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Population structure, morphometrics, moult, migration, and wintering of the Wrybill (*Anarhynchus frontalis*)

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ABSTRACT

Between 1987 and 1996, 2,383 Wrybills (*Anarhynchus frontalis*) were banded on their wintering grounds at two locations near Auckland; 690 of these were recaptured on 830 occasions. Birds started to arrive at their wintering grounds in December; and stayed at the more northern location until April, when they moved to wintering sites further south. First year birds comprised <15% of the population, and about 30% of birds were at least 5 years old. The maximum longevity in the wild was 16 years. Adults had significantly longer wings than younger birds, but there was no such difference in bill or tarsus length. Body mass generally increased during winter, and adults often were heavier than young birds. Wrybills moulted between late December and early May. A country-wide population census found 5,111 birds in May 1994. There is no reliable indication that the population ever exceeded this level.

KEYWORDS: Wrybill, population, morphometrics, moult, wintering

INTRODUCTION

The Wrybill (*Anarhynchus frontalis*) is a wader endemic to New Zealand. Its most distinctive feature is a lateral curve to the right of the final third of the bill. Although the sole member of its genus, the species is closely allied to *Charadrius* in genetic structure (A.J. Baker, pers. comm.), morphology (Bock 1958, Johnsgard 1981), the feather patterning of chicks (Jehl 1968), and behaviour (Phillips 1980, Hay 1984). Moreover, it shares with New Zealand Dotterel (*C. obscurus*) and Banded Dotterel (*C. bicinctus*) a display not found in other plovers (Phillips 1980) and, with Banded Dotterel, a feather louse (*Quadraceps cedemajori*) (Pilgrim & Palma 1982) not recorded on other species. Hay (1984) concluded that the retention of *Anarhynchus* as a monotypic genus is based solely on bill morphology and feeding behaviour.

Notwithstanding its distinctive character, confiding nature, small population, and the accessibility of major wintering sites, the Wrybill has been little studied. A notable exception was by Hay (1984), who offered a detailed analysis of breeding ecology, population dynamics, and migration, based on fieldwork conducted in 1975-1977.

Hay (1984) outlines the annual cycle for the species: Adults breed between late August and December on the braided river beds of the eastern side of the South Island from 42-45°S. The clutch consists of two eggs and a second nest may be attempted even if the first is successful. Juveniles from early nests head north at the end of December, while adults leave in mid-January or later, though some unsuccessful breeders depart earlier in the month. Migration from the breeding grounds is direct, with only a few birds stopping en route. The species winters in harbours and bays of the North Island north of 38°S. The vast majority (about 80%) congregate in the Firth of Thames and Manukau Harbour, 600-800 kilometres north of the breeding area. The first adults return south at the end of July, with the bulk of the flock departing in mid-August. Less than 10% of the total population remains in the north, these being birds hatched in the previous calendar year. Half or more of these first-years (that is, 5% of the population) move south about a month later, though theirs is a more leisurely migration than that of the adults. 14% of birds hatched in the previous calendar year reach their natal area, usually in November, but these do not breed.

In this paper I present new data collected mainly by the New Zealand Wader Study Group's Auckland cannon-netting team (hereafter NZWSG), as well as reviewing material published elsewhere. Information is presented on the timing of migration, movements between wintering sites, the wintering distribution, population size, longevity, the age structure of the population, morphometric data, the timing and duration of moult.

MATERIAL AND METHODS

Most of the data presented here were obtained from birds cannon-netted at high tide winter roosts. Where possible, age and weight were noted, moult was scored, and measurements were taken of wing, tarsus, and bill. Few individuals were subject to all these procedures, particularly when large catches (500+) were made.

