large flocks of the black phase Variable Oystercatcher fed on the mudflats of Paterson Inlet on Stewart Island, and occasionally they were accompanied by one or two South Island Pied Oystercatchers. On July 25th 1942 eight of the latter species were seen there, and since that time they have increased their numbers steadily to their present-day population of several hundreds. During the same period Variable Oystercatchers gradually became more scarce and have tended to feed increasingly on nearby rocky habitats (R.H. Traill, pers. comm.). A similar decrease in numbers of Variable Oystercatchers associated with an increase in South Island Pied Oystercatchers has been recorded at the Manawatu estuary since 1958, as shown in Table 2 (I. G. Andrews, pers. comm.).

At localities where the smaller South Island bird is absent or present only in small numbers, however, its larger Variable congener usually spreads back onto beaches and estuaries adjacent to rocky parts of the coast. Hinde (1966) considered that this type of behaviour was strong



TABLE 2. PEAK WINTER CENSUS FIGURES OF OYSTERCATCHERS AT MANAWATU ESTUARY SINCE 1958.

Year	Species	
	Variable Oystercatcher	South Island Pied Oystercatcher
	( <u>H. unicolor</u> )	( <u>H. ostralegus finschi</u> )
1958	27	24
1959	31	25
1960	12	30
1961	8	36
1962	13	55
1963	18	66
1964-66	No censuses made	
1967	6	80
1968	4	29*
1969	10	92
1970	5	72

\* Summer census only.

evidence of competition for feeding habitats, and in such cases he noted, "When one of two closely related species which occupy different habitats within the same general area is locally absent, the other may spread to occupy both habitats". Thus direct interspecific competition for food in heterogeneous habitats is largely prevented by differential habitat selection in regions of species overlap. In homogeneous habitats, competitive exclusion is not absolute as the effects of competition are reduced by interspecific differences in niche utilization (see section 3.4).

The Chatham Islands Oystercatcher (H. chathamensis) is most often found feeding in rocky habitats, though it does feed on sandy beaches close to rock platforms (Travers, 1872; pers. obs., 1970). Fleming (1939) noted this habitat

preference and suggested that this species was morphologically adapted to exploit rocky areas.

The selection of rocky habitats by North American Black Oystercatchers (H. bachmani) has been attributed to predator selection (Bancroft, 1927). This view contended that melanistic plumage gave protective colouration against dark rock backgrounds, whereas white-bellied forms were less conspicuous on sandy beaches. It is doubtful whether this hypothesis can account for the distribution of black phase Variable Oystercatchers in New Zealand. Adult Oystercatchers have very few natural predators, especially in New Zealand; no records of predation were found in the literature. However Jehl, (pers. comm., 1970) felt it would be unwarranted to consider that plumage has no selective value per se. He suggested that there was selection by aerial predators such as the Black-backed Gull (Larus dominicanus) for cryptic colouration in the chicks, and that this became apparent in the distribution of adult plumages. This view was based on the assumption that pied chicks are grey dorsally and black chicks brown. In New Zealand oystercatcher chicks the dorsal plumage exposed to predators is similar irrespective of the colour phase involved (see Plate 4), although some black chicks have dark heads. Further, where cryptically coloured substrate races occur among animal groups, they show exclusive selection for matching substrates. For example, the darkly coloured South African lark Miafra sabota is restricted to the dark soils of southwest Africa, while its reddish congener M. africanoides inhabits the red Kalahari sand. Substrate selection is rigorous even where the two substrates intermingle, and is thought to result from strong predator selection (Niethammer, 1940).

Habitat selection has been shown to have a strong genetic component by Harris (1952) who found that individuals

Plate 4.

Dorsal plumage of Variable Oystercatcher chicks.

Key to letters:

A. Black phase chick from Otago.

B. Pied phase chick from Northland.

Note the general similarity of the ground colour  
and the darker markings of both chicks.



**A**



**B**

of forest and prairie subspecies of the deer mouse Peromyscus maniculatus which had been bred and raised in standard cages differed in their preference for various artificial habitats. The prairie-dwelling P. m. bairdi preferred habitats that resembled grasslands, and the forest-dwelling P. m. gracilis preferred habitats that resembled woodland. The conservative and specialized habitat selection shown by oystercatchers is strong evidence for an associated genetic component.

In the last decade, South Island Pied Oystercatchers have shown greater flexibility in habitat selection (Falla et al., 1966). Following heavy rain, and often coinciding with high water, flocks of oystercatchers leave marine littoral areas and forage in coastal fields for earthworms washed to the surface. Black phase Variable Oystercatchers have also been recorded in coastal fields in South Westland. A similar tendency to feed inland during winter has been described by Dare (1966) for European oystercatchers in Great Britain. He suggested that from picking up these surfacing worms to actively probing for them would be a short step, particularly for those birds which were already inland breeders, and any temporary shortage of normal shellfish foods would tend to accelerate the adoption and spread of this feeding habit. Heppleston (1971) showed that pied oystercatchers (H. o. occidentalis) in Scotland could not obtain enough food for their daily requirements from marine habitats in mid-winter, so they sought extra food from terrestrial habitats during high water. When snow covered coastal fields for prolonged periods he found many birds which had presumably died from starvation.

The dichotomy of habitat selection shown by New Zealand oystercatchers would appear to be the result of a genetic component modified by habitat availability and interspecific competition. Habitat selection is a conservative

factor in species formation since it reduces the probability that new isolates will be established beyond the present species border (Mayr, 1963). The limited speciation within the genus Haematopus is no doubt partly attributable to this restrictive selection.

#### 3.4. NICHE UTILIZATION.

New Zealand oystercatchers possess a wide range of prey-specific feeding behaviour patterns to cope with the various sizes and species of prey found under the widely fluctuating environmental conditions of the sea shore. Each behaviour pattern is neatly adapted to the structure and habits of the prey.

South Island Pied Oystercatchers have strongly developed behaviour patterns for preying on bivalve molluscs. Gaping bivalves in shallow water are pierced between the valves with an initial sharp probe, followed by repeated pressure thrusts towards the centre of the prey until the adductor muscles are severed. The contents of the shell are then removed. Shellfish with their valves closed are hammered in the umbo region or at the edge of the gape with vertical jabs of the bill until access is gained to the flesh. Identical methods of preying on bivalves have been noted for European oystercatchers (H. ostralegus) by Dewar (1908) and Tinbergen and Norton-Griffiths (1964). In regions where Variable Oystercatchers feed in estuaries they also prey extensively on bivalve molluscs, though they seem to do so only by piercing.

Variable Oystercatchers have distinctive behaviour patterns for taking relatively large prey items such as mussels and limpets from rocky shores. Gaping mussels (Mytilus edulis and Modiolus neozelanicus) are pierced between the valves and prized open in situ. Mussels with closed valves are hammered until an access hole is made

through the shell. Small mussels may be removed from the substrate and orientated with their flatter ventral side uppermost for hammering. Dense concentrations of small Modiolus are dealt with simply by tearing shells from the substrate and swallowing them whole. Identical methods of preying on mussels were described by Norton-Griffiths (1967) for European oystercatchers. The only record of South Island Pied Oystercatchers feeding on mussels is that of Jackson (1964) who noted birds levering them open in Manakau Harbour.

The large shore limpet (Cellana denticulata) is a major prey item for H. unicolor. These gastropods are knocked off the rocks by sharp blows delivered with the bill, or by levering between the foot of the limpet and the substrate with the bill held almost horizontal. The contents of the shell are removed by placing the upturned animal in a suitable crevice, and paring the flesh from the shell with scissor-like movements of the bill. Identical behaviour was noted for North American Pied Oystercatchers (Audubon, 1840), European oystercatchers (Dewar, 1913) and North American Black Oystercatchers (Webster, 1941). Chitons (Sypharochiton pelliserpentis and Amaurochiton glaucus) are dealt with in essentially the same manner.

Gastropods such as the mudsnail (Amphibola crenata) and the common topshell (Melagraphia aethiops) are taken with the same method described by Dewar (1910) for the purple shell (Purpura lapillus). The bill is inserted into the aperture and a hole is punched in the outside whorl of the shell opposite to the operculum. The shell is then rotated and the hole enlarged until the exposed soft-parts can be removed. Smaller gastropods such as the scavenging whelk (Cominella glandiformis) and the long spired snail (Zeacumantus subcarinatus) are swallowed whole and the shells crushed in the stomach.

Although the three New Zealand species have similar prey-specific feeding behaviour patterns, their development within each species differs. This difference is most obvious in heterogeneous habitats where the species overlap. At Kaikoura Peninsula, extensive rock platforms are separated by occasional sandy beaches. Black, intermediate and pied phase Variable Oystercatchers feed almost exclusively on the rocky areas whereas South Island Pied Oystercatchers generally take bivalves from the beaches. When the latter venture on to rocks they feed chiefly on chitons and small gastropods. Small limpets (Cellana radians) are only rarely eaten. Thus where the two mainland species coexist on rocky habitats the effects of competition are mitigated by differential niche utilization.

The combined effects of habitat selection and niche utilization are clearly revealed in comparing the winter diet of mainland New Zealand oystercatchers (see Table 3). Unfortunately, detailed studies on the diet of Chatham Islands Oystercatchers have not been made.

The separation of feeding niches described above is probably related to the relative sizes of the trophic structure in the two species. Although they both have bills of similar length, South Island Pied Oystercatchers have a much slimmer and less robust bill (see Chapter 4.10, Table 26), which is especially suited for probing in soft substrates for bivalves and polychaete worms. The heavier bill and larger set of muscles associated with bill manipulation in Variable Oystercatchers are better suited to strenuous levering and hammering of large limpets from rocks.

The Chatham Islands Oystercatchers feeds mainly on chitons and small gastropods taken from rock surfaces. The bill of this bird, though considerably shorter than its mainland congeners, is slightly stouter than that of the South Island Pied Oystercatcher (see Chapter 4.10, Table 26),



Figure 10.

Comparative feeding rates of mainland New Zealand oystercatchers at Jackson Bay.

Key to numbers:

1. Pied and intermediate phase Variable Oystercatchers.
2. South Island Oystercatchers.
3. Black phase Variable Oystercatcher.

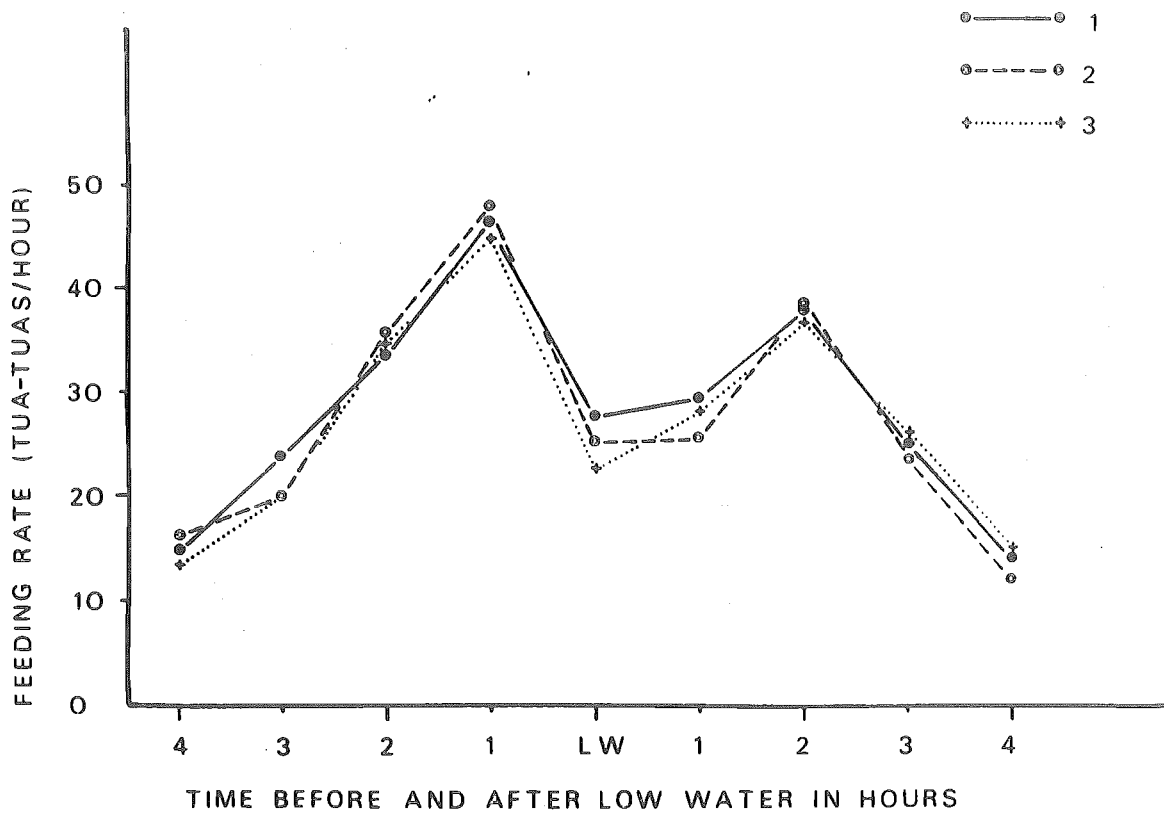


TABLE 3. THE WINTER DIET OF NEW ZEALAND OYSTERCATCHERS IN RELATION TO HABITAT.

Prey Species	Substratum	South Island Pied Oystercatcher	Black Phase Variable Oystercatcher	Pied Phase Variable Oystercatcher
COELENTERATA : ACTINOZOA				
<u>Isactinia olivacea</u>	Rock	X	-	-
MOLLUSCA : BIVALVIA				
<u>Chione stutchburyi</u>	Mud and sand	X	X	-
<u>Amphideme australe</u>	"	X	X	X
<u>A. subtriansulatum</u>	Sand	X	X	X
<u>Macomona liliata</u>	Mud	X	-	-
<u>Dorlinia anus</u>	Sand	X	X	-
<u>D. subrosea</u>	"	X	X	-
<u>Protorhaca crassicoata</u>	"	X	X	X
<u>Hydriddella menziesi</u>	Gravelly sand and mud	X	-	-
<u>Mytilus edulis</u>	Rock	-	X	X
<u>Perna canaliculus</u>	"	-	X	X
<u>Modiolus neozelandicus</u>	"	-	X	X
<u>Auleacomya maoriana</u>	"	-	X	X
: GASTROPODA				
<u>Cellana denticulata</u>	Rock	-	X	X
<u>C. radians</u>	"	X	X	X
<u>C. ornata</u>	"	-	X	X
<u>C. flava</u>	"	-	X	X
<u>Heliotis iris</u>	"	-	-	X
<u>Melaeoraphis aethiops</u>	"	X	X	X
<u>Amphibola crenata</u>	Mud	X	-	-
<u>Cominella glandiformis</u>	Mud and rocks	X	X	X
<u>Zacumantus subcarinatus</u>	"	X	X	X
: AMPHINEURA				
<u>Ameurochiton aleucus</u>	Rock	X	X	X
<u>Sypharochiton pelliserpentis</u>	"	X	X	X
CRUSTACEA : DECAPODA				
<u>Palaemon affinis</u>	Rock	X	-	-
<u>Helice crassa</u>	Mud	X	X	-
<u>Hemigrapsus edwardsii</u>	Rock	-	X	X
: AMPHIPODA				
<u>Talorchestia</u> spp.	Sand	X	X	X
: ISOPODA				
<u>Dynamenella huttoni</u>	Rock	X	X	X
ANNELIDA : POLYCHAETA				
<u>Glycera americana</u>	Mud	X	X	-
<u>Nicoa aestuariensis</u>	"	X	-	-
<u>Perinereis nuntia</u>	Sand	X	X	X
* : OLIGOCHAETA				
<u>Allobophora caliginosa</u>	Soil	X	X	-
* INSECTA : COLEOPTERA				
<u>Costelytra zelandica</u> (larvae)	Soil	X	-	-
: LEPIDOPTERA				
<u>Misana</u> spp. (larvae)	Soil	X	-	-
PISCES : ACTINOPTERYGII				
<u>Rhombosolen plebeia</u>	Sand	X	-	-

N.B. \* - prey species taken from coastal fields only during wet weather.

and seems better adapted for removing prey from rocks than for probing in sand or mud.

Although the three New Zealand species of oystercatcher are able to exploit invertebrate food supplies in most marine littoral habitats, their bills are best adapted to exploit different prey species. Where the mainland species overlap in homogeneous habitats, they are partly prevented from competing for food by differential niche utilization.

### 3.5 FOOD REQUIREMENTS AND INTERSPECIFIC COMPETITION.

It has been shown in a previous study (Baker, 1969) that the rate at which oystercatchers feed is extremely variable due to the modifying effect of several factors. Feeding rates vary with season, prey size, state of the tide, weather, and age of the birds. To reduce variation from these sources, comparative food intake estimations were made for adult South Island Pied and Variable Oystercatchers at Jackson Bay in June, 1967. At this time a flock of 59 Variable and 14 South Island Pied birds were feeding together along an oceanic beach rich in tua-tuas (Amphidesma subtriangulatum). Both species fed at approximately the same rate in this habitat (see Fig. 10), and for similar periods during each tidal cycle.

South Island Pied Oystercatchers ingested an average of 255.9 g dry weight of tua-tuas daily, or 51.8% of their body weight (N = 64 observations). Variable Oystercatchers (data for colour phases combined) had an average daily food intake of 245.3 g which represented 35.8% of their body weight (N = 68 observations).

Since Variable Oystercatchers are larger than South Island Pied Oystercatchers it might be expected that the latter would suffer proportionately greater heat losses. The metabolic rate of smaller animals is relatively greater

than that of large ones because of the greater ratio of surface area, concerned with heat loss, to body mass, concerned with heat production. Until recently it was maintained that as the rate of heat production was controlled by the rate of heat loss, the metabolic rate was proportional to external surface area rather than to body weight. However, both Kleiber (1961) and Kendeigh (1970) demonstrated some factors other than external surface area that operate in determining heat loss. Thus Kendeigh (op.cit.) formulated an equation for calculating the existence energy (energy metabolized to maintain constant weight in captive conditions) directly from body weight in non-passerine species at 30°C, as follows:

$$M = 0.5404 W^{0.7545}$$

$$\text{or } \log M = -0.2673 + 0.7545 \log W$$

where M = existence metabolism in Kcal/Bird-day  
and W = body weight in grams.

Taking the mean weights of South Island Pied and Variable Oystercatchers as 568 g and 692 g respectively (sexes combined, winter adults - see Appendices VI and VIII)

$$\begin{aligned} M_{\text{SIPO}} &= 64.69 \text{ Kcal/Bird-day} \\ M_{\text{Variable}} &= 75.09 \text{ Kcal/Bird-day} \end{aligned}$$

The larger Variable Oystercatcher therefore needs to ingest more food to maintain existence energy than does its smaller South Island congener. Since both species took similar amount of food at Jackson Bay, it is apparent that H. unicolor is at a considerable competitive disadvantage to H. o. finschi in habitats with soft substrates, especially where food resources are limited.

When feeding on rocky substrates at Kaikoura Peninsula in July 1967, Variable Oystercatchers ate an average of 298.3 g dry weight of limpets per day which was equivalent to 43.7% of their body weight (N = 46 observations). Since the calorific value of limpets and tua-tuas are similar (4.330 and 4.304 Kcals/g respectively), Variable Oystercatchers feeding on limpets at Kaikoura ingested more food and energy per bird than they did when feeding on tua-tuas at Jackson Bay. This indicates that H. unicolor is much more efficient at utilizing foods on hard substrates than on soft ones, and points to the survival value of habitat selection and niche utilization, especially where competitive exclusion by large flocks of South Island Pied Oystercatchers occurs.

### 3.6 BREEDING BIOLOGY.

The breeding biologies of the New Zealand species of oystercatcher are essentially similar in their broader perspectives. Major differences of relevance to systematics include time of breeding, dispersal to and from breeding areas, breeding dispersion, and egg weights and dimensions.

The two mainland species have different breeding seasons, although approximately three months overlap occurs. South Island Pied Oystercatchers breed from August to December, and Variable Oystercatchers from October to February. Peaks in breeding activity are well separated however, being September and December respectively. This asynchrony of breeding seasons is a major factor in ensuring the reproductive isolation of the two mainland species. Very little comparative data is available for the Chatham Islands Oystercatcher. Of ten clutches recorded on the Wildlife expedition in early summer 1970, eight were laid in October and two in early November. The peak in October is probably representative of the breeding activity

of this species, suggesting that it most closely approaches the South Island Pied Oystercatcher in timing of the breeding season.

Both mainland species have different dispersal patterns from their winter feeding areas to breeding localities. South Island Pied Oystercatchers possess a well developed migratory instinct, movement to breeding areas commencing in July and continuing to September. Distances as great as 1300 Km (C. 800 miles) are probably traversed by birds of northern populations moving south to breed. Variable and Chatham Islands Oystercatchers are non-migratory. They either undertake local movements from wintering areas to breeding localities, or they retain isolated territories throughout the year.

New Zealand oystercatchers have mutually exclusive breeding dispersions (cf Figs. 3 to 7). Although the breeding ranges of the two mainland species overlap latitudinally in the South Island, allopatry is effected by separation of breeding habitats within these ranges. South Island Pied Oystercatchers breed inland on the shingle beds of snow-fed rivers, though since 1950 this species has spread increasingly onto arable land and high country tussock grasslands. Variable and Chatham Islands Oystercatchers are strictly coastal breeders, the former commonly breeding on small offshore islands.

Following the fledging of broods, South Island Pied Oystercatchers migrate back to their winter haunts. Movement begins in late December, reaches a peak in February and continues in northern New Zealand until April. Juveniles tend to migrate further north than adults, as northern flocks contain high proportions of birds of this age class. Resightings of colour-banded adults suggest that they usually return to the same wintering areas year after year, although some notable exceptions have been recorded.

Variable and Chatham Islands Oystercatchers either stay in territories throughout the year or move into flocks at nearby feeding areas. Juveniles remain with their parents for several months, and then become independent. Banding returns indicate that Variable Oystercatchers wander most extensively in their second or third year of life before forming pair-bonds and localizing in an area. The greatest dispersal from natal sites of these immature birds so far recorded is 483 Km (c. 300 miles), but the average for 27 colour-marked birds is only 36 Km (c. 22 miles). Such local movements should be sufficient, however, to ensure adequate gene exchange between local populations, and to account for the sporadic appearance of pied and intermediate phase birds in southern localities where only the black phase is known to breed.

Egg dimensions and weights for New Zealand oystercatchers are species-specific (see Table 4).

TABLE 4. DIMENSIONS AND WEIGHTS OF EGGS OF NEW ZEALAND OYSTERCATCHERS.

Species	Mean Dimensions (mm)				Mean Weights(g)				
	Length	S.E.	N.	Width	S.E.	N.	Weight	S.E.	N.
South Island Pied Oyster- catcher	55.99	0.304	53	38.64	0.131	53	44.15	0.521	18
Variable Oystercatcher	58.76	0.377	35	40.93	0.165	35	49.36	0.492	14
Chatham Islands Oystercatcher	56.94	0.481	21	40.50	0.260	21	45.96	0.442	16

The eggs of South Island Pied Oystercatchers are smaller and lighter than those of Variable Oystercatchers



(length:  $t = 5.871$ ,  $p < 0.001$ ; width:  $t = 10.893$ ,  $p < 0.001$ ; weight:  $t = 7.105$ ,  $p < 0.001$ ). Chatham Islands Oystercatcher eggs are similar to those of the South Island Pied Oystercatcher in length, but most closely resemble those of the Variable Oystercatcher in width, the respective differences not being statistically significant. These dimensions account for the weight of eggs from the Chathams lying between those for the mainland species (Chatham v. S.I.P.O.:  $t = 2.608$ ,  $0.05 < p < 0.01$ ; Chatham v. Variable:  $t = 5.138$ ,  $p < 0.001$ ). Since most of the eggs used in this comparison were collected from similar latitudes, it seems probable that the differences are unbiased and reflect genetic differences between these species.

The broad similarity of the breeding biologies of New Zealand Oystercatchers outlined above is punctuated by significant species differences. Reproductive isolation of the two mainland species is assured by allopatric breeding dispersions and largely asynchronous breeding seasons. Chatham Islands Oystercatchers resemble South Island Pied Oystercatchers in time of breeding and in some egg parameters, and differences such as coastal breeding and non-migratory habits that indicate affinity with Variable Oystercatchers, may simply result from lack of opportunity for expression on such a limited land mass.

### 3.7 PARASITES.

Parasites are of value to systematic studies of their hosts since they evolve together, and in some cases parasites are more conservative than their hosts (Mayr, 1969). Evidence provided by parasites must, however, be evaluated with caution, as they sometimes randomly shift hosts (Baer, 1957). Clay (1951) has pointed out the limitations of applying the general principle that "the phylogenetic relationships of the Mallophaga reflect those of their hosts" to

birds, as similarity of feather structure between unrelated birds can result in them having identical Mallophaga. However, she concluded that Mallophaga were often valuable as supporting evidence where the taxonomic status of a bird was in doubt.

Three genera and four species of Mallophaga occur on the feathers of New Zealand oystercatchers. The largest of these, Saemundssonina haematopi, is found on the head and upper neck of each species (see Plate 5A). Two body lice (Actornithophilus grandiceps and Quadriceps auratus) are common to all three oystercatchers, occurring on the feathers of the trunk and wings (see Plates 5B and 5C). A fourth species of Mallophaga (Quadriceps ridgwayi) is peculiar to the Variable Oystercatcher, occurring on all colour phases throughout their range (see Plate 5D). This louse is found on the feathers of the wings, the back, and on the scapulars. Hence the mainland species of oystercatcher can be distinguished on the presence or absence of Q. ridgwayi, and its absence from the Mallophagan fauna of the Chatham Islands Oystercatcher points to the affinity of this bird with the South Island Pied Oystercatcher.

The internal helminth parasites of mainland New Zealand oystercatchers also show a dichotomy paralleling that of the Mallophaga, but to some extent this is due to different foods (and thus secondary hosts) taken by the species rather than species-specific differences. South Island Pied and Variable Oystercatchers have three genera of trematodes in common: Echinoparyphium sp. in the intestine, Notocotylus sp. in the caecae, and Cloacatrema sp. in the cloaca. They have different cestodes, however, as South Island Pied Oystercatchers host the small tapeworms Progy-notaenia sp. and Hymenolepis sp., whereas Variable Oystercatchers have larger as yet unidentified sp. Nematodes and an Acanthocephalan have also been recorded from South Island

Plate 3.

Halliday's from New Zealand systematics.

Key to letters:

- A. Stenandrena huamatoi.
- B. Actonithenailux grandiceps.
- C. Quadracus auratus.
- D. Quadracus sidgwayi.

In all photographs, males are on the left and females on the right.



A



B



C



D

Pied Oystercatchers, but they also are unidentified. Unfortunately, the helminth fauna of the Chatham Islands Oystercatcher is unknown.

More extensive sampling of Variable Oystercatchers is needed to describe its helminths adequately, but it does seem likely that, as with the Mallophaga, the New Zealand species of oystercatcher can be separated on differences in their helminth parasites. It seems equally likely that these differences reflect differences in the phylogeny of their hosts.

### 3.8 BEHAVIOUR.

Since ethological differences between species in the breeding season may function as reproductive isolating mechanisms, the comparative breeding behaviour of species is important to systematic studies. The behaviour of the New Zealand species of oystercatcher is similar, although differences do occur in the various displays and vocalizations associated with breeding.

Pair formation in the mainland species of oystercatcher is usually effected whilst the birds are still in their winter flocks. Courtship leading to pair formation manifests itself primarily in vocalized piping displays (see Plate 6A). Such piping contains a dominant social element in contrast to aggressive piping which is agonistic in nature and frequently involves disputes over food and feeding sites (see Plate 6B). Social and aggressive piping also differ in that the former is mutually stimulating to several birds, groups of up to six birds being common in displays. Fighting between members of a group engaged in social piping is extremely rare, whereas it often follows aggressive piping. The sexual element in social piping of South Island Pied Oystercatchers is apparent because it is restricted to adult-plumaged birds

Plate 6.

Piping displays of New Zealand oystercatchers.

Key to letters:

- A. Social piping display of the Variable Oystercatcher, during which the participating birds pipe in unison and frequently turn towards each other.
- B. Aggressive piping display of the South Island Pied Oystercatcher. Note the depressed tail, the wing raised upward and away from the body at the carpal flexure, the extended neck and the mandibles pointed downward.



A



B

(presumably sexually mature), and the frequency of these displays increases markedly with the onset of the breeding season (see Table 5).

TABLE 5. OCCURRENCE OF SOCIAL PIPING DISPLAYS BY SOUTH ISLAND PIED OYSTERCATCHERS AT THE HEATHCOTE-AVON ESTUARY DURING 1967.

Month	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
Mean No. of displays/ 1 hr obs. period	0	2	11	19	5	3	0
% of total	0	5	27.5	47.5	12.5	7.5	0

Ceremonial social piping parties of the European Oystercatcher (H. ostralegus) have received a great deal of attention from ornithologists (Selous, 1901; Huxley and Montague, 1925; Dirckson, 1932; Perry, 1938; Armstrong, 1947; Makkink, 1942). Two to a dozen birds were noted to participate, though three was the usual number, especially during the months of February, March, April (August, September, October of the New Zealand breeding season). Social piping of the conspecific South Island Pied Oystercatcher seems similar in both form and timing to that of the European bird.

Social piping is similar in the three New Zealand species of oystercatcher. It involves specific posturing in which the participating birds move forward together, aligned side by side. Their tails are depressed, wings raised upwards and away from the body at the carpal flexure, necks extended forward and mandibles pointed downward (see Plate 6A). The vocalizations associated with the piping display are characteristic of oystercatchers, beginning with sharp "pic" notes and gathering quickly into a prolonged chorus of high-pitched calls "kervee-kervee-kervee-kervee" etc., finally ending in a short lower trilling phrase.



Figure 11.

Sound spectrographs of social piping vocalizations of New Zealand oystercatchers. Spectrographs were made at a tape speed of  $7\frac{1}{2}$  inches per second over the frequency range 80-3000Hz.

Key to letters:

- A. Pied phase Variable Oystercatcher.
- B. Intermediate phase Variable Oystercatcher.
- C. Black phase Variable Oystercatcher.
- D. South Island Pied Oystercatcher.
- E. Chatham Islands Oystercatcher.

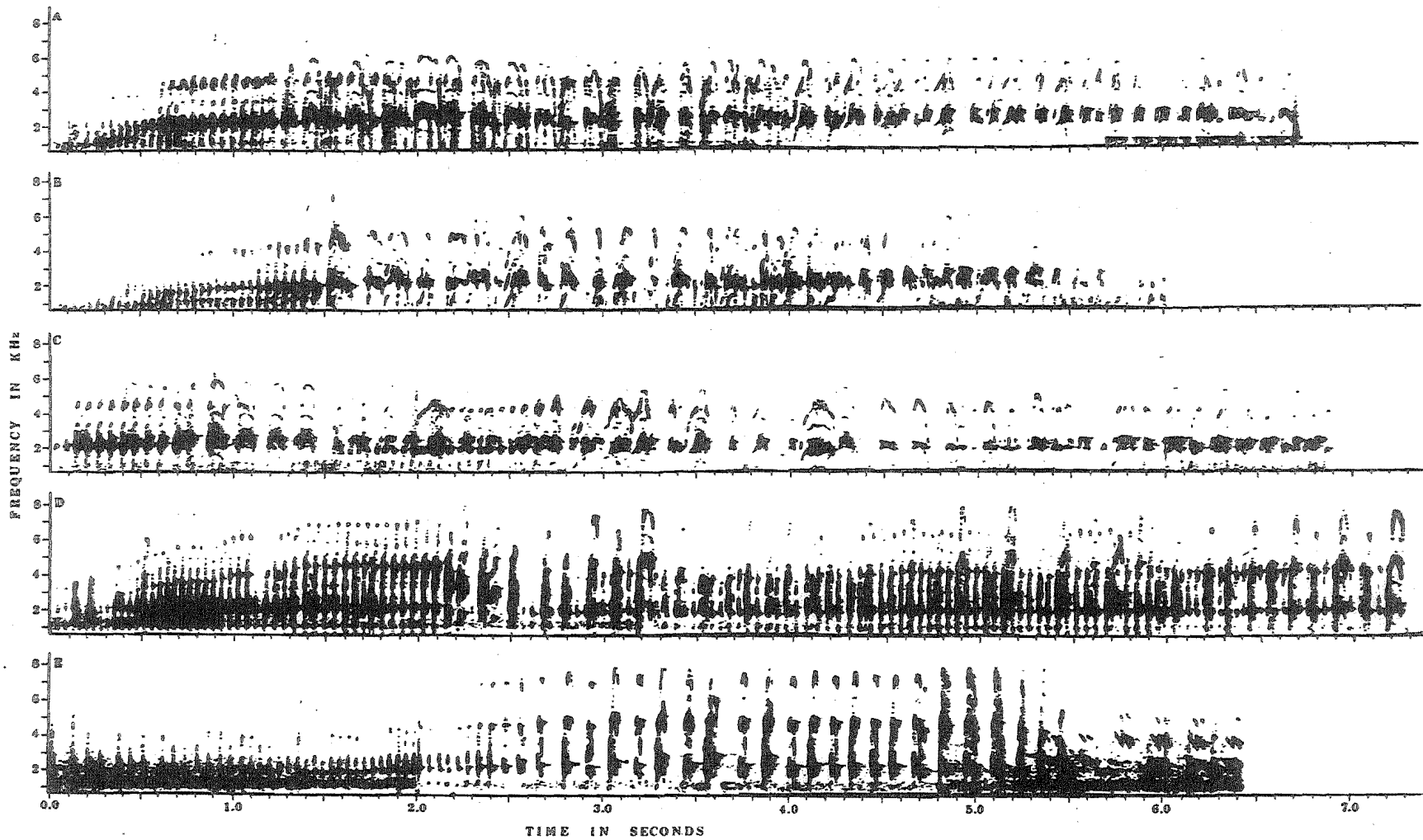
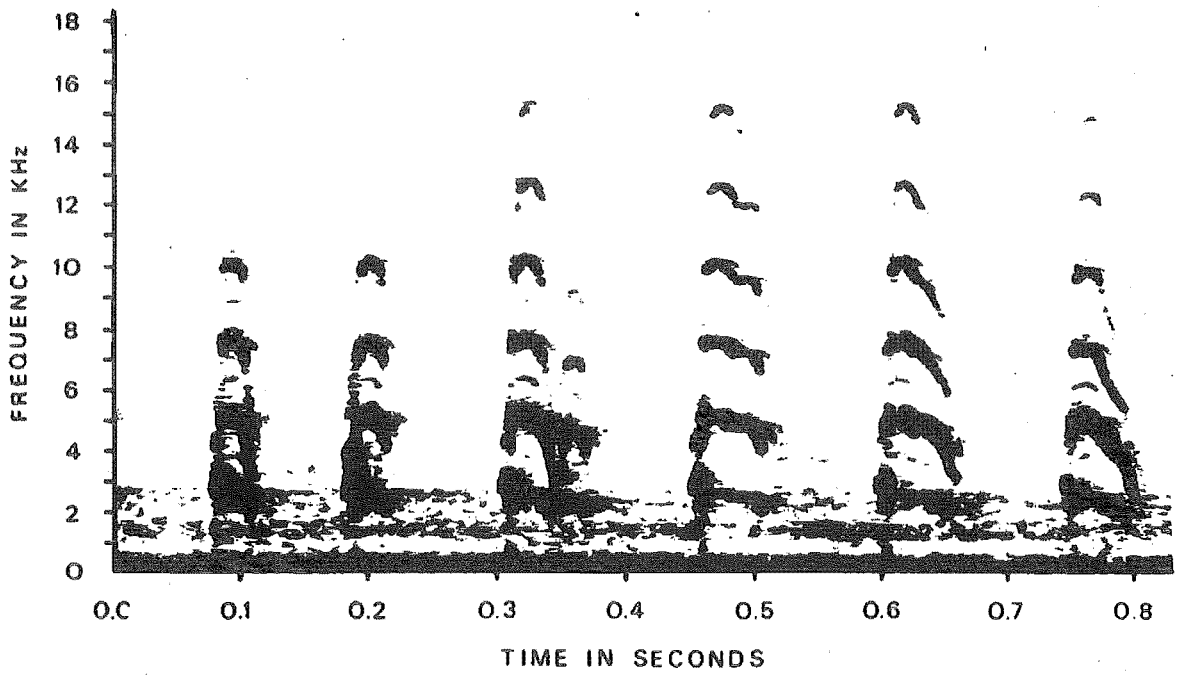


Figure 12.

Sound spectrograph of a segment of the social piping vocalization of a Chatham Islands Oystercatcher. This spectrograph was made from a segment of spectrograph B in Figure 11 (above the 5.0 second marker), at a tape speed of  $7\frac{1}{2}$  inches per second over a frequency range of 160-16,000 Hz.



Sound spectrographs of the social piping vocalizations are similar in their general pattern (see Fig. 11). Each spectrograph records piping vocalizations of two courting birds whose calls may or may not be in unison. Thus differences along the time axis are not likely to be significant, but are probably the result of the calls from the two birds being out of phase with one another. As the length of the piping call varies considerably even for the same pair of courting birds, differences in the length of the spectrographs are also not relevant.

The basic difference between the vocalizations of the species is that associated with pitch (and thus frequency). On each spectrograph a fundamental dominant frequency is depicted at approximately 2KHz, above which is superimposed a first harmonic at approximately 4KHz. The higher pitch of the calls of South Island Pied and Chatham Islands Oystercatchers discernable by ear is represented by a second harmonic on their spectrographs at about 7.5KHz. The truncated tops of the "kervee" calls of these two species extend to approximately 15KHz, far in excess of those of the Variable Oystercatcher (see Fig. 12). Hence although the social piping vocalizations of the New Zealand species of oystercatcher are similar in structure, they do differ in their pitch. The vocalizations of the Chatham Islands and South Island Pied Oystercatchers are very similar in pitch and indicate affinity of the two species.

Courtship behaviour of the South Island Pied Oystercatcher begins in June, reaches its greatest development in August, and ends in October. Similar social piping, involving identical posturing (Watt, 1955) reaches a peak in September for Variable Oystercatchers at Jackson Bay (D. Greaney, pers. comm.). The later seasonal development of social piping in this species is in accordance with its later breeding season.

Pair formation marks the culmination of courtship behaviour, and is indicated by copulation between members of a pair. Most pair formation of South Island Pied Oystercatchers is accomplished by mid-August, and seems to occur mainly at winter haunts. Before the inland migration of this species, it is common to see copulations at wintering areas, and pairs are often seen feeding and roosting together. Further evidence for pair formation at wintering localities is provided by observations of pairs sighted on migration in the MacKenzie Basin and on Canterbury riverbeds. Pair formation in European oystercatchers (H. ostralegus) also seems to occur mainly within roosting flocks before territories are taken up (Harris, 1967).

In contrast to the foregoing, it also seems likely that at least some pair-bonds are formed on arrival at the breeding grounds. Small flocks of up to 50 birds have been occasionally recorded migrating inland in the breeding season, and such flocks probably contain some unpaired birds. The differential migration and partial sexual segregation of South Island Pied Oystercatchers in winter suggested by the cyclical changes in the sex-ratio at the Heathcote-Avon estuary (see Chapter 4.5, p. 62), would necessitate some pair-bonds to be formed at the breeding grounds as this would be the only opportunity for potential mates to meet.

The formation of new pairs of Variable Oystercatchers is accomplished by September, and precedes the establishment of territories. At Waipu estuary in northern New Zealand, colour-banded birds retained their pair-bonds throughout 1970, even though they roosted in a flock in winter. Pairs of Variable Oystercatchers on isolated stretches of coastline maintain their pair-bonds throughout the year and drive off any intruding birds.

The courtship behaviour and pair formation of the Chatham Islands Oystercatcher is unknown.

The copulatory behaviour of the three New Zealand species of oystercatcher is identical. Copulation is usually, but not always, preceded by specific posturing. The male posture involves a stealthy approach, with the head drawn between the shoulders and held to one side of the body. This hunched-up attitude is accentuated by a general lowering of the body, and a pressing down and fanning of the tail. Females willing to copulate assume a passive posture, raising the body higher above the ground than is usual and at the same time erecting the tail feathers above the horizontal. The male mounts from behind and during coition maintains balance by flapping his wings. Occasionally, in all species, copulations occurred in which the male did not adopt the pre-copulatory posture, but either walked up to the female and mounted or flew onto her back from a short distance. Webster (1941) noted that copulation of American Black Oystercatchers did not involve any special preliminary ceremony, the male commonly flying onto the female as described above.

The maintenance of pair-bonds throughout the year by Variable Oystercatchers is probably related to their copulatory behaviour. I have observed pairs copulating in the winter months of May, June and July, and since it is extremely unlikely that these copulations could have resulted in fertilization of ova, they probably served to strengthen the pair-bonds between the participants. Such markedly aseasonal mating has not been recorded for South Island Pied or Chatham Islands Oystercatchers, and suggests perhaps that they do not always retain their pair-bonds throughout the year. However, South Island Pied Oystercatchers were seen copulating at the Heathcote-Avon estuary at least five weeks before egg-laying. Huxley and Montague (1925)

noted the same behaviour in European oystercatchers and concluded that "the physiological capacity of the eggs to be fertilized was not synchronous with the psychological readiness for insemination". Applying this reasoning Makkink (1942) suggested that early copulations were part of the behavioural mechanism whereby pair-bonds were established and secured. Copulations occur at the breeding grounds up to the time of egg-laying, and it seems probable that these later acts bring about fertilization of the ova.

The behaviour associated with courtship and pair formation of New Zealand oystercatchers is similar for each species. Temporal separation in the forming of pair-bonds serves to reinforce reproductive isolation between the mainland species. Social piping, the display through which pairs are formed, is similar in structure for the three species, but the pitch of piping vocalizations is higher for South Island Pied and Chatham Islands Oystercatchers than it is for Variable Oystercatchers, suggesting an affinity of the former two. However, it is unlikely that this difference could function as an ethological isolating mechanism between the two mainland species.

### 3.9 SUMMARY.

Genetic isolation between the New Zealand species of oystercatcher is maintained by species differences in habitat selection, niche utilization, food requirements, breeding biology and pair formation.

South Island Pied Oystercatchers (Haematopus ostralegus finschi) usually feed in large flocks in estuaries and mudflats where bivalves are abundant. Variable Oystercatchers (H. unicolor), especially the black phase in the South Island, are sparsely distributed over rocky shores from which they take mainly large limpets and mussels.



Where rocky areas are limited and competing South Island Pied Oystercatchers absent or scarce, Variable Oystercatchers may also feed on bivalve molluscs in estuaries. Thus habitat selection, which is most marked in regions of species overlap, is enhanced by competitive exclusion of H. unicolor from habitats with soft substrates. In such habitats, the disproportionately long and slender bill of H. o. finschi is well adapted for probing for bivalve molluscs, whereas on rocky shores the stouter and heavier bill of H. unicolor enables it to exploit foods unavailable to the smaller South Island bird. The short and relatively slender bill of H. chathamensis is probably a rock-dwelling adaptation of the probing bill of H. o. finschi. Competitive exclusion probably operates through the food requirements of the species, South Island Pied Oystercatchers faring best on bivalves and Variable Oystercatchers on limpets.

In the breeding season the mainland species of oystercatcher have allopatric dispersions and largely asynchronous breeding cycles. Since pair formation occurs at different times of the year for these species, and as some South Island Pied Oystercatcher pairs are formed following migration to inland breeding sites, the mainland species are therefore effectively reproductively isolated. Variable Oystercatchers maintain their pair-bonds throughout the year, strengthening them with aseasonal mating. The partial segregation of sexes of South Island Pied Oystercatchers coupled with their absence of aseasonal mating suggests that they do not always remain paired throughout the year.

The affinities of the Chatham Islands Oystercatcher as indicated by ecological and behavioural evidence lie mainly with the South Island Pied Oystercatcher. Both of these species have similar breeding seasons, social piping

vocalizations, and eggs. They also both lack the louse Quadriceps ridgwayi which is found on the Variable Oyster-catcher. The rock-dwelling, coastal breeding and non-migratory habits of H. chathamensis probably do not indicate relationship with H. unicolor, but rather result from the limited land mass available in which to feed and breed.

## Chapter 4.

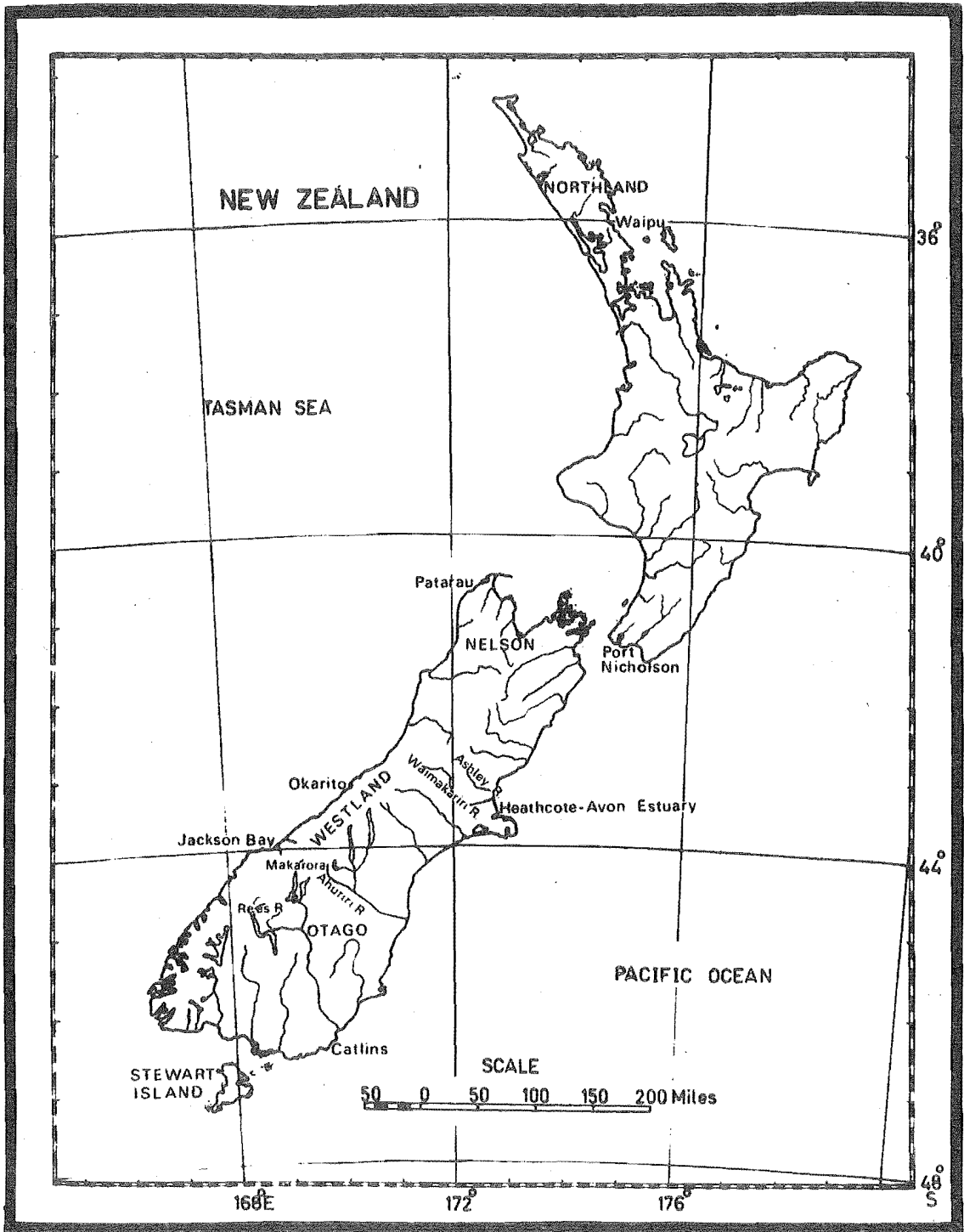
MORPHOLOGICAL VARIATION IN NEW ZEALAND OYSTERCATCHERS.4.1 INTRODUCTION.

The analysis of phenetic variation in animal populations is fundamental to modern systematic methodology. With the development of the biological species concept, the arbitrary and biologically misleading nature of typological systematics was clearly revealed. Thus Mayr (1959) was led to predict that avian systematists of the future would largely dispense with the services of types, and instead analyse variation within and between species populations, for which he coined the term population systematics.

Since this prediction was made, major advances have occurred in the detection and analysis of clines, hybridization, and geographical variation of species, largely through the application of multivariate statistical techniques. Special emphasis has been placed on the analysis of character variation in populations of species, since the systematics of these populations must allow for interpopulational and intrapopulational variability. Such analyses have frequently invalidated subspecies erected arbitrarily on the basis of types taken from a population continuum. Yet Michener (1969) noted at that time there was still a tendency among authors to let recognition of subspecies replace genuine studies of variation in relation to geography, ecology or chronology. He urged young systematists to investigate such variation intensively because of its importance to evolutionary biology, but not to do so by subjective recognition and delimitation of types. Rather, studies should be made of variation of individual characters or groups of characters, over the whole range of the species. It seems certain that future progress in systematics will

Figure 13.

Major sampling localities for black phase  
Variable Oystercatchers.



depend upon this methodology.

In accordance with this view, this chapter presents an analysis of morphological variation in New Zealand oystercatchers.

#### 4.2 METHODS.

##### A. Trapping of samples.

Two methods were used for trapping samples of birds for measurement of morphological characters, depending on the date of sampling. Outside the breeding season, birds were trapped with a projectile net (see Plate 7), since at this time they were gathered in accessible flocks. During the breeding season, adults were trapped at the nest using an automatic drop trap set over the eggs.

##### B. Time and Location of Samples.

Major sampling effort was timed for the winter months of May, June and July in 1970 and 1971, as this was the period following the autumn moult. An initial sample was taken at the Heathcote-Avon estuary in August, 1969. Nine more samples of South Island Pied Oystercatchers were trapped there over a 12 month period commencing June 1970. These samples were spaced at approximately equal intervals so that seasonal variation in the morphological characters could be examined. An additional sample of this species was obtained at Nelson to provide information on geographic variation in morphological characters, sex ratio and age class structure. Winter samples of Variable Oystercatchers were trapped at a number of localities in New Zealand which were accessible and which covered a wide geographic range (see Fig. 13).

Breeding adults of all three New Zealand species of oystercatcher were trapped during the 1970 and/or 1971 breeding seasons. South Island Pied Oystercatchers were

Plate 7.

Method of projectile-netting South Island  
Pied Oystercatchers. (Photo:H. Best).





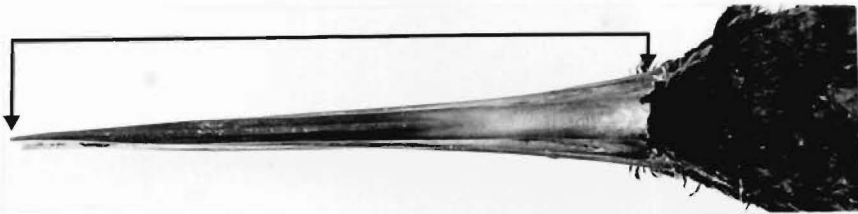
trapped during September and November at the Ashley riverbed in Canterbury, and the Makarora, Ahuriri and Rees riverbeds in North Otago (see Fig. 13). Breeding Variable Oystercatchers were trapped in the period December to January during surveys of breeding habitats from Stewart Island to Northland (see Chapter 3.2 D). Most trapping was carried out at Stewart Island, the Catlins coast in Otago, Jackson Bay, northwest Nelson Province, Port Nicholson and Northland (see Fig. 13). Chatham Island Oystercatchers were trapped at the nest in November, 1970.

### C. Measurement of Characters.

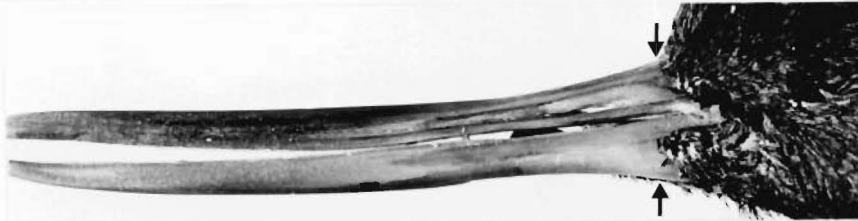
#### (i) Linear measurements and body weight.

The following characters, classically associated with avian systematics, were recorded for each trapped bird:

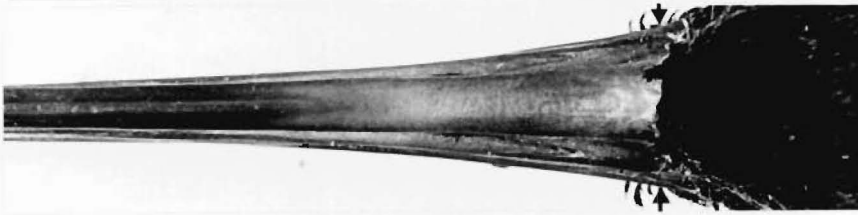
1. Bill length - measured along the dorsal surface of the culmen from the tip to the junction of the feathers (see Plate 8A).
2. Bill height - measured from the junction of the feathers with the culmen on the upper mandible to the exposed portions of the mandibular rami on the lower mandible (see Plate 8B).
3. Bill width - measured at the widest point of the bill beneath the dorsal feather margin on the upper mandible (see Plate 8C).
4. Tarsus length - measured diagonally from the posterior aspect of the joint between the tibio-tarsus and the tarsometatarsus, to the anterior aspects of the joint between the tarsometatarsus and the middle toe (see Plate 8D).
5. Middle toe length - measured dorsally from the joint with the tarsometatarsus to the base of the claw (see Plate 8E).
6. Tail length - measured from the point of emergence



A



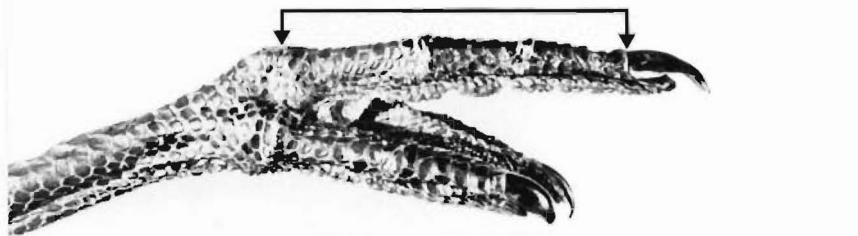
B



C



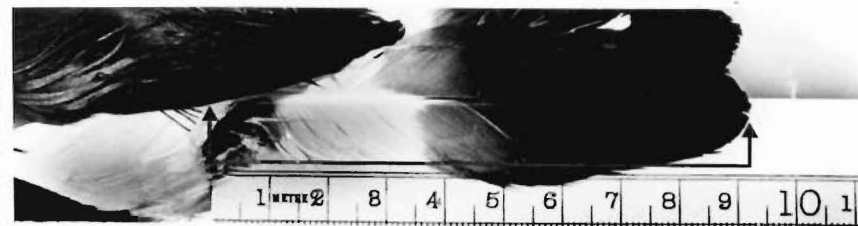
D



E



F



G

of the two central rectrices to the tip of the longest rectrix (see Plate 8G).

7. Wing length - measured as the chord of the flattened wing from the carpal flexure to the tip of the outermost primary feather. (see Plate 8F).
8. Body weight.

The first five linear measurements above were taken with dial calipers to the nearest 0.1 mm. Wing and tail were measured with a steel rule accurate to 1.0 mm. Body weight were recorded on a spring balance accurate to 5g.

D. Fat-free weights and lipid extraction.

From each of the ten samples of South Island Oystercatchers trapped at the Heathcote-Avon estuary, some birds were anaesthetized and skinned to provide a reference collection and material for an investigation of fat-free weights. These birds were weighed, sexed by dissection, and their discrete perivisceral and ventral subcutaneous fat depots were removed and weighed as a measure of total lipid content. Weighings were carried out on a Mettler balance to the nearest 0.01g.

Forty-eight birds from the March and June samples in 1971 were selected for extraction of total lipids. The undigested food was removed from the alimentary tract and the feathers plucked from the body. The carcass was jointed and put through a commercial meat mincing machine. The resulting mixture was further homogenized in a Waring blender with 95% ethanol as a blending agent and preservative. The homogenate from each bird was dried in an oven at 65°C for approximately 7 days until constant dry weight was achieved. These dried samples were ground to a coarse powder with a mortar and pestle, and then placed in separate 180 x 60 mm fat-free extraction thimbles. Lipids were extracted from the samples in a 5 litre soxhlet extractor, using petroleum

Figure 14.

Regression of total fat on  $\log_{10}$  fat amount,  
data from the extraction sample only.

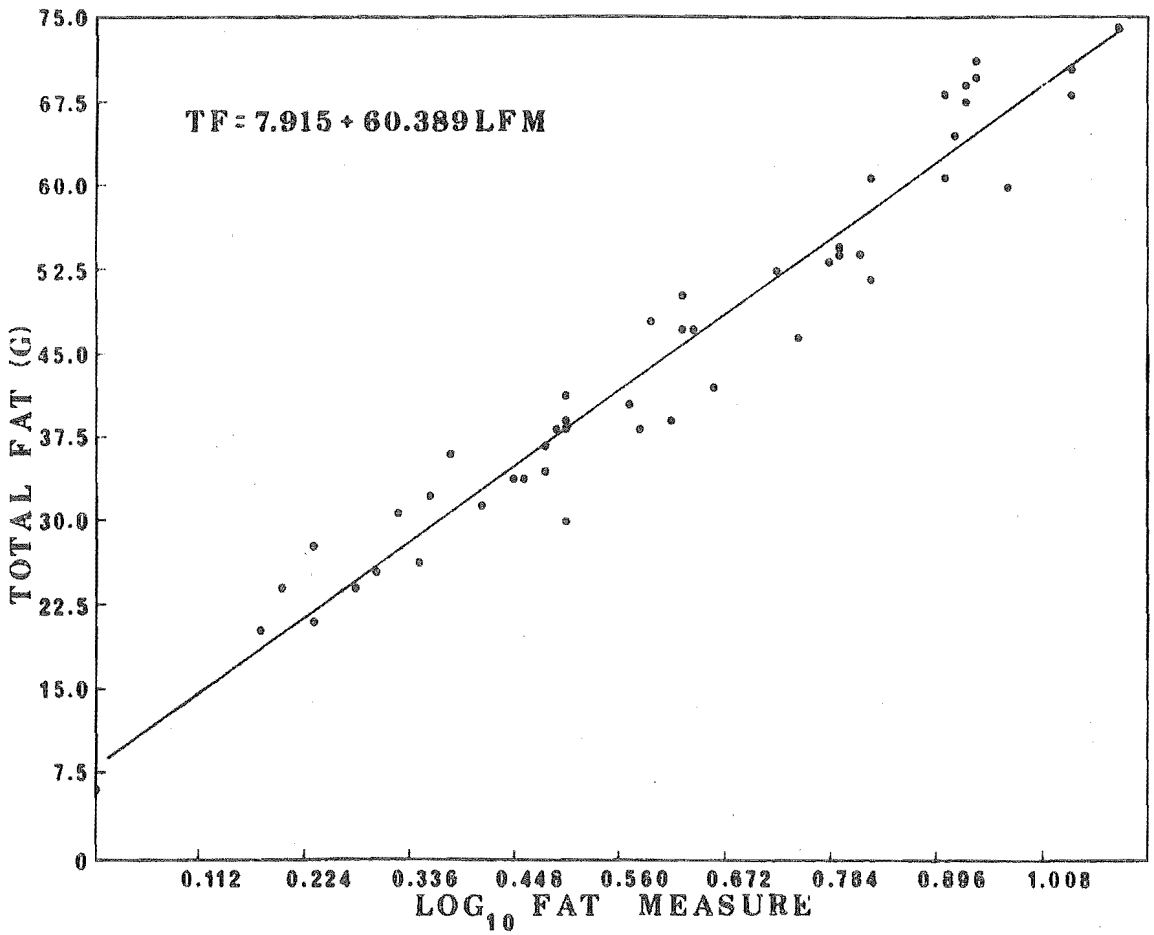
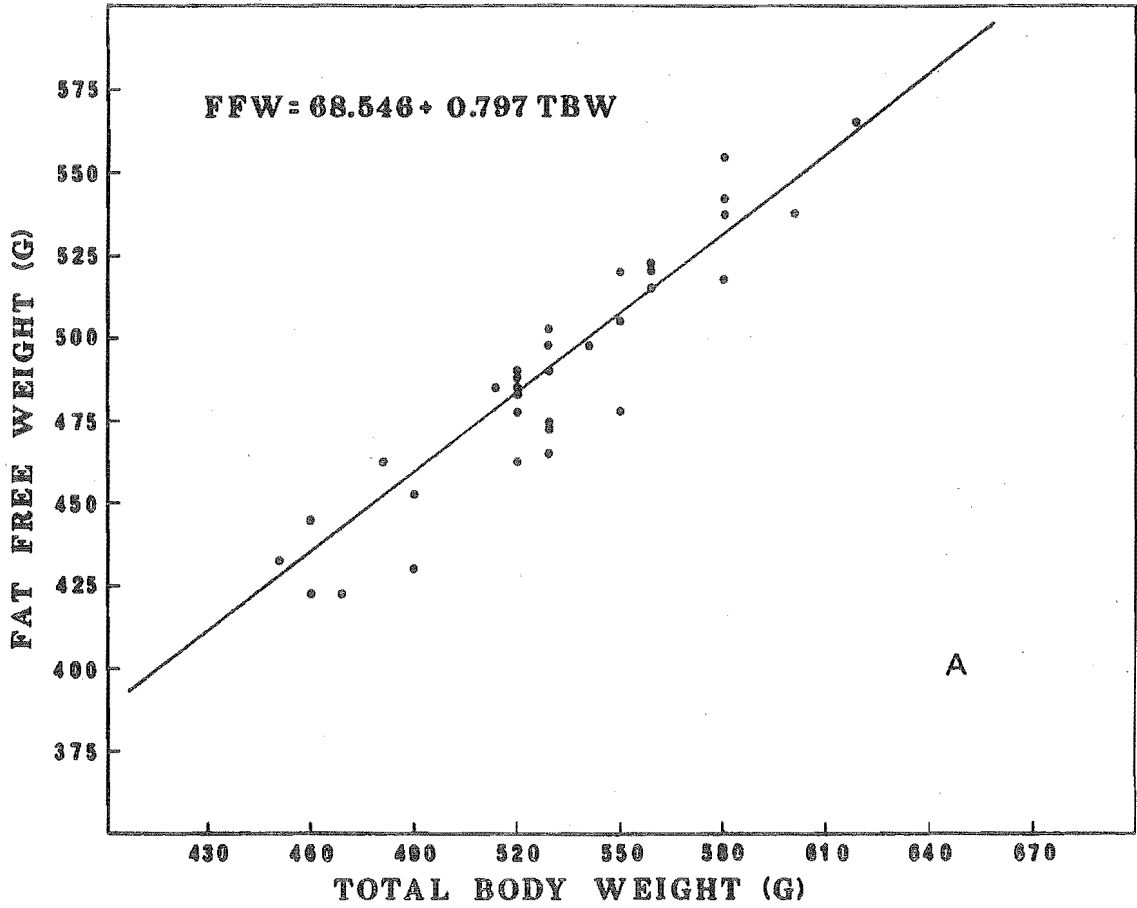


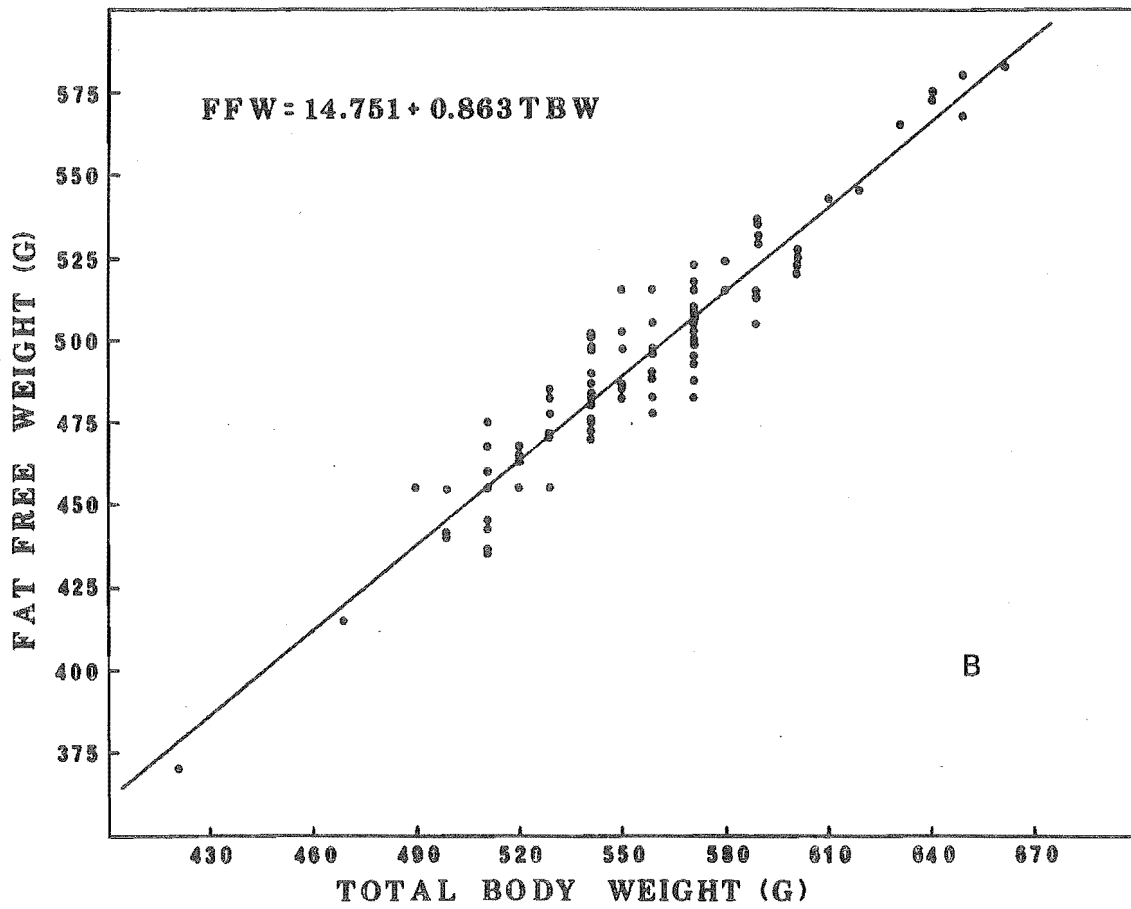
Figure 14.

Seasonal regressions of fat-free weight on  
total body weight.

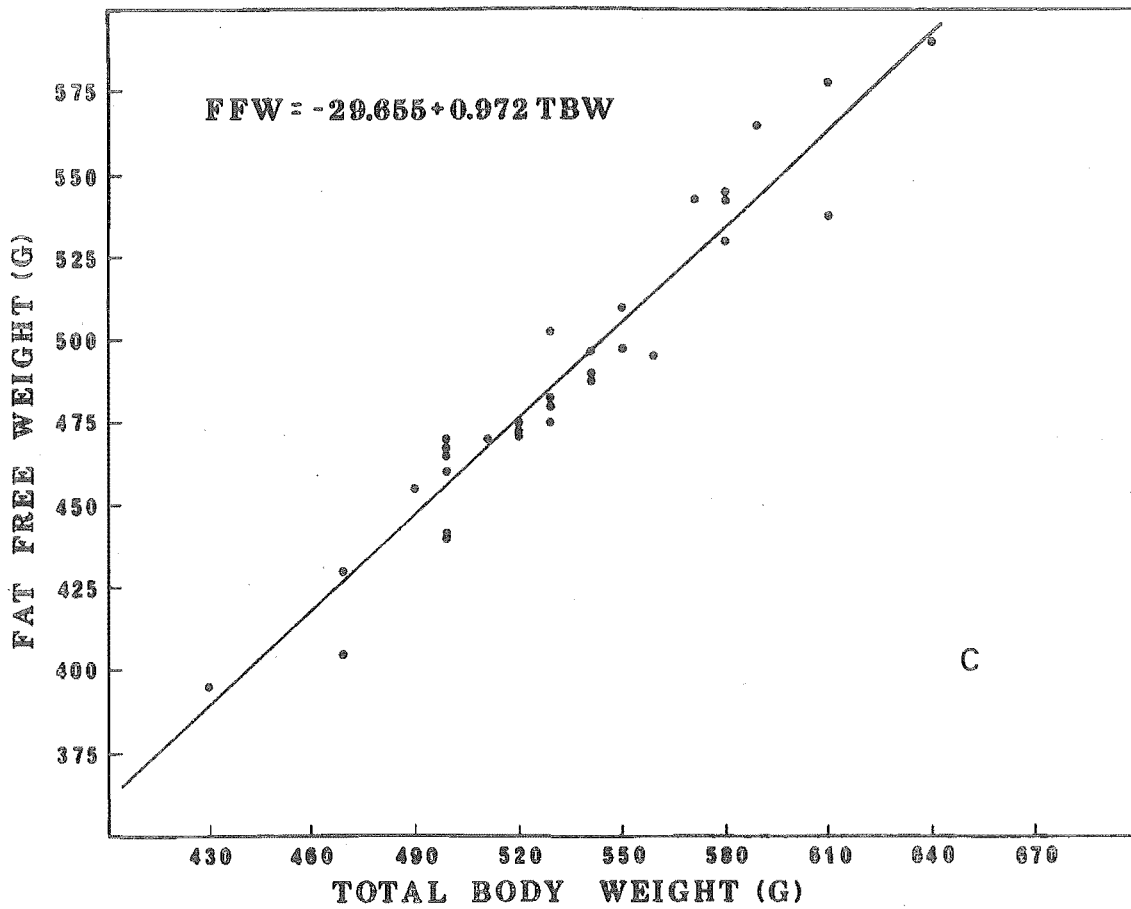
Key to letters:

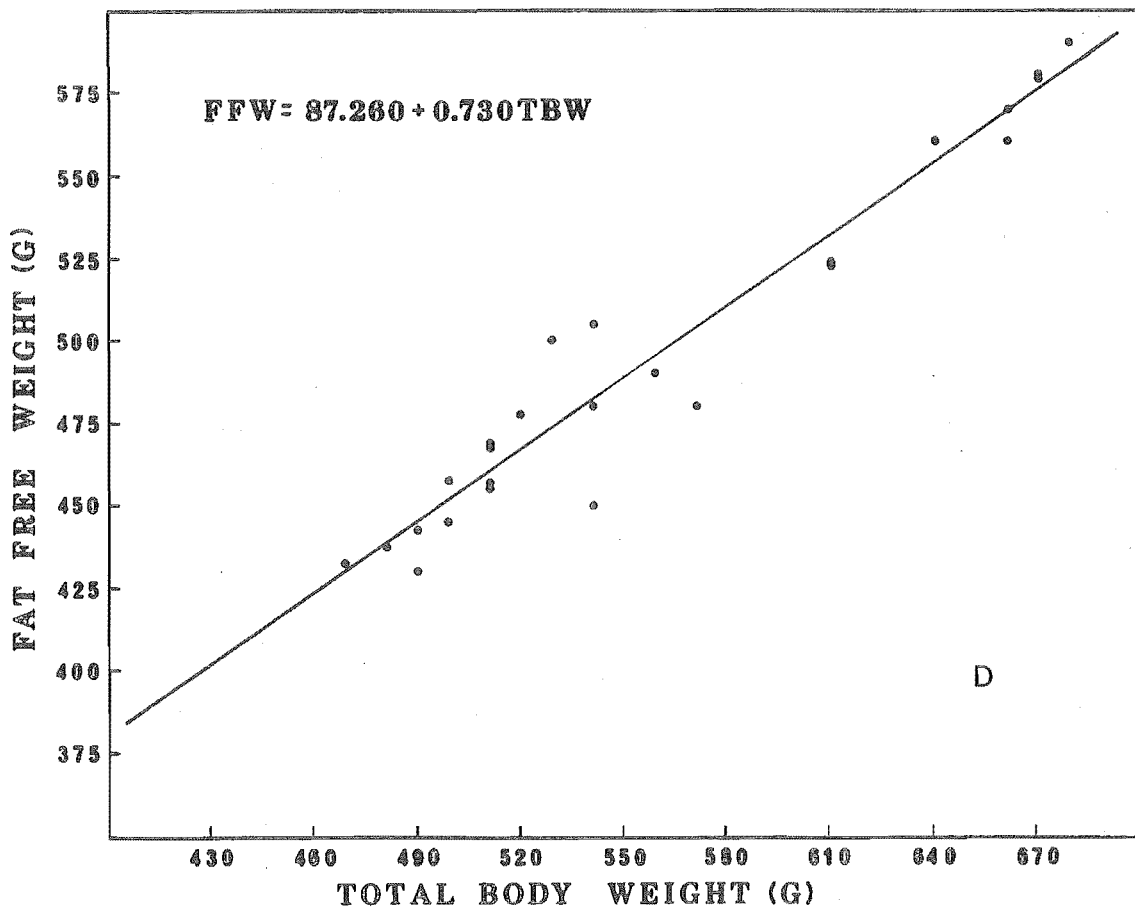
- A. Autumn sample.
- B. Winter sample.
- C. Spring sample.
- D. Summer sample.











ether as a solvent. Six reflux cycles were necessary to extract all lipids from the samples, but the considerable time involved in this extraction was partly offset by the simultaneous processing of four samples. The fat-free residues were dried in an oven to constant weight, and the total lipids for each bird calculated from the difference between the dry-weighted samples before and after extraction of lipids.

Odum and Perkinson (1951) showed that the total lipids in the White-throated Sparrow (Zonotrichia albicollis) were closely paralleled by the subcutaneous fat deposits, especially in the abdominal region. It follows, therefore, that fat deposits might be of value in estimating total lipids of a bird. Since total lipids of South Island Pied Oystercatchers in the extraction sample increased exponentially with fat measure (weight of perivisceral and subcutaneous fat depots), total fat was regressed on  $\log_{10}$  fat measure, yielding a highly significant relationship ( $F = 16.81$ ,  $P < 0.001$ ; see Fig. 14). By substituting the fat measures of all birds in the reference collection in this regression equation, total fat contents (and thus fat-free weights) were computed. The fat-free weights thus derived were then partitioned according to season, and four separate seasonal regressions were established between fat-free weight and total body weight (see Fig. 15A to D). The resultant equations were used to estimate fat-free weights of all birds live-trapped at the estuary.

#### E. Melanin pigmentation in mantle feathers.

Since there is speculation on possible geographic variation in plumage pigmentation of Variable Oystercatchers (see Chapter 1.5), four feathers were removed from the mantle of each breeding adult caught on the nest. Similar feather samples were obtained from South Island Pied and Chatham Islands Oystercatchers. The intensity of melanin

pigmentation in the distal 5mm of each feather was analysed with a Beckman DK-2A ratio-recording spectrophotometer, using white standards of 100% reflectance prepared from magnesium sulphate. Curves of percentage diffuse spectral reflectance over the wavelength range 380 to 770m $\mu$  were used to calculate tristimulus values (X, Y, Z) using the weighted-ordinate method (Judd and Wyszecki, 1963). This method involves breaking down the reflectance curve into 10m $\mu$  intervals and reading off reflectance values (R $\lambda$ ) on the ordinate at these intervals. Tristimulus values may then be calculated from the equations:

$$X = k \sum_{\lambda=380}^{770} R\lambda H\lambda \bar{x}\lambda \Delta\lambda \dots\dots\dots(1)$$

$$Y = k \sum_{\lambda=380}^{770} R\lambda H\lambda \bar{y}\lambda \Delta\lambda \dots\dots\dots(2)$$

$$Z = k \sum_{\lambda=380}^{770} R\lambda H\lambda \bar{z}\lambda \Delta\lambda \dots\dots\dots(3)$$

where H $\lambda$   $\Delta\lambda$  is the spectral-radiant flux incident on the object being evaluated. In this study, H $\lambda$   $\bar{x}\lambda$ , H $\lambda$   $\bar{y}\lambda$  and H $\lambda$   $\bar{z}\lambda$  values were those of CIE\* standard source C, listed in Table 2.6 of Judd and Wyszecki (op. cit.: 132-133). The wavelength interval  $\Delta\lambda$  was set at 10m $\mu$ , and for source C, k = 1. Thus by reading R $\lambda$  values into equations (1), (2) and (3), tristimulus values were obtained.

Chromaticity co-ordinates (x, y, z) were computed from the expressions:

$$x = \frac{X}{X+Y+Z}$$

$$y = \frac{Y}{X+Y+Z}$$

and  $z = 1 - (x+y)$

\*CIE = Commission Internationale de l'Eclairage.

The x and y co-ordinates were transformed to the illustrative terms dominant wavelength ( $\lambda_d$ ) and excitation purity ( $\phi$ ) respectively, using Table 18 of Hardy (1936). The tristimulus value Y was converted to a brightness term from the equation:

$$Y = 100y_s$$

where  $y_s$  is the trichromatic coefficient of the sample. Dominant wavelength, brightness and excitation purity correspond to the psychological attributes of hue, brilliance and saturation respectively (Selander and Johnson, 1967).

Before commencing colorimetric determinations, several practice runs were made on the same reference sample to check on experimental error. Acceptable standards of repeatability (< 1% error) were achieved providing the feathers were positioned identically at the sample port between each run.

#### F. Plumage patterns.

To provide information on variation in plumage patterns, photographs were taken of the ventral plumage, the alar bar, and the rump patch of all pied and intermediate phase Variable Oystercatchers trapped during this study. Comparative photographic series were also gathered for South Island Pied and Chatham Islands Oystercatchers. The inheritance of colour phases of Variable Oystercatchers was investigated by photographing broods of previously photographed adults. The ontogeny of plumages from the chick to adult stages were checked by retrapping banded birds and were recorded photographically.

#### G. Statistical Methods.

All computations were performed on an IBM 360/44 computer at the University of Canterbury Computer centre.

Quantitative data were initially screened with either program A<sub>1</sub> or A<sub>8</sub> from the Department of Zoology program library. A<sub>1</sub> computes basic statistics of location and dispersion, the latter for testing the normality of frequency distributions of data. A<sub>8</sub> performs Bartlett's test of homogeneity of variances of samples before analysis of variance (anova), and computes  $F_{\max}$  values for checking against Bartlett's chi-square values. Both programs contain options for transforming non-normal data (see Sokal and Rohlf, 1969).

Conventional univariate statistical techniques such as analysis of variance, sum of squares simultaneous test procedure (SS - STP) (Gabriel, 1964), Student's t-tests and chi-square tests were used to study variation in characters.

In some sections beyond, data were analysed with multivariate techniques. Multivariate statistical methods involve the analysis of simultaneous variation in two or more variables. As these methods require heavy computation, their widespread application has not been feasible until recently, when the introduction and availability of high-speed digital computers has shortened computation to practical limits.

Systematic studies are usually based on comparison of groups of organisms through multiple characters. Although variation in the characters themselves can best be studied by univariate statistical techniques, the grouping of organisms and the relationships of groups are most efficiently studied by considering simultaneous variation in as many characters as possible, as for example by canonical variates analysis (Power, 1970a).

The multivariate technique of canonical variates analysis (= discriminant function analysis) was first brought to the attention of biologists by R.A. Fisher (1936, 1938).

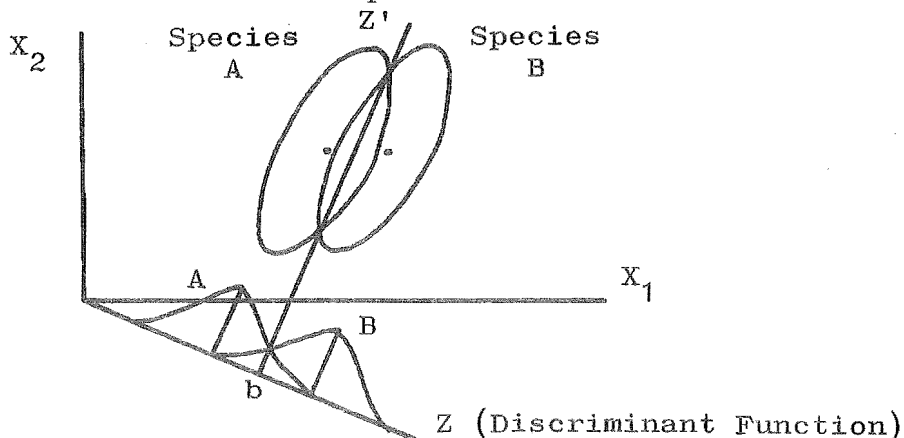
who initially applied discriminant functions to taxonomic problems. Despite Fisher's foresight, the application of discriminant function analysis to the separation of groups of organisms has been popularized only in very recent years e.g. Jolicoeur (1959), Lubischew (1962), Dupraw (1965), Jameson, Mackey and Richmond (1966), Power (1970a), and Atchley (1970).

The technique and advantages of discriminant function analysis can be simply explained in terms of two samples representing two different populations, such as two species. Suppose that two characters ( $X_1$  and  $X_2$ ) were measured for each species sample, but that neither character was sufficiently distinct to allow separation of the species with any degree of certainty i.e. the species character means are different but the distributions on which they are based overlap considerably. Discriminant function analysis computes a new variable  $Z$  which is a linear combination of both variable  $X_1$  and  $X_2$  such that:

$$Z = k_1 X_1 + k_2 X_2$$

where  $k_1$  and  $k_2$  are discriminant coefficients. This function is developed so that as many as possible of the members of one species have high values of  $Z$  and as many as possible of the other species have low values. Thus  $Z$  serves as a much better discriminator of the two species than does either  $X_1$  or  $X_2$  taken singly.

Discriminant analysis can be geometrically represented in the above simple case as follows:



In this diagram  $X_1$  and  $X_2$  are represented by the two axes in the normal two-dimensional bivariate graph. The ellipses about the two species centroids indicate confidence regions for bivariate means (see Sokal and Rohlf, 1969). If the significance level for describing differences between the means was set at 0.95, and this value substituted in equations for generating ellipses, then these ellipses would define regions in which 95% of the species A and species B would lie respectively. By projecting a line  $Z'$  through the points of intersection of the ellipses, it is possible to construct another line  $Z$  perpendicular to it. This line is given by the discriminant equation, and if the original data points from which the centroids were derived in the two-dimensional space were projected on to it as shown in the diagram (giving two normal curves), then the overlap between the groups would be smaller than for any other possible line. The point  $b$  where  $Z'$  meets  $Z$  divides the one-dimensional space into two regions, one for probable membership in species A and one for probable membership in species B (Cooley and Lohnes, 1971).