Wrybills were first cannon-netted under the direction of C.R. Veitch in 1979-1982 near Miranda on the Firth of Thames (37°10'S 175°20'E) and at Jordan's Farm on the south-east Kaipara Harbour (36°34'S 174°21'E). About 1,600 were banded, but few morphometric data were collected at this time. Catching at the same sites resumed under the direction of S. Davies and A. Riegen in 1987. Also, a small catch was made at Pollok's Spit, western Manukau Harbour, in 1995.

Metal bands on Wrybills wear quickly, with many being difficult to read after only two or three years. 111 bands were replaced and 10 of these were themselves replaced. One band was completely illegible, three digits were erased from two, a further 10 lost two digits, and another 12 lost one.

Ageing

While the suggestion (Hayman *et al.* 1986) that first-years may retain white-fringed juvenile inner median coverts was not confirmed by NZWSG, separating them from older birds was not difficult. Young birds arrived on the wintering grounds with fresh plumage, while adults had worn feathers. Adults moulted their primaries between early January and late April, whereas birds in their first year showed no primary moult at this time. From May to August adults possessed fresh plumage, while birds in their first year exhibited

some wear on the outer primaries. Birds in their second year could be distinguished from mature adults between late December and early March. Their primaries were more abraded and bleached and their moult was more advanced. When the outer primaries had been dropped toward the close of the moult, second-year birds could not be distinguished from older birds.

I refer to birds in their first year of life as "first-years." Birds known to be more than one year and less than two years are called "second-years." Except where explicitly stated, second-years are classed along with mature adults as "adults" or "non-juveniles." Wrybills not aged at the time of first capture are called "unaged."

Birds were regarded as living at least as long as the period between first and last captures. Where digits on bands were illegible and the date of first banding could not be established, the banding date was notionally assigned to the most recent date on which the relevant number sequence was used. To determine the minimum ages of birds first banded at wintering sites, it was assumed that juveniles and unaged birds had hatched on the previous 15 October (the middle of the breeding season) and that adults had hatched a year earlier, though some adults were obviously much older. Where birds were first banded in the South Island (by R. Maloney) and later retrapped by NZWSG at wintering sites, it was assumed that breeding adults were not less than 23 months old and that chicks or unaged birds hatched in the season of banding.

Sexing

Although males and females in breeding plumage can be distinguished, and there are significant differences between the sexes in bill, tarsus, and other measurements (Hay 1984), no combination of characters allowed for reliable sexing in the hand outside the breeding season (that is, from January to August). Wrybills processed by NZWSG were not sexed.

Movements and distribution

In addition to captures of banded birds and field counts, observation of breeding birds marked in the South Island with individual combinations of colour bands by Richard Maloney of the Department of Conservation provided information concerning the dates of their arrivals at northern wintering sites. Captures and recaptures of birds at wintering sites (about 100 kilometres apart) on the Kaipara Harbour and Firth of Thames provided evidence of movement between these places.

A national census of Wrybills conducted on 29 May 1994 was organised and co-ordinated by Adrian Riegen. Visits were made to over 40 sites where Wrybills had been recorded in earlier censuses. Two locations in the Far North (Great Exhibition Bay and Rangaunu Beach) and one in Northland (Waipu) were not visited, however. Figures for Neil's Beach and Pollen Island were based on examination of photographs of flying flocks, as well as on counts of roosting birds. Counts from photographs were higher than those based on direct observation at these sites.

Morphometrics and moult

Wing length was measured (to the nearest mm) by the maximum chord method. Most measurements were taken by the author, who obtained consistent and repeatable results. Birds moulting the outer primaries were excluded from any analysis. Marchant & Higgins (1993) used the same method, but Hay (1984) recorded the minimum chord (that is, did not flatten and straighten the wing in taking its length).

Bill length was measured (to the nearest 0.1 mm) from the bill-tip to the farthest point of exposed, non-feathered culmen ridge. Vernier dial callipers were used. Because of the bill's lateral asymmetry, the measurement recorded a chord rather than the absolute length of the bill.