When more than two variables are considered simultaneously for several groups, as in multiple discriminant analysis, it is possible to generate several discriminant functions. These functions can then serve as axes on which to plot the discrimination of the group. In this study, multiple discrimination analysis was carried out using computer programs from Cooley and Lohnes (1962). Such an analysis involves the production of canonical axes (= discriminant functions), one axis being generated for each character. Thus if there are  $m$  characters there are  $m$  canonical axes which describe the variation in the characters in  $m$ -dimensional hyperspace. The canonical variates procedure rotates these axes through the character



space so that within-group variation is minimized and among-group variation maximized. Since it is only possible to depict graphically two or three-dimensional space, the dispersions of the group centroids in  $m$ -dimensional space are reduced to appropriate co-ordinates in two or three-dimensional space. The projection of the group centroids onto the first two or three canonical axes usually accounts for the vast majority of variation contained within the original  $m(\text{variables}) \times n(\text{groups})$  data matrices. The axes of the characters used in deriving the discriminant functions may also be projected onto the canonical axes to indicate the magnitude and direction of the separation of groups afforded by each character. Thus, as Power (1970a) lucidly points out, "one may place the emphasis on among-group relationships and neatly summarize most of the information given in univariate comparisons as well as provide new information by considering character jointly."

The method of canonical variates analysis involves the following calculations. A mean squared deviations and cross products matrix is generated for each group and these are pooled to produce a within-group variance-covariance matrix  $W$ . The dispersion of the groups means about their grand means is contained in another matrix, the among-group variance-covariance matrix  $B$ . This matrix is standardized by matrix  $W(BW^{-1})$ , which serves to adjust each character measurement by the variance of every other character, and thus maximizes among-group variation relative to within-group variation. The discriminant functions (canonical axes) are then derived as principal components of the standardized matrix  $B$ . The proportion of among-group variation extracted by each principal component decreases with each successive extraction, and therefore two or three principal components usually contain most of the variation.

For each axis there are discriminant function coefficients (K) so that the discriminant equations can be written as:

$$K_1 X_1 + K_2 X_2 + \dots \dots \dots K_n X_n = P$$

where  $K_1, \dots \dots \dots K_n$  are eigenvectors,  $X_1, \dots \dots \dots X_n$  are group means for the n characters, and P is the point on the axis for a group. Each canonical axis has an eigenvalue which indicates the dispersion of group means along the axis. The per cent variation described by each discriminant function is derived from the ratio of each eigenvalue to that of the sum of all eigenvalues.

In the multivariate case, homogeneity of dispersion matrices as tested by the Wilks' Lambda converts to an F-value for significance testing. The robustness of this value plus the probability that the K discriminant functions are more likely to be normally distributed than the original characters on which they are based, make moderate departures from homogeneous dispersions unlikely to effect seriously the validity of results (Cooley and Lohnes, 1962).

For increased value in viewing the group centroids in two-dimensional space, 95% confidence ellipses were superimposed about them. The calculation of ellipse parameters followed the method of Barlow and Power (1970).

In all statistical tests, the significance level was set at 0.95, as this level strikes an optimal balance between the possibility of type I error (rejection of a true null hypothesis) and type II error (acceptance of a false null hypothesis). Throughout the text, the probability ranges associated with significance tests are designated by asterisks as follows:

\* =  $0.05 > P > 0.01$ , \*\* =  $0.01 > P > 0.001$ , \*\*\* =  $P > 0.001$ ,  
ns = not significant. In tables, degrees of freedom are abbreviated to D.F.

### 4.3 AGE DETERMINATION.

Age classes of South Island Pied Oystercatchers can be determined accurately on the basis of progressive changes in the colours of the dorsal plumage, irides, bill and legs, as shown in Table 6.

TABLE 6. COLOUR CHARACTERS USED IN AGE DETERMINATION OF SOUTH ISLAND PIED OYSTERCATCHERS.

Age Class	Dorsal Plumage	Iris	Bill	Leg
Juvenile	Very brown, with buff edges to feathers	Brown	Pale orange with dark tip	Grey
Second Year	Browny-black	Orange-red	Orange	Light pink
Sub-adult	Black	Red	Orange	Pink
Adult	Black	Scarlet	Bright orange	Coral pink to purple

The colour changes listed above were determined from retraps and sight records of colour-banded birds at the Heathcote-Avon estuary over the period 1967 to 1971. Juvenile birds moult their brownish first year plumage in the spring following their first winter and assume the darker plumage typical of second year birds. At approximately the same time the iris changes gradually from brown through yellow to orange-red, the bill loses its dark tip and the legs become light pink in colour. Sub-adult colours appear in the summer moulting period marking the end of the second year of life. Of 74 banded sub-adults subsequently retrapped or sighted as four year olds, 58 (78.4%) maintained their third year colourings and 16 (21.6%) achieved adult colourings. Twenty-one of the above fourth year sub-adults were

resighted in 1971 as five year olds, and of these 15 (71.4%) were in adult colours. The change from sub-adult to adult colourings occurs in the autumn moulting period of these age classes. Since only birds in adult colourings breed, it seems likely that some birds may breed when 4 years old, but the majority do not reach breeding condition until they are at least 5 years of age. These findings agree closely with those of Harris (1967) for European Oystercatchers (H. ostralegus).

Variable and Chatham Islands Oystercatchers can also be separated into four groups on the basis of identical colour changes, and presumably they also indicate the same age-specific changes as in the South Island Pied Oystercatcher.

#### 4.4 SEX DETERMINATION.

The absence of obvious sexually dimorphic characters in oystercatchers has in the past made the correct field identification of sexes difficult. Similar difficulties associated with sexing of the Fulmar (Fulmarus glacialis) and Great Black-backed Gull (Larus marinus) were largely resolved by Dunnet and Anderson (1961) and Harris (1964) respectively, who separated the sexes by discriminant analysis of bill lengths and bill depths. Heppleston and Kerridge (1970) extended this method of sexing to European Oystercatchers (H. ostralegus), but found that it was mathematically equivalent to using the less sophisticated ratio of bill length to bill depth.

New Zealand oystercatchers can be sexed with a high degree of accuracy using the ratio of bill length/bill width in combination with the ratio of bill length/bill height. Since males have a shorter, wider and deeper bill than females, the ratios are small for males and large for females, and have the effect of maximizing sexual dimorphism

in bill measurements.

A sexed sample of adult South Island Pied Oystercatchers was established from dissected birds subsampled from the regular projectile-netted catches, and from breeding birds caught at the nest and sexed by either external cloacal inspection or copulatory behaviour. For approximately two weeks after egg-laying females can be distinguished by the distended nature and deep pink colouration of the cloaca. Sexes were discriminated in the sample as follows:

bill length  $>$  89mm = female  
 $<$  81mm = male

In the overlap range 81 to 89mm, the ratio of bill length/bill width was computed to effect separation:

if bill length/bill width  $\geq$  6.60 = female  
 $<$  6.60 = male

Since there was slight overlap about this discriminating point, L/W ratios in the range 6.50 to 6.70 were checked against bill length/bill height ratios:

if bill length/bill height  $\geq$  5.30 = female  
 $<$  5.30 = male

Using this method, the sex of 136 adults (78 males and 58 females) in the sexed sample were predicted with 97.8% accuracy (three errors).

The other three age classes of South Island Pied Oystercatchers can also be sexed in this manner. Sub-adults have bills of adult dimensions and thus can be sexed with the same ratios as adults. Of 33 sub-adults (21

males and 12 females) in the sample, the sex of 32 were correctly predicted (97.0% accuracy).

Although the bill of South Island Pied Oystercatchers reaches adult length in approximately the first six months of life, it continues to grow in both width and height until the end of the second year (see section 4.7A). The ratios for sexing the juvenile first year and second year birds are therefore different, and are higher than those for adults and sub-adults. For second year birds, the discriminating point between the sexes in the bill length overlap zone of 81 to 89mm was 6.80 for the L/W ratio, and 5.60 for the L/Ht ratio. Corresponding values for juveniles were 7.15 for the L/W ratio, and 5.70 for the L/Ht ratio. With these ratios, the sex of 38 second year birds (23 males and 15 females) and 36 juveniles (23 males and 13 females) were predicted with 97.4% (1 error) and 100% accuracy respectively.

Without comparative data from localities in the far south and north of New Zealand, it is difficult to assess the utility of the above method of sexing. However it seems likely that the ratios derived for adults encompass a reasonably representative New Zealand sample, and thus have wide application. The 58 breeding adults included in the sexed sample probably had diverse wintering origins, as most were captured in inland North Otago which could draw birds from Stewart Island, Southland, Otago, Canterbury and possibly even northern New Zealand populations. Certainly Canterbury birds breed there, as one bird breeding in the Rees riverbed in October 1970 had been colour-banded at the Heathcote-Avon estuary six months previously. It is sobering to note the divergent bill length/bill height ratios obtained by Heppleston and Kerridge (1970) for two British populations of oystercatchers, but it seems likely

that their data were obtained from mixed populations of Scottish, Faerøe and Icelandic birds, representing a tremendous range of geographic variation.

Significant geographic variation in the bill lengths of Variable Oystercatchers made the sexing of this species more difficult than H. ostralegus finschi. The relatively low numbers of H. unicolor in New Zealand precluded the establishment of a dissected reference collection, so only adults caught at the nest and sexed by cloacal examination and copulatory behaviour were used to develop a sexing method. The overlap in sexual dimorphism generated by geographic variation in bill dimensions was reduced considerably by developing separate sexing ratios for southern and northern New Zealand populations. In the South Island, Variable Oystercatchers can be sexed as follows:

bill length  $> 89\text{mm}$  = female  
 $< 81\text{mm}$  = male.

In the overlap range 81 to 89mm, the ratio bill length/bill width was used to separate the sexes thus:

if  $L/W \geq 6.10$  = female  
 $< 6.10$  = male.

Around this discriminating point, ratios were checked against the ratio of bill length/bill height:

if  $L/Ht \geq 4.70$  = female  
 $< 4.70$  = male.

The sex of 43 of a sample of 44 birds (20 males and 24 females) were correctly assigned with these ratios (97.7% accuracy).

In Northland, appropriate discriminating ratios were 5.80 for L/W and 4.90 for L/Ht, but the overlap region in which these ratios were used had to be extended to cover the range 81 to 94mm due to the increase in bill length of this species with decreasing latitude. One bird from a sample of 20 (10 males and 10 females) was incorrectly sexed with these ratios (95% accuracy).

The total sample of 16 Chatham Islands Oystercatchers used in this study were captured at the nest, and sexed by cloacal examination and copulatory behaviour. It was therefore unnecessary to develop a method of sexing, but for completeness and for possible use in further studies, sexing ratios were computed. The short compact bill of this species has resulted in a lowering of ratios relative to those for the mainland species. Sexes may be distinguished for H. chathamensis as follows:

bill length > 75mm = female  
< 67mm = male

In the bill length range 67 to 75mm, sexes are separable on L/W ratios:

if L/W  $\geq$  5.20 = female  
< 5.20 = male

As a check on L/W ratios from 5.10 to 5.30, L/Ht ratios provide supplementary information:

if L/Ht  $\geq$  4.30 = female  
< 4.30 = male.

The sex of 15 of the 16 birds (8 males, 8 females) were correctly predicted with this method (93.8% accuracy).



TABLE 7. AGE COMPOSITION AND SEX RATIOS OF PROJECTILE-NETTED SAMPLES OF SOUTH ISLAND PIED OYSTERCATCHERS.

Date	Locality	N	Age Classes				Sex Ratio	Chi <sup>2</sup>
			Juv	2Yr	Sub-ad	Ad	Males:Females	
26.8.69	H.-Avon	43	6	5	18	14	1.53:1.00	3.94*
30.4.70	H.-Avon	47	4	7	18	18	1.14:1.00	0.20ns
16.6.70	H.-Avon	116	3	9	0	104	1.87:1.00	10.32***
29.7.70	H.-Avon	71	18	27	14	12	2.09:1.00	8.80***
24.9.70	H.-Avon	82	38	27	7	10	1.41:1.00	2.39ns
11.11.70	H.-Avon	40	16	10	9	5	2.64:1.00	9.10***
5.2.70	H.-Avon	110	17	23	24	46	0.67:1.00	4.40*
12.4.71	Nelson	53	31	7	4	11	1.79:1.00	4.24*
23.4.71	H.-Avon	34	5	8	2	19	1.20:1.00	0.12ns
18.6.71	H.-Avon	78	5	10	16	47	1.60:1.00	4.15*

#### 4.5 AGE COMPOSITION AND SEX RATIOS OF PROJECTILE-NETTED SAMPLES.

The age composition and sex ratios of samples of South Island Pied Oystercatchers projectile-netted at the Heathcote-Avon estuary and Nelson are shown in Table 7.

The proportion of each age class captured in a sample was largely dependent on the date of netting. The samples in June of both years were composed mainly of adults, consistent with the great preponderance of this age class present at the estuary in mid-winter. Their numbers begin to decline in late July as the migration of breeding adults away from the estuary to inland breeding sites commences. Accordingly, the frequencies of the other age classes increase through spring to summer. However, some sub-adults and second year birds also migrate inland during the breeding season, and thus deplete coastal summering populations. Five such birds were trapped in November 1970 on the Waimakariri riverbed approximately 40 Km inland from the Canterbury coastline, and of these, three were second year birds and two were sub-adults. In late summer, there is a considerable influx of adults and juveniles at the estuary, as most breeding birds and their progeny leave inland breeding sites and migrate back to coastal wintering localities at this time. This influx is clearly revealed in the February sample. The onset of autumn saw the departure of some juveniles for northern localities, and thus accounts for their drop in numbers in the April sample. The tendency for juveniles to migrate further northwards than adults is also apparent from the concurrent April sample captured at Nelson, approximately 240 Km north of the Heathcote-Avon estuary. In that sample 58.5% of the birds caught were juveniles and only 20.8% were adults.

TABLE 8. AGE COMPOSITION AND SEX RATIOS OF PROJECTILE-NETTED SAMPLES OF VARIABLE OYSTERCATCHERS.

Date	Locality	N	Age Classes				Sex Ratio
			Juv	2Yr	Sub-ad	Ad	Males:Females
16.8.69	Okarito	12	1	2	3	6	1.40:1.00
7.5.70	Port Nicholson	4	1	1	0	2	1.00:1.00
12.5.70	Waipu Estuary	32	5	10	1	16	1.00:1.00
8.9.70	Patarau	14	2	2	2	7	1.33:1.00
15.5.71	Waipu Estuary	13	0	3	3	7	2.25:1.00
5.6.71	Stewart Island	30	1	2	5	22	1.14:1.00
9.6.71	Jackson Bay	10	1	1	1	7	1.50:1.00

For all samples lumped, sex ratio = 1.25 males : 1.00 females,  
and  $\chi^2 = 1.4696$  (  $0.1 > P > 0.05$  ).

At the Heathcote-Avon estuary, the sex ratio in most samples favoured males. The sample taken in February when migrating breeding birds and their progeny were arriving back at the estuary, contained a small excess of females. The proportion of females progressively declined through the autumn and winter samples, the July 1970 sample containing two males to each female. Since this disparity was sustained within each age class and is therefore unlikely to have resulted solely from differential mortality of the sexes, and since it is also unlikely that there was a sexual trapping bias, it seems that there may be some geographic segregation of the sexes at their winter haunts. The progressive decrease of females in the samples suggests that there is a differential movement of sexes away from the estuary, and could be explained if females tend to migrate further north than males. However, the predominance of males in the samples is probably accentuated by differential mortality in the sexes, as is the case for many winter populations of monogamous birds (Mayr, 1939).

The age composition and sex ratios of samples of Variable Oystercatchers projectile-netted at various localities in New Zealand are shown in Table 8.

As all the samples were trapped in winter when the birds were gathered in flocks, the best represented age class was the adult one. Oystercatchers are comparatively long-lived, and according to Harris (1967) average life expectancy for H. ostralegus reaching breeding age is 11.8 years. Allowing an average of four years to reach adulthood, then it follows that the adult age class contains birds where ages span at least seven years thus explaining their preponderance in populations. Although there is an excess of males in most samples of Variable Oystercatchers, the sex ratio in all samples lumped together does not deviate significantly from 1:1. It therefore seems probable that mortality occurs independently of sex in H. unicolor.

#### 4.6 SEASONAL NON-GENETIC VARIATION.

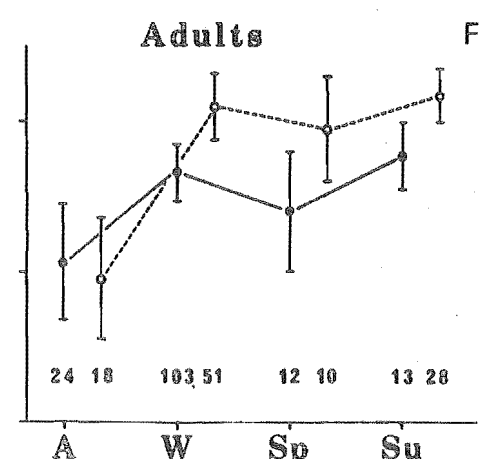
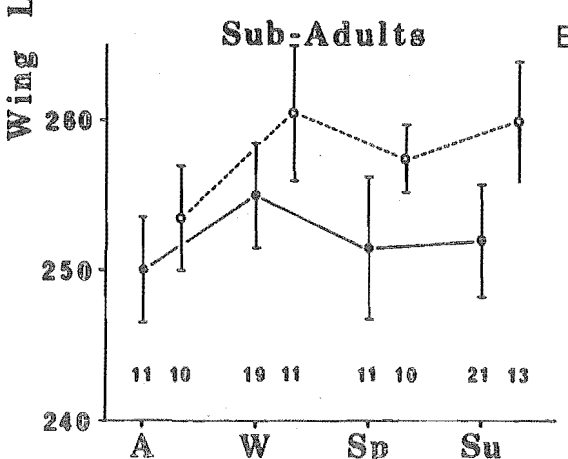
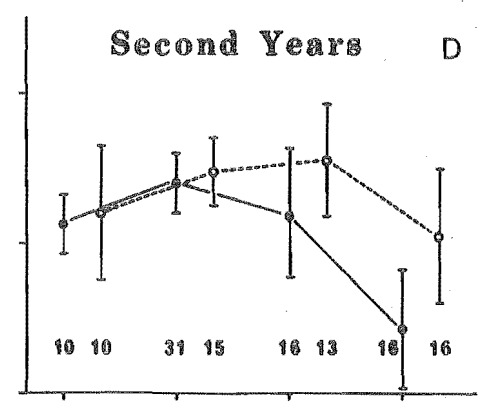
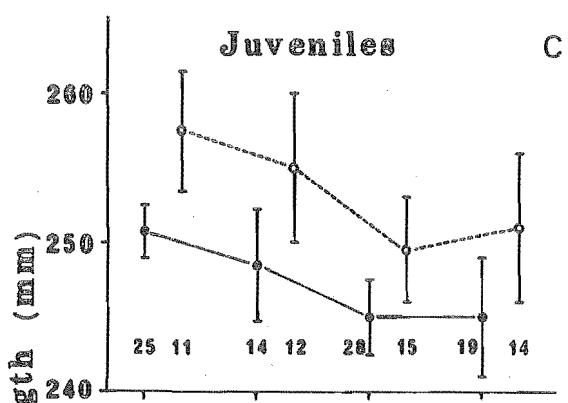
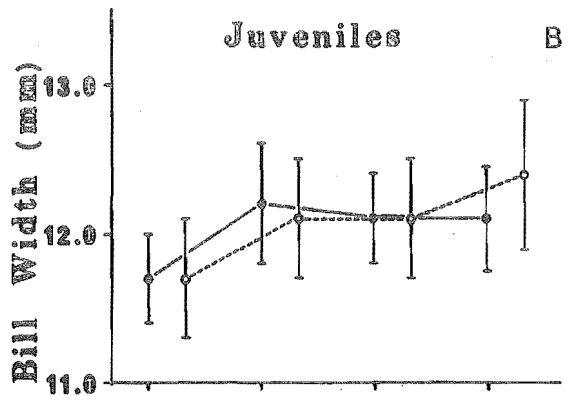
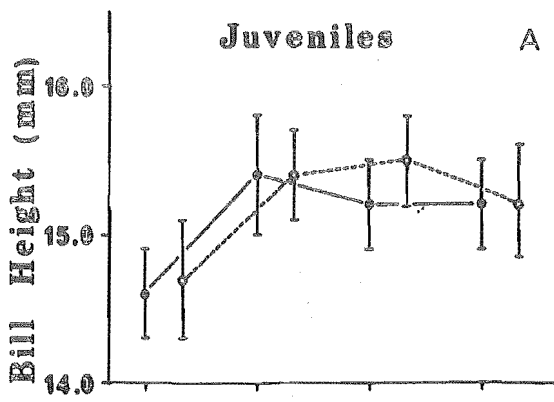
Before beginning to partition components of the total variance of characters that are genetically determined, it is important to eliminate or minimize the effects of seasonal non-genetic variation. Seasonal variation in bill length, wing length, tail length and body weight has been recorded for many species of birds. White and Gittens (1964) emphasized the seasonal variation in bill length measurements of some European Oystercatchers (H. ostralegus) when contesting Evan's (1964) claim that migrant wader populations of diverse geographic origins might be separable from within mixed flocks on the basis of bill length, wing length and total length measurements. Most modern studies of variation in characters seek to eliminate the seasonal component by confining the collection of specimens to a short period following the completion of the annual moult, at which time abrasion of the tips of the wing and tail feathers is insignificant (Packard, 1967; Selander and Johnston, 1967). Where this has not been possible, other researchers have reduced the discordant effects of differential seasonal wear by collecting specimens at a specified time of year, such as the breeding season (Yang and Selander, 1968; Barlow and Power, 1970; Power, 1971). Since seasonal variation of characters is assumed in these studies, little attention has been focused on the magnitude or direction of this variation, or its contribution to the total variance of characters.

The seasonal character means by sex and age of South Island Pied Oystercatchers trapped at the Heathcote-Avon estuary are shown in Appendix VI. Tests of the significance of differences between the seasonal means are tabulated in Appendix VII. The main findings of this analysis are summarized below:

- A. Bill length. The differences between the four seasonal bill length means for each sex and age class grouping were not statistically significant, indicating an absence of seasonal variation in the character. This result contrasts sharply with the major seasonal changes recorded in bill lengths of some European oystercatchers by White and Gittens (1964), but both Evans (1964) and Harris (1967) suggested that much of the "seasonal" variation listed in White and Gittens measurements was due to inaccurate measurement and poor repeatability. Nevertheless, seasonal changes in bill length have been demonstrated for many passerine species (Clancey, 1948; Davis, 1954; Selander, 1958; Selander and Johnston, 1967). It has been postulated that these changes may be due to variation in the rate of wear of the constantly growing horny bill tip associated with seasonal dietary changes. Presumably, the lack of seasonal variation in the bill lengths of South Island Pied Oystercatchers at the Heathcote-Avon estuary results from approximately equal and opposite growth and abrasion. The rate of abrasion of the bill tip is likely to be reasonably constant, since the birds at the estuary feed on the same foods in the same areas throughout the year. Of the nine birds recaptured and remeasured in different seasons during this study, four had bill lengths identical with those previously recorded, three differed by 0.3mm or less and the other two differed by 0.5 and 0.6mm respectively. Clearly then, the small variation in bill lengths which could be attributed to season falls within or near to the limits of measurement error (see section 4.2 C), and thus would not contribute significantly to the total variance.
- B. Bill height and bill width. The height and width of the bills of juvenile South Island Pied Oystercatchers are subject to seasonal variation, although the heterogeneity in

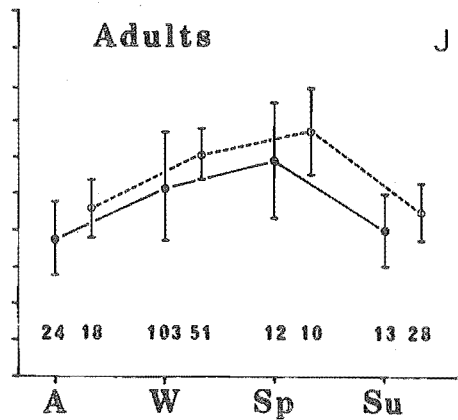
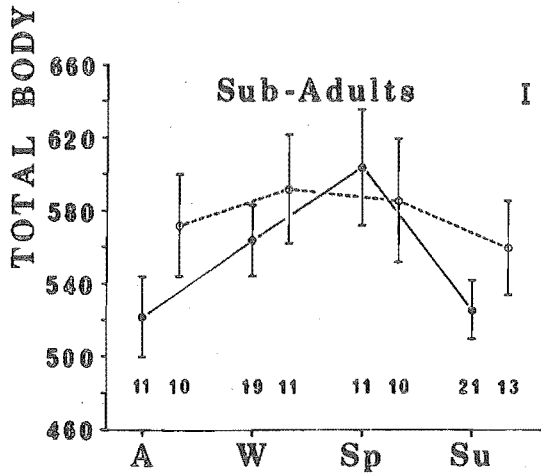
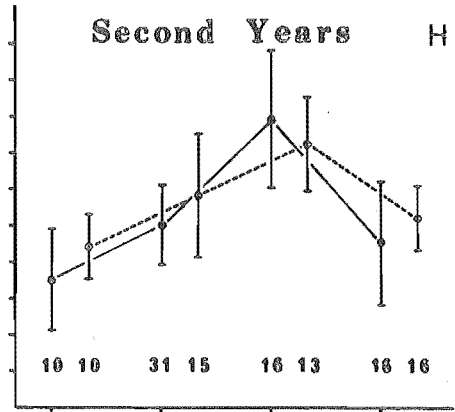
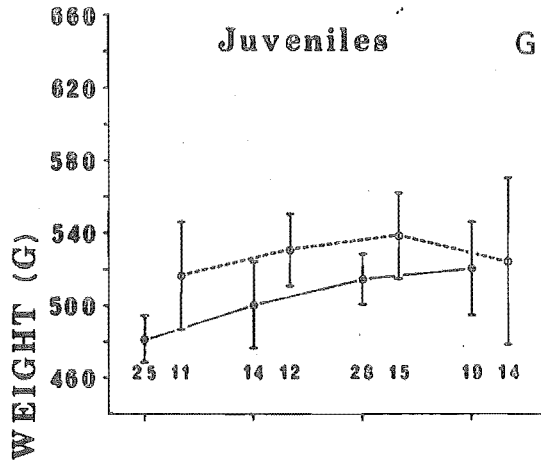
Figure 16.

Seasonal variation in some morphological characters of South Island Pied Oystercatchers.



SEASON





SEASON

means is solely attributable to the autumn samples (see Fig. 16A and B). At this time the juvenile age class contains young birds, most of which are less than four months old and which have only recently arrived at the estuary from inland breeding sites. Although the bill of these birds has reached maturity in length, it is still growing in both height and width during autumn, and does not reach constant proportions until winter. This pattern of variation is similar in both sexes.

C. Wing length. Seasonal variation is evident in wing lengths of all age classes (see Figs. 16C to F). The variant seasons differ for each age class, coincident with their respective moult periods. Juveniles moult their flight feathers in late spring and early summer, and although all birds in wing moult or with obvious wear or damage to the primaries were excluded from the samples, the cumulative effects of gradual abrasion are apparent in the spring sample for both sexes and in the summer sample for males (see Fig. 16C). Second year birds moult their flight feathers in summer, so about this time feather wear is maximal, and this is clearly depicted in Fig. 16D. Both sub-adults and adults experience greatest feather wear in autumn just before the seasonal moult (see Figs. 16E and F). For all the above age classes, the seasonal component of variation can be reduced to statistically acceptable levels if the samples from the seasons in which moult occurs is excluded. Ideally, wing lengths used in size comparisons of the age classes would be of greatest value if they were taken from specimens collected after the annual moult had been completed and the new feathers had completed growth. Calhoun (1947) found a statistically significant difference between mean wing lengths of North American Sparrows (Passer domesticus) collected in autumn and spring even though he omitted any birds from the sample that showed obvious wear, and this

was subsequently confirmed by Selander and Johnston (1967). However, the latter authors found differences of only 0.43mm and 0.35mm for males and females respectively, amounting to approximately 0.5% of the mean. These small differences must surely lie within the range of measurement and repeatability error. Although the wear of the primaries of South Island Pied Oystercatchers is gradual, it seems that the rate of abrasion is not constant between moults, but becomes pronounced near the moulting period. At this time the feather tips may become shredded and thus wear very quickly, whereas at other times of the year the heavily pigmented tips remain quite resistant to abrasion (Averill, 1923; Welty, 1964:46).

- D. Tail, tarsus and middle toe lengths. No significant seasonal variation was detected in tail, tarsus or middle toe lengths. The constancy of tail lengths is perhaps unexpected in view of the abrasion to which the rectrix tips could be subject, but as for the primaries, it seems that the intense melanin pigmentation in the feather tips prevents measurable wear. The exclusion of specimens that were moulting or which had obviously worn rectrices undoubtedly contributed to the similarity in seasonal mean tail lengths. The seasonal invariance of tarsus and middle toe lengths is evident for all age classes, suggesting that stability in these measurements is reached very early in life.
- E. Total body weight and fat-free weight. The total body weight of South Island Pied Oystercatchers varies considerably with season (see Figs. 16G to I), but fat-free weight is relatively constant, indicating that seasonal variation in the former is largely due to the accumulation of fat in the various depots. The pronounced rise in fat storage begins in winter when feeding rates reach a peak (Baker, 1969), and continues into spring just before the departure of birds

on inland migration. The enormous amount of fat deposition in the subcutaneous and perivisceral fat depots of pre-migratory birds is well established (e.g. Odum and Perkinson, 1951; King and Farner, 1959; George and Berger, 1966). This probably accounts for the major portion of the spring fattening of adults, also of some subadults and second year birds which also undertake migrations (see section 4.5). In addition to this pre-migratory fattening, many species of birds display an annual cycle of weight change in which weights are inversely correlated with ambient temperature (Baldwin and Kendeigh, 1938; Helms and Drury, 1960). Although this seasonal pattern may result partly from concomitant seasonal changes in liver weights and water content of the tissues, by far the greatest component is attributable to the deposition of fat in the subcutaneous depot (George and Berger, 1966). Such winter fattening is apparent in the samples of juveniles, as these birds remain at the estuary throughout the year and do not deposit pre-migratory fat reserves in the visceral depot.

- F. Pooling of samples. The seasonal variation in characters of South Island Pied Oystercatchers outlined above indicates the extent to which samples can be pooled for analysis of age differences and sexual dimorphism in the ensuing sections. Seasonal samples of bill lengths, tarsus lengths, middle toe lengths, tail lengths and fat-free weights were pooled to increase sample sizes. To reduce seasonal variation in the remaining four characters to statistically acceptable levels, variant samples were excluded before pooling. The autumn sample of juvenile bill heights and bill widths, the winter and spring samples of total body weights of all age classes, and the wing length samples taken in the moulting periods were all excluded from further analyses.

TABLE 9. ANALYSIS OF VARIANCE OF SIZE CHARACTERS IN SOUTH ISLAND PIED OYSTERCATCHERS.

Source of variation	F-ratio								
	Bill length	Bill height	Bill width	Tarsus	Middle toe	Wing	Tail	Weight	Fat-free weight
Sex	351.892 <sup>***</sup>	0.591	1.294	20.827 <sup>***</sup>	10.900 <sup>***</sup>	38.989 <sup>***</sup>	6.756 <sup>**</sup>	15.254 <sup>***</sup>	53.490 <sup>***</sup>
D.F.	1,588	1,566	1,559	1,588	1,588	1,482	1,588	1,258	1,588
Age	0.763	19.675 <sup>***</sup>	35.177 <sup>***</sup>	2.783 <sup>*</sup>	2.727 <sup>*</sup>	23.091 <sup>***</sup>	0.528	9.711 <sup>***</sup>	20.657 <sup>***</sup>
D.F.	3,588	3,566	3,559	3,588	3,588	3,482	3,588	3,258	3,588
Sex-Age	0.075	1.622	1.793	3.061 <sup>*</sup>	0.176	1.356	4.804 <sup>**</sup>	1.117	0.122
D.F.	3,588	3,566	3,559	3,588	3,588	3,482	3,588	3,258	3,588

Since it was not possible to trap samples of Variable or Chatham Islands Oystercatchers at any one locality for each season, it was therefore impractical to attempt to investigate seasonal variation of characters in these species. For analytical purposes, it was assumed that similar seasonal variation occurs in each species, and therefore similar pooling procedures were universally applied. In species comparisons of adults (see section 4.10), the sample of South Island Pied Oystercatchers was restricted to the winter catch, as this contained adequate numbers of males and females. The winter sample of Variable Oystercatchers was relatively small, so summer samples were included to boost the sample size. The only sample of Chatham Islands Oystercatchers available was a summer one, so this had to be used.

#### 4.7 SIZE VARIATION.

Variation in size was investigated mainly for South Island Pied Oystercatchers as this was the only species on which adequate data were available. Where possible, however, interspecific comparisons were made to substantiate findings and increase their applicability. The significance of variation arising from age and sex differences in size was determined for each character by a Model I two-way factorial analysis of variance, as shown in Table 9.

Unbiased estimates of differences between sex and age groups were calculated from unweighted mean differences where significant sex-age interaction was present, and from weighted mean differences where significant sex-age interaction was absent (see Steel and Torrie, 1960:265-270).

##### A. Age Variation in Size.

With the exception of bill and tail lengths, all of the morphological characters show significant age variation

TABLE 10. AGE VARIATION IN SIZE IN SOUTH ISLAND PIED OYSTERCATCHERS.

(Unbiased estimates of differences between age classes)

Morphological character	Mean differences between:					
	Juv & 2yr	Juv & Sub-ad	Juv & Ad	2yr & Sub-ad	2yr & Ad	Sub-ad & Ad
Bill height	-0.1mm 0.6%	-0.1mm 0.6%	-0.3mm 1.9%	-0.1mm 0.6%	-0.3mm 1.9%	-0.2mm 1.3%
Bill width	-0.2mm 1.6%	-0.4mm 3.2%	-0.8mm 6.4%	-0.2mm 1.6%	-0.6mm 4.8%	-0.3mm 2.4%
Tarsus length	-0.2mm 0.4%	-0.1mm 0.2%	-0.1mm 0.2%	-0.1mm 0.2%	-0.2mm 0.4%	-0.2mm 0.4%
Middle toe length	-0.3mm 0.9%	-0.2mm 0.6%	-0.3mm 0.9%	-0.2mm 0.6%	-0.2mm 0.6%	-0.1mm 0.3%
Wing length	-2.4mm 0.9%	-6.9mm 2.7%	-9.6mm 3.8%	-4.4mm 1.7%	-7.0mm 2.8%	-2.6mm 1.0%
Total weight	-13.9g 2.6%	-35.5g 6.7%	-35.1g 6.6%	-21.8g 4.1%	-22.3g 4.2%	0.9g 0.2%
Fat-free weight	-24.5g 4.9%	-49.2g 9.9%	-38.8g 7.8%	-24.6g 5.0%	-14.2g 2.9%	10.8g 2.2%

(see Table 9). The magnitude of these differences were calculated using Steel and Torrie's (1960:271) approximation of the method of fitting constants (see Table 10).

The pattern of age variation in size is similar in all characters, the gradual increase in size from juvenile to adult dimensions reflecting slow growth. Because of this significant age variation it is not permissible to pool measurements of characters from all age classes when making species comparisons in taxonomic studies. However, the similarity of measurements of sub-adults and adults indicates that these two age classes can be pooled to increase sample sizes without introducing significant heterogeneity.

#### B. Sexual Dimorphism in Size.

Significant sexual dimorphism in size occurs in all mensural characters except bill height and bill width (see Table 9). Unbiased estimates of the magnitude of sexual dimorphism in each of these characters is tabulated in Table 11.

Sexual dimorphism in size undoubtedly has a strong adaptive basis. Oystercatchers are monomorphic in plumage, and lack conspicuous morphological "signals" which might function as releasers in pair formation and courtship displays. Thus any difference in body size is likely to be subject to Darwinian sexual selection. Bill size appears to be the result of several contrasting adaptive strategies. Selander (1966) developed the thesis that the degree of sexual dimorphism in bill size is linked with niche utilization. Small amounts of sexual dimorphism in bill size characteristically occur in omnivorous birds where food supplies are sufficiently abundant to allow extensive sexual overlap in niche utilization, whereas marked dimorphism occurs amongst food specialists, and functions to reduce competition for food between the sexes.



TABLE 11. SECONDARY SEXUAL DIMORPHISM IN SIZE IN  
SOUTH ISLAND PIED OYSTERCATCHERS.

Morphological character	Mean Difference between Females and Males	
	Absolute	Percentage
Bill length	9.4mm	11.0
Tarsus length	1.0mm	2.0
Middle toe length	0.4mm	1.3
Wing length	4.4mm	1.7
Tail length	2.1mm	2.2
Total weight	22.7g	4.3
Fat-free weight	16.0g	3.2

While differential niche utilization is a plausible explanation for sexual dimorphism in bill length of South Island Pied Oystercatchers, it probably forms only part of the selective pressure. Of 44 pairs of birds caught at the nest during this study, the female had the longer bill in all cases. Harris (1967, and pers. comm., 1972) reported the same finding for European oystercatchers (H. ostralegus). Since there is considerable sexual overlap in bill length, the dimorphism of bill lengths in pairs suggests that it is associated with sex recognition in courtship and pair formation. The prominent displaying attitude of the bill in courtship social piping indicates such a function.

The monomorphism in bill width and bill depth is in sharp contrast to the dimorphism in length. Presumably, any inherent dimorphism in width and depth is suppressed by an overriding selection for shape, as probing bills are most

TABLE 12. SECONDARY SEXUAL DIMORPHISM IN SIZE IN NEW ZEALAND OYSTERCATCHERS

Character	South Island Pied Oystercatcher				Chatham Islands Oystercatcher				Black Phase Variable Oystercatcher				Pied Phase Variable Oystercatcher				Intermediate Phase Variable Oystercatcher			
	Character Means		Anova <sup>1</sup>		Character Means		Anova <sup>1</sup>		Character Means		Anova <sup>1</sup>		Character Means		Anova <sup>1</sup>		Character Means		Anova <sup>1</sup>	
	M	F	D.F.	F-ratio	M	F	D.F.	F-ratio	M	F	D.F.	F-ratio	M	F	D.F.	F-ratio	M	F	D.F.	F-ratio
Bill length	81.0mm	90.7mm	1,225	261.910	67.8mm	76.8mm	1,14	17.661	78.8mm	88.5mm	1,142	208.880	83.6mm	94.1mm	1,38	50.141	84.4mm	95.3mm	1,33	47.188
Bill height	15.6mm	15.7mm	1,225	1.861	16.2mm	16.9mm	1,14	7.072	17.5mm	17.8mm	1,142	3.353	18.7mm	18.9mm	1,38	1.065	19.0mm	19.6mm	1,33	2.443
Bill width	12.9mm	13.0mm	1,225	1.623	13.1mm	14.1mm	1,14	11.100	14.4mm	14.3mm	1,142	0.131	14.9mm	14.8mm	1,38	0.247	15.5mm	15.5mm	1,33	0.006
Tarsus length	49.9mm	50.6mm	1,225	16.290	51.3mm	53.7mm	1,14	8.100	58.3mm	59.5mm	1,142	11.608	58.4mm	60.0mm	1,38	7.878	60.2mm	61.8mm	1,33	3.681
Middle toe length	31.8mm	32.1mm	1,225	7.154	34.9mm	36.7mm	1,14	9.578	38.3mm	38.8mm	1,142	3.927	37.7mm	38.0mm	1,38	0.240	38.4mm	39.6mm	1,33	2.258
Wing length	256.1mm	260.5mm	1,207	19.975	251.6mm	265.8mm	1,14	15.360	270.1mm	274.7mm	1,142	16.180	267.3mm	270.5mm	1,38	1.519	271.2mm	277.0mm	1,33	3.254
Tail length	95.8mm	97.7mm	1,225	24.078	96.1mm	99.4mm	1,14	5.621	104.1mm	105.8mm	1,142	8.905	102.4mm	104.4mm	1,38	2.510	104.8mm	105.9mm	1,33	0.815
Total weight	539g	561g	1,81	4.218	540g	640g	1,14	30.303	678g	724g	1,142	45.319	717g	750g	1,38	7.546	710g	779g	1,33	24.087
Fat-free weight	499g	512g	1,225	24.796																

<sup>1</sup> Single classification analysis of variance, sexes compared pair-wise for each character (see Johnston and Selander, 1971).

efficient when their cross-section is thin and restricted in height.

The highly significant sexual dimorphism in the remaining morphological characters probably results from correlation of these characters with general body size rather than specific selection for individual characters. The longer wing and tail of females would seem to be necessitated by increased body size. Such selection could operate through flight characteristics such as wing loadings and manoeuvrability. Annan (1965) suggested that sexual dimorphism in wing length of the White-crowned Sparrow (Zonotrichia leucophrys) was related to sexual differences in the distance of migration. This hypothesis is consistent with the suggestion that female South Island Pied Oystercatchers migrate further northwards than males (see section 4.5).

The degree of sexual dimorphism in the morphological characters of adults varies in the New Zealand species of oystercatcher (see Table 12). It is most marked in the Chatham Islands Oystercatcher, possibly because the original founders were by chance very dimorphic i.e. due to the Founder effect (Mayr, 1965). South Island Pied Oystercatchers and black phase Variable Oystercatchers are less dimorphic. Pied phase Variable Oystercatchers are considerably less dimorphic with only bill length, tarsus length and body weight differences being significant. The sexes of intermediate phase Variable Oystercatchers differ only in bill length and body weight. Such a reduction in the degree of sexual dimorphism could be attributable to a reduction in the range of variation between the parentals, due to hybridization (see section 4.9). In most characters the hybrids introgress towards the less sexually dimorphic pied phase, and thus reduce sexual differences.

TABLE 13. INTRAPOPULATION VARIABILITY IN SIZE IN BLACK PHASE  
VARIABLE OYSTERCATCHERS.

Character	No. of samples	Males		Females		* F-ratio
		Mean sample size	Mean CV(%)	Mean sample size	Mean CV(%)	
Bill length	5	14	4.144	15	3.206	1.1906ns
Bill height	5	14	3.621	15	3.945	1.061ns
Bill width	5	14	4.815	15	4.671	1.019ns
Tarsus length	5	14	2.805	15	2.877	1.021ns
Middle toe	5	14	3.772	15	3.596	1.034ns
Wing length	5	14	2.190	15	2.165	1.011ns
Tail length	5	14	2.655	15	2.947	1.089ns
Body weight	5	14	5.759	15	4.292	1.191ns

\*To reduce effects of absolute size, F values calculated from expression

$$F = \frac{0.4343 \log [1+(C.V.x)^2]}{0.4343 \log [1+(C.V.y)^2]}$$

where C.V.x > C.V.y (Bader and Lehmann, 1965).

TABLE 14. INTRAPOPULATION VARIABILITY IN SIZE IN SOUTH ISLAND  
PIED OYSTERCATCHERS FROM THE HEATHCOTE-AVON ESTUARY AND  
NELSON. (All age classes included).

Character	Males		Females		* F-ratio
	N	C.V.(%)	N	C.V.(%)	
Bill length	345	4.397	225	4.910	1.072
Bill height	320	4.802	214	4.337	1.076
Bill width	320	6.392	214	6.162	1.024
Tarsus length	345	3.636	225	3.563	1.011
Middle toe length	345	4.429	225	3.813	1.102
Wing length	266	3.175	166	2.778	1.116
Tail length	345	4.385	225	3.972	1.072
Total weight	111	8.351	88	8.173	1.014
Fat-free weight	345	7.993	225	7.750	1.010

\* F- values calculated as for Table 13.

The considerable sexual dimorphism outlined above in most morphological characters has important implications for taxonomic studies. Clearly, morphological comparisons of the New Zealand species of oystercatcher are meaningful only if the sexes are considered separately.

#### 4.8 POPULATION VARIABILITY AND GEOGRAPHIC VARIATION.

Before proceeding to species comparisons involving samples from several geographically widespread localities, it is necessary to examine intrapopulation variability. Any geographical trend in such variability would obviously bias the comparisons, especially if samples were taken mostly from localities where high or low variability occurred. Since widespread sampling was possible only for black phase Variable Oystercatchers, the analysis of population variability and geographic variation was restricted largely to this colour phase. The mean coefficients of variation for each of the morphological characters of black phase Variable Oystercatchers are shown in Table 13.

None of the F-ratios are statistically significant, indicating that the sexes do not differ in their variability. The similarity of the sample coefficients of variation on which the means are based point to the absence of geographic variation in intrapopulation variability, thus allowing direct comparisons of samples.

According to Selander and Johnston (1967), the "standard" sequence of increasing variability for linear measurements is from wing length as the least variable character, to bill length as the most variable. Neither black phase Variable Oystercatchers (see Table 13) nor South Island Pied Oystercatchers (see Table 14) conform to this generality, as the most variable linear character is bill width.

The sequence of variability differs slightly for the two species, but is broadly similar in that the least variable linear character in both is wing length and the most variable bill width. It is noteworthy that fat-free weight is only slightly less variable than total body weight.

All of the morphological characters of black phase Variable Oystercatchers show significant interlocality (= interpopulation) variability indicative of geographic variation (see Table 15).

TABLE 15. INTERLOCALITY VARIATION IN SIZE IN BLACK PHASE  
VARIABLE OYSTERCATCHERS.

Character	No. of localities	Sex		D.F.	F-ratio <sup>1</sup>
		♂♂(N=69)	♀♀(N=75)		
Bill length	5	Males		4,64	8.304***
		Females		4,69	4.382**
Bill height	5	Males		4,64	6.069***
		Females		4,69	10.500***
Bill width	5	Males		4,64	23.735***
		Females		4,69	15.181***
Tarsus length	5	Males		4,64	7.089***
		Females		4,69	6.114***
Middle toe length	5	Males		4,64	2.648*
		Females		4,69	2.920*
Wing length	5	Males		4,64	2.525*
		Females		4,69	3.847**
Tail length	5	Males		4,64	3.251*
		Females		4,69	7.546***
Total weight	5	Males		4,64	4.148**
		Females		4,69	2.528*

<sup>1</sup>Single classification anova.

The border-line significance of variation in wing length for males and total weight for females may partly result from the marginal sample sizes involved in the analysis. Using the procedure outlined by Sokal and Rohlf (1969:247) for predicting the sample size needed for a priori significance testing, iteration to stability was achieved with a sample size of 13.88 at a significance level of 0.95. Thus 14 birds were needed from each locality to be reasonably sure of detecting differences between means. Unfortunately, the Northland sample was composed of 12 males and 13 females, but it was decided that it would be instructive to include these marginal-sized samples in the analyses as they represented the only samples from the northern extreme of the character range. Locality character means and standard errors are tabulated in Appendix VIII.

Patterns of geographic variation were investigated by the sum of squares simultaneous test procedure (SS-STP), an a posteriori analysis of variance multiple comparisons test (Gabriel, 1964). This procedure has several advantages over the more conventional t-test; for "a" localities  $a(a-1)/2$  t-tests between means are required, the t-tests are mathematically equivalent to F-tests yet they lack the simplicity and elegance of the latter, and F-tests follow naturally from anova. Analyses were performed using Power's (1971) version of a computer program called UNIVAR, which ranks the means in descending order and graphs the homogeneous (= non-significant) subset of means. The results of this analysis are shown below, with each line covering a statistically homogeneous subset of means:

BILL LENGTH\*

	Northland	Nelson	Westland	Otago	Stewart Island
Females	<u>91.3</u>	<u>88.8</u>	<u>88.0</u>	87.3	86.9mm

	Northland	Nelson	Westland	Otago	Stewart Island
Males	<u>83.9</u>	<u>79.8</u>	<u>79.5</u>	78.5	76.5mm

BILL HEIGHT

	Northland	Nelson	Otago	Stewart Island	Westland
Females	<u>18.7</u>	<u>18.1</u>	17.7	17.3	17.2mm

	Northland	Nelson	Otago	Westland	Stewart Island
Males	<u>18.2</u>	<u>17.6</u>	<u>17.6</u>	17.2	17.0mm

BILL WIDTH

	Northland	Otago	Stewart Island	Nelson	Westland
Females	<u>15.6</u>	<u>14.2</u>	14.0	14.0	13.8mm

	Northland	Nelson	Otago	Westland	Stewart Island
Males	<u>16.1</u>	<u>14.3</u>	14.1	14.0	13.5mm

TARSUS LENGTH

	Northland	Nelson	Stewart Island	Otago	Westland
Females	<u>61.6</u>	<u>59.4</u>	59.0	58.8	56.8mm

	Northland	Otago	Nelson	Stewart Island	Westland
Males	<u>61.2</u>	<u>58.3</u>	<u>58.3</u>	56.9	56.8mm



MIDDLE TOE LENGTH

	Stewart Island	Northland	Westland	Nelson	Otago
Females	<u>39.7</u>	<u>39.0</u>	<u>38.6</u>	<u>38.6</u>	<u>37.9mm</u>

	Stewart Island	Northland	Westland	Nelson	Otago
Males	<u>39.4</u>	<u>39.0</u>	<u>38.1</u>	<u>38.0</u>	<u>37.8mm</u>

WING LENGTH

	Stewart Island	Otago	Westland	Nelson	Northland
Females	<u>278</u>	<u>276</u>	<u>276</u>	<u>274</u>	<u>270mm</u>

	Stewart Island	Otago	Westland	Nelson	Northland
Males	<u>275</u>	<u>272</u>	<u>270</u>	<u>270</u>	<u>267mm</u>

TAIL LENGTH

	Stewart Island	Otago	Westland	Nelson	Northland
Females	<u>109</u>	<u>107</u>	<u>106</u>	<u>104</u>	<u>103mm</u>

	Stewart Island	Westland	Otago	Nelson	Northland
Males	<u>106</u>	<u>105</u>	<u>104</u>	<u>103</u>	<u>103mm</u>

TOTAL BODY WEIGHT

	Northland	Stewart Island	Otago	Nelson	Westland
Females	<u>755.0</u>	<u>730</u>	<u>725</u>	<u>720</u>	<u>715 g</u>

	Northland	Stewart Island	Otago	Westland	Nelson
Males	<u>720</u>	<u>680</u>	<u>675</u>	<u>670</u>	<u>665 g</u>

\* The listings may be interpreted as follows: any means not covered by two or more lines are significantly different from the others.

Two major contrasting trends are apparent from the analysis. Bill dimensions and tarsus length increase clinally from north to south, though the variation in bill width and tarsus length is not strictly clinal as geographically contiguous localities are not always grouped together. With the exception of the Stewart Island mean, there is a tendency for middle toe length to increase on transition northwards. In contrast to the above characters, wing and tail lengths decrease from south to north. Total body weight tends to increase in the southern part of the range, though the Northland mean is an exception to this trend.

Putative causal agencies of geographic variation were examined by linear regressions of character means on average yearly locality values of mean maximum temperature, mean minimum temperature, precipitation, relative humidity and isophane. The isophane is a statistic developed by Hopkins (1938) which broadly summarizes climatic variables, especially temperature (Thomas, 1968). It is calculated from the formula:

$$\text{Isophane (}^{\circ}\text{S)} = (\text{latitude in }^{\circ}\text{S)} + \frac{1}{5} (100 - \text{longitude in }^{\circ}\text{E}) + (\text{altitude in feet}/400).$$

Data on all the above climatic variables were collated from the annual meteorological observations over the period 1959 to 1969, published by the New Zealand Meteorological Service (see Table 16).

Twenty-one significant and ten near-significant regressions resulted, all involving temperature and/or isophane values. Neither precipitation nor relative humidity contributed to significant regressions, although the latter

TABLE 17. LINEAR REGRESSIONS OF CHARACTER MEANS OF BLACK PHASE VARIABLE  
OYSTERCATCHERS ON CLIMATIC VARIABLES.

Character	Sex	Regression Equation	F-ratio	Coefficient of Determination
Bill length	F	Y= 76.436+ 0.746 Mean Max. Temp.	110.066***	0.793
	M	Y= 61.816+11.071 Mean Max. Temp.	24.174**	0.890
	F	Y= 88.448+ 0.693 Mean Min. Temp.	27.535**	0.902
	M	Y= 72.153+ 0.110 Mean Min. Temp.	50.985**	0.944
	F	Y= 98.012- 0.335 Isophane	197.372***	0.985
	M	Y= 93.974- 0.503 Isophane	33.839**	0.919
Bill height	F	Y= 13.730+ 0.254 Mean Max. Temp.	23.344*	0.886
	M	Y= 14.623+ 0.180 Mean Max. Temp.	13.223*	0.815
	F	Y= 20.874- 0.107 Isophane	11.696*	0.796
	M	Y= 19.716- 0.007 Isophane	8.884a	0.748
Bill width	F	Y= 10.010+ 0.268 Mean Max. Temp.	8.496a	0.739
	M	Y= 7.812+ 0.408 Mean Max. Temp.	30.374*	0.910
	M	Y= 11.915+ 0.363 Mean Min. Temp.	10.268*	0.774
	F	Y= 17.561- 0.113 Isophane	5.855a	0.661
	M	Y= 19.450- 0.179 Isophane	21.165*	0.876
Tarsus length	F	Y= 51.538+ 0.494 Mean Max. Temp.	29.765*	0.908
	M	Y= 10.864+ 0.643 Mean Max. Temp.	16.902*	0.849
	F	Y= 65.607- 0.214 Isophane	17.580*	0.854
	M	Y= 9.707-10.286 Isophane	9.437a	0.759
Wing length	F	Y=297.670- 0.149 Mean Max. Temp.	11.994*	0.800
	M	Y=286.761- 0.996 Mean Max. Temp.	9.155a	0.753
	F	Y=282.497- 0.129 Mean Min. Temp.	5.567a	0.669
	M	Y=278.092- 0.108 Mean Min. Temp.	66.914*	0.957
	F	Y=254.801+ 0.664 Isophane	11.978*	0.800
	M	Y=257.454+ 0.465 Isophane	13.877*	0.822
Tail length	F	Y=119.558- 0.857 Mean Max. Temp.	7.850a	0.724
	M	Y=112.271- 0.532 Mean Max. Temp.	7.244a	0.707
	F	Y=111.868- 0.898 Mean Min. Temp.	17.330*	0.852
	M	Y=107.450- 0.487 Mean Min. Temp.	5.611a	0.632
	F	Y= 94.345+ 0.400 Isophane	11.316*	0.790
	M	Y= 97.365+ 0.238 Isophane	7.181a	0.705

<sup>a</sup> Near-significant regression,  $0.10 > P > 0.05$ .

TABLE 16. CLIMATIC VARIABLES USED IN REGRESSION ANALYSIS.

Sampling Locality	*Climate Station	Mean Max. Temp. (°C)	Mean Min. Temp. (°C)	Relative Humidity (%)	Total Precip. (mm)	Isophane (°S)
Northland	Kerikeri	19.8	10.2	79.5	1680	20.4
Nelson	Nelson Airport	16.9	7.3	79.1	1005	26.6
Westland	Haast	14.9	7.4	81.5	3390	30.1
Otago	Balclutha	14.7	5.1	78.5	650	32.3
Stewart Island	Oban	14.2	4.0	82.0	1448	33.1

\*Climate stations were selected as the ones nearest to the centres of the sampling ranges for each locality.

did account for 56% of the scatter about regression of female middle toe length. The regression equations, F-ratios for significance of regression, and coefficients of determination (indicating the proportion of the variation accounted for by regression) are depicted in Table 17.

The strict clinal decrease in bill length from the warmer northern part to the cooler southern part of the range is in accordance with Allen's ecogeographic rule i.e. in polytypic species of endotherms, extensions of the body tend to be larger in warmer parts of the species range and shorter in cooler parts. The significant regressions involving temperature extremes and isophane (which also largely reflects temperature) indicate that geographic variation in bill length is an adaptive response to thermoregulatory dictates of the bill. Heavy vascularization of the bill of oystercatchers revealed by the sectioning techniques of Heppleston (1970) suggests that it could be subject to considerable heat exchange. Clinal trends in bill

height and width presumably also relate to thermoregulation. The lack of strict clinal variation in these two characters probably results from interacting selective pressures exerted by non-clinal climatic variables such as precipitation, and by factors other than climatic ones.

Clinal variation in bill size of other species of birds similar to that described above has also been attributed to thermoregulatory properties of the bill subsumed by Allen's rule (Johnston, (1969) for House Sparrows, Power (1970 a and b) for Red-winged Blackbirds, and Barlow and Power (1970) for vireos). However, much evidence has accumulated relating variation in bill morphology to dietary adaptations (Beecher, 1951; Pitelka, 1951; Betts, 1955; Hinde, 1959; Bowman, 1961; Kear, 1962; Myton and Ficken, 1967; Power, 1970b; Willson, 1971). It seems unlikely that dietary differences could account for a significant proportion of the variation in the bill of black phase Variable Oystercatchers as they take similar foods throughout their range (see Chapter 3.4).

Clinal increase in tarsus length from cooler southern latitudes to warmer northern latitudes is also predicted by Allen's rule. In long-legged birds like oystercatchers the tarsus could provide a site for a significant amount of heat dissipation. Scholander (1955) demonstrated that the legs of many birds contain arterio-venous countercurrent retes which function in heat conservation by restricting blood flow to the legs at low ambient temperatures. Heat loss through the tarsus has been experimentally proven for the American Kestrel (Falco sparverius) and Californian Quail (Lophorytx californicus) by Bartholomew and Cade (1957) and Brush (1965) respectively.

Middle toe length varies randomly from locality to locality. The lack of significant regressions with climatic variables indicates that this character varies independently

of climate.

Wing length and tail length are inversely correlated with temperature. Although temperature does not seem to exert a selective force on feather growth per se, the usual explanation for this inverse relationship centres on the correlation of wing length with body size (Hamilton, 1961). It is argued that increased wing lengths in cooler parts of the range are a reflection of an increase in body size, correlated with winter temperature extremes (Rensch, 1939; Mayr, 1942; Huxley, 1942; Snow, 1954).

Excluding the Northland sample of body weights, there is a general tendency for body weight to decrease from south to north (see page 76) in accordance with Bergmann's rule i.e. body size in geographically variable homeotherms is larger in cooler parts of the range of a species. The increased mean weight of the Northland birds probably results in part from introgression with the larger pied phase Variable Oystercatcher (see section 4.9). Thus it seems plausible that clinal variation in wing and tail length is associated with similar variation in body size, the latter necessitating the former through flight dynamics.

Summarizing, it is apparent that the clinal variation outlined above for most characters results from adaptive sensitivity to environmental variables that are similarly clinal, and that within the clinal continuum the birds are close to optimal adaptation to local conditions (Rising, 1970).

#### 4.9 VARIATION DUE TO HYBRIDIZATION.

The correct interpretation of natural hybridization of closely related taxa is critical to their systematic study. The term hybridization is used here in the sense of Short (1969) as "the interbreeding of individuals of morphologically and presumably genetically distinct populations,

regardless of the taxonomic status of such populations". Such a definition has considerably utility since it does not require a taxonomic decision to decide whether or not the interbreeding should be designated hybridization (Bigelow, 1965). The interbreeding of black and pied phase Variable Oystercatchers in New Zealand meets the requirements of the above definition and thus may be justifiably termed hybridization.

According to Short (1969) the following biological information is necessary for a taxonomic decision on hybridizing forms:

- (1) the occurrence of hybrids;
- (2) the distribution and habitats of parentals and hybrids;
- (3) the relative frequencies of parental and hybrid phenotypes in areas of hybridization;
- (4) the types of crosses that are occurring and generations involved;
- (5) the occurrence and extent of introgression; and,
- (6) the population dynamics of the forms involved.

The first two of these requirements have already been described (see Chapters 2 and 3); the remaining four will be the subject of this section.

#### A. Morphology of parentals and Hybrids.

##### (i) Univariate Tests.

The considerable geographic variation in the morphological characters as outlined in the previous section requires phenetic comparisons between parentals and hybrids to be restricted to samples taken from a relatively small geographic range. Accordingly, the Northland region was chosen for analysis, mainly because this was the only area in which all three phenotypes were adequately represented. The comparative morphology of the parentals and hybrids is

TABLE 18. CHARACTER MEANS AND STANDARD ERRORS OF VARIABLE OYSTERCATCHER PARENTALS AND HYBRIDS IN NORTHLAND.

Character	Sex	Character Mean $\pm$ S.E.		
		Black phase <sup>1</sup>	Intermediate (=hybrid) phases <sup>2</sup>	Pied phase <sup>3</sup>
Bill length	M	83.9 $\pm$ 0.73	84.4 $\pm$ 0.92	83.6 $\pm$ 0.83mm
	F	91.3 $\pm$ 1.40	95.3 $\pm$ 1.26	94.1 $\pm$ 1.31
Bill height	M	18.2 $\pm$ 0.10	19.0 $\pm$ 0.17	18.7 $\pm$ 0.16mm
	F	18.7 $\pm$ 0.21	19.2 $\pm$ 0.17	18.9 $\pm$ 0.22
Bill width	M	16.1 $\pm$ 0.09	15.5 $\pm$ 0.13	14.9 $\pm$ 0.13mm
	F	15.6 $\pm$ 0.21	15.5 $\pm$ 0.16	14.8 $\pm$ 0.18
Tarsus length	M	61.2 $\pm$ 0.34	60.2 $\pm$ 0.40	59.4 $\pm$ 0.34mm
	F	61.6 $\pm$ 0.52	61.8 $\pm$ 0.47	60.0 $\pm$ 0.53
Middle toe length	M	39.0 $\pm$ 0.26	38.4 $\pm$ 0.42	37.9 $\pm$ 0.36mm
	F	39.0 $\pm$ 0.27	39.1 $\pm$ 0.31	38.0 $\pm$ 0.42
Wing length	M	267 $\pm$ 1.4	270 $\pm$ 2.1	267 $\pm$ 1.8mm
	F	270 $\pm$ 1.3	277 $\pm$ 1.8	274 $\pm$ 2.1
Tail length	M	103 $\pm$ 0.5	105 $\pm$ 0.9	102 $\pm$ 0.8mm
	F	104 $\pm$ 0.6	106 $\pm$ 0.8	104 $\pm$ 0.9
Body weight	M	718 $\pm$ 10.5	710 $\pm$ 8.0	717 $\pm$ 8.5g
	F	754 $\pm$ 7.4	769 $\pm$ 11.8	750 $\pm$ 9.6

<sup>1</sup>N (Males) = 12, N(Females) = 13.

<sup>2</sup>N (Males) = 21, N(Females) = 19.

<sup>3</sup>N (Males) = 17, N(Females) = 18.



evident from their character means and standard errors, tabulated in Table 18.

Homogeneity of the character means in the three phenotypes was tested with an a posteriori SS-STP procedure following single classification anova. Significant differences were found in bill width of both sexes, in bill height of males, and in wing length of females. The patterns of non-significant subsets are shown below:

BILL HEIGHT

	Hybrid	Pied	Black
Males	<u>19.0</u>	<u>18.7</u>	18.2mm

BILL WIDTH

	Black	Hybrid	Pied
Males	<u>16.1</u>	<u>15.5</u>	<u>14.9mm</u>

	Black	Hybrid	Pied
Females	<u>15.6</u>	<u>15.5</u>	<u>14.8mm</u>

WING LENGTH

	Hybrid	Pied	Black
Females	<u>277</u>	<u>274</u>	270mm

Apart from the differences noted above, the parentals and their hybrids are morphologically similar. Since many characters are highly correlated through ontogenetic processes and natural selection (Olson and Miller, 1958; Berg, 1960; Power, 1971), it is reasonable to assume that at least some of the differences that now exist between the morphology of the parentals are remnants of former differences which existed before secondary contact. It therefore follows from this reasoning that considerable introgression (incorporation of genes from one gene pool into that of

Plate 17.

Male Variable Oystercatcher phenotype means and bivariate 0.95 confidence ellipses projected onto the first and second canonical axes (discriminant functions). This view of the character space describes 93.5% of the variation among phenotypes. The phenotypes are identified by A (Black phase), B (hybrid) and C (pied phase). The vectors plotted on the left hand side of the figure are projections of eigenvectors scaled relative to the pooled within-groups standard deviations, and show the magnitude and direction of the separation of the phenotypes afforded by each character.

Key to characters:

- BL. Bill length.
- BH. Bill height.
- BW. Bill width.
- Tar. Tarsus length.
- MT. Middle toe length.
- W. Wing length.
- T. Tail length.
- Wt. Body weight.

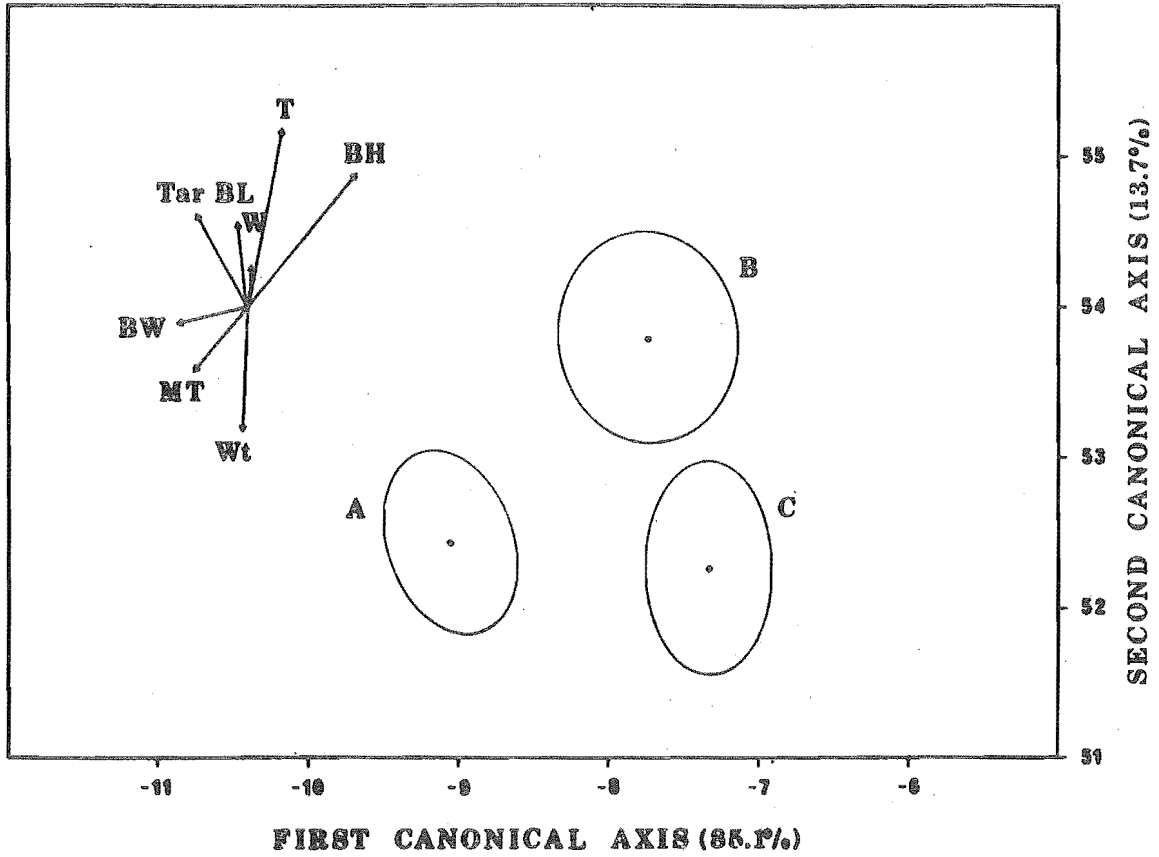
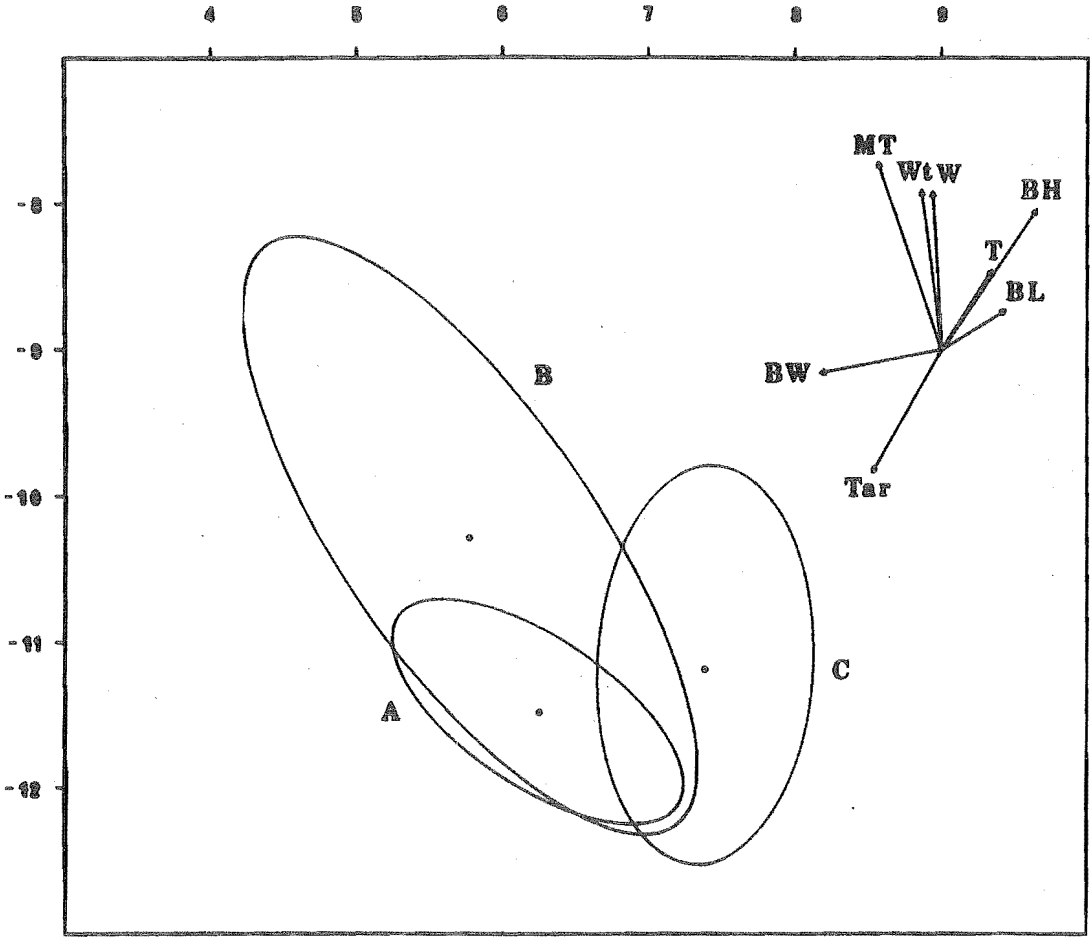


Figure 18.

Female Variable Oystercatcher phenotype means and bivariate 0.95 confidence ellipses projected onto the first and second canonical axes. This view of the character space describes 95.5% of the variation among phenotypes. For further explanation see the legend to Figure 17 and the text.

FIRST CANONICAL AXIS (67.3%)

SECOND CANONICAL AXIS (26.2%)



another) has occurred between the parentals, resulting in gradual genetic swamping and merging of the two gene pools. Where significant differences do occur, as for example in bill height and bill width of the parentals, they are bridged by the intermediate phenetic position of the hybrids. With further generations of F1, F2 and backcrosses, it seems likely that genetic swamping will be complete, and morphological differences between the parentals will disappear.

(ii) Multivariate Tests.

To determine whether phenetic differences exist between parentals and hybrids when all characters are considered simultaneously in the multivariate case, the three phenotypes were subjected to a canonical variates analysis.

The results of canonical variates analysis for male and female parentals and hybrids are shown in Figs. 17 and 18. For males, the test of  $H_2$  (equality of group centroids), Wilks' Lambda was 0.2205 which converted to a highly significant F-value of 5.79 ( $P < 0.001$ ) with 16 and 82 degrees of freedom. For females, Wilks' Lambda was 0.3252 corresponding to a highly significant F-value of 3.58 ( $P < 0.001$ ) with 16 and 76 degrees of freedom. Thus in both sexes, there are significant phenetic differences between parentals and hybrids. Unfortunately, there are no a posteriori methods available for identifying which of the centroids are significantly different from the others, although Power (pers. comm.) is currently developing one.

Inspection of Figs. 17 and 18, however, reveals that in both sexes the hybrids are phenetically intermediate between the two parentals, as their centroids lie between those of the parentals. It therefore seems likely that the significant discrimination between the group centroids in 2-D space is largely due to morphological differences between the parentals. The hybrids form a "genetic bridge"

between the parentals through which genes can introgress. Hence, even when the characters are all considered simultaneously and the differences compounded, the three phenotypes are sufficiently similar to be interpreted as one taxonomic cluster, especially in the case of females where the three confidence ellipses overlap (see Fig.18).

(iii) Variation in dorsal melanin pigmentation.

To test the hypothesis that the northern black phase of the Variable Oystercatcher may be brownish black and lack the purple gloss of the southern black phase (Falla et. al., 1966), the pigmentation of the mantle feathers was compared from samples taken all over New Zealand. Comparative data were included for Chatham Islands and South Island Pied Oystercatchers to test for possible affinities. Mean values and standard errors of the pigmentation parameters of hue, excitation purity and brightness are tabulated in Table 19.

TABLE 19. MELANIN PIGMENTATION IN MANTLE FEATHERS OF NEW ZEALAND OYSTERCATCHERS.

	N	Mean Hue value + S.E.	Mean Excitation Purity + S.E.	Mean Brightness + S.E.
Chatham	28	584.0+0.08	63.5+0.07	8.1+0.07
SIPO	20	583.8+0.07	63.8+0.08	8.4+0.18
Black Variable	12	583.8+0.03	63.4+0.05	8.0+0.05
Pied Variable	24	583.8+0.04	63.4+0.05	8.1+0.04
Hybrid	32	584.1+0.05	63.8+0.08	8.0+0.08

The data were subjected to a three-level mixed model hierarchical analysis of variance (see Sokal and Rohlf, 1969). Feather replicates were arranged within individuals, sexes and taxa. The results of this analysis are shown in Table 20.

TABLE 20. ANALYSIS OF VARIANCE OF PIGMENTATION PARAMETERS  
IN NEW ZEALAND OYSTERCATCHERS.

Source of Variation	D.F.	F-ratio		
		Hue	Excitation Purity	Brightness
Among taxa	4,162	2.68	1.31	0.13
Among sexes	5,162	1.47	1.28	0.27
Among individuals	44,162	5.90***	11.49***	18.02***

For each parameter, the only significant variance component is among individuals. Both the sexes and taxa do not seem to differ in their plumage pigmentation.

Geographic variation in the pigmentation of the mantle feathers of the black phase Variable Oystercatchers was investigated by single classification anova on means of the latitude groupings 34-39°, 39-44°, and 44-48°S. (see Table 21).

TABLE 21. GEOGRAPHIC VARIATION OF MELANIN PIGMENTATION  
IN BLACK PHASE VARIABLE OYSTERCATCHERS.

Pigmentation Parameter	D.F.	F-ratio
Hue	2,108	2.01
Excitation Purity	2,108	0.97
Brightness	2,108	1.16



There is thus no indication of geographic variation of melanin pigmentation in black phase Variable Oystercatchers, as none of the means are significantly different.

B. Relative Frequencies of Hybrids in the Area of Hybridization.

The great majority of hybridization between pied and black phase Variable Oystercatchers occurs in Northland, as this is the only large area in New Zealand in which the pied phase is relatively abundant (see Chapter 2.3C). The relative frequencies of the parentals and their hybrids in Northland as a whole, and in the specific locality of Waipu are shown in Table 22.

TABLE 22. RELATIVE FREQUENCIES OF PARENTALS AND HYBRIDS IN NORTHLAND.

	Phenotype		
	Black	Hybrid	Pied
*Numbers in Northland	258	267	179
Per cent occurrence	36.7	37.9	25.4
Number at Waipu, May 1971	16	56	43
Per cent occurrence	13.9	48.7	37.4

\*Data from Appendices II, III and IV.

In the whole of Northland, hybrids are the most abundant of the three phenotypes, although the black phase closely approximates it in numbers. All three phenotypes are well represented, although the proportions of each phenotype vary considerably from locality to locality as evidenced by the Waipu figures. Such good representation of each parental in the area of hybridization has important taxonomic implications (see Chapter 5).

### C. Genetic Basis of Colour Phase Hybridization.

The genetic basis of the hybridization of black and pied phase Variable Oystercatchers as reflected by the inheritance of colour phases is of primary interest in interpreting their interbreeding. It has been tacitly assumed in the past that plumage variation between the two parental extremes of black and pied is continuous, as for example in the statement of Oliver (1955): "There is no fixed pattern, every individual being differently marked".

The range of plumage variation in breast, rump and alar bar patterns of birds captured during this study is shown in Plate 9. Although these patterns do not include all those evident in live-trapped and museum specimens, they do cover the observed range of variation. The correspondence of the loss of white parts in the breast, rump and alar bar patterns from pied through to black, indicates that there is effective linkage between the genes controlling these traits.

For descriptive purposes, the phenotypes were classified as pied (1 in Plate 9), pied hybrid (2,3 and 4), intermediate hybrid (5, 6 and 7), black hybrid (8 and 9) or black (10). The inheritance of colour phases was studied by examining broods from various parentages. Data were gathered on 57 such broods involving a total of 108 chicks. The phenotypes of the progeny are discernible at hatching, as black chicks have brown bellies, pied chicks have white bellies, and hybrids have a mixture of brown and white down on the belly (see Plate 10 & 11). However, the degree of hybridization in the plumage characters cannot be gauged until the chicks have gained their juvenile feathers at the age of approximately 6 weeks. It was therefore necessary to follow the development of chick plumages for about 6 weeks after hatching. This was achieved by retrapping banded chicks just



Plate 9.

Variation in the plumage patterns of the breast, alar bar and rump patch of Variable Oystercatchers, ranging from pied (1) to black (10) phases.

See text for explanation of numbers.



6



7



8



9



10

Plate 10.

Ventral plumage of hybrid chicks from a pied  
x black phase mating combination.

Key to letters:

- A. Three day old chicks showing dark markings  
on the breast.
- B. Same chicks at three weeks of age.



A

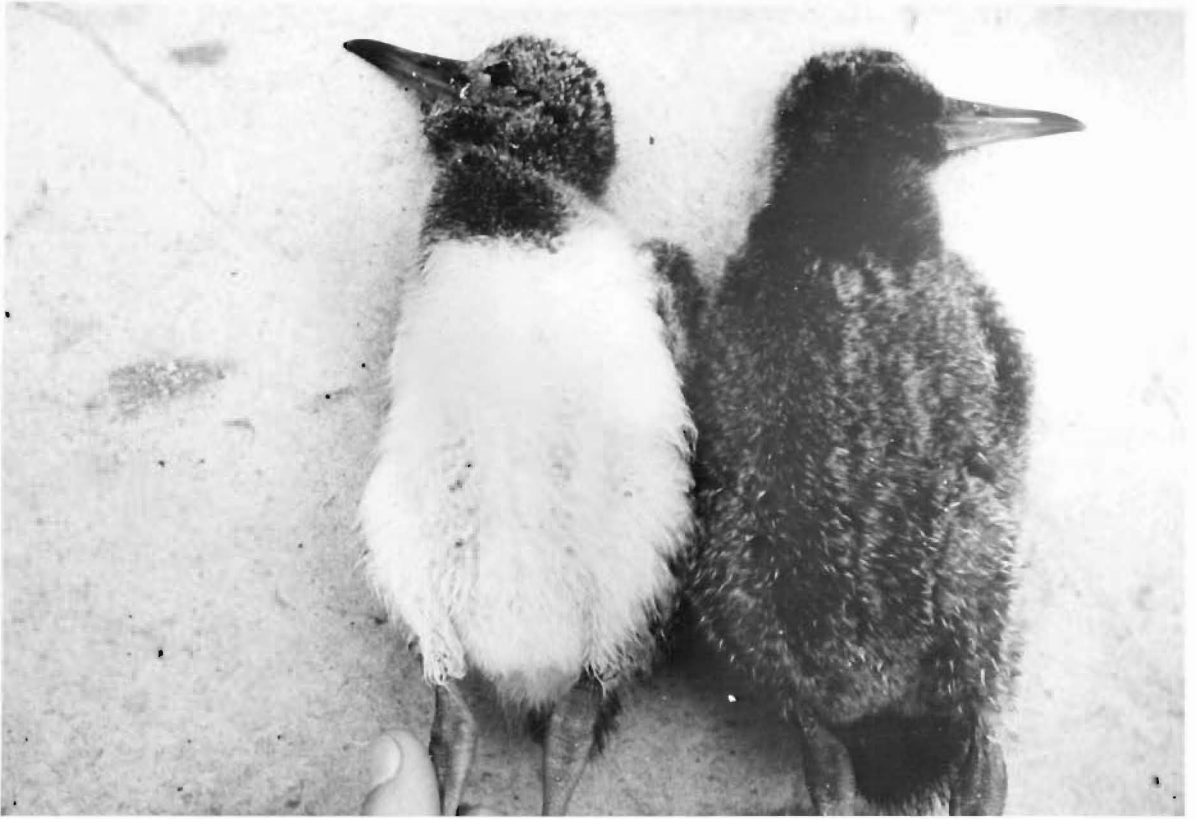


B

Plate 11.

Black and pied phase Variable Oystercatcher  
chicks, the progeny of a mating between  
a phenotypically black and an almost black  
hybrid.





before they were able to fly. The results of this analysis are summarized in Table 23.

TABLE 23. PROGENY FROM MATING COMBINATIONS.

Mating combinations	Progeny
(1) Black x black	Black
(2) Black x black hybrid	All phenotypes
(3) Black hybrid x black hybrid	Black and all hybrid phenotypes
(4) Black hybrid x intermediate hybrid	Black and all hybrid phenotypes
(5) Black x pied	All phenotypes
(6) Black hybrid x pied hybrid	All phenotypes
(7) Black hybrid x pied	Intermediate and pied hybrids
(8) Intermediate hybrid x intermediate hybrid	All phenotypes
(9) Intermediate hybrid x pied hybrid	Pied hybrid and pied
(10) Intermediate hybrid x pied	Intermediate and pied hybrids, pied
(11) Pied hybrid x pied hybrid	Pied hybrid and pied
(12) Pied hybrid x pied	Pied
(13) Pied x pied	Pied

The inheritance pattern can be explained in terms of polygenes, as it is apparent that such variation is likely to be due to genes at several loci. If the pied condition is inherited through a dominant W gene, then the double recessive ww at this locus would account for the black condition. Hybrids would therefore have a basic Ww genotype.