Tarsus length was measured by two methods, using Vernier dial callipers accurate to the nearest 0.1 mm. Method (A) measured from the notch at the back of the "knee" to the front of the top of the down-folded foot. This technique allowed for speed and accuracy under field conditions. Method (B) recorded the length of the tarsus from the centre of the back of the "knee" to the middle of the joint between tarsus and middle toe on the front (last scale before toes divide). It was found difficult to obtain reliable measurements by method (B) under field conditions.

Body mass was measured to the nearest gram, using 100 g Pesola spring balances.

Measurements were tested for significance using Student's t-test.

Moult data were collected between 1987 and 1996. Primary moult in Wrybills follows the descendant pattern. Moult was scored for each primary (of one wing) on the scale of 0 (old) to 5 (new, with growth completed). Missing primaries or unbroken pins were rated as 1; primaries showing a waxy base and more than two-thirds growth were scored 4; 2 and 3 recorded intermediate stages. Prior to dropping the innermost primary the total score was 0. When moult was completed with full growth of the outermost primary, the total score was 50.

RESULTS

A total of 2,383 Wrybills were banded in the Auckland region by NZWSG. Since 1987, 830 recaptures have involved 699 birds. Four birds were trapped four times after first banding, a further 15 were recaptured three times, 89 were retrapped twice, and 591 were retrapped once.

Arrival of adults to the wintering grounds

Sightings of birds first banded as adults at Taramaire, near Miranda on the Firth of Thames, and subsequently fitted with colour-bands while breeding in the South Island (by R. Maloney) provided evidence of arrival dates at wintering sites. Individuals last seen on the Tekapo River on 27 October and 30 November 1993 were observed at Taramaire on 1 January 1994 and 27 December 1993, respectively. Individuals at Ohau River on 13 and 18 October 1992 were seen at Taramaire on 31 December 1992 and 11 January 1993, respectively.

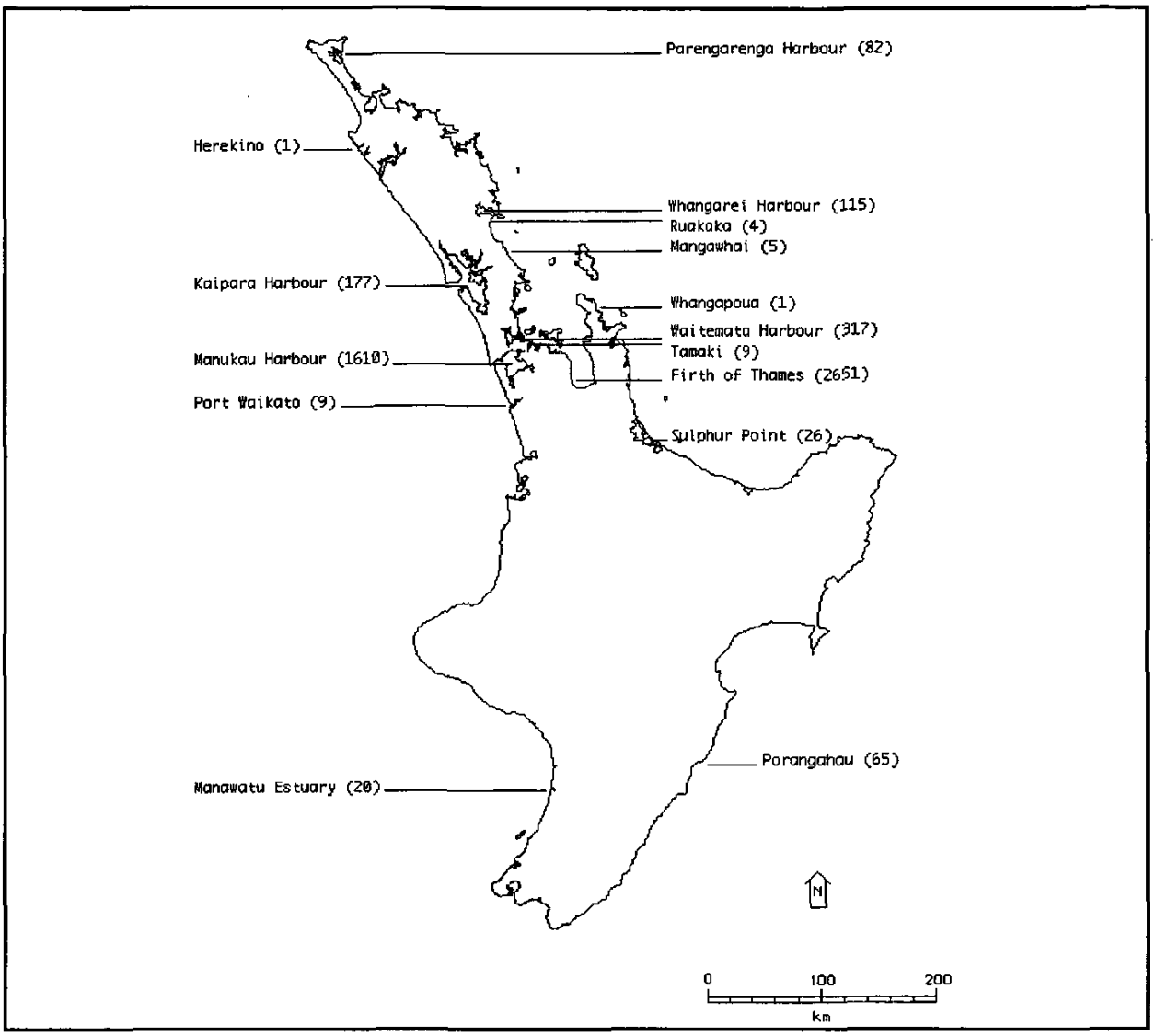

FIGURE 1 – Results of the winter census of Wrybills on the North Island, 29 May 1994.

This pattern was supported by other observations. An adult captured at Taramaire on 21 April 1992 was there on 27 December 1993 (T. Harbracken, pers. comm.). A single bird observed by the author at Jordan's Farm, Kaipara Harbour, on 27 December 1994 was joined by two more the next day. By 3 January 1995, 48 were present, including many banded individuals. At Miranda, the flock of 30 birds resident in early December 1994, was augmented by an influx of 300 birds, around 28 December (K. Woodley, pers. comm.). Many of these birds were also banded.

Movements between wintering sites

A total of 683 Wrybills have been retrapped by NZWSG at the same (wintering) site where banded. Some birds used more than one wintering area, however: 33 birds have been captured at both the Kaipara Harbour and the Firth of Thames. These recaptures occasionally spanned several years. One bird present in the Miranda region in 1980, 1992, and 1993 was caught at Jordan's Farm in 1988; another, present in the Miranda region in