The degree of hybridization in the plumage characters could then be expressed through the action of modifying genes at other loci, specific in the sense that they interact only with the Ww genotype, as for example in variegated spotting in house mice (Sinnott, Dunn and Dobzhansky, 1958). If the modifiers were present as a polygenic complex of say four genes, then the crosses in Table 19 would be simply explained e.g.

Ww with 4 modifiers could give pied (or nearly so) phenotypes

Ww with 3 modifiers could give pied hybrids

Ww with 2 modifiers could give intermediate hybrids

Ww with 1 modifier could give black hybrids

Ww with 0 modifiers could give black (or nearly so) phenotypes.

Thus the modifiers would act additively in determining the degree of dominance of the major gene W, as is common in these polygenic systems (Sinnott, et.al, op. cit). The hybrid phenotypes could therefore range between the parental extremes of black and pied, even though they all had the same basic genotype. The actual number of modifiers involved in controlling dominance of the major gene is likely to be greater than four, since there are more phenotypes discernable than are listed in the simplistic example above.

I prefer this mechanism of colour phase inheritance to other possible polygenic models because it is the only one that explains the frequent generation of parental phenotypes from hybrid mating combinations. Instead of the parentals disappearing in a morass of increasingly variable phenotypes, they would commonly be regenerated as a consequence of recombination.

D. Mating Combinations and Types of Crosses.

As outlined in Table 23, all possible mating combinations occur. The observed frequencies and those expected from the overall frequencies of the three phenotypes in Northland (see Table 22) are tabulated in Table 24.

TABLE 24. TYPES OF CROSSES AND FREQUENCIES OF 101 MATING COMBINATIONS IN NORTHLAND.

Type of Cross	Mating Combination	Observed Frequency	Expected Frequency* Assuming Random Mating
True breeding	Black x black	17	13
	Pied x pied	7	7
Parental cross	Pied x black	14	18
F <sub>1</sub> and F <sub>2</sub>	Hybrid x hybrid	22	15
Backcross	Black x hybrid	24	28
	Pied x hybrid	17	20

\*Expected frequencies calculated on the assumption that Ww is pied, Ww is hybrid and ww is black. Thus mating frequency of WW is given by:

$$\begin{aligned} WW (\text{♀♀}) \times WW (\text{♂♂}) &= (179/704) \times (179/704) \\ &= 0.065 \end{aligned}$$

For 101 pairs, we would expect 101 x 0.065 pied matings i.e. approximately 7 pairs. Similarly, the mating frequencies of Ww x Ww, Ww x ww and ww x ww can be calculated.

The close correspondence of the expected frequency (based on the premise that mating is random with respect to colour phase) with the observed frequency indicates that

mating is non-assortative. The preponderance of  $F_1$ ,  $F_2$  and backcrosses demonstrates that gene exchange between the parental gene pools via the hybrids is extensive.

#### E. Viability of Hybrids.

The viability of hybrids, as measured by conventional attributes such as fecundity and hatching success, is similar to that of the parentals (see Table 25).

TABLE 25. FECUNDITY AND HATCHING SUCCESS OF PARENTALS AND HYBRIDS.

Phenotype	*N	Mean clutch Size	N	Mean Hatching Success (%)
Black parental	58	2.3	16	69.9
Pied parental	50	2.2	9	74.2
Hybrids	38	2.3	21	71.6

\*Data from this study plus O.S.N.Z. nest-record cards.

It seems likely that the parentals and hybrids also have similar breeding success (number of chicks fledged/clutch size) as there is no indication from the banding returns so far to hand, that differential mortality is occurring in the progeny of the phenotypes. Of 54 chicks (16 pied, 26 hybrid and 12 black) banded in 1970, 22 were resighted in 1971 (6 pied, 11 hybrid and 5 black), representing respective first year mortalities of 62.5%, 57.7% and 58.3%. These mortality estimates are probably too high as undoubtedly some birds not resighted are still alive. However, the similarity in the estimates argues against differential mortality in the parentals and hybrids. The hybrids do not, therefore, appear to suffer from inviability associated with the production of disharmonious genotypes

through the incompatibility of parental gene recombinations.

In summary, evidence from the foregoing sections points to extensive gene exchange between the parentals. Both parentals and hybrids occur in the area of hybridization in relative abundance, their mating is non-assortative with respect to colour phase, and they seem to be equally viable. Introgression of parental characters via the "hybrid bridge" has probably resulted in the gradual reduction of morphological differences which existed before secondary contact occurred.

#### 4.10 PHENETIC COMPARISON OF NEW ZEALAND SPECIES.

The ultimate aim in systematic studies of related taxa is to compare their morphology, though ecological, genetical and physiological studies provide powerful aids in the interpretation of the morphological characters (Jameson et. al., 1966). In the following account the New Zealand species of oystercatcher are firstly compared by univariate tests and then by multivariate tests. The rationale behind this dual approach has been previously outlined in section 4.9.

##### A. Univariate Comparisons.

Although there are only three New Zealand species of oystercatcher listed in the Annotated Checklist of New Zealand Birds (Kinsky, 1970), there seemed considerable heuristic value in including both the pied and black phase of the Variable Oystercatcher in the "species" comparisons. The character means and standard errors for black and pied phase Variable Oystercatchers in Northland were listed in Table 18. The Northland sample of this species was chosen for interspecific comparisons because variability associated with geographic variation could be minimized. Standard statistics of South Island Pied and Chatham Islands Oyster-

TABLE 26. CHARACTER MEANS AND STANDARD ERRORS FOR CHATHAM ISLANDS  
AND SOUTH ISLAND PIED OYSTERCATCHERS.

Character	Sex	Character Mean $\pm$ S.E.	
		Chatham Islands <sup>1</sup> Oystercatcher	South Island Pied <sup>2</sup> Oystercatcher
Bill length	M	67.8 $\pm$ 0.97mm	80.9 $\pm$ 0.35mm
	F	76.8 $\pm$ 1.99	90.0 $\pm$ 0.68
Bill height	M	16.2 $\pm$ 0.14mm	16.0 $\pm$ 0.16mm
	F	16.9 $\pm$ 0.23	16.0 $\pm$ 0.12
Bill width	M	13.1 $\pm$ 0.09mm	13.1 $\pm$ 0.41mm
	F	14.1 $\pm$ 0.28	13.1 $\pm$ 0.10
Tarsus length	M	51.3 $\pm$ 0.45mm	49.9 $\pm$ 0.24mm
	F	53.7 $\pm$ 0.75	51.0 $\pm$ 0.29
Middle toe length	M	34.9 $\pm$ 0.40mm	31.8 $\pm$ 0.41mm
	F	36.7 $\pm$ 0.45	32.1 $\pm$ 0.18
Wing length	M	251 $\pm$ 2.2mm	257 $\pm$ 0.8mm
	F	266 $\pm$ 3.0	261 $\pm$ 0.9
Tail length	M	96 $\pm$ 1.0mm	95 $\pm$ 0.6mm
	F	99 $\pm$ 1.1	98 $\pm$ 0.5
Body weight	M	540 $\pm$ 8.7g	555 $\pm$ 5.6g
	F	640 $\pm$ 16.7g	580 $\pm$ 6.4

<sup>1</sup>N(Males) = 8, N(Females) = 8.

<sup>2</sup>N(Males) = 103, N(Females) = 51.

catchers are shown in Table 26.

The significance of the differences between the character means of New Zealand oystercatchers was tested with single classification anovas, followed by a posteriori SS-STP analysis to identify variant means. The results of this analysis are presented below:

BILL LENGTH

	Black Variable	Pied Variable	SIPO	Chatham
Males	<u>83.9</u>	<u>83.6</u>	<u>80.9</u>	<u>67.8</u> mm

	Pied Variable	Black Variable	SIPO	Chatham
Females	<u>94.1</u>	<u>91.3</u>	<u>90.0</u>	<u>76.8</u>

BILL HEIGHT

	Pied Variable	Black Variable	Chatham	SIPO
Males	<u>18.7</u>	<u>18.2</u>	<u>16.2</u>	<u>16.0</u> mm

	Pied Variable	Black Variable	Chatham	SIPO
Females	<u>18.9</u>	<u>18.7</u>	<u>16.9</u>	<u>16.0</u>

BILL WIDTH

	Black Variable	Pied Variable	Chatham	SIPO
Males	<u>16.1</u>	<u>14.9</u>	<u>13.1</u>	<u>13.1</u> mm

	Black Variable	Pied Variable	Chatham	SIPO
Females	<u>15.6</u>	<u>14.8</u>	<u>14.1</u>	<u>13.1</u>

TARSUS LENGTH

	Black Variable	Pied Variable	Chatham	SIPO
Males	<u>61.2</u>	<u>58.4</u>	<u>51.3</u>	<u>49.8</u> mm



<u>TARSUS LENGTH</u>	Black Variable	Pied Variable	Chatham	SIPO
Females	<u>61.6</u>	<u>60.0</u>	<u>53.7</u>	<u>51.0</u>

MIDDLE TOE LENGTH

	Black Variable	Pied Variable	Chatham	SIPO
Males	<u>39.0</u>	<u>37.7</u>	<u>34.9</u>	<u>31.8 mm</u>

	Black Variable	Pied Variable	Chatham	SIPO
Females	<u>39.0</u>	<u>38.0</u>	<u>36.7</u>	<u>32.1</u>

WING LENGTH

Males No significant differences between the means.

	Black Variable	Pied Variable	Chatham	SIPO
Females	<u>274</u>	<u>270</u>	<u>266</u>	<u>261 mm</u>

TAIL LENGTH

	Black Variable	Pied Variable	Chatham	SIPO
Males	<u>103</u>	<u>102</u>	<u>96</u>	<u>95 mm</u>

	Pied Variable	Black Variable	Chatham	SIPO
Females	<u>104</u>	<u>103</u>	<u>99</u>	<u>98</u>

BODY WEIGHT

	Black Variable	Pied Variable	Chatham	SIPO
Males	<u>720</u>	<u>720</u>	<u>555</u>	<u>540 g</u>

	Pied Variable	Black Variable	Chatham	SIPO
Females	<u>750</u>	<u>735</u>	<u>640</u>	<u>580</u>

Figure 19.

Male New Zealand oystercatcher character means and bivariate 0.95 confidence ellipses projected onto the first and second canonical axes. This view of the character space describes 96.8% of the variation among taxa. For further explanation see the legend to Figure 17 and the text.

Key to letters:

- A. South Island Pied Oystercatcher
- B. Black phase Variable Oystercatcher
- C. Pied phase Variable Oystercatcher
- D. Chatham Islands Oystercatcher

FIRST CANONICAL AXIS (88.6%)

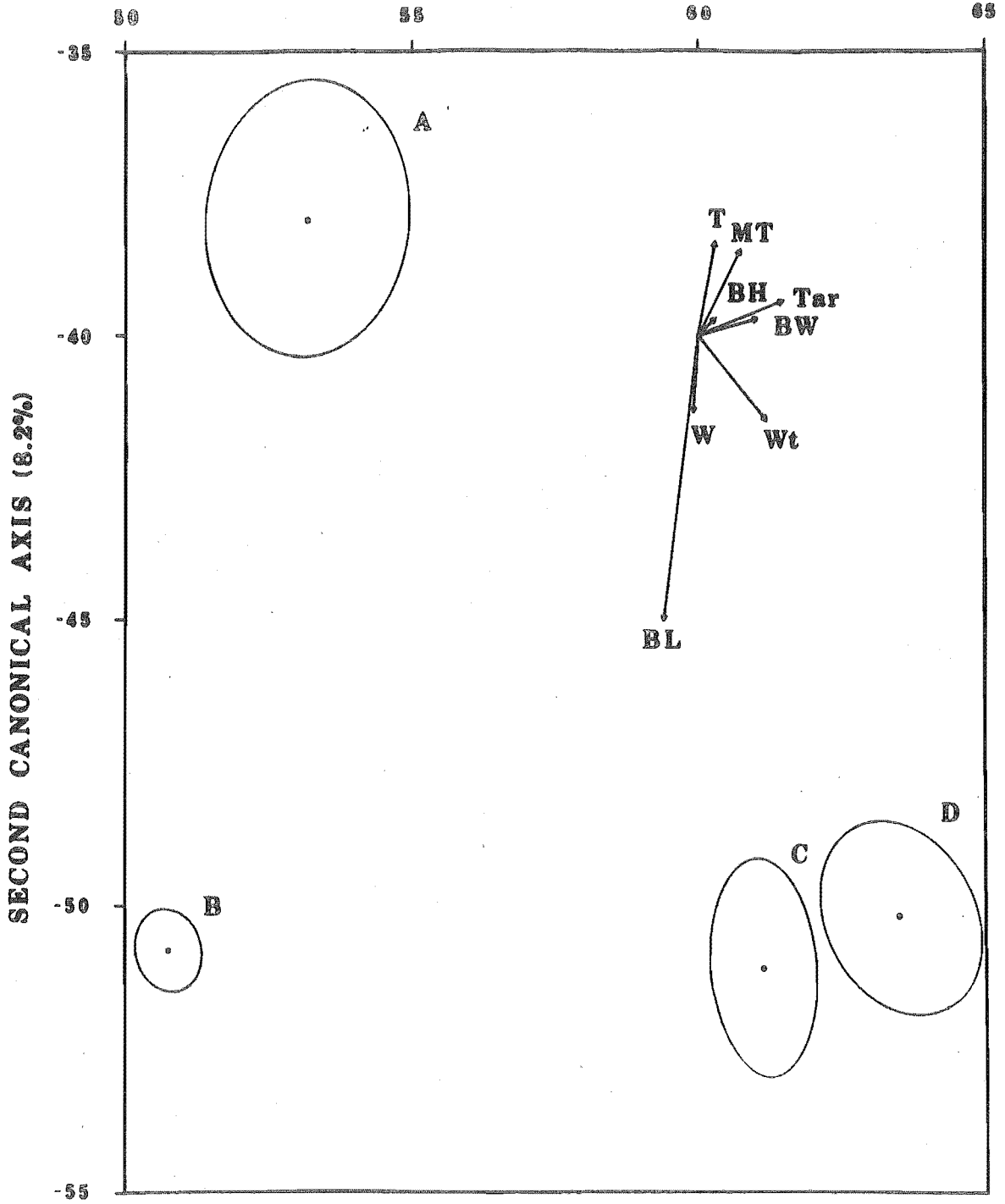
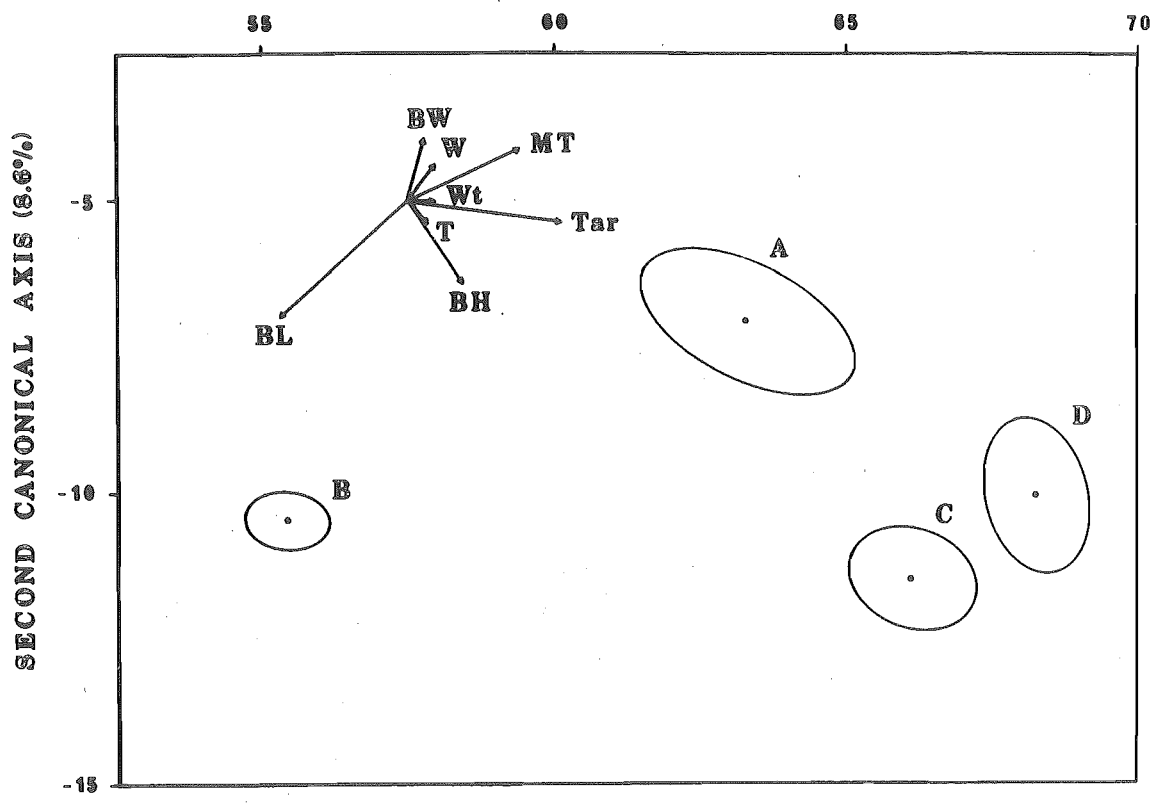


Figure 20.

Female New Zealand cyprinid character means and bivariate 0.95 confidence ellipses projected onto the first and second canonical axes. This view of the character space describes 96.9% of the variation among taxa. For further explanation see the legend to Figure 17 and the text.

Letters define the taxa as in Figure 19.

FIRST CANONICAL AXIS (88.3%)



In all characters except bill width, and tarsus length for males, black and pied phase Variable Oystercatchers appear in the same non-significant subset, thus emphasizing their general phenetic similarity. Chatham Islands Oystercatchers means either group with those of the South Island Pied Oystercatcher or they are intermediate between the mainland species. In some characters, such as middle toe length of both sexes, and tarsus length of females, South Island Pied Oystercatchers are phenetically distinct from the other taxa.

#### B. Multivariate Comparisons.

The results of separate canonical variates analysis for males and females are depicted in Figs. 19 and 20 respectively. These two dimensional projections are of two-fold value in comparing taxa in character space. Firstly, they provide graphic representation of the phenetic positions of each taxa and show the contributions of the individual characters to these positionings. Secondly, like other clustering procedures, they provide insight into the taxonomic relationships of the projected groups, as morphologically similar groups will tend to cluster in proximity, and vice versa.

For males, Wilks' Lambda was 0.0233 which converted to a highly significant F-value of 43.74 ( $P < 0.001$ ) with 24 and 386 degrees of freedom. Similarly for females, Wilks' Lambda of 0.0301 converted to a highly significant F-value of 22.47 ( $P < 0.001$ ) with 24 and 230 degrees of freedom. Thus in both sexes there are real phenetic differences between the taxa. When all characters are considered simultaneously, it is bill length which contributes most substantially to separate the phenetic groups, especially in males (see Fig. 19). Smaller differences in the other morphological characters serve to discriminate mainly between the Variable Oystercatcher on the one hand, and South

Island Pied and Chatham Islands Oystercatchers on the other. Although the relative positioning of the taxa are different for males and females, the clustering patterns are essentially similar. In two-dimensional character space, three phenetic entities emerge: these entities are entirely compatible with the present nomenclatorial system which recognises three species. The close proximity of the centroids of the pied and black phase Variable Oystercatcher indicate their close affinity.

#### 4.11 SUMMARY.

New Zealand oystercatchers show considerable morphological variation, both within and between species. South Island Pied Oystercatchers and also probably the other species, can be aged on the basis of progressive colour changes in the dorsal plumage, irides, bill and legs. Sex determination can be accomplished with a high degree of accuracy using the ratio of bill length to bill width. Males have short stout bills and thus low ratios; females have long thin bills and high ratios. Projectile-netted samples contained a high proportion of males, and the cyclic change in sex ratio of South Island Pied Oystercatchers at the Heathcote-Avon estuary suggests there may be some segregation of the sexes of this species at winter haunts.

Considerable seasonal variation occurs in the morphological characters of bill height and bill width in juvenile birds, and in wing length and total body weight of all age classes. Differential pooling of samples with respect to each of the characters was necessary so that sample sizes could be increased without introducing significant seasonal bias. Analysis of variance revealed that there is significant variation in size due to both age differences and sexual dimorphism. Only measurements from sub-adults and adults are sufficiently similar to permit pooling for taxonomic comparisons, and the sexes have to be treated separately.

Sexual dimorphism is apparent in all morphological characters of South Island Pied Oystercatchers except bill height and bill width. Since the phenotype is the product of selection by several contrasting adaptive strategies, sexual dimorphism probably results from Darwinian sexual selection, differential niche utilization and character correlations. Sexual dimorphism is most strongly expressed in the Chatham Islands Oystercatcher, presumably because of the Founder effect from the originally dimorphic colonists. Variable Oystercatchers are least dimorphic, with hybrids between the parental pied and black phases showing sexual differences only in bill length and body weight. This loss in dimorphism could result from a reduction of the range of variation in the hybrids, due to their intermediate phenetic position, and introgression towards the least dimorphic parental.

Black phase Variable Oystercatchers show considerable clinal variation in morphological characters, and much of this variation is directly attributable to local adaptive responses to climatic variables, especially temperature. Increase in bill size and tarsus length with increasing temperature follows Allen's ecogeographic rule, and suggests thermoregulatory adaptation. Clinal increase of wing and tail lengths against the temperature gradient are due to the correlation of these characters with body size, which also tends to be inversely correlated with temperature as predicted by Bergmann's rule.

Black and pied phase Variable Oystercatchers hybridize extensively wherever their ranges overlap, but more especially in Northland. Both parentals and hybrids are relatively abundant in the area of hybridization ; their mating with respect to colour phase is non-assortative, and they seem equally viable. Gene exchange between the parentals via the hybrids is therefore extensive, indicating their lack of



reproductive isolation. The inheritance of colour phases can be explained by a simple polygenic system involving a major gene whose dominance is expressed through the cumulative effects of several specific modifying genes at other loci.

In both univariate and multivariate comparisons of the New Zealand taxa, three phenetic entities are apparent, suggestive of three species.

## Chapter 5.

AFFINITIES OF NEW ZEALAND OYSTERCATCHERS AND SYSTEMATIC  
CONCLUSIONS.

5.1 INTRODUCTION.

The assessment of the affinities of taxa is a crucial step in formulating their systematic relationships. Much of the taxonomic splitting that has occurred in the past e.g. Sharpe (1896); Mathews (1913); and Ridgway (1919), is the direct result of considering various forms in isolation rather than in a wider geographic context. The New Zealand nomenclature seems to have suffered as much as that of other countries at the hands of splitters. For example, the exemplary researches of Fleming (1950a and b) on the New Zealand flycatchers of the genus Petroica reduced an unstable complex of six genera and ten species to one genus and three species. Fleming was able to bring about this drastic revision simply by assessing the morphological affinities of the New Zealand taxa and their extralimital relations, notably in Australia.

When looking for affinities of New Zealand birds, it is usual to turn to the continent of Australia (e.g. Falla, 1953) where considerably greater bird species diversity exists. The Tasman Sea acts as a barrier to dispersal of Australian species to New Zealand via the pronounced west-wind drift. Nevertheless, several species have colonized New Zealand within the last 150 years e.g. White-eye (Zosterops lateralis) White-faced Heron (Notophox novaehollandiae), Spur-winged Plover (Lobibyx novaehollandiae), Welcome Swallow (Hirundo neoxena) and Black-fronted Dotterel (Charadrius melanops). It therefore seems expedient, as a first measure, to compare Australian and New Zealand oystercatchers.

This chapter presents an analysis of the affinities of New Zealand oystercatchers, and culminates in a systematic revision which aims to express inferred phyletic relationships.

## 5.2 METHODS AND MATERIAL.

As the only Australian material available for measurement was museum skins, it was desirable to test for differences between measurements taken from freshly collected and from skinned birds, especially since Kinsky and Harper (1968) established that the bill width of some prions (Pachyptila sp.) shrunk as much as 23% during drying of the skins. Comparative measurements of ten birds collected and measured in August 1968, and then remeasured three years later as dried skins are shown in Table 27.

TABLE 27. COMPARISON OF MEASUREMENTS FROM 10\* FRESHLY COLLECTED SOUTH ISLAND PIED OYSTERCATCHERS AND THEIR DRIED SKINS.

Character	<sup>1</sup> Mean (mm) $\pm$ S.E. (freshly collected material)	<sup>2</sup> Mean (mm) $\pm$ S.E. (skin material)	Percent Change
Bill length	81.5 $\pm$ 1.39	81.6 $\pm$ 1.38	--
Bill height	16.2 $\pm$ 0.18	15.0 $\pm$ 0.20	7.4
Bill width	13.3 $\pm$ 0.17	12.8 $\pm$ 0.22	3.8
Tarsus length	44.3 $\pm$ 0.66	44.1 $\pm$ 0.67	--
Middle toe length	33.7 $\pm$ 0.54	33.5 $\pm$ 0.51	--
Wing length	240 $\pm$ 3.0	241 $\pm$ 3.1	--
Tail length	100 $\pm$ 1.1	100 $\pm$ 1.1	--

<sup>1</sup> Measured 14th August, 1968.

<sup>2</sup> Measured 23rd October, 1971.

\* 9 Males, 1 Female; 9 Adults, 1 Juvenile.

Both bill height and bill width are clearly smaller in the skinned specimens, due to the drying and shedding of the soft orange epidermis covering the proximal part of the bill. It therefore seems unwise to include live-trapped specimens in phenetic comparisons of Australian and New Zealand taxa, so the data were gathered only from prepared skins. With the exception of some Chatham Islands Oystercatcher measurements, that were obtained through the courtesy of curatorial assistants in overseas museums, all measurements included in this section were made by the author. From each specimen the following seven characters were recorded: bill length, bill height, bill width, tarsus length, middle toe length, wing length and tail length. For the method of measuring each of these characters, see Chapter 4.2 C. In addition, the plumage characters of the white patterning on the breast, wing and rump were recorded photographically for most specimens, and each specimen was searched for Mallophaga.

Although the analytical technique of canonical variates analysis is again used in this section, the extra variation stemming from the data on Australian oystercatchers required added (statistical) computations for meaningful interpretation. It was not possible to account for a high proportion of the total variation in the original data matrices without utilizing three discriminant functions. This required the production of three-dimensional graphs, each dimension being represented by a separate discriminant function. To aid the interpretation of these graphs and to obviate any visual distortion resulting from the plotting of a three-dimensional diagram on a two-dimensional surface, minimum distance networks (= Prim networks) were fitted between the taxa projections. Since these networks are based on all the data in the original matrices, they give an estimate of phenetic resemblance which takes into account all

TABLE 28. CHARACTER MEANS AND STANDARD ERRORS OF AUSTRALASIAN OYSTERCATCHERS.

Character	Sex	Mean (mm) $\pm$ S.E.					
		<sup>1</sup> South Island Pied Oystercatcher	<sup>2</sup> Chatham Islands Oystercatcher	<sup>3</sup> Black Phase Variable Oystercatcher	<sup>4</sup> Pied Phase Variable Oystercatcher	<sup>5</sup> Australian Pied Oystercatcher	<sup>6</sup> Sooty Oystercatcher
Bill length	M	81.4 $\pm$ 0.88	68.1 $\pm$ 0.91	78.6 $\pm$ 1.31	83.0 $\pm$ 0.92	73.9 $\pm$ 0.86	68.3 $\pm$ 1.07
	F	91.0 $\pm$ 1.07	76.9 $\pm$ 1.76	88.2 $\pm$ 0.69	94.1 $\pm$ 1.41	84.8 $\pm$ 1.01	81.1 $\pm$ 2.08
Bill height	M	15.6 $\pm$ 0.19	15.5 $\pm$ 0.14	16.6 $\pm$ 0.23	17.5 $\pm$ 0.22	16.6 $\pm$ 0.21	16.6 $\pm$ 0.22
	F	15.7 $\pm$ 0.21	16.1 $\pm$ 0.20	16.7 $\pm$ 0.12	18.0 $\pm$ 0.21	17.0 $\pm$ 0.15	16.9 $\pm$ 0.20
Bill width	M	12.6 $\pm$ 0.15	12.6 $\pm$ 0.12	13.8 $\pm$ 0.25	14.2 $\pm$ 0.17	12.9 $\pm$ 0.18	14.3 $\pm$ 0.21
	F	12.7 $\pm$ 0.12	13.3 $\pm$ 0.26	13.5 $\pm$ 0.11	14.4 $\pm$ 0.19	13.3 $\pm$ 0.19	13.9 $\pm$ 0.22
Tarsus length	M	49.4 $\pm$ 0.39	51.6 $\pm$ 0.44	56.6 $\pm$ 0.56	57.8 $\pm$ 0.35	56.4 $\pm$ 0.55	55.0 $\pm$ 0.61
	F	51.7 $\pm$ 0.44	53.2 $\pm$ 0.71	59.2 $\pm$ 0.51	60.6 $\pm$ 0.47	59.6 $\pm$ 0.64	55.6 $\pm$ 0.54
Middle toe length	M	31.8 $\pm$ 0.89	34.9 $\pm$ 0.38	37.2 $\pm$ 0.45	37.8 $\pm$ 0.41	34.7 $\pm$ 0.47	39.9 $\pm$ 0.63
	F	31.9 $\pm$ 0.27	36.2 $\pm$ 0.43	38.2 $\pm$ 0.43	38.5 $\pm$ 0.33	35.6 $\pm$ 0.70	38.6 $\pm$ 0.89
Wing length	M	257 $\pm$ 1.7	253 $\pm$ 2.1	274 $\pm$ 2.1	266 $\pm$ 2.4	275 $\pm$ 1.8	283 $\pm$ 2.8
	F	260 $\pm$ 1.4	265 $\pm$ 2.9	273 $\pm$ 2.4	271 $\pm$ 2.2	281 $\pm$ 1.8	286 $\pm$ 3.4
Tail length	M	94 $\pm$ 1.2	96 $\pm$ 0.98	105 $\pm$ 0.8	103 $\pm$ 1.3	112 $\pm$ 1.6	114 $\pm$ 1.7
	F	98 $\pm$ 0.9	99 $\pm$ 1.0	106 $\pm$ 1.1	104 $\pm$ 0.6	115 $\pm$ 2.1	115 $\pm$ 1.6

<sup>1</sup> N(Males) = 22, N(Females) = 18

<sup>2</sup> N(Males) = 9, N(Females) = 10

<sup>3</sup> N(Males) = 20, N(Females) = 16

<sup>4</sup> N(Males) = 15, N(Females) = 16

<sup>5</sup> N(Males) = 21, N(Females) = 17

<sup>6</sup> N(Males) = 18, N(Females) = 9

of the variation. The networks were computed using the simplified algorithm of Farris (1970:87-88).

### 5.3 MORPHOLOGICAL AFFINITIES.

Means and standard errors of the morphological characters measured for the Australasian taxa of oystercatchers are shown in Table 28.

The statistical significance of the differences between the character means was tested using single classification anova followed by a posteriori SS-STP analysis. The results of this procedure are shown below:

#### BILL LENGTH

	Pied Var.	SIPO	Black Var.	Aust. Pied	Sooty	Chatham	
Males	<u>83.0</u>	81.4	<u>78.6</u>	73.9	<u>68.3</u>	68.1	mm

	Pied Var.	SIPO	Black Var.	Aust. Pied	Sooty	Chatham	
Females	<u>94.1</u>	<u>91.0</u>	<u>88.2</u>	<u>84.8</u>	<u>81.1</u>	76.9	

#### BILL HEIGHT

	Pied Var.	Black Var.	Aust. Pied	Sooty	SIPO	Chatham	
Males	<u>17.5</u>	16.6	16.6	<u>16.6</u>	<u>15.6</u>	15.5	mm

	Pied Var.	Aust. Pied	Sooty	Black Var.	Chatham	SIPO	
Females	<u>18.0</u>	<u>17.0</u>	<u>16.9</u>	<u>16.7</u>	<u>16.1</u>	15.7	

BILL WIDTH

	Sooty	Pied Var.	Black Var.	Aust. Pied	SIPO	Chatham	
Males	<u>14.3</u>	<u>14.2</u>	<u>13.8</u>	12.9	12.6	12.6	mm

	Pied Var.	Sooty	Black Var.	Chatham	Aust. Pied	SIPO	
Females	<u>14.4</u>	<u>13.9</u>	13.5	13.3	13.3	12.7	

TARSUS LENGTH

	Pied Var.	Black Var.	Aust. Pied	Sooty	Chatham	SIPO	
Males	<u>57.8</u>	<u>56.6</u>	<u>56.4</u>	55.0	51.6	49.4	mm

	Pied Var.	Aust. Pied	Black Var.	Sooty	Chatham	SIPO	
Females	<u>60.6</u>	<u>59.6</u>	<u>59.2</u>	55.6	53.2	51.7	

MIDDLE TOE LENGTH

	Sooty	Pied Var.	Black Var.	Chatham	Aust. Pied	SIPO	
Males	<u>39.9</u>	<u>37.8</u>	<u>37.2</u>	34.9	34.7	31.8	mm

	Sooty	Pied Var.	Black Var.	Chatham	Aust. Pied	SIPO	
Females	<u>38.6</u>	<u>38.5</u>	<u>38.2</u>	<u>36.2</u>	<u>35.6</u>	<u>31.9</u>	

WING LENGTH

	Sooty	Aust. Pied	Black Var.	Pied Var.	SIPO	Chatham	
Males	<u>283</u>	<u>275</u>	<u>274</u>	266	257	253	mm
	Sooty	Aust. Pied	Black Var.	Pied Var.	Chatham	SIPO	
Females	<u>286</u>	<u>281</u>	<u>273</u>	271	265	260	

TAIL LENGTH

	Sooty	Aust. Pied	Black Var.	Pied Var.	Chatham	SIPO	
Males	<u>114</u>	<u>112</u>	<u>105</u>	103	96	94	mm
	Aust. Pied	Sooty	Black Var.	Pied Var.	Chatham	SIPO	
Females	<u>115</u>	<u>115</u>	<u>106</u>	104	99	98	

With the exception of bill length, a clear pattern emerges from the analysis. The Australian Pied Oystercatcher (H. longirostris)\* and the Sooty Oystercatcher (H. fuliginosus) usually group with both colour phases of the Variable Oystercatcher (H. unicolor) in the same non-significant subsets, indicating their morphological affinity. The Chatham Islands Oystercatcher (H. chathamensis) is phenetically intermediate in most characters between the above group and the South Island Pied Oystercatcher (H. ostralegus finschi).

\* longirostris is accepted in preference to ostralegus (Peters, 1934) for reasons beyond (see page 117).



Figure 21.

Character means and bivariate 0.95 confidence ellipses of male Australian oystercatchers projected onto the first and second canonical axes. This view of the character space described 70.9% of the variation among taxa. For further explanation see the legend to Figure 17 and the text.

Key to letters:

- A. South Island Pied Oystercatcher
- B. Black phase Variable Oystercatcher
- C. Pied phase Variable Oystercatcher
- D. Chatham Islands Oystercatcher
- E. Australian Pied Oystercatcher
- F. Sooty Oystercatcher

FIRST CANONICAL AXIS (35.5%)

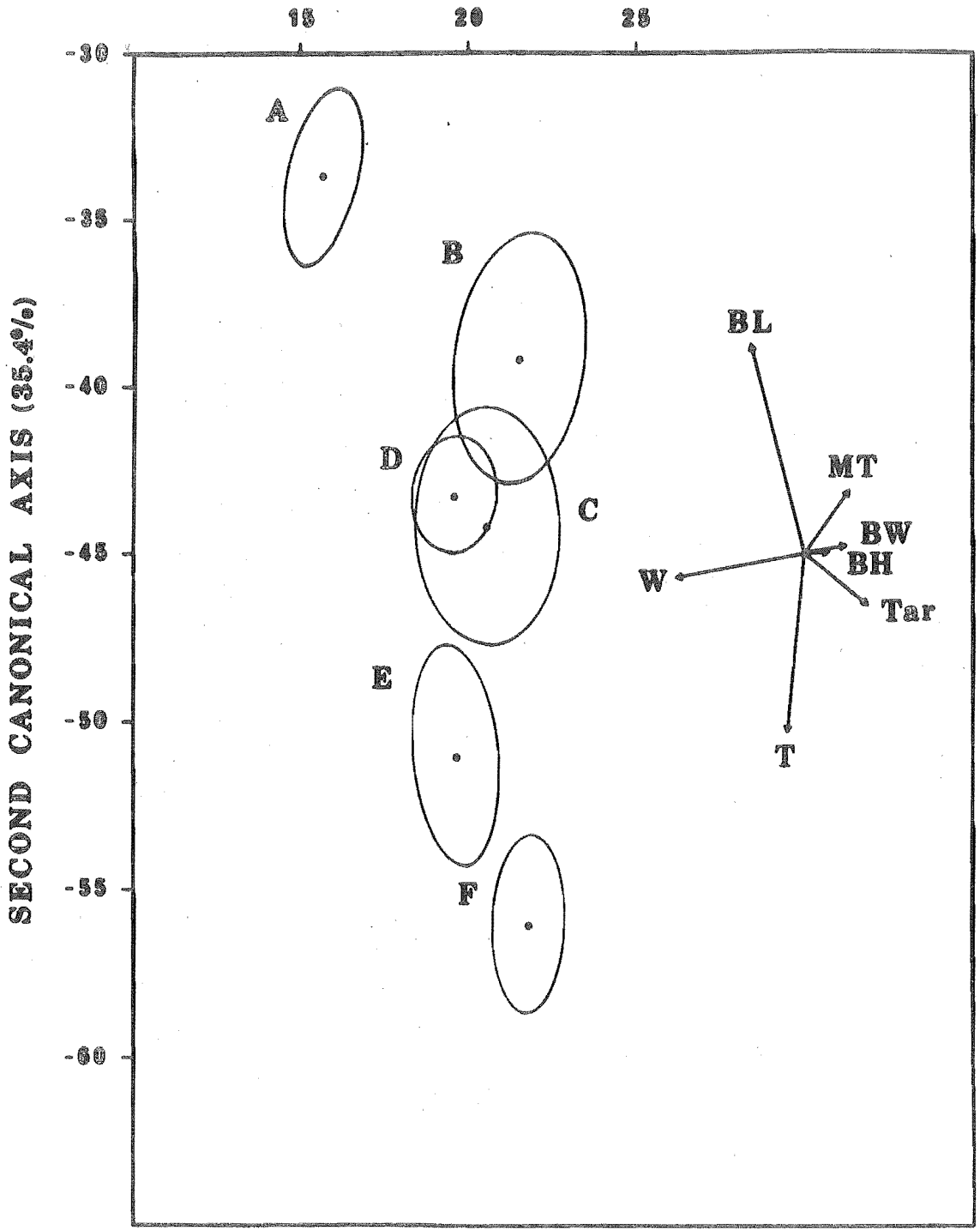
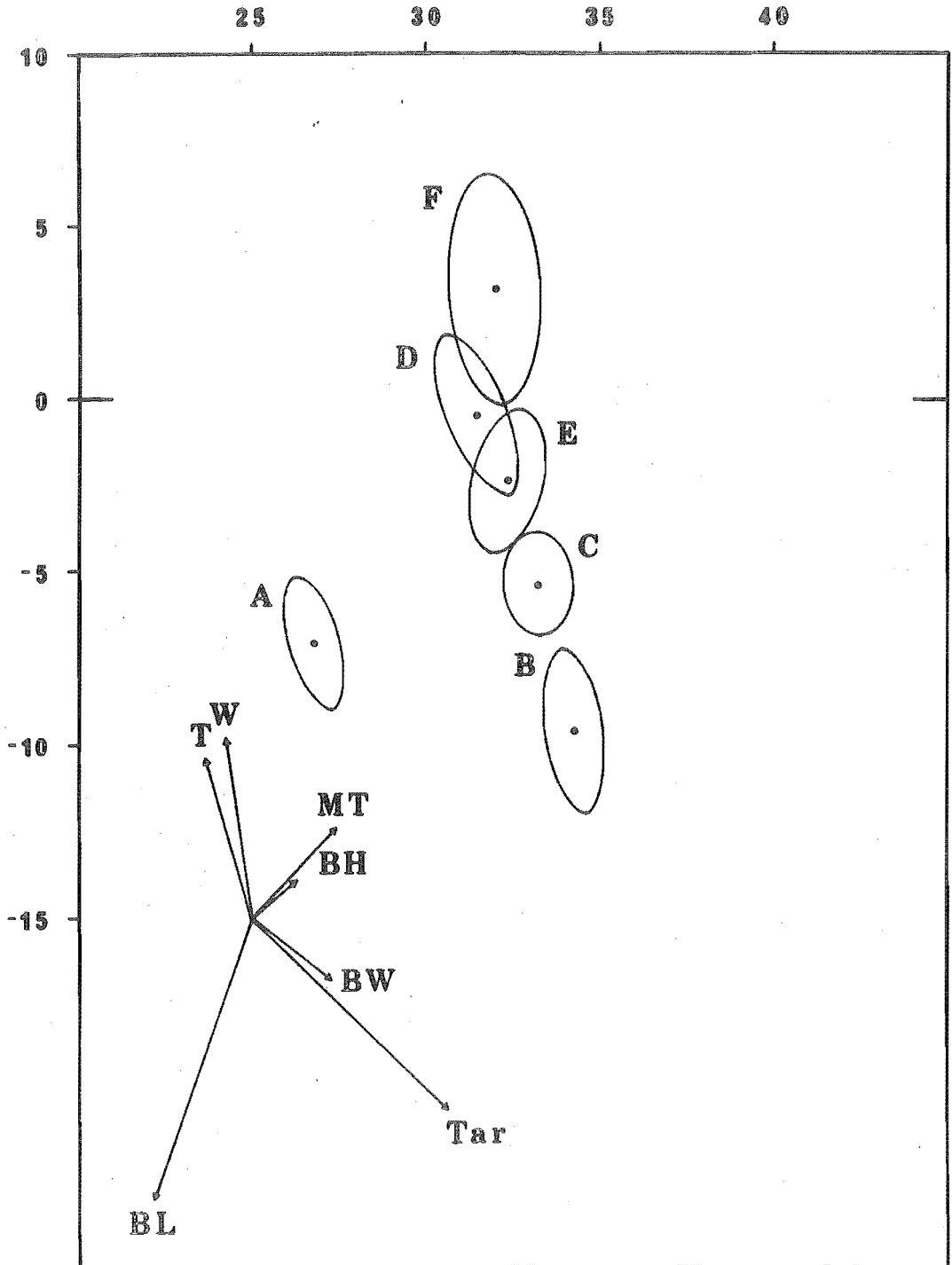


Figure 23.