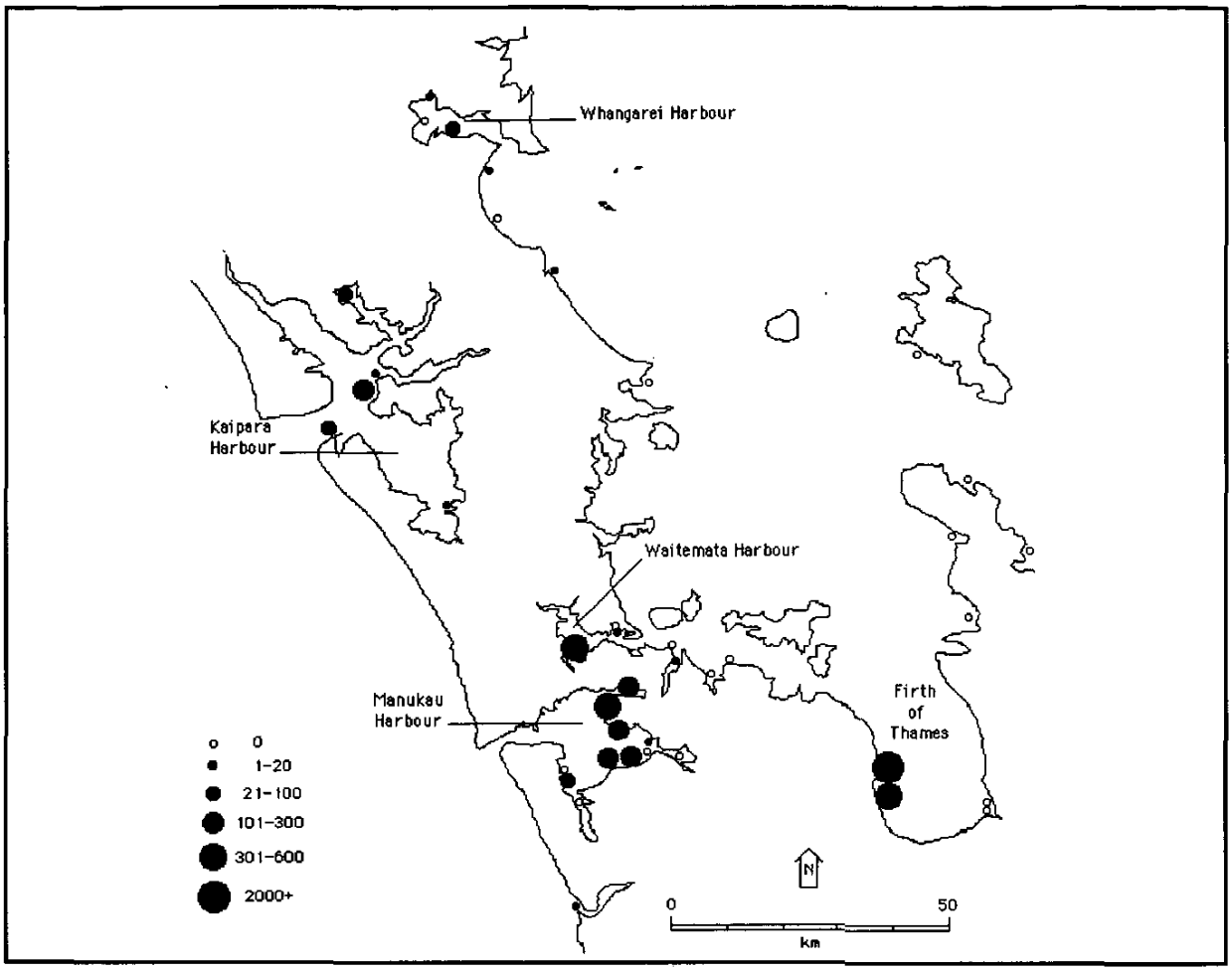

FIGURE 2 – The distribution of Wrybills in the northern part of the North Island, 29 May 1994.

1980 and 1993 was trapped at Jordan's Farm in 1995. Seven individuals have been captured at both sites within the same calendar year: six caught at Jordan's Farm on 7 March 1993 were recaptured near Miranda on 25 July 1993; another bird, present at Jordan's Farm on 17 March 1991 was near Miranda on 20 April 1991. Counts taken by the author indicated that many birds departed Jordan's Farm before April. The pattern for 1994 was consistent with other years: though more than 150 birds were present in February, only 10 were resident from the end of April through May. All 33 of the birds captured at different wintering sites were at Jordan's Farm between 10 January and 19 March and in the Miranda region between 7 April and 17 August.

Only one bird has been shown to moult at different sites in successive years. Of 19 birds captured at Pollok's Spit on the western edge of the Manukau Harbour on 19 February 1995, one moulting adult was already banded. This bird had also been trapped in mid-moult on 27 February 1994 at Jordan's Farm (about 70 kilometres due north).

Population size

A total of 5,111 birds was recorded on 29 May 1994. More than 83% were found in the Manukau Harbour and Firth of Thames, which long have been known as wintering

TABLE 1 - Known minimum ages of wintering Wrybill population near Auckland, based on known minimum ages of birds captured between 1987-1996

years	16+	15+*	14+	13+	12+	11+	10+	9+	8+	7+
N	1	2	9	19	26	30	31	33	40	55

*A bird of 10+ years is also counted as having survived 9+ years, and so on.

strongholds for the species (see Figures 1 and 2). Only 19 (0.37%) were located in the South Island (8 at Motueka Sandspit in Nelson and, in Canterbury, 7 at Ashley Estuary and 4 at Lake Ellesmere). No birds were seen at Houhora Harbour and Kowhai Beach (Far North), Whitianga and Tairua (Coromandel), Waihi, Matakana and Maketu (Bay of Plenty), Ahuriri Point (Hawke's Bay), Farewell Spit, Waimea Estuary and Nelson Haven (Nelson), as well as at sites indicated on Figure 2. The results of the Ornithological Society of New Zealand's national mid-winter (June) counts from 1985-1994 (covering all shorebird species) are given in Figure 3.

Age structure and longevity

Of 1,614 birds aged at the time of first capture, 9.3% (151) were first-year birds. The highest percentage of first-year birds in a catch of more than 100 was 15% (20/134 on 19 March 1995).

One individual was recaptured 14.6 years and another 14.1 years after banding. Taking into account the age of birds at first banding, the time elapsed between banding and last capture indicates birds' *known minimum ages* (see Table 1). The oldest bird was at least 16.4 years of age. In addition, of 12 birds first banded in the South Island and captured subsequently by NZWSG, two were not less than 9 years, two were 8 years, one was 7 years, one was 6 years, and one was 5 years of age. Of 50 banded non-juveniles caught on 19 March 1995, 32% (16) were at least 5 years old.

Morphometrics and moult

Wing measurements are summarised in Table 2. In birds processed by NZWSG, the difference between adult and first-years was significant (Student's $t_{249} = 5.51$, $P<0.0002$). The outer primaries of second-years and adults showed wear in January. After the moult, their wing-lengths were slightly longer. (The difference was statistically significant: old primaries, $\bar{x} = 122.1$ mm, S.D. = 3.4 mm, N = 102; new primaries, $\bar{x} = 123.8$ mm, S.D. = 2.3 mm, N = 79; $t_{179} = 4.10$, $P<0.0002$.)

Neither the bill length nor the tarsus length of adults and first-years were significantly different (Table 3: $t_{112} = 1.50$, N.S.; Table 4: method A, $t_{78} = 1.47$, N.S. and method B, $t_{79} = 0.77$, N.S.).

The active moult (that is, score 1-49) of 278 adults is graphed in Figure 4. Moult progresses quickly at first, when several inner primaries are dropped at once, but slows as the longer outer primaries are grown. Wrybills moult between late December and the beginning of May.

TABLE 2 - Wing length (mm) of Wrybills measured on the wintering grounds

	Mean	S.D.	Range	Sample size
Present study				
All birds	122.3	3.0	114-129	251
Adult	122.8	3.1	114-129	181
First year	120.8	2.0	117-124	70
Marchant & Higgins (1993)				
Adult male	122.5	2.3	118-126	13
Adult female	123.0	2.0	121-128	12
First year male	120.0	3.2	116-125	5
First year female	117.0	1.9	114-120	8

Hay (1984) measured minimum chord. Males: $\bar{x}$ = 119.3 mm, S.D. = 2.0, N = 39.
Females: $\bar{x}$ = 118.6 mm, S.D. = 2.3, N = 67.