Character means and bivariate 95% confidence ellipses of female Australasian cysterobathra projected onto the first and second canonical axes. This view of the character space described 78.6% of the variation among taxa. For further explanation see the legend to Figure 17 and the text. Letters define the taxa as in Figure 21.

FIRST CANONICAL AXIS (56.4%)

SECOND CANONICAL AXIS (22.2%)



Both the Sooty and the Australian Pied Oystercatchers have short stout bills, and long wings and tails. They differ from each other principally in that the Sooty Oystercatcher has a much longer middle toe, a phenomenon common in rock-dwelling species of Haematopus (Murphy, 1925 ; Fleming, 1939).

Simultaneous variation in the morphological characters was investigated by canonical variates analysis. For males, Wilks' Lambda for equality of group centroids was 0.0173 which converted to a highly significant F-value of 18.05 ( $P < 0.001$ ) with 35 and 390 degrees of freedom. For females, Wilks' Lambda was 0.0158 which gave a highly significant F-value of 14.66 ( $P < 0.001$ ) with 35 and 306 degrees of freedom. In both sexes, therefore, there are real phenetic differences between the taxa.

The clustering pattern of the taxa in two-dimensional character space is similar for both sexes (see Figs. 21 and 22). Two basic clusters emerge, with South Island Pied Oystercatchers separating off from the other species. Bill length, tarsus length, tail length and wing length provide the greatest contributions to separation of the groups. Somewhat surprisingly, the morphologically distinctive Chatham Islands Oystercatcher clusters near the Variable and Australian oystercatchers. As the Chathams bird is phenetically intermediate between the South Island Pied Oystercatcher and the other taxa in the univariate case, it could be reasonably expected to cluster between them in the multivariate case. The first two canonical axes accounted for only 70.9% of the variation of males and 78.6% of that of females, and it was evident from the eigenvalues (see statistical methods Chapter 4.2 D) that a significant component of variation was present on the third axis. It was therefore decided to plot the first three canonical axes in a three-dimensional diagram to increase the amount of

Figure 23.

Character means of male Australasian oystercatchers projected onto the first three canonical axes. This view of the character space describes 91.5% of the variation among taxa. Broken lines show the shortest simply connected network between the taxa, based on distance coefficients (see Michener, 1970). See text for further explanation. Letters define the taxa as in Figure 21.

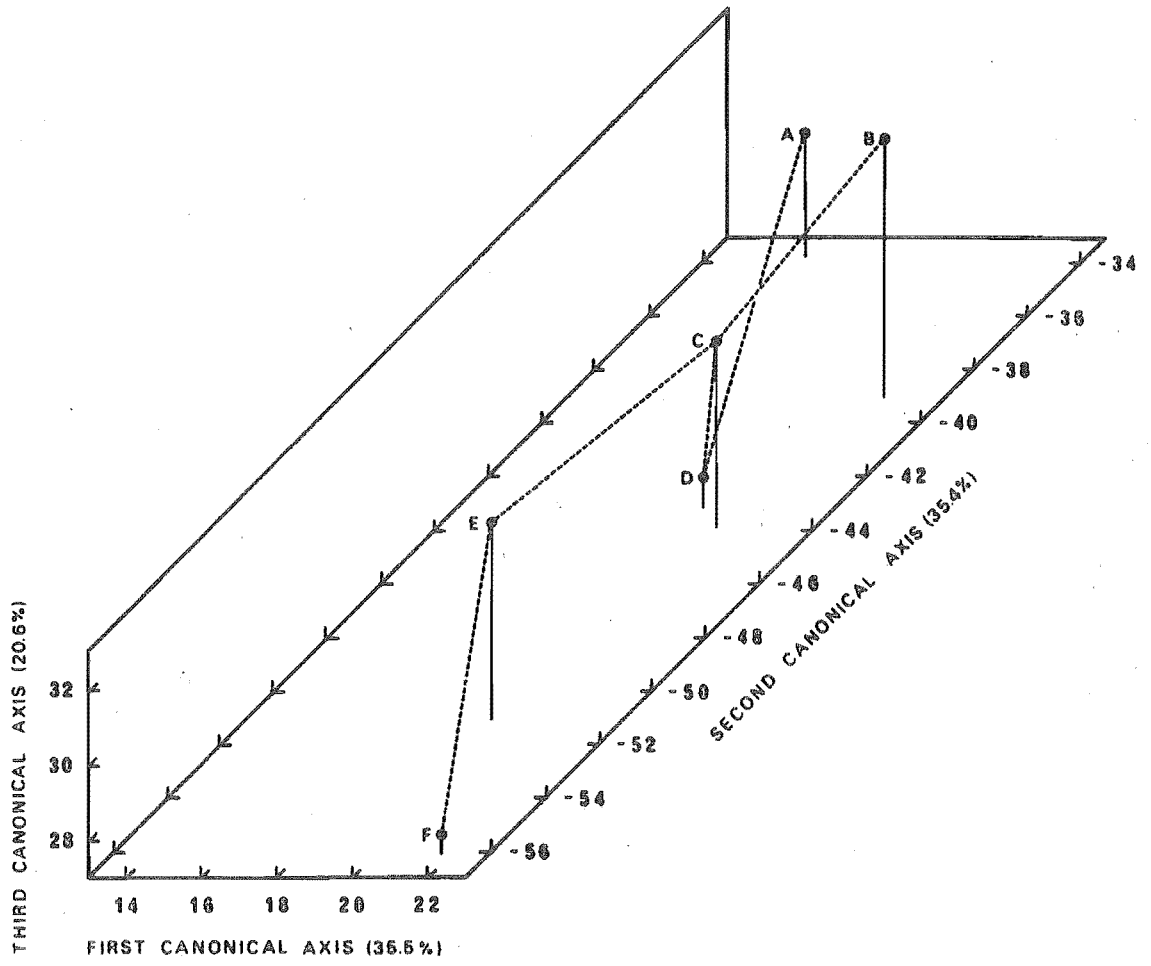
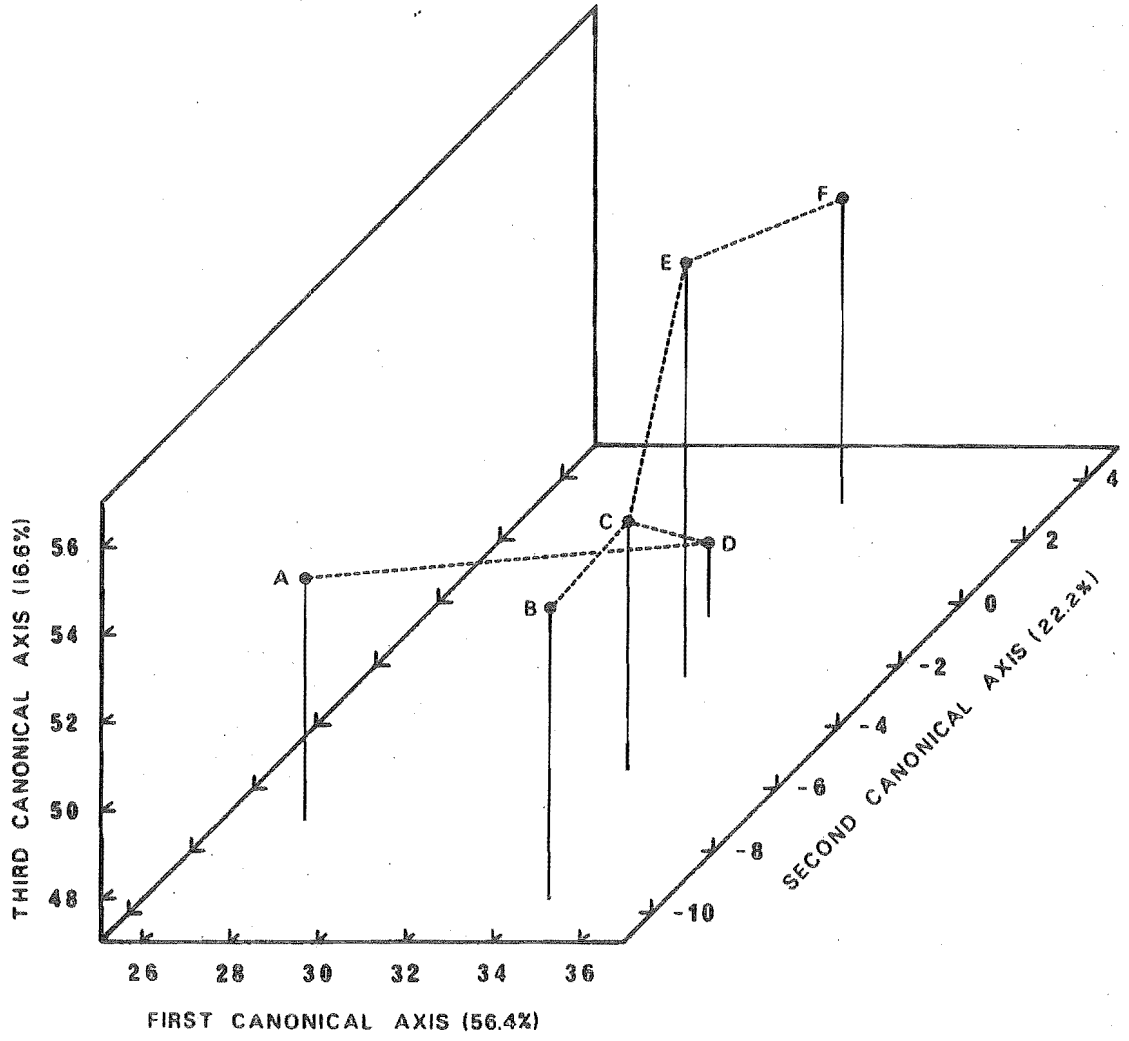


Figure 21.

Character means of female Australasian cyprinid fish projected onto the first three canonical axes. This view of the character space describes 95.2% of the variation among taxa. Broken lines show the shortest simply connected network between the taxa, based on distance coefficients. See text for further explanation. Letters define the taxa as in Figure 21.





variation accounted for to over 90%, and to check the unexpected clustering patterns arising from the two-dimensional plots. The three-dimensional projections with a minimum-distance network fitted between the projected points are shown in Figs. 23 and 24. It is readily seen from these figures that the Chatham Islands Oystercatcher is actually phenetically distinct from the Variable and Australian oystercatchers. The clustering pattern produced in the two-dimensional case was illusory as the separation of the constituent taxa was largely effected on the third axis. Thus where the third axis contains a significant proportion of the variation of the original data matrices, it seems imperative that three-dimensional projections are used. Further, it is evident that clustering patterns based on two-dimensional plots which account for less than 80% of the variation should be viewed with care.

#### 5.4 PLUMAGE AFFINITIES.

Old and New World oystercatchers are divisible on the basis of their plumage patterns, particularly the extent of white on the breast, rump and outer webbing of the primary flight feathers.

##### A. Breast Pattern.

Several of the New World species are characterized by black mottling on an otherwise white breast. The pied phase Variable Oystercatcher (H. unicolor), the Galapagos Islands Oystercatcher (H. palliatus galapagensis), the Frazar Oystercatcher (H. p. frazari), and the Patagonian Oystercatcher (H. p. durnfordi) all show mottling of the breast, especially at the junction of black and white areas on the upper breast (see Plate 12). In addition, this same mottling occurs sporadically on eastern specimens of the American Pied Oystercatcher (H. p. palliatus). As Murphy (1925) remarked "... the mottling of the breast... appears to be carried by a

Plate 12.

Breast patterns of some American oystercatchers, showing mottling at the boundary between black and white plumage.

Key to letters:

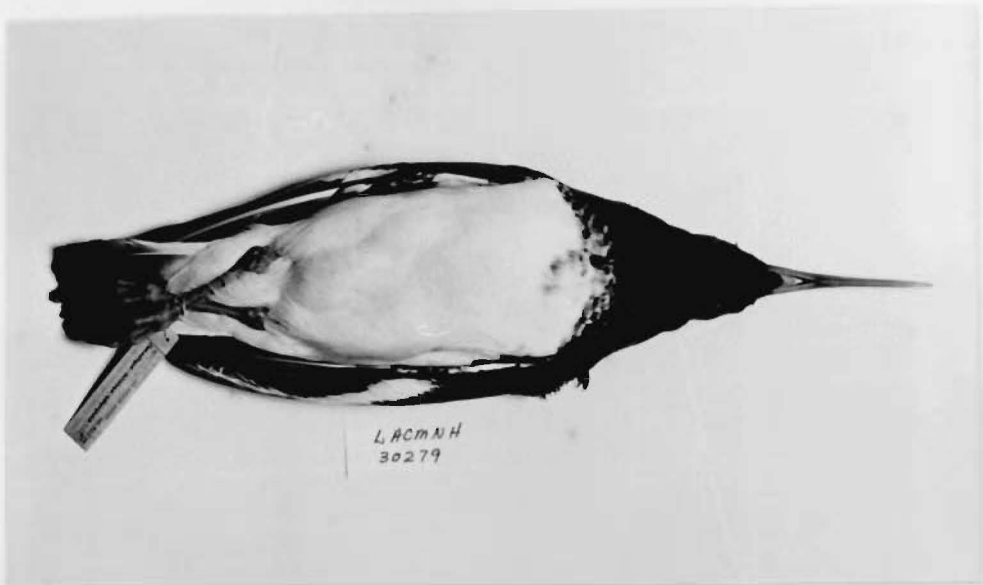
A. Galapagos Islands Oystercatcher

(H. galapagensis).

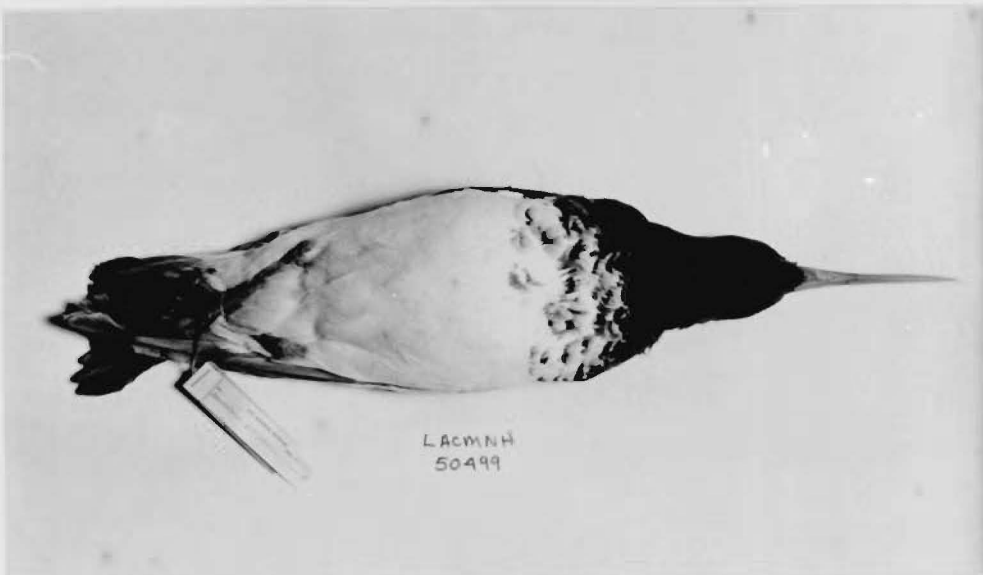
B and C. Frazer Oystercatcher (H. palliatus

frazeri).

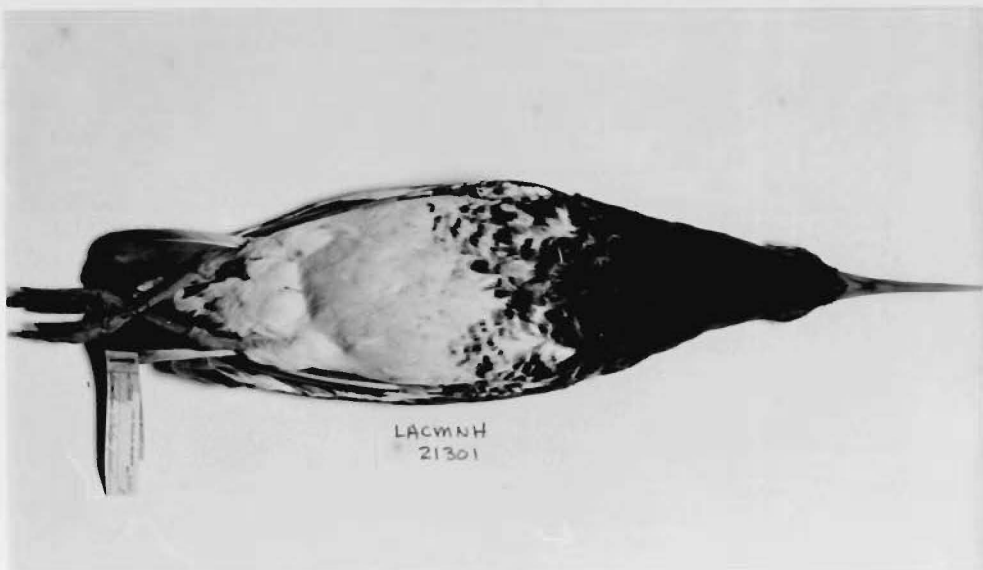
(Photos: James E. Northern, Los Angeles County  
Museum of Natural History).



A



B



C

genetic factor deep-rooted in the species palliatus as a whole." In the pied phase Variable Oystercatcher such mottling arises partly through introgressive hybridization with the black phase of this species. Whether or not this indicates that the above-mentioned New World oystercatchers are of hybrid origin is uncertain at this stage, but certainly the American species are within range of the area of hybridization of the Frazar and North American Black Oystercatcher (H. bachmani) (see Fig.1). In general, the mottling of the breast is largely confined to species in the Pacific Basin. The Old World species (H. ostralegus), including the South Island Pied Oystercatcher, all have immaculate white breasts with clear cut margins between black and white areas of the plumage. The Chatham Islands Oystercatcher (H. chathamensis) has a small amount of mottling on the breast (see Plate 3), although 6 of the 16 birds trapped in 1970 had clear cut boundaries similar to those of the South Island Pied Oystercatcher.

#### B. Rump Patch.

Reduction of the extent of the white rump patch is largely confined to oystercatchers of the Pacific area (see Plate 13 A-C). All of the New World species have small rump patches which commonly cover only the lower back. In contrast, the Old World oystercatchers all have an extensive rump patch which runs in a bright wedge on the back between the wings, as in the South Island Pied Oystercatcher (see Plate 1). The rump patch of the Chatham Islands Oystercatcher is similar in size to those of New World species (see Plate 13D).

#### C. White Markings on the Outer Primary Webs.

As noted by Murphy (1925, 1936) the Old World pied oystercatchers (H. ostralegus) are characterized by white quill markings which extend over the outer webs of each

Plate 19.

Rump patches of some New World oystercatchers.

Key to letters:

- A. American Pied Oystercatcher  
(H. palliatus palliatus).
- B. Australian Pied Oystercatcher  
(H. longirostris).
- C. Pied phase Variable Oystercatcher  
(H. unicolor).
- D. Chatham Islands Oystercatcher  
(H. chathamensis).

Note that the rump patches do not extend in a triangular wedge between the wings, as in Old World H. ostralegus.



A



B



C



D

primary feather. Moving eastwards from the Palaearctic region, eastern populations of H. palliatus have their markings reduced so they extend at maximum from the inner primaries to the fourth primary. Further eastwards and southward of eastern United States there is a progressive reduction in the amount of white on the outer primary webs. All Pacific pied species have unmarked outer webs. Finschi differs from the nominate ostralegus in that the white markings appear on the inner webs of the primaries (see Plate 14).

Summarizing, the plumage patterns of New Zealand Oystercatchers indicate a dichotomy of affinities. The tendency for mottling of the breast, the reduced rump patch and the lack of white markings on the outer webs of the primaries are common to most New World species. All Australasian oystercatchers share these features, with the exception of the South Island Pied Oystercatcher which has plumage affinities with the Old World H. ostralegus.

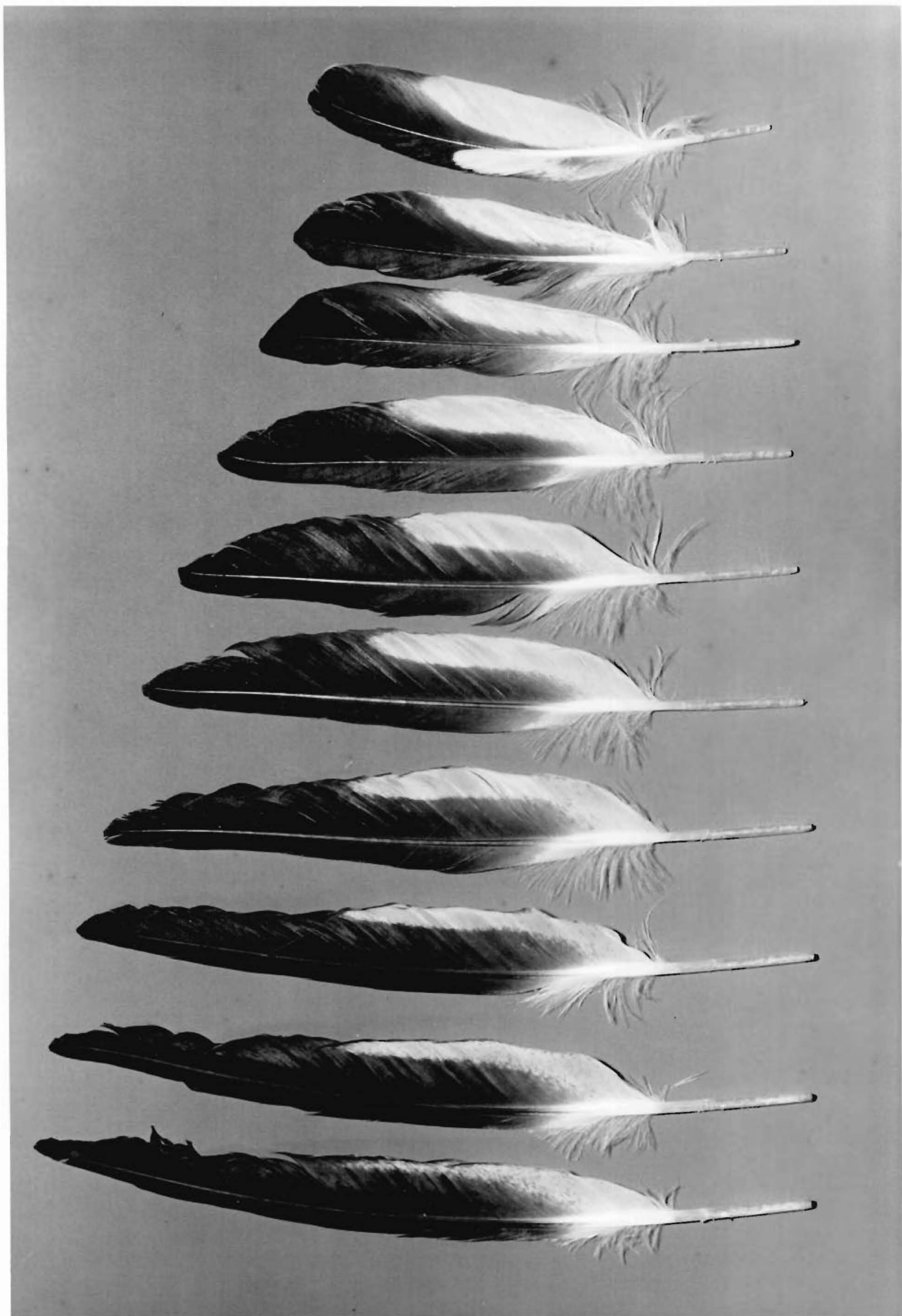
#### 5.5 AFFINITIES SUGGESTED BY THE MALLOPHAGA.

Unfortunately, the Mallophaga of some species of oystercatcher are either undescribed or described from inadequate material. However, Mallophaga so far described do indicate dual affinities for New Zealand oystercatchers in line with morphological and plumage divisions. As noted in Chapter 3.7, the New Zealand taxa can be separated on the presence or absence of the louse Quadriceps ridgwayi. All colour phases of the Variable Oystercatcher are host to this ectoparasite, whereas the South Island Pied and Chatham Islands Oystercatchers lack it. This louse was also present on Australian Pied Oystercatcher skins that were prepared over 80 years ago, but was absent from the 26 Sooty Oystercatcher skins which were examined. Theresa Clay (pers. comm.) also found Q. ridgwayi on a pair of



Plate 14.

The pattern of white markings on the webs of primary flight feathers of **the** South Island Pied Oystercatcher. Note that the white markings are confined to the inner webs.



Australian Pied Oystercatchers, and Timmermann (1971) did not record it on the Sooty Oystercatcher.

The original description of Q. ridgwayi was by Kellogg (1906) who found it on the Galapagos Islands Oystercatcher. Recently, Emerson (pers. comm.) reported this louse from a specimen of H. ostralegus? osculans collected in Korea, thus indicating that ridgwayi is found around the Pacific Basin.

#### 5.6 EVOLUTIONARY RELATIONSHIPS OF AUSTRALIAN OYSTERCATCHERS.

Synthesis of the affinities suggested by morphological, plumage and Mallophaga evidence provides clues to the evolutionary relationships of the Australasian oystercatchers. The following is an attempt to reconstruct the major steps in the evolution of the genus Haematopus in Australasia.

As for much of the avian fauna of New Zealand, it seems likely that the New World oystercatchers colonized this country from Australia. Presumably, the first colonization was one of the Australian Pied Oystercatcher which secondarily became melanistic here, as have several other colonists such as the Black Fantail (Rhipidura fuliginosa), the Black Stilt (Himantopus novaezealandiae), the Snares Island Tomtit (Petroica macrocephala dannefaerdi) and the Black Robin (Petroica traversi).

The secondary contact of pied and black phase Variable Oystercatchers now evident in northern New Zealand seems a relatively recent phenomenon, probably marking another invasion of the Australian Pied Oystercatcher. The occurrence of hybrids between black and pied phase Variable oystercatchers in New Zealand was not noted until as late as 1899 when Rothschild described a mottled specimen as a new species H. reischeki.

The origin of the Sooty Oystercatcher is hard to determine on the available knowledge, but it obviously is a

good species as it is reproductively isolated from the Australian Pied Oystercatcher. Two subspecies of the Sooty Oystercatcher have been described; H. fuliginosus fuliginosus which occurs around much of the Australian coastline, and H. f. ophthalmicus which occurs principally in the Cape York area and is distinguished by a large fleshy ring around the eye. Although the original type description of ophthalmicus stated that this bird was smaller than typical fuliginosus in bill dimensions and body size, this is incorrect as several of the specimens in Australian Museum collections are actually larger (pers. obs., pers. comm. A. R. McEvey). The only other oystercatcher with a similar fleshy eye ring is also a black form, the South African Black Oystercatcher (H. moquini). This could indicate affinity of fuliginosus and moquini, and suggest an origin for the Sooty Oystercatcher independent of that for the Australian Pied Oystercatcher. The latter seems most closely related to the Pacific species group and probably draws its origins from America.

Mayr (in Falla, 1953) considered that the pied phase Variable Oystercatcher was derived from a single invasion of the stock from which the Australian Pied Oystercatcher is descended. Following the invasion, the pied phase has become increasingly melanistic towards the south of New Zealand. He suggested that the black phase Variable Oystercatcher may have given rise to the Sooty Oystercatcher by returning to southern Australia. The weight of evidence seems against these views for the following reasons:

(1) melanism in New Zealand birds tends to develop in geographically isolated populations, and proceeds to an exclusive frequency e.g. the Black Robin on Little Mangere Island and the Black Tit on Snares Island;

(2) many of the melanistic forms in New Zealand have

their nearest non-melanistic relatives in Australia;

(3) hybridization of sympatric melanistic and non-melanistic forms is strongly suggestive of secondary contact (second invasion) following a period of isolation in which the two forms diverged i.e. one form became melanistic; and,

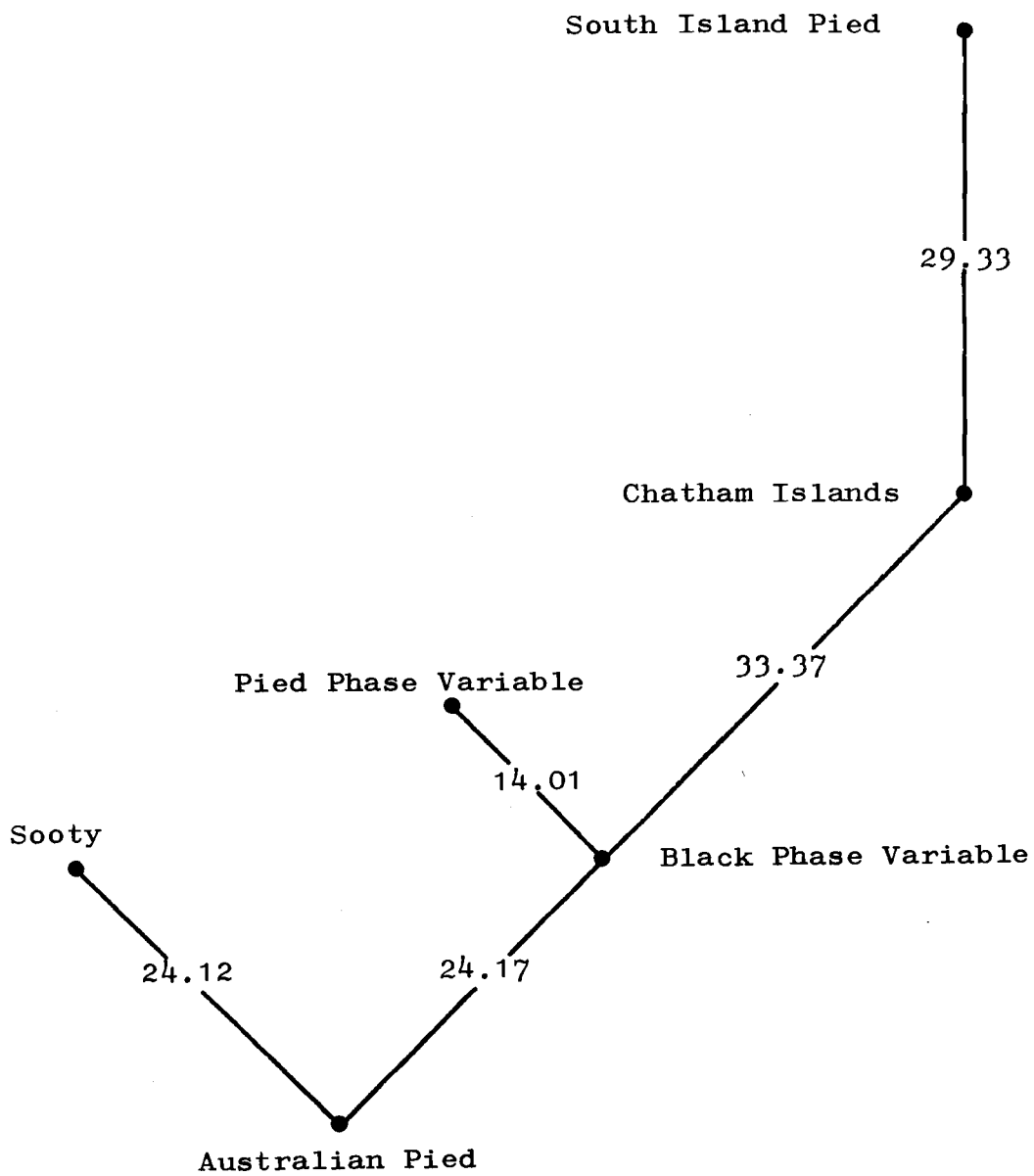
(4) the derivation of the Sooty Oystercatcher from the black phase Variable Oystercatcher is unlikely, as it seems to lack the louse Q. ridgwayi, it has a distinctive eye-ring suggesting affinity with the South African Black Oystercatcher, and because the "reverse dispersal" of New Zealand elements to the Australian avifauna is extremely rare.

The South Island Pied Oystercatcher has clear-cut Old World affinities. Apart from the lack of either white markings on the outer primary webs or a white winter chin-strap, it is morphological very similar to European oystercatchers. Although it was not possible to obtain adequate data on European H. ostralegus, the published measurements of Salomonsen (1930) and Harris (1967) agree closely with those of the South Island Pied Oystercatcher.

The Chatham Islands Oystercatcher has a curious mixture of affinities with both the pied phase Variable and the South Island Pied Oystercatcher. Morphologically it is most similar to the latter species, it lacks the louse Q. ridgwayi and its piping vocalizations are similar to those of the South Island Pied Oystercatcher. Yet some of its plumage characters resemble those of the Australian Pied and the Variable Oystercatchers, as also noted by Oliver (1955). It may represent an ancient ancestral form, or it may be the product of the operation of the founder principle (Mayr, 1965) on aberrant H. ostralegus colonists. The founder principle is based on the idea that the few founding individuals of a species which colonize isolated areas such as islands, rarely if ever include the whole

Figure 25.

Wagner tree suggesting phylogenetic relationships of male Australasian cysterentelers, based on morphological characters. Figures on the diagram show morphological distance between the taxa nodes. For further explanation see the text.



genetic repertory of the species. Especially if the founding sample is small, they may right from the beginning of colonization differ markedly and in a more or less random way from the parental population. If the Chatham Islands were colonized by a few morphologically aberrant South Island Pied Oystercatchers, then their contemporary derivatives could well be similarly aberrant. Phylogenetic relationships within the Australasian taxa were investigated objectively on morphological grounds by computing a Wagner tree (Wagner, 1961). However, the "Wagner method" employed by Kluge and Farris (1969) was not used, but instead the Prim Network approximation of Farris (1970) was employed as this was easier to compute and involved little loss of information. The Prim approximation for computing a Wagner Network involves finding a taxon which is morphologically closest to the arbitrary ancestor, and then linking it to the network. The difference between each unplaced taxon and the network is then computed, and the taxon that is closest to the network is added to the node from which it differs least. This process is repeated until all taxa are placed on the network. The phylogenetic tree thus produced for Australasian oystercatchers was similar for both sexes, that of males being shown in Fig. 25.

In computing Wagner trees it is necessary to choose arbitrarily an ancestral taxon. Obviously, any of the taxa could have been selected as ancestral, but this would in no way affect the "morphological distance" between the taxa nodes or the pattern of relationships; it would simply alter the hierarchial positions in the tree. It seemed logical to select the Australian Pied Oystercatcher as the hypothetical Australasian ancestor, since this species could reasonably be expected to have given rise to the New Zealand Variable Oystercatcher, and because it is generally accepted that the South Island Pied Oystercatcher was a



later Eurasiatic immigrant to New Zealand (Falla, 1953; Larsen, 1957; Fleming, 1962a and b). It should be noted that, by rearranging the tree, the Chatham Islands Oystercatcher could also be regarded as an ancestral species near the divergence of Old and New World species.

In Fig. 25 the New World species are phylogenetically closest and the derivation of the pied and black phase Variable Oystercatchers from the Australian Pied Oystercatcher is confirmed. The Chatham Islands Oystercatcher is phylogenetically nearer to the South Island Pied Oystercatcher than the pied phase Variable Oystercatcher.

I interpret the above phylogeny to mean that the oystercatchers in the Pacific Basin represent the ancestral form which once ranged around the northern Arctic shores in the warm Tertiary climate. The oldest fossil oystercatcher (Paractiornis) is of Miocene age (Brodkorb, 1967) and according to Larsen (1957) it is a primitive form. Thus oystercatchers are probably of Miocene age. The gradual cooling of the Tertiary climate resulted in the southwards expansion of the temperate and cold zones to their present day positions (Larsen, op. cit.). Since the oystercatchers were largely tied to the temperate zone, to judge from their present climatic distribution, it seems that they would have been forced into temperate North America and Eurasia. Thus in the late Pliocene, the American and Eurasiatic populations would have been isolated.

According to Larsen (op. cit.) the Old World H. ostralegus could have arisen on the American Atlantic coast during the late Pliocene-early Pleistocene when the area was a glacial refugium. He suggested that during the first interglacial this new form could have been introduced into Eurasia through Greenland. Accepting this hypothesis, the New Zealand H. ostralegus would therefore be a later immigrant from Eurasia, an interpretation also expressed by

Falla (1953) and Fleming (1962a and b), though their views were based on morphological evidence.

Further evidence for this primarily zoogeographic and climatic hypothesis is provided by American Atlantic coast oystercatchers which are phenetically intermediate to those of the Pacific Basin and Eurasia (Murphy, 1936).

Larsen (op. cit.) was led to predict that black oystercatchers were the ancestral form from which pied mutants arose, but in view of the marked phenetic differences of such black species as the South African Black Oystercatcher (H. moquini) and the South American Black Oystercatcher (H. ater), it seems more likely that black forms arose independently from several pied forms. Clearly, a detailed phenetic study of the world species would be the next logical step in determining the evolutionary history of oystercatchers.

#### 5.7 SYSTEMATIC CONCLUSIONS.

The South Island Pied Oystercatcher is obviously a good species because of its reproductive isolation from the Variable Oystercatcher. Its affinities are with the Old World H. ostralegus, from which it differs in small but constant plumage characters. Since subspecies are defined by Mayr (1969) as "a geographically defined aggregate of local populations which differs taxonomically from other such subdivisions of the species", it is apparent that finschi is a valid subspecies, and that the practice of Falla et. al. in raising finschi to species status on the grounds that it is a "strong" race has no biological basis.

The Chatham Islands Oystercatcher seems closest to the South Island Pied Oystercatcher, yet it has some conspicuous morphological and ecological differences. It seems therefore prudent to refer it to a separate species H. chat-hamensis as is done by the Annotated Checklist of New Zealand Birds (Kinsky, 1970).

The taxonomy of black and pied phase Variable Oystercatchers has to be based on an interpretation of their hybridization. Hybrids occur wherever the parentals are sympatric, and all three phenotypes occur in the same habitats in the area of hybridization. There is no compressed hybrid zone, as hybridization occurs through much of New Zealand, although the greatest amount of interbreeding occurs in Northland where both parentals are relatively abundant. All types of crosses occur, hybrids are fully fertile, and they do not seem to suffer from selective mortality. Introgression of parental characters via the hybrids is probably quite extensive.

Short (1969) regarded a zone of overlap and hybridization as a general term for all situations involving hybridization and backcrossing between formerly allopatric forms in a secondary contact. He defined such a zone as "an area of secondary intergradation occupied by numerous hybrids and both parental forms as well." He further considered that the joint maintenance of parental phenotypes in a zone of overlap and hybridization in numbers greater than 5% indicated that the parentals comprised a part of the population and were not simply recombinants representing extreme hybrid phenotypes. He went on to conclude that selection must be operating against the hybrids, indicating that gene flow is being impeded through partial isolating mechanisms. This view, however, takes no account of the complexity of the system of recombination. A relatively simple system of recombination involving a small number of genes could produce both parental phenotypes in numbers far greater than 5%. Thus, in my view, the arbitrary decision to accept the occurrence of parentals in numbers greater than 5% in a zone of hybridization as evidence for reproductive isolation between them is of dubious value.

In most cases of avian hybridization, identification

of hybrids is based on plumage characters, often involving simple differences as in the classical case of the European crows Corvus corone and C. cornix. Unless plumage characters by which parentals and hybrids are distinguished are linked with the other morphological characters under study (a highly unlikely event considering the differential recombination and introgression of gene complexes in most cases of hybridization) then the plumage recombinants of Variable Oystercatchers will quite frequently be mistaken as true parentals. Therefore, it is probable that the frequencies of true parentals in the area of hybridization are grossly overestimated (see Chapter 4.9B) as they were made on the basis of plumage identification. In reality, hybrids are probably considerably more numerous than the true parentals taken together, and it is not possible to estimate whether the latter exceed the suggested 5% limit.

It is tempting to apply Short's (1969) reasoning and suggest that because of the presence of parentals in the hybrid zone, the hybrids are being selected against, and thus black and pied forms are partially reproductively isolated semispecies which should be accorded the taxonomic rank of species. However, without information on the age of the secondary contact or of temporal trends in the frequencies of the phenotypes, and with the knowledge that hybrids are equally viable, there can be few grounds for postulating selection against hybrids. Hence, I consider that the black and pied phase Variable Oystercatchers are better regarded as conspecific, not as semispecies as suggested by Oliver (1955). Until such time as partial isolating mechanisms between the parentals can be demonstrated conclusively, there can be no justification for according the black phase Variable Oystercatcher full species status as H. unicolor. Since the function of a taxonomy is to most clearly depict relationships, and as the Variable and

Australian Pied Oystercatchers have close affinities, they should be referred to a single species, the earliest name for which is longirostris. I conclude therefore that New Zealand has three species of oystercatcher as follows:

- (1) Haematopus ostralegus finschi Martens, 1897-  
South Island Pied  
Oystercatcher.
- (2) Haematopus chathamensis Hartert, 1927 - Chatham  
Islands Oyster-  
catcher.
- (3) Haematopus longirostris Vieillot, 1817- Variable  
Oystercatcher.

GENERAL SUMMARY.

This study of the systematics and affinities of New Zealand oystercatchers was initiated in the light of their unstable taxonomy. It aimed to clarify existing taxonomic confusion by examining, on a comparative basis, the distribution and abundance of the New Zealand taxa, their ecology and ethology, their morphology and their affinities.

Outside the breeding season the ranges of the mainland oystercatchers overlap, as the more abundant South Island Pied Oystercatcher (H. ostralegus finschi) leaves inland breeding sites for major coastal wintering haunts. The less numerous Variable Oystercatcher (H. longirostris) remains on the coast all year round, so in the breeding season the mainland species have allopatric distributions. The Chatham Islands Oystercatcher (H. chathamensis) is a rare form restricted to the islands, approximately 800 Km east of New Zealand.

Reproductive isolation of mainland species is assured by their allopatric breeding distribution and asynchronous breeding cycles, and is further enhanced by differential habitat selection, niche utilization and food requirements. The South Island Pied Oystercatcher breeds inland through most of the South Island in the period August to December, whereas Variable Oystercatchers breed coastally from late October to February. The breeding season of Chatham Islands Oystercatchers lies between that of the mainland species, but most closely resembles that of the South Island Pied Oystercatcher.

In winter, large flocks of South Island Pied Oystercatchers are concentrated on major harbours, estuaries and bays where they take mainly bivalve molluscs. Variable

Oystercatchers are common on rocky shores where they prey extensively on limpets. In northern New Zealand they do, however, spread onto sandy beaches and estuaries when the South Island Pied Oystercatcher is scarce or absent.

Competitive exclusion in terms of food requirements seems to explain the movement of Variable Oystercatchers away from the areas in which South Island Pied Oystercatchers are abundant.

New Zealand oystercatchers vary considerably in their morphology, both within and between species. Significant variation arises through age and sex, so that species comparisons have to be based on separate analyses of adult males and females. Sexual dimorphism, presumably due to Darwinian sexual selection, is most pronounced in the Chatham Islands Oystercatcher and the South Island Pied Oystercatcher, and is least pronounced in hybrids between black and pied phase Variable Oystercatchers.

Black phase Variable Oystercatchers show clinal variation in morphological characters, much of which can be accounted for as adaptive responses to climatic variables which are similarly clinal.

Wherever black and ~~pied~~ pied phase Variable Oystercatchers are sympatric they hybridize, although most hybridization occurs in Northland where both parentals are relatively abundant. Their mating is non-assortive with respect to colour phase, the hybrids are viable and do not seem subject to selective mortality, and parentals are present in the area of hybridization. The data on inheritance of colour phases are most simply explained in terms of polygenes involving a major gene whose dominance is expressed through the cumulative effects of several modifying genes at other loci.

Skin measurements divide the Australasian oystercatchers into two groups, one representing the South Island Pied Oystercatcher and one involving the other taxa. The

Chatham Islands Oystercatcher separates out of the second group in the multivariate case, and possibly represents an ancient form near the junction of H. ostralegus and H. longirostris, or it may be the result of colonization of the Chathams by a few aberrant H. ostralegus.

The black phase Variable Oystercatcher is thought to have arisen through an invasion of Australian H. longirostris, which became melanistic in New Zealand. The hybridization now evident between the pied and black phases is probably due to a secondary contact following another invasion of the Australian Pied Oystercatcher.

Without any evidence for the existence of partial isolating mechanisms between the parentals and the hybrids, it must be concluded that black and pied phase Variable Oystercatchers are conspecific. Because of the obvious affinities of the Australian Pied and Variable Oystercatchers, they are referred to a single species, the oldest name for which is longirostris. It is recommended that three species be recognized in New Zealand: H. ostralegus finschi (South Island Pied Oystercatcher), H. chathamensis (Chatham Islands Oystercatcher), and H. longirostris (Variable Oystercatcher).



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Any mistakes that remain in the final copy are my own.

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APPENDIX I.CENSUS DATA FOR SOUTH ISLAND PIED OYSTERCATCHERS.

Locality	Number	Date	Source	Latitude and Longitude
			Informant	Reference
NORTH ISLAND				
1. Parengarenga	35	May 1970	A.J.Baker	
2. The Bluff	1	Jan. 1971	A.J.Baker	
3. Kaimaumau	37	Jan. 1971	A.J.Baker	
4. Wainui Bay	24	May 1970	A.J.Baker	
5. Marsden Bay	130	Aug. 1970	M.Munro	Pers.comm.
6. Ruakaka	107	May 1971	A.J.Baker	
7. Waipu Estuary	2	May 1971	A.J.Baker	
8. Great Barrier Island	2	Jun. 1957	B.D.Bell & D.H.Brathwaite	Notornis 10(8):374 1964
9. Kaipara Harbour	5741	Jun. 1967	G.D.Leitch	O.S.N.Z. Rec.Scheme
10. Waitemata Harbour	62	Jun. 1967	A.J.Baker	
11. Whitford	7	Jun. 1958	H.R.McKenzie	Notornis 8(3):70 1959
12. Mataitai	35	May 1965	Miss A.J.Goodwin	O.S.N.Z. Rec.Scheme
13. Clevedon Estuary	48	May 1965	Miss A.J.Goodwin	O.S.N.Z. Rec.Scheme
14. Manakau Harbour	8804	Jun. 1970	H.R.McKenzie	Pers.comm.
15. Tairua	17	May 1970	A.J.Baker	
16. Firth of Thames	2503	Jul. 1970	H.R.McKenzie	Pers.comm.

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
17. Waikato Heads	77	Jun. 1967	Mrs. B. Brown	O.S.N.Z. Rec. Scheme	37°21'	174°42'
18. Athenree	40	Jun. 1966	R. St. Paul	O.S.N.Z. Rec. Scheme	37°27'	175°55'
19. Bowentown	18	Aug. 1960	M. J. Imber	Notornis 9(3):74 1960	37°28'	175°59'
20. Maketu	2	May 1958	H. R. McKenzie	Notornis 8(3):70 1959	37°45'	176°26'
21. Raglan Harbour	2	Apr. 1954	H. R. McKenzie	Notornis 6(3):94 1955	37°48'	174°54'
22. Whakatane Heads	1	Jun. 1954	Mrs. d'Auvergne	Notornis 6(3):94 1955	37°56'	176°59'
23. Aotea Harbour	40	Jun. 1956	C. R. Buckeridge	Notornis 7(3):79 1957	37°58'	174°51'
24. Ohiwa Harbour	2	Sep. 1950	J. C. Davenport	Notornis 4(3):44 1951	38°00'	177°04'
25. Kawhia Harbour	56	Jan. 1962	Mrs. Templer	O.S.N.Z. Rec. Scheme	38°05'	174°50'
26. Muriwai, Gisborne	3	Apr. 1967	A. Blackburn	O.S.N.Z. Rec. Scheme	38°45'	177°55'
27. Ahuriri Estuary (Napier)	7	May 1971	A. J. Baker		39°28'	176°51'
28. Rangitikei Estuary	4	Jun. 1963	I. G. Andrew	Pers. comm.	40°17'	175°13'
29. Porangahau	62	Jun. 1952	D. H. Brathwaite	Notornis 5(3):92 1953	40°19'	176°38'



Locality	Number	Date	Source		Latitude and Longitude
			Informant	Reference	
30. Manawatu Estuary	60	May 1969	I.G.Andrew	Pers.comm.	40°28' 175°08'
31. Hokio Beach	10	May 1967	E.B.Jones	O.S.N.Z. Rec.Scheme	40°36' 175°12'
32. Waikanae	6	Apr.1961	M.J.Imber	Notornis 9(7):241 1961	40°52' 175°00'
33. Plimmerton	6	Aug.1969	L.R.Moran	Pers.Comm.	41°04' 174°51'
34. Lake Wairarapa	2	Jun.1952	R.H.D.Stidolph	Notornis 5(3):92 1953	41°14' 174°51'
35. Port Nicholson	17	May 1970	A.J.Baker		41°16' 174°52'
	<u>17946</u>				
SOUTH ISLAND					
36. Farewell Spit	6160	Jun.1971	A.J.Baker		40°30' 172°50'
37. Whanganui Inlet	680	Aug.1970	A.J.Baker		40°35' 172°35'
38. Golden Bay	3700	Jun.1967	A.J.Baker		40°40' 172°48'
39. Marahau Estuary	400+	Sep.1956	M.J.Breen	Notornis 7(3):80 1957	41°00' 173°01'
40. Sandy Bay	22	May 1970	A.J.Baker		41°01' 173°01'
41. Kaiteriteri	27	May 1970	A.J.Baker		41°03' 173°01'
42. Riwaka	850	May 1967	A.T.Edgar	O.S.N.Z. Rec.Scheme	41°04' 172°58'
43. Motueka	1000	Jun.1970	A.J.Baker		41°05' 173°01'
44. Karamea	60	Jun.1959	H.R.McKenzie	Notornis 8(7):203 1960	41°15' 172°06'

Locality	Number	Date	Source		Latitude and Longitude
			Informant	Reference	
45. Mapua	17	Jun. 1969	A. J. Baker		41°15' 173°06'
46. Nelson Harbour	350	May 1967	A. J. Baker		41°16' 173°16'
47. Ngakuta Bay	21	Mar. 1971	R. M. Weston	Pers. comm.	41°17' 174°01'
48. Wairau River- mouth	14	Aug. 1970	A. J. Baker		41°30' 174°03'
49. Cape Campbell	11	Aug. 1970	A. J. Baker		41°44' 171°16'
50. Westport	30	Oct. 1961	E. W. Crack	O. S. N. Z. Rec. Scheme	41°45' 171°36'
51. Okari River- mouth	100+	Jan. 1955	T. J. Packer	Notornis 6(7):203 1956	41°50' 171°27'
52. Fox Rivermouth	1	Jun. 1956	J. R. Jackson	Notornis 7(3):80 1957	42°02' 171°23'
53. Kaikoura Penin- sula	28	Jun. 1970	A. J. Baker		42°25' 173°42'
54. Motunau River- mouth	12	Feb. 1964	R. H. Taylor	D. S. I. R. Bull. 178:60 1967	43°02' 173°05'
55. Waipara River- mouth	500+	Nov. 1956	B. D. Heather	Notornis 7(3):80 1957	43°08' 172°50'
56. Okarito Lagoon	92	Jul. 1970	A. J. Baker		43°12' 170°13'
57. Ashley River- mouth	102	Jun. 1966	A. J. Baker		43°17' 172°43'
58. Waimakariri Estuary	285	Jun. 1970	A. J. Baker		43°27' 172°31'
59. Spencer Park	104	Apr. 1966	A. J. Baker		43°28' 172°42'
60. Heathcote-Avon Estuary	4100	Jun. 1971	A. J. Baker		43°33' 172°44'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
61. Governors Bay	60	Jun.1967	I.Stirling	Pers.comm.	43°38'	172°39'
62. Okain's Bay	18	Jun.1967	J.D.Coleman	Pers.comm.	43°43'	173°02'
63. Le Bons Bay	30	Jul.1967	J.D.Coleman	Pers.comm.	43°46'	173°03'
64. Robinson's Bay	46	May 1971	Mrs. S.M.Baker	Pers.comm.	43°48'	172°58'
65. Duvauchelles	100	May 1971	A.J.Baker		43°48'	172°59'
66. Rakaia River- mouth	27	Jul.1969	A.J.Baker		43°53'	172°17'
67. Okuru River- mouth	12	Feb.1963	H.R.McKenzie	O.S.N.Z. Rec.Scheme	43°54'	168°55'
68. Jackson Bay	14	May 1967	A.J.Baker		43°57'	168°40'
69. Orari Rivermouth	2	May 1968	A.J.Baker		44°10'	171°30'
70. Awarua Bay	20	Jan.1947	L.T.Bell	N.Z.Bird Notes 3(1):20 1948	44°18'	168°05'
71. Martin's Bay	3	Jan.1947	L.T.Bell	N.Z.Bird Notes 3(1):20 1948	44°22'	167°59'
72. Washdyke Lagoon	62	Jul.1970	P.Sagar	Pers.comm.	44°22'	171°15'
73. Katiki Beach	4	Jun.1970	A.J.Baker		45°26'	170°49'
74. Karitane	6	Mar.1962	Dunedin Natura- lists Club	O.S.N.Z. Rec.Scheme	45°38'	170°39'
75. Blueskin Bay	984	Mar.1965	Mrs.J.A.Hamel	O.S.N.Z. Rec.Scheme	45°44'	170°34'
76. Purakanui Bay	132	Jun.1963	W.T.Poppelwell	O.S.N.Z. Rec.Scheme	45°46'	170°37'
77. Otago Harbour	3238	Jun.1963	J.A.Watt	O.S.N.Z. Rec.Scheme	45°50'	170°36'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
78. Papanui Inlet	400	Jul.1965	A.Cunninghame	O.S.N.Z. Rec.Scheme	45°51'	170°41'
79. Hooper's Inlet	80	Jun.1965	B.Cunninghame	O.S.N.Z. Rec.Scheme	45°52'	170°40'
80. Kuri Bush	40+	Sep.1952	Mrs.I.Tily	Notornis 5(8):92 1953	46°02'	170°14'
81. Taieri River- mouth	203	Feb.1961	W.T.Poppelwell	Notornis 9(4):241 1961	46°03'	170°12'
82. Te Wae Wae Bay	52	Jun.1969	A.J.Baker		46°09'	167°27'
83. Lake Tuakitoto	60+	Feb.1963	H.R.McKenzie	O.S.N.Z. Rec.Scheme	46°14'	169°49'
84. Riverton Estuary	511	Jun.1971	A.J.Baker		46°21'	168°01'
85. Colac Bay	7	Jun.1969	A.J.Baker		46°22'	167°53'
86. Waimatuku River- mouth	98	Jan.1969	P.Muller	Notornis 16(2):126 1969	46°22'	168°10'
87. Kaka Point	17	Jun.1970	A.J.Baker		46°23'	169°47'
88. Owaka Heads	359	Jun.1970	A.J.Baker		46°23'	169°40'
89. Oreti Beach	22	Aug.1964	Mrs.Barlow	O.S.N.Z. Rec.Scheme	46°26'	168°14'
90. Oreti Estuary	2150	Jan.1969	P.Muller	Notornis 16(2):126 1969	46°28'	168°19'
91. Pounawea	350	Jun.1967	A.J.Baker		46°28'	169°42'
92. Surat Bay	5	Jun.1970	A.J.Baker		46°29'	169°45'
93. Jack's Bay	5	Jun.1970	A.J.Baker		46°30'	169°43'

Locality	Number	Date	Source		Latitude and Longitude
			Informant	Reference	
94. Tahakopa Bay	72	Jun. 1970	A.J. Baker		46° 31' 169° 21'
95. Bluff Harbour	56	Jun. 1970	A.J. Baker		46° 34' 168° 21'
96. Awarua Bay	453	Jan. 1969	P. Muller	Notornis 16(2):126 1969	46° 34' 168° 25'
97. Waituna Lagoon	78	Jan. 1969	P. Muller	Notornis 16(2):126 1969	46° 34' 168° 35'
98. Toetoes Harbour	452	Jan. 1969	P. Muller	Notornis 16(2):126 1969	46° 34' 168° 46'
99. Fortrose	210	Jun. 1970	A.J. Baker		46° 34' 168° 48'
100. Tautuku Bay	7	Feb. 1963	H.R. McKenzie	O.S.N.Z. Rec. Scheme	46° 35' 169° 26'
101. Waikawa	700	Mar. 1963	B.D. Bell & B.D. Heather	O.S.N.Z. Rec. Scheme	46° 38' 169° 00'
102. Porpoise Bay	3	Nov. 1970	A.J. Baker		46° 39' 169° 06'
103. Port William	1	Jan. 1952	W.A. Watters	Notornis 5(3):92 1953	46° 51' 168° 05'
104. Paterson Inlet	360	Jan. 1964	Mrs. M.L. Barlow	O.S.N.Z. Rec. Scheme	46° 55' 168° 00'
105. The Neck	142	Jun. 1971	A.J. Baker		46° 57' 168° 13'
106. Mutton Bird	1-2	Jun. 1965	A. Blackburn	Notornis 12(4):205 1965	47° 13' 167° 23'

S.I.	30851
N.I.	17946
G.Total	48797
<u>    </u>	49000

APPENDIX II.CENSUS DATA FOR BLACK OYSTERCATCHERS.

Locality	Number	Date	Source		Latitude and	
			Informant	Reference	Longitude	
NORTH ISLAND						
1. Tom Bowling Bay	3	Jan. 1967	A.T. Edgar	Pers. comm.	34°25'	172°58'
2. Waikuku Beach	6	Jan. 1971	D.E. Crockett	Pers. comm.	34°26'	173°00'
3. Spirits Bay	4	Jan. 1971	W. Campbell	Pers. comm.	34°27'	172°50'
4. Te Werahi	4	Jan. 1971	A.J. Baker		34°28'	172°40'
5. Whareana Beach	4	Jan. 1971	T.R. Calvert	Pers. comm.	34°28'	173°00'
6. Twilight Beach	2	Jan. 1971	C.R. Veich	Pers. comm.	34°30'	172°42'
7. Ngakino	4	Jan. 1970	A.J. Baker		34°30'	172°44'
8. Coal Point	3	Jan. 1970	A.J. Baker		34°31'	173°00'
9. Parengarenga	3	Jan. 1970	A.J. Baker		34°31'	172°56'
10. Scott Point	13	May 1970	A.T. Edgar	Pers. comm.	34°31'	172°42'
11. Bluff to Te Paki Stream	19	May 1970	A.T. Edgar	Pers. comm.	34°36'	172°46'
12. The Bluff	21	May 1970	A.T. Edgar	Pers. comm.	34°41'	172°53'
13. Great Exhibition Bay	33	Jan. 1971	T.R. Calvert	Pers. comm.	34°42'	173°04'
14. Rarawa	1	Jan. 1971	A.J. Baker		34°44'	173°05'
15. Ninety Mile to Bluff	6	May 1970	A.T. Edgar	Pers. comm.	34°46'	172°58'
16. Henderson Bay	4	Jan. 1971	R. Slack	Pers. comm.	34°47'	173°09'
17. Kowhai Beach	2	Jan. 1971	A.J. Baker		34°47'	173°09'
18. Houhora Harbour	2	Jan. 1971	R. Slack	Pers. comm.	34°49'	173°10'
19. Rangaunu Bay	5	Jan. 1971	A.J. Baker		34°49'	173°19'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
20. Karikari Bay	7	Jan.1971	Mrs.S.Reed	Pers.comm.	34°54'	173°20'
21. Kaimaumau	8	Jan.1971	A.J.Baker		34°55'	173°16'
22. Tokerau	6	Jan.1971	A.J.Baker		34°59'	173°25'
23. Taipa	2	Jan.1970	A.J.Baker		35°00'	173°28'
24. Taupo Bay	1	Jan.1968	A.T.Edgar	Pers.comm.	35°00'	173°43'
25. Wainui Bay	1	Jan.1968	A.T.Edgar	Pers.comm.	35°01'	173°51'
26. Matauri Bay	2	Jan.1970	A.J.Baker		35°02'	173°55'
27. Takou Bay	6	Jan.1971	A.J.Baker		35°06'	173°58'
28. Taronui Bay	4	Jan.1971	A.J.Baker		35°07'	173°58'
29. Kerikeri Inlet	3	Mar.1968	A.T.Edgar	Pers.comm.	35°12'	174°01'
30. Whangamumu	2	Jan.1970	A.J.Baker		35°15'	174°16'
31. Herekino Heads	7	Jan.1968	A.T.Edgar	Pers.comm.	35°17'	173°11'
32. Bland Bay	1	Jan.1970	A.J.Baker		35°20'	174°22'
33. Mitimiti	4	Jan.1970	A.J.Baker		35°26'	173°16'
34. Mimiwhangata	2	Jan.1970	A.J.Baker		35°26'	174°24'
35. Whangape-Hoki- anga	14	Jan.1960	A.T.Edgar	Pers.comm.	35°27'	173°14'
36. Waimamaku	3	Jan.1968	A.T.Edgar	Pers.comm.	35°36'	173°25'
37. Waipoua	7	Jan.1968	A.T.Edgar	Pers.comm.	35°40'	173°29'
38. Ngunguru Bay	2	Apr.1970	M.Munro	Pers.comm.	35°40'	174°31'
39. McLeods Bay	5	May 1970	M.Munro	Pers.comm.	35°46'	174°32'
40. Taurikura	1	May 1970	M.Munro	Pers.comm.	35°48'	174°31'
41. Marsden Bay	2	Aug.1970	M.Munro	Pers.comm.	35°50'	174°30'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
42. Bream Bay	1	Nov. 1970	M. Munro	Pers. comm.	35°51'	174°36'
43. Ruakaka	7	May 1970	A. J. Baker		35°54'	174°26'
44. Waipu Estuary	7	May 1971	A. J. Baker		36°00'	174°28'
45. Mangawai Estuary	3	Jan. 1970	A. J. Baker		36°07'	174°35'
46. Great Barrier Is.	18	Dec. 1960	B. D. Bell & D. H. Brathwaite	Notornis 10(8):374 1968	36°11'	175°25'
47. Te Arai	4	Jan. 1967	J. F. Bell	O. S. N. Z. Rec. Scheme	36°12'	174°35'
48. Pakiri	2	Jan. 1970	A. J. Baker		36°15'	174°44'
49. Kaipara Harbour	5	Jan. 1965	H. R. McKenzie	Notornis 12(2):76 1965	36°24'	174°15'
50. Waikawau Bay	5	Dec. 1964	B. D. Bell	Pers. comm.	36°36'	175°32'
51. Kennedy Bay	2	Dec. 1964	B. D. Bell	Pers. comm.	36°40'	175°33'
52. Otama Beach	2	Dec. 1964	B. D. Bell	Pers. comm.	36°42'	175°45'
53. Kuaotunu Beach	1	Dec. 1964	B. D. Bell	Pers. comm.	36°43'	175°44'
54. Opito Bay	1	Dec. 1964	B. D. Bell	Pers. comm.	36°43'	175°49'
55. Whangapoua Harbour	4	Dec. 1964	B. D. Bell	Pers. comm.	36°44'	175°38'
56. Buffalo Beach	1	Dec. 1964	B. D. Bell	Pers. comm.	36°49'	175°42'
57. Cook's Beach	6	Dec. 1964	B. D. Bell	Pers. comm.	36°50'	175°44'
58. Kawakawa Bay	2	Nov. 1968	Mrs. J. A. Brown	Pers. comm.	36°57'	175°10'
59. Manakau Harbour	1	Dec. 1970	H. R. McKenzie	Pers. comm.	36°59'	174°46'
60. Tairua Harbour	6	Jan. 1970	A. J. Baker		37°00'	175°51'



Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
61. Pawanui Beach	7	Dec.1964	B.D.Bell	Pers.comm.	37°00'	175°52'
62. Opoutere	20	Jun.1967	H.R.McKenzie	Pers.comm.	37°06'	175°53'
63. Firth of Thames	5	Oct.1970	H.R.McKenzie	Pers.comm.	37°06'	175°24'
64. Waikato Heads	6	May 1971	Mrs.J.A.Brown	Pers.comm.	37°21'	175°02'
65. Hicks Bay	9	Mar.1954	Miss A.J.Goodwin	Notornis 6(3):96 1955	37°35'	178°18'
66. Mount Maunganui	2	Sep.1952	M.Hodgkin	Notornis 5(3):92 1953	37°38'	176°11'
67. Motiti Island	2	Jan.1953	B.Sladden	Notornis 5(7):224 1954	37°38'	176°25'
68. Maketu	9	Aug.1966	H.R.McKenzie	Pers.comm.	37°45'	176°26'
69. Waihi Estuary	7	May 1970	A.J.Baker		37°46'	176°28'
70. Rurima Rocks	8	Jan.1953	B.Sladden	Notornis 5(7):224 1954	37°50'	176°53'
71. Rangitaiki River- mouth	1	Jan.1970	A.J.Baker		37°55'	176°53'
72. Whakatane Heads	3	Jan.1970	A.J.Baker		37°56'	176°59'
73. Ohope Beach	12	Aug.1965	R.M.Weston	Pers.comm.	37°58'	177°00'
74. Ohiwa Harbour	5	Jan.1970	A.J.Baker		38°00'	177°04'
75. Kawhia Harbour	2	Jul.1954	H.R.McKenzie	Notornis 6(3):96 1955	38°05'	174°50'
76. Tolaga Bay	3	Jan.1970	A.J.Baker		38°22'	178°19'
77. Tatapouri	1	Jan.1970	A.J.Baker		38°39'	178°09'

Locality	Number	Date	Source	Informant	Reference	Latitude and Longitude
78. Muriwai, Gisborne	2	Jan. 1971	A. J. Baker			38°45' 177°56'
79. Mahia Peninsula (Opoutotama)	9	Jan. 1970	A. Blackburn		O.S.N.Z. Rec. Scheme	39°10' 177°53'
80. Waitotara	2	Nov. 1970	D. E. Crockett		Pers. comm.	39°50' 174°40'
81. Kaitoke	1	Nov. 1970	D. E. Crockett		Pers. comm.	39°58' 175°05'
82. Turakina River- mouth to Rangitikei	8	Jun. 1969	I. G. Andrew & D. E. Crockett		Pers. comm.	40°09' 175°10'
83. Rangitikei Estuary	8	Mar. 1968	I. G. Andrew		Pers. comm.	40°17' 175°13'
84. Porangahau	2	Nov. 1950	K. Wodzicki		Notornis 4(7):183 1952	40°19' 176°38'
85. Rangitikei to Foxton	4	Jun. 1969	I. G. Andrew		Pers. comm.	40°22' 175°12'
86. Manawatu Heads	8	Aug. 1969	I. G. Andrew		Pers. comm.	40°27' 175°07'
87. Manawatu Estuary	3	Aug. 1969	I. G. Andrew		Pers. comm.	40°28' 175°08'
88. Ohau to Manawatu Heads	7	Aug. 1969	I. G. Andrew		Pers. comm.	40°38' 175°10'
89. Waikawa Beach	1	Feb. 1969	I. G. Andrew		Pers. comm.	40°41' 175°09'
90. Ohau Estuary	6	Aug. 1969	I. G. Andrew		Pers. comm.	40°42' 175°15'
91. Otaki Rivermouth	2	Aug. 1970	A. J. Baker			40°46' 175°06'
92. Mataikona River- mouth	2	Dec. 1951	R. H. D. Stidolph		Notornis 5(3):92 1953	40°48' 176°17'
93. Waikanae	2	Nov. 1970	A. J. Baker			40°52' 175°00'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
94. Castlepoint	3	Dec. 1951	R.H.D. Stidolph	Notornis 5(3):92 1953	40°55'	176°14'
95. Port Nicholson	26	Aug. 1970	A.J. Baker		41°16'	174°52'
96. Palliser Bay	2	Nov. 1970	R.A. Falla	Pers. comm.	41°27'	175°09'
	509					
SOUTH ISLAND						
97. Cape Farewell	17	May 1971	A.J. Baker		40°30'	172°41'
98. Farewell spit	18	Dec. 1970	A.J. Baker		40°35'	172°50'
99. Whanganui Inlet	7	Dec. 1970	A.J. Baker		40°35'	172°35'
100. Stephens Island	1	Dec. 1896	G.E. & E.W. Dawson	Notornis 8(2):42 1958	40°40'	174°00'
101. Collingwood	3	May 1971	A.J. Baker		40°41'	172°41'
102. Patarau	16	Aug. 1970	A.J. Baker		40°42'	172°30'
103. Ligar Bay	2	Aug. 1970	A.J. Baker		40°49'	172°54'
104. D'Urville Island	16	Aug. 1969	A.J. Baker		40°50'	173°51'
105. Chetwode Islands	17	Dec. 1970	C.R. Veitch	Pers. comm.	40°54'	174°05'
106. French Pass	4	Aug. 1969	A.J. Baker		40°56'	173°51'
107. Duffers Reef	4	Dec. 1970	C.R. Veitch	Pers. comm.	40°57'	174°03'
108. Heaphy River- mouth	12	Dec. 1966	R.J. Scarlett	Notornis 14(1):32 1969	40°58'	172°08'
109. Sandy Bay	2	Jan. 1970	J.D. Coleman	Pers. comm.	41°01'	173°01'

Locality	Number	Date	Source		Latitude and	
			Informant	Reference	Longitude	
110. Kaiteriteri	4	Jan. 1970	J.D. Coleman	Pers. comm.	41°03'	173°01'
111. Ship Cove	1	Nov. 1942	R.H.D. Stidolph	N.Z. Bird Notes 1(3):22 1943	41°06'	174°14'
112. Croiselles Harbour	2	Jun. 1969	A.J. Baker		41°06'	173°35'
113. Long Island	1	Dec. 1970	R. Simpson & T. Walker	Pers. comm.	41°07'	174°17'
114. Pickersgill Island	2	Jan. 1939	R.H.D. Stidolph	N.Z. Bird Notes 1(3):22 1943	41°10'	174°17'
115. Mapua	1	Jan. 1969	A.J. Baker		41°15'	173°06'
116. Nelson Harbour	8	Aug. 1969	A.J. Baker		41°16'	173°16'
117. Arapawa Island	2	Jan. 1939	R.H.D. Stidolph	N.Z. Bird Notes 1(3):22 1943	41°11'	174°19'
118. Port Underwood	2	Aug. 1970	A.J. Baker		41°20'	174°07'
119. Wairau Rivermouth	1	Aug. 1970	A.J. Baker		41°30'	174°03'
120. Awatere River- mouth	2	Aug. 1970	A.J. Baker		41°36'	174°10'
121. Cape Campbell	7	Aug. 1970	A.J. Baker		41°44'	174°16'
122. Orowaiti	2	Feb. 1969	J. Jenkins	O.S.N.Z. Rec. Scheme	41°45'	171°38'
123. Okari Rivermouth	5	Jan. 1955	T.J. Packer	Notornis 6(7):203 1956	41°50'	171°27'
124. Punakaiki	2	Jul. 1971	A.J. Baker		42°07'	171°20'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
125. Barrytown	5	Jun. 1970	A. J. Baker		42°14'	171°20'
126. Kaikoura	2	Jul. 1970	A. J. Baker		42°25'	173°42'
127. Waiau Rivermouth	7	Dec. 1969	A. J. Baker		42°45'	173°20'
128. Totara Rivermouth	4	Dec. 1950	T. J. Packer	Notornis 5(3):92 1953	42°52'	171°30'
129. Motunau Island	1	Nov. 1967	J. Warham	Pers. comm.	43°04'	173°05'
130. Waipara River- mouth	2	Dec. 1968	A. J. Baker		43°08'	172°50'
131. Okarito Lagoon	27	Aug. 1971	A. J. Baker		43°12'	170°13'
132. Ashley Rivermouth	2	Dec. 1968	A. J. Baker		43°17'	172°43'
133. Gillespies Beach	3	Aug. 1971	A. J. Baker		43°25'	169°49'
134. Heathcote-Avon Estuary	2	Jul. 1971	A. J. Baker		43°33'	172°44'
135. Bruce Bay	11	Jul. 1971	A. J. Baker		43°35'	169°42'
136. Pigeon Bay	1	Jun. 1968	A. J. Baker		43°41'	172°53'
137. Waita Rivermouth	1	Jun. 1971	A. J. Baker		43°47'	169°07'
138. Haast Rivermouth	3	Jun. 1971	A. J. Baker		43°50'	169°02'
139. Open Bay Islands	26	Jun. 1971	E. H. Miller	Pers. comm.	43°52'	168°53'
140. Robinson's Bay	2	May 1971	A. J. Baker		43°56'	172°58'
141. Jackson Bay	18	Jun. 1971	A. J. Baker		43°57'	168°40'
142. Cascade River- mouth	2	Jul. 1948	D. Greaney	Pers. comm.	44°01'	168°22'
143. Awarua Bay	20	Jan. 1947	L. J. Bell	N. Z. Bird Notes 3(1):20 1948	44°18'	168°05'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
144. Washdyke Lagoon	4	Jan.1971	A.J.Baker		44°22'	171°21'
145. Martin's Bay	3	Jul.1948	D.Greaney	Pers.comm.	44°22'	167°49'
146. Milford Sound	2	Dec.1948	L.W.McCaskill	N.Z.Bird Notes 3(8): 208 1950	44°34'	167°48'
147. Routeburn Valley	27	Jan.1947	Dunedin N.F.C.	N.Z.Bird Notes 2(6):145 1947	44°44'	168°19'
148. George Sound	20	Feb.1948	P.C.Bull	D.S.I.R.Bull. 83, 1949	44°50'	167°20'
149. Caswell Sound	2	Feb.1948	P.C.Bull	D.S.I.R.Bull. 83, 1949	44°59'	166°57'
150. Charles Sound	20	Feb.1948	P.C.Bull	D.S.I.R.Bull. 83, 1949	45°02'	167°04'
151. Secretary Island	2	Feb.1948	P.C.Bull	D.S.I.R.Bull. 83, 1949	45°13'	166°46'
152. Doubtful Sound	4	Apr.1963	W.T.Poppelwell	O.S.N.Z. Rec.Scheme	45°16'	166°37'
153. Moeraki	4	Jun.1971	A.J.Baker		45°21'	170°50'
154. Kaitiki	11	Jan.1965	W.T.Poppelwell	O.S.N.Z. Rec.Scheme	45°26'	170°49'
155. Pleasant River- mouth	2	Dec.1969	A.J.Baker		45°34'	170°43'
156. Karitane	2	Jul.1965	I.McVinnie	O.S.N.Z. Rec.Scheme	45°38'	170°39'
157. Goose Cove	50	Feb.1948	P.C.Bull	D.S.I.R.Bull. 83, 1949	45°39'	166°33'
158. Resolution Island	3	Feb.1948	P.C.Bull	D.S.I.R.Bull. 83, 1949	45°40'	166°35'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
159. Duck Cove	4	Feb. 1948	P.C. Bull	D.S.I.R. Bull.	45°44'	166°38'
				83, 1949		
160. Aramoana	15	Nov. 1967	Mrs. J.A. Hamel	O.S.N.Z. Rec. Scheme	45°47'	170°42'
161. Dusky Sound	20	Apr. 1965	J. Hall-Jones	Notornis 13(2):93 1966	45°47'	166°30'
162. Otago Peninsula	10	Dec. 1970	A. J. Baker		45°51'	170°45'
163. St. Kilda Beach	2	Dec. 1970	A. J. Baker		45°55'	170°31'
164. Green Island Lagoon	1	Dec. 1970	A. J. Baker		45°57'	170°23'
165. Taiari Rivermouth	2	Dec. 1970	A. J. Baker		46°03'	170°12'
166. Akatore	1	Dec. 1970	A. J. Baker		46°07'	170°11'
167. Waiiau Rivermouth	4	Dec. 1969	A. J. Baker		46°09'	167°40'
168. Te Waewae Bay West	7	Dec. 1969	A. J. Baker		46°09'	167°27'
169. Tokomairiro Rivermouth	2	Dec. 1970	A. J. Baker		46°13'	170°03'
170. Howells Point	24	Jun. 1971	A. J. Baker		46°20'	168°02'
171. Riverton Estuary	36	Jun. 1971	A. J. Baker		46°21'	168°10'
172. Colac Bay	4	Dec. 1970	A. Moeed	Pers. comm.	46°22'	167°53'
173. Kaka Point	2	Jun. 1971	A. J. Baker		46°23'	169°47'
174. Nugget Point	2	Jun. 1971	A. J. Baker		46°27'	169°49'
175. New River Harbour	4	Dec. 1969	A. J. Baker		46°28'	168°19'
176. Pounaweia	2	Nov. 1971	Mrs. J.A. Hamel	Pers. comm.	46°28'	169°42'
177. Jack's Bay	2	Nov. 1971	Mr. J.A. Hamel	Pers. comm.	46°30'	169°43'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
178. Purakaunui Bay	2	Dec.1970	A.Moeed	Pers.comm.	46°30'	169°33'
179. Tahakopa Bay	6	Dec.1970	A.Moeed	Pers.comm.	46°31'	169°21'
180. Hinahina Cove	2	Dec.1970	A.Moeed	Pers.comm.	46°32'	169°39'
181. Pillan's Head	4	Nov.1971	Mrs.J.A.Hamel	Pers.comm.	46°34'	169°33'
182. Toetoes Harbour	10	Jan.1969	P.Muller	Notornis 16(2):130 1969	46°34'	168°46'
183. Waituna Lagoon	3	Jan.1969	P. Muller	Notornis 16(2):130 1969	46°34'	168°35'
184. Long Point	11	Dec.1970	A. Moeed	Pers.comm.	46°35'	169°28'
185. Mahaka	2	Nov.1970	Mrs.J.A.Hamel	Pers.comm.	46°35'	169°27'
186. Tautuku Beach	5	Nov.1970	Mrs.J.A.Hamel	Pers.comm.	46°35'	169°26'
187. Bluff	4	Jun.1971	A.J.Baker		46°36'	168°21'
188. Waipati Beach	6	Dec.1970	A.Moeed	Pers.comm.	46°37'	169°21'
189. Waikawa	2	Dec.1969	A.J.Baker		46°38'	169°08'
190. Porpoise Bay	2	Dec.1970	A.Moeed	Pers.comm.	46°39'	169°06'
191. Ruapuke Island	Several pairs	Dec.1963	W.A.Watters	Notornis 10(6):305 1963	46°46'	168°21'
192. Codfish Island	4	Dec.1966	A.Blackburn	Notornis 15(2):61 1968	46°47'	167°29'
193. Port William	2	Jan.1950	Mrs. I.Tily	Notornis 4(6):150 1951	46°51'	168°55'
194. Butterfields Beach	19	Jun.1971	H.Best	Pers.comm.	46°53'	168°08'
195. Paterson Inlet	43	Jun.1971	H.Best	Pers.comm.	46°55'	168°00'



Locality	Number	Date	Source Informant	Reference	Latitude and Longitude
196. Mason Bay	17	Feb. 1951	E.W. Dawson	Notornis 4(6):147 1951	46°55' 167°39'
197. The Neck	34	Jun. 1971	H. Best	Pers. comm.	46°57' 168°13'
198. Port Pegasus	16	Dec. 1969	A.J. Baker		47°12' 167°39'
199. Mutton Bird Islands	Present	Aug. 1964	A. Blackburn	Notornis 12(5):205 1965	47°13' 167°23'
	S.I.	774			
	N.I.	509			
G. Total		<u>1283</u>			
		<u>1300</u>			

APPENDIX III.CENSUS DATA FOR NORTHERN PIED OYSTERCATCHERS.

Locality	Number	Date	Source	Latitude and Longitude
			Informant	Reference
NORTH ISLAND				
1. Te Werahi	1	Jan.1971	A.J.Baker	34°28' 172°40'
2. Ngakino	2	Jan.1971	A.J.Baker	34°30' 172°44'
3. Parengarenga	5	Jan.1970	A.J.Baker	34°31' 172°56'
4. Scott Point	10	May 1970	A.T.Edgar	Pers.comm. 34°31' 172°42'
5. Bluff to Te Paki Stream	11	May 1970	A.T.Edgar	Pers.comm. 34°36' 172°46'
6. The Bluff	20	May 1970	A.T.Edgar	Pers.comm. 34°41' 172°53'
7. Great Exhibition Bay	7	Jan.1971	T.R.Calvert	Pers.comm. 34°42' 173°04'
8. Ahipara to Bluff	1	May 1970	A.T.Edgar	Pers.comm. 34°46' 172°58'
9. Henderson Bay	2	Jan.1971	R.Slack	Pers.comm. 34°47' 173°08'
10. Kowhai Beach	9	Jan.1971	A.J.Baker	34°47' 173°09'
11. Kaimaumu	3	Jan.1971	A.J.Baker	34°55' 173°16'
12. Tokerau	1	Jan.1971	A.J.Baker	34°59' 173°25'
13. Wainui Bay	1	Sep.1967	A.T.Edgar	Pers.comm. 35°01' 173°53'
14. Takou Bay	3	Jan.1971	A.J.Baker	35°06' 173°58'
15. Taronui Bay	1	Jan.1971	A.J.Baker	35°07' 173°58'
16. Kerikeri Inlet	4	Mar.1967	A.T.Edgar	Pers.comm. 35°12' 174°01'
17. Herekino Heads	1	Jan.1968	A.T.Edgar	Pers.comm. 35°18' 173°11'
18. Mimiwhangata	1	Jan.1970	A.J.Baker	35°26' 174°24'

Locality	Number	Date	Source	Latitude and Longitude
			Informant	Reference
19. Mitimiti	1	Jan. 1970	A. J. Baker	35°26' 173°16'
20. Whangape-Hokianga	15	Sep. 1966	A. T. Edgar	Pers. comm. 35°27' 173°14'
21. Waimamaku	3	Jan. 1968	A. T. Edgar	Pers. comm. 35°36' 173°25'
22. Waipoua	9	Jan. 1968	A. T. Edgar	Pers. comm. 35°40' 173°29'
23. Ngunguru Bay	1	Apr. 1970	M. Munro	Pers. comm. 35°40' 174°31'
24. McLeods Bay	7	Apr. 1970	M. Munro	Pers. comm. 35°46' 174°32'
25. Ruakaka Estuary	26	May 1971	A. J. Baker	35°54' 174°26'
26. Waipu Estuary	13	May 1971	A. J. Baker	36°00' 174°28'
27. Mangawhai Estuary	5	May 1970	A. J. Baker	36°07' 174°25'
28. Great Barrier Island	4	Dec. 1960	B. D. Bell & D. H. Brathwaite	Notornis 10(8):374 1964 36°11' 175°25'
29. Pakiri	1	May 1970	A. J. Baker	36°15' 174°44'
30. Kaipara Harbour	8	Jan. 1965	H. R. McKenzie	Notornis 12(2):76 1965 36°24' 174°15'
31. Wairiri (Coromandel)	1	Dec. 1964	B. D. Bell	Pers. comm. 36°43' 175°36'
32. Kuaotunu Beach	1	Dec. 1964	B. D. Bell	Pers. comm. 36°43' 175°44'
33. Opito Bay	2	Dec. 1964	B. D. Bell	Pers. comm. 36°43' 175°49'
34. Cooks Beach	2	Dec. 1964	B. D. Bell	Pers. comm. 36°50' 175°44'
35. Tairua Harbour	1	Jan. 1970	A. J. Baker	37°00' 175°51'
36. Pawanui Beach	2	Dec. 1964	B. D. Bell	Pers. comm. 37°00' 175°52'
37. Waikato Heads	7	May 1971	Mrs. J. A. Brown	Pers. comm. 37°21' 175°02'
38. Athenree	2	Jan. 1970	A. J. Baker	37°27' 175°55'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
39. Bowentown	4	Aug. 1970	R.B. Sibson	Notornis 9(3):75 1960	37°28'	175°59'
40. Mt. Maunganui	2	Mar. 1964	M. Hodgkins	O.S.N.Z. Rec. Scheme	37°38'	176°11'
41. Waihi Estuary	2	May 1970	A.J. Baker		37°46'	176°28'
42. Tarawera Estuary	3	Sep. 1960	P.D.G. Skegg	Notornis 9(3):75 1960	37°53'	176°47'
43. Whakatane Heads	2	Jan. 1970	A.J. Baker		37°56'	176°59'
44. Aotea Harbour	1	Apr. 1954	C.K. Buckeridge	Notornis 6(3):96 1955	37°58'	174°51'
45. Ohiwa Harbour	2	Jan. 1970	A.J. Baker		38°00'	177°04'
46. Kawhia	1	May 1961	W.S. Sutherland	Notornis 9(7):242 1961	38°05'	174°50'
47. Kaitoke	1	Nov. 1970	D.E. Crockett	Pers. comm.	39°58'	175°05'
48. Rangitikei Estuary	1	Mar. 1968	I.G. Andrew	Pers. comm.	40°17'	175°13'
49. Manawatu Heads	1	Aug. 1969	I.G. Andrew	Pers. comm.	40°27'	175°07'
50. Ohau Estuary	1	Aug. 1969	I.G. Andrew	Pers. comm.	40°42'	175°15'
51. Otaki Rivermouth	2	Nov. 1970	A.J. Baker		40°46'	175°06'
52. Waikanae	1	Nov. 1970	A.J. Baker		40°52'	175°00'
53. Port Nicholson	3	Aug. 1970	A.J. Baker		41°16'	174°52'

Locality	Number	Date	Source Informant	Reference	Latitude and Longitude
SOUTH ISLAND					
54. Farewell Spit (inner Beach)	1	May 1971	A.J.Baker		40°29' 172°50'
55. Whanganui Inlet	1	Dec.1970	A.J.Baker		40°35' 172°35'
56. D'Urville Island	1	Aug.1969	A.J.Baker		40°50' 173°51'
57. Chetwode Islands	1	Dec.1970	C.R.Veitch	Pers.comm.	40°54' 174°05'
58. Kaiteretere	1	Jan.1967	J.D.Coleman	Pers.comm.	41°03' 173°01'
59. Long Island	2	Dec.1970	R.Simpson	Pers.comm.	41°07' 174°17'
60. Queen Charlotte Sound	4	Jul.1954	B.D.Heather	Notornis 6(3):96 1955	41°12' 174°16'
61. Wairau Rivermouth	1	Aug.1970	A.J.Baker		41°30' 174°03'
62. Kaikoura	1	Dec.1970	A.J.Baker		42°25' 173°42'
63. Waitangi River- mouth	1	Feb.1961	A.B.Mundew	O.S.N.Z. Rec.Scheme	43°19' 170°16'
64. Gillespies Beach	1	Aug.1971	A.J.Baker		43°25' 169°49'
65. Open Bay Islands	1	Jun.1971	E.H.Miller	Pers.comm.	43°52' 168°53'
66. Okura Rivermouth	1	Jun.1971	A.J.Baker		43°54' 168°55'
67. Jackson Bay	1	Jun.1971	A.J.Baker		43°57' 168°40'
68. Awarua Bay	20	Jan.1947	L.J.Bell	N.Z.Bird Notes 3(1): 20, 1948	
69. Martin's Bay	Few	Jan.1947	L.J.Bell	N.Z.Bird Notes 3(1): 20, 1948	44°22' 167°59'
70. Milford Sound	1	Feb.1963	H.R.McKenzie	O.S.N.Z. Rec.Scheme	44°34' 167°48'



APPENDIX IV.CENSUS DATA FOR HYBRIDS OF BLACK AND NORTHERN PIED OYSTERCATCHERS.

Locality	Number	Date	Source		Latitude and Longitude
			Informant	Reference	
NORTH ISLAND					
1. Tom Bowling Bay	8	Jan. 1971	T.R. Calvert	Pers. comm.	34°25' 172°58'
2. Waikuku Beach	3	Jan. 1971	T.R. Calvert	Pers. comm.	34°26' 173°00'
3. Spirits Bay	2	Jan. 1971	T.R. Calvert	Pers. comm.	34°27' 172°50'
4. Te Werahi	8	Jan. 1971	A.J. Baker		34°28' 172°40'
5. Ngakino	2	Jan. 1970	A.J. Baker		34°30' 172°44'
6. Coal Point	1	Jan. 1970	A.J. Baker		34°31' 173°00'
7. Parengarenga	9	Jan. 1970	A.J. Baker		34°31' 172°56'
8. Scott Point	21	May 1970	A.T. Edgar	Pers. comm.	34°31' 172°42'
9. Bluff to Te Paki Stream	20	May 1970	A.T. Edgar	Pers. comm.	34°36' 172°46'
10. The Bluff	19	May 1970	A.T. Edgar	Pers. comm.	34°41' 172°53'
11. Great Exhibition Bay	23	Jan. 1971	T.R. Calvert	Pers. comm.	34°42' 173°04'
12. Rarawa	2	Jan. 1971	A.J. Baker		34°44' 173°05'
13. Ahipara to Bluff	2	May 1970	A.T. Edgar	Pers. comm.	34°46' 172°58'
14. Kowhai Beach	9	Jan. 1971	A.J. Baker		34°47' 173°09'
15. Rangaunu Bay	3	Jan. 1971	A.J. Baker		34°49' 173°19'
16. Karikari Bay	1	Jan. 1971	Mrs. S. Reed	Pers. comm.	34°54' 173°20'
17. Taipa	1	Jan. 1971	A.J. Baker		35°00' 173°28'
18. Matauri Bay	1	Jan. 1970	A.J. Baker		35°02' 173°55'

Locality	Number	Date	Source		Latitude and Longitude
			Informant	Reference	
19. Takou Bay	6	Jan. 1971	A. J. Baker		35°06' 173°58'
20. Taronui Bay	5	Jan. 1971	A. J. Baker		35°07' 173°58'
21. Kerikeri Inlet	5	Mar. 1967	A. T. Edgar	Pers. comm.	35°12' 174°01'
22. Herekino Heads	20	Jan. 1968	A. T. Edgar	Pers. comm.	35°17' 173°11'
23. Mitimiti	2	Jan. 1970	A. J. Baker		35°26' 173°16'
24. Mimiwhangata	1	Jan. 1970	A. J. Baker		35°26' 174°24'
25. Whangape-Hokianga	20	Sep. 1966	A. T. Edgar	Pers. comm.	35°24' 173°14'
26. Waimamaku	3	Jan. 1968	A. T. Edgar	Pers. comm.	35°36' 173°25'
27. Waipoua	13	Jan. 1968	A. T. Edgar	Pers. comm.	35°40' 173°29'
28. Ngunguru Bay	7	Apr. 1970	M. Munro	Pers. comm.	35°40' 174°31'
29. McLeods Bay	1	Apr. 1970	M. Munro	Pers. comm.	35°46' 174°32'
30. Bream Bay	1	Nov. 1971	M. Munro	Pers. comm.	35°51' 174°36'
31. Ruakaka Estuary	18	May 1971	A. J. Baker		35°54' 174°26'
32. Waipu Estuary	22	May 1971	A. J. Baker		36°00' 174°28'
33. Mangawhai Estuary	4	May 1970	A. J. Baker		36°07' 174°35'
34. Pakiri	1	May 1970	A. J. Baker		36°15' 174°44'
35. Great Barrier Island	2	Dec. 1960	B. D. Bell & D. H. Brathwaite	Notornis 10(8):374 1964	36°11' 175°25'
36. Waikawau Bay	3	Dec. 1964	B. D. Bell	Pers. comm.	36°36' 175°32'
37. Kennedy Bay	1	Dec. 1964	B. D. Bell	Pers. comm.	36°40' 175°33'
38. Kuaotuna Beach	6	Dec. 1964	B. D. Bell	Pers. comm.	36°43' 175°44'
39. Opito Bay	2	Dec. 1964	B. D. Bell	Pers. comm.	36°43' 175°49'
40. Whangapoua Harbour	2	Dec. 1964	B. D. Bell	Pers. comm.	36°44' 175°38'



Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
41. Buffalo Beach	1	Dec. 1964	B.D. Bell	Pers. comm.	36°49'	175°42'
42. Cooks Beach	2	Dec. 1964	B.D. Bell	Pers. comm.	36°50'	175°44'
43. Muriwai (Auckland)	4	Jul. 1960	R.B. Sibson	Notornis 9(3):74 1965	36°50'	174°26'
44. Tairua Harbour	3	Jan. 1970	A.J. Baker		37°00'	175°51'
45. Pawanui Beach	3	Dec. 1964	B.D. Bell	Pers. comm.	37°00'	175°52'
46. Firth of Thames	1	Mar. 1968	H.R. McKenzie	Pers. comm.	37°05'	175°24'
47. Opoutere	8+	Jun. 1967	H.R. McKenzie	Pers. comm.	37°06'	175°53'
48. Waikato Heads	13	May 1971	Mrs. J.A. Brown	Pers. comm.	37°21'	175°02'
49. Athenree	3	Jan. 1970	A.J. Baker		37°27'	175°55'
50. Maketu	2	Aug. 1966	H.R. McKenzie	Pers. comm.	37°45'	176°26'
51. Waihi Estuary	4	May 1970	A.J. Baker		37°46'	176°28'
52. Whakatane Heads	2	Jan. 1970	A.J. Baker		37°56'	176°59'
53. Tatapouri	1	Jan. 1970	A.J. Baker		38°59'	178°09'
54. Kaitoke	1	Nov. 1970	D.E. Crockett	Pers. comm.	39°58'	175°05'
55. Rangitaiki Estuary	1	Mar. 1968	I.G. Andrew	Pers. comm.	40°17'	175°13'
56. Manawatu Heads	1	Aug. 1969	I.G. Andrew	Pers. comm.	40°27'	175°07'
57. Ohau-Manawatu Heads	3	Aug. 1969	I.G. Andrew		40°38'	175°10'
58. Ohau Estuary	2	Aug. 1969	I.G. Andrew	Pers. comm.	40°42'	175°10'
59. Otaki Rivermouth	2	Nov. 1970	A.J. Baker		40°46'	175°06'
60. Mataikona River- mouth	1	Jan. 1941	R.H.D. Stidolph	Notornis 1(3):22 1943	40°48'	176°17'

Locality	Number	Date	Source		Latitude and Longitude	
			Informant	Reference		
61. Waikanae	2	Nov. 1970	A. J. Baker		40°52'	175°00'
62. Port Nicholson	3	Aug. 1970	A. J. Baker		41°16'	174°52'
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SOUTH ISLAND						
63. Farewell Spit (Outer Beach)	2	May 1971	A. J. Baker		40°29'	172°50'
64. Cape Farewell	1	May 1971	A. J. Baker		40°30'	172°41'
65. D'Urville Island	1	May 1969	A. J. Baker		40°50'	173°51'
66. Duffers Reef	1	Dec. 1970	C. T. Veitch	Pers. comm.	40°57'	174°03'
67. Long Island	1	Dec. 1970	R. Simpson	Pers. comm.	41°07'	174°17'
68. Wakapuaka (Nelson)	1	Winter 1965	W. T. Poppelwell	O. S. N. Z. Rec. Scheme	41°13'	173°21'
69. Queen Charlotte Sound	2	Jan. 1939	R. D. H. Stidolph	Notornis 1(3):22 1943	41°12'	174°16'
70. Kaikoura	2	Dec. 1971	A. J. Baker		42°25'	173°42'
71. Oaro	2	Dec. 1970	A. J. Baker		42°31'	173°30'
72. Motanau Island	1	Dec. 1970	C. W. Challies	Pers. comm.	43°04'	173°05'
73. Gillespie Point	2	Jan. 1961	R. B. Sibson	Notornis 9(7):242 1961	43°24'	169°43'
74. Open Bay Islands	2	Jun. 1971	E. H. Miller	Pers. comm.	43°52'	168°53'
75. Okuru Rivermouth	1	Jun. 1971	A. J. Baker		43°54'	168°55'
76. Jackson Bay	2	Jun. 1971	A. J. Baker		43°57'	168°40'

Locality	Number	Date	Source Informant	Reference	Latitude and Longitude
77. Awarua Bay	2	Jan.1947	L.J.Bell	N.Z.Bird Notes 3(1):20 1948	44°18' 168°05'
78. Routeburn Valley	1	Jan.1947	Miss C.White	N.Z.Bird Notes 2(6):145 1947	44°44' 168°19'
79. Charles Sound	Some	Feb.1948	A.G.Henderson	D.S.I.R. Bull.83 1949	45°02' 167°04'
80. Waiau Rivermouth	1	Mar.1962	B.D.Heather	O.S.N.Z. Rec.Scheme	46°09' 167°40'
81. Waikawa	2	Mar.1961	B.D.Bell & B.D.Heather	O.S.N.Z Rec.Scheme	46°38' 169°08'

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S.I. 27

N.I. 346

G.Total 373

      
400

APPENDIX V.CENSUS DATA FOR CHATHAM ISLANDS OYSTERCATCHERS.

Locality	Number	Date	Source		Latitude and	
			Informant	Reference	Longitude	
CHATHAM ISLAND						
Cape Young	2	Sep. 1961	B. D. Bell	Pers. comm.	43°42'	176°37'
Wharekauri	2	Oct. 1961	B. D. Bell	Pers. comm.	43°42'	176°35'
Taupeka Point	2	Nov. 1970	A. J. Baker		43°43'	176°31'
Cape Pattison	2	1957	C. J. Lindsay, W. J. Phillips & W. A. Watters	Notornis 8(4):102 1959	43°44'	176°48'
Waitangi West	2	Oct. 1970	R. A. Stanley	Pers. comm.	43°47'	176°49'
Waitangi Beach	1	Nov. 1961	B. D. Bell	Pers. comm.	43°56'	176°33'
Shelley Beach	2	Sep. 1961	B. D. Bell	Pers. comm.	44°00'	176°24'
Manakau Point	1	Sep. 1961	B. D. Bell	Pers. comm.	44°02'	176°20'
The Pinnacles	2	1957	C. J. Lindsay, W. J. Phillips & W. A. Watters	Notornis 8(4):102 1959	44°04'	176°25'
Kawhaki Creek	2	Sep. 1961	B. D. Bell	Pers. comm.	44°06'	176°39'
PITT ISLAND						
Moutapu Point	2	1957	C. J. Lindsay, W. J. Phillips & W. A. Watters	Notornis 8(4):102 1959.	44°12'	176°13'
Tupuangi Creek	2	1957	C. J. Lindsay, W. J. Phillips & W. A. Watters	Notornis 8(4):102 1959	44°13'	176°12'
Glory Bay	1	Nov. 1970	A. J. Baker		44°19'	176°18'

Locality	Number	Date	Source	Reference	Latitude and Longitude
MANGERE ISLAND	6	Nov. 1970	D.V. Merton	Pers. comm.	44°17' 176°18'
RANGATIRA ISLAND	23	Nov. 1970	A.J. Baker		44°21' 176°10'
	<hr/>				
G. Total	52				
	<hr/>				
	50				

## APPENDIX VI.

SOUTH ISLAND PIED OYSTERCATCHER SEASONAL MEANS FOR 9 VARIATES  
BY SEX AND AGE.

Character	Age	Sex	Season	N	Mean	<u>±</u>	S.E.
Bill length	Juvenile	M	Spring	28	80.8		0.68
"	"	F	Spring	15	88.4		0.81
"	"	M	Summer	19	81.0		0.85
"	"	F	Summer	14	89.7		0.93
"	"	M	Autumn	25	79.9		0.69
"	"	F	Autumn	11	89.6		0.83
"	"	M	Winter	14	79.6		0.80
"	"	F	Winter	12	91.7		1.55
"	2yr	M	Spring	16	81.9		1.06
"	"	F	Spring	13	93.8		1.03
"	"	M	Summer	16	80.5		0.91
"	"	F	Summer	16	90.9		1.22
"	"	M	Autumn	10	78.9		0.79
"	"	F	Autumn	10	89.4		0.80
"	"	M	Winter	31	82.1		0.42
"	"	F	Winter	15	88.9		1.24
"	Sub-ad	M	Spring	11	82.4		1.50
"	"	F	Spring	10	91.5		0.75
"	"	M	Summer	21	80.7		0.65
"	"	F	Summer	13	92.1		1.26
"	"	M	Autumn	11	81.8		0.90
"	"	F	Autumn	10	90.1		0.78
"	"	M	Winter	19	80.7		0.82
"	"	F	Winter	11	91.6		1.48
"	Adult	M	Spring	12	81.9		0.72
"	"	F	Spring	10	91.0		0.97
"	"	M	Summer	13	81.1		0.62
"	"	F	Summer	28	91.7		0.92
"	"	M	Autumn	24	80.0		0.77

Character	Age	Sex	Season	N	Mean	$\pm$	S.E.
Bill length	Adult	F	Autumn	18	89.9		1.22
"	"	M	Winter	103	80.9		0.35
"	"	F	Winter	51	90.0		0.68
Bill height	Juvenile	M	Spring	28	15.2		0.13
"	"	F	Spring	15	15.5		0.12
"	"	M	Summer	19	15.2		0.14
"	"	F	Summer	14	15.2		0.21
"	"	M	Autumn	25	14.6		0.12
"	"	F	Autumn	11	14.7		0.16
"	"	M	Winter	14	15.4		0.19
"	"	F	Winter	12	15.5		0.12
"	2yr	M	Spring	16	15.3		0.14
"	"	F	Spring	13	15.3		0.13
"	"	M	Summer	16	15.0		0.15
"	"	F	Summer	16	15.1		0.16
"	"	M	Autumn	10	15.2		0.13
"	"	F	Autumn	10	15.4		0.10
"	"	M	Winter	31	15.8		0.12
"	"	F	Winter	15	15.4		0.16
"	Sub-ad	M	Spring	11	15.5		0.18
"	"	F	Spring	10	15.2		0.13
"	"	M	Summer	21	15.1		0.18
"	"	F	Summer	13	15.6		0.16
"	"	M	Autumn	11	15.3		0.10
"	"	F	Autumn	10	15.3		0.09
"	"	M	Winter	19	15.6		0.14
"	"	F	Winter	11	15.6		0.14
"	Adult	M	Spring	12	15.6		0.22
"	"	F	Spring	10	15.7		0.22
"	"	M	Summer	13	15.3		0.26
"	"	F	Summer	28	15.4		0.15
"	"	M	Autumn	24	15.6		0.19
"	"	F	Autumn	18	15.6		0.17

Character	Age	Sex	Season	N	Mean	$\pm$	S.E.
Bill height	"	M	Winter	103	16.0		0.16
"	"	F	Winter	51	16.0		0.12
Bill width	Juvenile	M	Spring	28	12.1		0.15
"	"	F	Spring	15	12.1		0.18
"	"	M	Summer	19	12.2		0.22
"	"	F	Summer	14	12.4		0.25
"	"	M	Autumn	25	11.7		0.10
"	"	F	Autumn	11	12.1		0.25
"	"	M	Winter	14	12.2		0.21
"	"	F	Winter	12	11.7		0.26
"	2yr	M	Spring	16	12.2		0.20
"	"	F	Spring	13	12.0		0.16
"	"	M	Summer	16	12.2		0.15
"	"	F	Summer	16	12.3		0.16
"	"	M	Autumn	10	12.4		0.17
"	"	F	Autumn	10	12.3		0.20
"	"	M	Winter	31	12.7		0.11
"	"	F	Winter	15	12.4		0.13
"	Sub-ad	M	Spring	11	12.5		0.10
"	"	F	Spring	10	12.6		0.09
"	"	M	Summer	21	12.4		0.17
"	"	F	Summer	13	12.2		0.17
"	"	M	Autumn	11	12.4		1.20
"	"	F	Autumn	10	13.0		0.26
"	"	M	Winter	19	12.8		0.12
"	"	F	Winter	11	12.8		0.17
"	Adult	M	Spring	12	12.8		0.16
"	"	F	Spring	10	13.2		0.14
"	"	M	Summer	13	12.6		0.21
"	"	F	Summer	28	12.6		0.14
"	"	M	Autumn	24	13.1		0.15
"	"	F	Autumn	18	13.0		0.19
"	"	M	Winter	103	13.1		0.41



Character	Age	Sex	Season	N	Mean	$\pm$	S.E.
"	"	F	Winter	51	13.1		0.10
Tarsus	Juvenile	M	Spring	28	50.2		0.27
"	"	F	Spring	15	52.1		0.50
"	"	M	Summer	19	50.8		0.48
"	"	F	Summer	14	50.7		0.55
"	"	M	Autumn	25	49.1		0.30
"	"	F	Autumn	11	51.4		0.45
"	"	M	Winter	14	49.9		0.49
"	"	F	Winter	12	51.3		0.31
"	2yr	M	Spring	16	50.9		0.42
"	"	F	Spring	13	52.1		0.65
"	"	M	Summer	16	49.4		0.45
"	"	F	Summer	16	50.7		0.51
"	"	M	Autumn	10	49.6		0.33
"	"	F	Autumn	10	50.1		0.72
"	"	M	Winter	31	50.2		0.28
"	"	F	Winter	15	51.2		0.30
"	Sub-ad	M	Spring	11	50.4		0.48
"	"	F	Spring	10	51.4		0.26
"	"	M	Summer	21	49.6		0.40
"	"	F	Summer	13	50.7		0.59
"	"	M	Autumn	11	49.8		0.38
"	"	F	Autumn	10	50.9		0.32
"	"	M	Winter	19	50.1		0.31
"	"	F	Winter	11	52.0		0.39
"	Adult	M	Spring	12	49.6		0.41
"	"	F	Spring	10	50.1		0.46
"	"	M	Summer	13	50.2		0.37
"	"	F	Summer	28	50.8		0.32
"	"	M	Autumn	24	49.7		0.39
"	"	F	Autumn	18	50.3		0.37
"	"	M	Winter	103	49.9		0.24
"	"	F	Winter	51	51.0		0.29

Character	Age	Sex	Season	N	Mean	$\pm$	S.E.
Middle toe	Juvenile	M	Spring	28	32.4		0.23
"	"	F	Spring	15	33.0		0.25
"	"	M	Summer	19	32.2		0.29
"	"	F	Summer	14	32.4		0.45
"	"	M	Autumn	25	31.5		0.16
"	"	F	Autumn	11	32.7		0.15
"	"	M	Winter	14	31.5		0.41
"	"	F	Winter	12	32.4		0.36
"	2yr	M	Spring	16	32.6		0.17
"	"	F	Spring	13	32.5		0.30
"	"	M	Summer	16	31.6		0.35
"	"	F	Summer	16	31.9		0.31
"	"	M	Autumn	10	32.0		0.33
"	"	F	Autumn	10	31.9		0.34
"	"	M	Winter	31	32.0		0.23
"	"	F	Winter	15	32.0		0.23
"	Sub-ad	M	Spring	11	31.9		0.44
"	"	F	Spring	10	32.4		0.19
"	"	M	Summer	21	31.5		0.28
"	"	F	Summer	13	31.9		0.25
"	"	M	Autumn	11	31.8		0.19
"	"	F	Autumn	10	31.5		0.16
"	"	M	Winter	19	31.9		0.30
"	"	F	Winter	11	33.4		0.40
"	Adult	M	Spring	12	32.1		0.35
"	"	F	Spring	10	32.2		0.30
"	"	M	Summer	13	31.8		0.26
"	"	F	Summer	28	32.0		0.22
"	"	M	Autumn	24	31.6		0.29
"	"	F	Autumn	18	31.7		0.42
"	"	M	Winter	103	31.8		0.41
"	"	F	Winter	51	32.1		0.18
Wing	Juvenile	M	Spring	28	245		1.2
"	"	F	Spring	15	250		1.6

Character	Age	Sex	Season	N	Mean	$\pm$	S.E.
Wing	Juvenile	M	Summer	19	245		2.3
"	"	F	Summer	14	251		2.5
"	"	M	Autumn	25	251		0.8
"	"	F	Autumn	11	258		1.7
"	"	M	Winter	14	248		1.7
"	"	F	Winter	12	253		1.6
"	2yr	M	Spring	16	252		2.0
"	"	F	Spring	13	256		2.0
"	"	M	Summer	16	244		2.0
"	"	F	Summer	16	251		2.1
"	"	M	Autumn	10	252		0.9
"	"	F	Autumn	15	255		2.2
"	"	M	Winter	31	254		1.1
"	"	F	Winter	31	255		1.1
"	Sub-ad	M	Spring	11	252		2.1
"	"	F	Spring	10	257		1.6
"	"	M	Summer	21	252		1.8
"	"	F	Summer	13	260		1.7
"	"	M	Autumn	11	250		1.5
"	"	F	Autumn	10	254		1.6
"	"	M	Winter	19	255		1.7
"	"	F	Winter	11	261		2.2
"	Adult	M	Spring	12	254		1.9
"	"	F	Spring	10	259		1.3
"	"	M	Summer	13	258		1.1
"	"	F	Summer	28	262		0.9
"	"	M	Autumn	24	251		1.9
"	"	F	Autumn	18	249		2.1
"	"	M	Winter	103	257		0.8
"	"	F	Winter	51	261		0.9
Tail	Juvenile	M	Spring	28	91		0.7
"	"	F	Spring	15	94		0.9
"	"	M	Summer	19	92		1.1

Character	Age	Sex	Season	N	Mean	$\pm$	S.E.
Tail	Juvenile	F	Summer	14	95		1.1
"	"	M	Autumn	25	93		0.7
"	"	F	Autumn	11	96		1.0
"	"	M	Winter	14	92		1.2
"	"	F	Winter	12	92		0.7
"	2yr	M	Spring	16	94		0.9
"	"	F	Spring	13	96		1.3
"	"	M	Summer	16	93		0.8
"	"	F	Summer	16	95		1.0
"	"	M	Autumn	10	94		1.0
"	"	F	Autumn	10	96		1.6
"	"	M	Winter	31	95		0.8
"	"	F	Winter	15	93		0.7
"	Sub-ad	M	Spring	11	93		0.9
"	"	F	Spring	10	96		0.7
"	"	M	Summer	21	95		1.2
"	"	F	Summer	13	99		0.9
"	"	M	Autumn	11	93		0.6
"	"	F	Autumn	10	97		0.8
"	"	M	Winter	19	95		0.7
"	"	F	Winter	11	99		1.1
"	Adult	M	Spring	12	95		0.8
"	"	F	Spring	10	98		0.4
"	"	M	Summer	13	97		1.0
"	"	F	Summer	28	99		0.8
"	"	M	Autumn	24	96		0.8
"	"	F	Autumn	18	96		1.0
"	"	M	Winter	103	95		0.6
"	"	F	Winter	51	98		0.5
Weight	Juvenile	M	Spring	28	515		5.8
"	"	F	Spring	15	538		11.0
"	"	M	Summer	19	520		12.3
"	"	F	Summer	14	524		17.3

Character	Age	Sex	Season	N	Mean	$\pm$	S.E.
Weight	Juvenile	M	Autumn	25	481		6.5
"	"	F	Autumn	11	576		12.6
"	"	M	Winter	14	501		11.0
"	"	F	Winter	12	530		9.1
"	2yr	M	Spring	16	598		16.1
"	"	F	Spring	13	582		12.3
"	"	M	Summer	16	515		8.9
"	"	F	Summer	16	542		8.5
"	"	M	Autumn	10	509		12.6
"	"	F	Autumn	10	528		9.4
"	"	M	Winter	31	539		6.1
"	"	F	Winter	15	547		11.7
"	Sub-ad	M	Spring	11	605		14.0
"	"	F	Spring	10	580		12.2
"	"	M	Summer	21	526		7.5
"	"	F	Summer	13	561		11.7
"	"	M	Autumn	11	523		8.7
"	"	F	Autumn	10	572		12.5
"	"	M	Winter	19	565		9.2
"	"	F	Winter	11	593		14.1
"	Adult	M	Spring	12	578		15.2
"	"	F	Spring	10	593		11.3
"	"	M	Summer	13	541		9.8
"	"	F	Summer	28	550		7.8
"	"	M	Autumn	24	517		9.1
"	"	F	Autumn	18	553		8.7
"	"	M	Winter	103	553		5.6
"	"	F	Winter	51	582		6.4
Fat free weight	Juvenile	M	Spring	28	463		5.3
"	"	F	Spring	15	481		8.0
"	"	M	Summer	19	476		11.9
"	"	F	Summer	14	470		16.8

Character	Age	Sex	Season	N	Mean	<u>±</u>	S.E.
Fat free weight	Juvenile	M	Autumn	25	452		5.2
"	"	F	Autumn	11	479		10.9
"	"	M	Winter	14	447		9.5
"	"	F	Winter	12	472		7.9
"	2yr	M	Spring	16	524		11.7
"	"	F	Spring	13	512		8.9
"	"	M	Summer	16	471		8.6
"	"	F	Summer	16	498		8.7
"	"	M	Autumn	10	474		10.0
"	"	F	Autumn	10	489		6.9
"	"	M	Winter	31	480		5.2
"	"	F	Winter	15	487		10.2
"	Sub-ad	M	Spring	11	531		10.0
"	"	F	Spring	10	514		9.4
"	"	M	Summer	21	482		7.4
"	"	F	Summer	13	516		11.4
"	"	M	Autumn	11	485		7.9
"	"	F	Autumn	10	515		9.6
"	"	M	Winter	19	502		9.7
"	"	F	Winter	11	526		12.2
"	Adult	M	Spring	12	510		10.6
"	"	F	Spring	10	519		8.4
"	"	M	Summer	13	496		8.7
"	"	F	Summer	28	505		7.7
"	"	M	Autumn	24	496		7.3
"	"	F	Autumn	18	509		6.8
"	"	M	Winter	103	492		5.2
"	"	F	Winter	51	517		5.5



Age & Sex                    N    t or adjusted t values for Significance of Differences  
between Seasonal Means

<u>III. BILL WIDTH</u>			Spring & Summer	Spring & Autumn	Spring & Winter	Summer & Autumn	Summer & Winter	Autumn & Winter
Juveniles	Male	86	0.424	2.566*	0.335	2.413*	0.073	2.717*
	Female	52	0.767	2.722*	0.421	2.815*	0.997	2.642*
Second years	Male	73	0.076	0.709	2.017	0.795	2.021	1.260
	Female	54	1.277	1.239	1.789	1.249	0.367	1.039
Sub-adults	Male	62	0.275	1.357	1.914	1.584	1.673	2.081
	Female	44	2.018	1.427	1.030	2.091	2.061	0.469
Adults	Male	152	0.648	0.109	0.623	0.808	1.136	0.762
	Female	107	2.026	0.423	0.367	2.005	2.008	0.126

IV. TARSUS LENGTH

Juveniles	Male	86	1.020	2.035	0.560	2.196	1.374	1.444*
	Female	52	1.900	1.035	1.266	0.927	0.933	0.124
Second years	Male	73	2.097	2.038	1.445	0.329	1.650	1.184
	Female	54	1.691	2.107	1.337	0.681	0.778	1.536
Sub-adults	Male	62	1.172	0.946	0.385	0.289	0.722	0.386
	Female	44	0.915	1.192	1.212	0.227	1.668	2.004
Adults	Male	152	1.099	0.068	0.671	0.921	0.198	0.800
	Female	107	1.149	0.387	1.351	0.916	0.533	1.298

V. MIDDLE TOE LENGTH

Juveniles	Male	86	0.515	2.110	2.082	2.113	1.492	0.067
	Female	52	1.193	0.916	1.372	0.614	0.052	0.727
Second years	Male	73	2.138	1.926	1.795	0.718	0.970	0.064
	Female	54	1.294	1.140	1.334	0.109	0.184	0.051



Age & Sex . . . . . N . . . . . t or adjusted t values for Significance of Differences  
between Seasonal Means

<u>V. MIDDLE TOE LENGTH</u>			Spring & Summer	Spring & Autumn	Spring & Winter	Summer & Autumn	Summer & Winter	Autumn & Winter
Sub-adults	Male	62	0.883	0.376	0.004	0.637	1.082	0.432
	Female	44	1.545	1.492	2.140	1.125	1.274	2.073
Adults	Male	152	0.646	1.076	0.083	0.535	0.315	0.682
	Female	107	0.649	0.943	0.364	0.716	0.377	0.920
<u>VI. WING</u>								
Juveniles	Male	86	0.007	3.893*	1.638	2.421*	1.226	1.229
	Female	52	0.606	4.385*	1.718	2.695*	0.699	2.095
Second years	Male	73	2.666*	0.079	1.005	3.526*	4.684*	1.343
	Female	54	1.537	2.211*	0.518	0.482	1.571	1.275
Sub-adults	Male	62	0.453	1.173	1.579	1.657	1.249	2.280*
	Female	44	0.425	3.101*	1.170	2.991*	0.189	2.725*
Adults	Male	152	2.190*	0.926	1.816	3.333*	0.798	3.037*
	Female	107	1.768	4.760*	1.040	6.512*	0.654	6.159*
<u>VII. TAIL</u>								
Juveniles	Male	86	0.226	1.304	0.364	0.761	0.111	0.590
	Female	52	0.833	1.334	1.038	0.446	1.848	1.617
Second years	Male	73	0.416	0.173	0.739	0.571	1.183	0.462
	Female	54	0.264	0.093	2.011	0.269	1.872	1.830
Sub-adults	Male	62	1.705	0.414	2.019	1.633	0.243	1.764
	Female	44	1.890	1.005	2.066	1.432	0.062	1.216
Adults	Male	152	1.040	1.082	0.074	0.034	1.054	1.330
	Female	107	0.847	0.840	0.704	1.837	0.234	1.910

Age & Sex                      N    t or Adjusted t values for Significance of Differences  
between Seasonal Means

VIII. TOTAL BODY WEIGHT

			Spring & Summer	Spring & Autumn	Spring & Winter	Summer & Autumn	Summer & Winter	Autumn & Winter
Juveniles	Male	86	0.334	3.968*	1.294	2.780*	1.092	1.665
	Female	52	2.217*	1.304*	0.543	0.069	2.706*	0.903
Second years	Male	73	4.493*	3.896*	3.405*	0.400	2.269*	2.340*
	Female	54	2.745*	3.511*	2.057*	1.181	0.337	1.234
Sub-adults	Male	62	4.935*	5.774*	2.478*	0.326	3.267*	4.427*
	Female	44	2.291*	0.457	0.676	0.649	1.762	1.090
Adults	Male	152	2.119*	2.437*	2.297*	0.291	1.112	1.840
	Female	107	2.945*	3.109*	0.731	0.275	3.082*	2.968*

IX. FAT-FREE WEIGHT

Juveniles	Male	86	0.971	1.724	1.574	1.827	1.881	0.496
	Female	52	0.457	0.028	0.676	0.376	0.094	0.554
Second years	Male	73	1.566	1.906	1.909	0.215	0.890	0.517
	Female	54	1.178	2.003	1.849	0.750	0.847	0.179
Sub-adults	Male	62	1.951	1.536	2.019	0.303	1.836	1.578
	Female	44	0.118	0.089	0.788	0.040	0.629	0.706
Adults	Male	152	1.764	1.881	1.913	0.008	0.496	0.643
	Female	107	1.762	1.961	0.951	0.458	1.258	0.737

APPENDIX VIII.LOCALITY CHARACTER MEANS AND S.E. FOR ADULT BLACK OYSTER-  
CATCHERS.

Character	Locality	Sex	N	Mean	S.E.	
Bill length	Stewart Island	M	14	76.5	1.40	
		F	15	86.9	0.76	
	Otago	M	14	78.5	0.96	
		F	14	87.3	0.52	
	Westland	M	14	79.5	0.96	
		F	16	88.0	0.86	
	Nelson	M	15	79.8	0.96	
		F	17	88.8	0.74	
	Northland	M	12	83.9	0.73	
		F	12	91.3	1.40	
	Bill height	Stewart Island	M	14	17.0	0.22
			F	15	17.3	0.13
Otago		M	14	17.6	0.20	
		F	14	17.7	0.21	
Westland		M	14	17.2	0.22	
		F	16	18.1	0.18	
Nelson		M	15	17.6	0.20	
		F	17	18.1	0.18	
Northland		M	12	18.2	0.10	
		F	12	18.7	0.21	
Bill width		Stewart Island	M	14	13.5	0.22
			F	15	14.0	0.16
	Otago	M	14	14.2	0.20	
		F	14	14.2	0.20	
	Westland	M	14	14.0	0.22	
		F	16	13.9	0.26	
	Nelson	M	15	14.1	0.29	
		F	17	14.0	0.16	

Character	Locality	Sex	N	Mean	S.E.	
	Northland	M	12	16.1	0.09	
		F	12	15.6	0.21	
Tarsus length	Stewart Island	M	14	56.9	0.52	
		F	15	59.0	0.33	
	Otago	M	14	58.3	0.48	
		F	14	58.8	0.43	
	Westland	M	14	56.8	0.59	
		F	16	58.7	0.60	
	Nelson	M	15	58.3	0.52	
		F	17	59.4	0.70	
	Northland	M	12	61.2	0.34	
		F	12	61.6	0.52	
Middle toe length	Stewart Island	M	14	39.9	0.45	
		F	15	39.7	0.34	
	Otago	M	14	37.7	0.46	
		F	14	37.9	0.38	
	Westland	M	14	38.1	0.56	
		F	16	38.6	0.53	
	Nelson	M	15	38.0	0.43	
		F	17	38.6	0.62	
	Northland	M	12	39.0	0.26	
		F	12	39.0	0.27	
	Wing length	Stewart Island	M	14	275	1.3
			F	15	278	1.2
Otago		M	14	272	1.8	
		F	14	276	1.5	
Westland		M	14	270	1.8	
		F	16	276	2.1	
Nelson		M	15	270	2.3	
		F	17	274	2.2	
Northland		M	12	267	1.4	
		F	12	270	1.3	

Character	Locality	Sex	N	Mean	S.E.
Tail length	Stewart Island	M	14	106	0.7
		F	15	109	0.9
	Otago	M	14	104	1.0
		F	14	107	0.9
	Westland	M	14	105	1.1
		F	16	106	1.0
	Nelson	M	15	103	1.0
		F	17	104	1.2
	Northland	M	12	103	0.5
		F	12	103	0.6
Total body weight	Stewart Island	M	14	679	11.6
		F	15	729	11.0
	Otago	M	14	676	12.7
		F	14	723	8.0
	Westland	M	14	671	9.9
		F	16	714	12.8
	Nelson	M	15	667	9.9
		F	17	719	12.8
	Northland	M	12	716	10.5
		F	12	754	7.4