TABLE 3 - Bill length measurements (mm) of Wrybills by different authors

	Mean	S.D.	Range	Sample size
Present study				
All birds	29.0	0.89	26.8-31.0	114
Adults	29.1	0.85	27.3-31.0	93
First year birds	28.8	1.03	26.8-30.4	21
Hay (1984)				
Males	29.9	0.8	—	48
Females	28.8	1.2	—	75
Marchant & Higgins (1993)				
Adult males	29.5	1.2	28.0-30.8	13
Adult females	29.1	1.1	26.9-30.9	12
First year males	27.8	1.0	26.2-28.9	5
First year females	27.7	0.7	27.0-29.0	6

Of 11 adults examined on 6 January 1996, 9 had commenced primary moult. Whereas mature adults scored 4 or less, the moult of two of three second-years was more advanced at 15 and 17. Similarly, three second-years captured on 31 January 1987 scored 22, 23, and 31, whereas a mature adult scored 3. Of 108 non-juveniles inspected on 19 March 1995, 5 (4.6%) had already completed their moult (score 50) and a further 8 were rated at 49. Of 59 non-juveniles examined on 5 April 1992, 9 (13.6%) had completed.

Body mass variation

Adult Wrybills weighed by NZWSG were heavier than first-year birds (Table 5; t_{474} = 2.59, P<0.01). Body mass of adults gradually decreased during winter, but increased again before migration to the breeding grounds (Table 6). Body mass variation of first year birds was lowest in January, then increased to about 53 g. This level was maintained throughout the winter (Table 6).

TABLE 4 - Tarsus length measurements (mm) of Wrybills by different authors

	Mean	S.D.	Range	Sample size
Present study - method A				
All birds	33.6	0.89	31.4-35.4	80
Adult	33.7	0.93	31.4-35.4	65
First year	33.3	0.62	31.8-34.1	15
Present study - method B				
All birds	31.7	0.85	29.7-33.6	81
Adult	31.7	0.85	29.7-33.6	61
First year	31.5	0.83	30.0-32.7	20
Hay (1984)*				
Males	30.0	1.1	—	48
Females	29.3	1.2	—	74
Marchant & Higgins (1993)*				
Adult male	29.2	0.8	27.7-30.4	14
Adult female	29.0	0.9	27.0-30.7	12
First year male	29.1	1.0	29.0-29.2	4
First year female	28.8	0.4	28.4-29.4	6

* Both Hay and Marchant & Higgins used method 'B'. See text for details.

TABLE 5 - Body mass data (g) of Wrybills by different authors

	Mean	S.D.	Range	Sample size
Present study				
All birds	53.9	3.7	43-68	476
Adult	54.1	3.7	43-68	401
First year	52.9	3.2	44-60	75
Hay (1984)*				
Males	58.6	5.3	—	46
Females	56.7	3.7	—	75
Marchant & Higgins (1993)**				
Males	59.9	5.7	50.4-66.5	7
Females	64.8	0.0	—	1

*Hay's data include breeding birds.
**Marchant & Higgins' data were from labels of specimens at the Museum of New Zealand.

Table 6 indicates variability in body mass during autumn and winter. Adults were significantly heavier in July than in April (t_{190} = 11.60, P<0.0001). Adults were heavier than first-years in January (t_{18} = 7.03, P<0.0002) and July (t_{109} = 4.59, P<0.0001), but not in March (t_{119} = 1.11, N.S.).

Body mass values in the same month of different years were not always similar. Adults at Jordan's Farm on 3 February 1991 ($\bar{x}$ = 55.7 g, S.D.= 2.9 g, N = 10) and at Pollok's Spit on 19 February 1995 ($\bar{x}$ = 56.9 g, S.D. = 3.6 g, N = 15) were not significantly different from each other (t_{23} = 0.90, N.S.), adults at Jordan's Farm on 27 February 1994 ($\bar{x}$ = 52.3 g, S.D. = 1.9 g, N = 67) were significantly lighter than those in either February 1991 or 1995 (t_{75} = 4.82, P<0.0001; t_{80} = 6.97, P<0.0001, respectively).

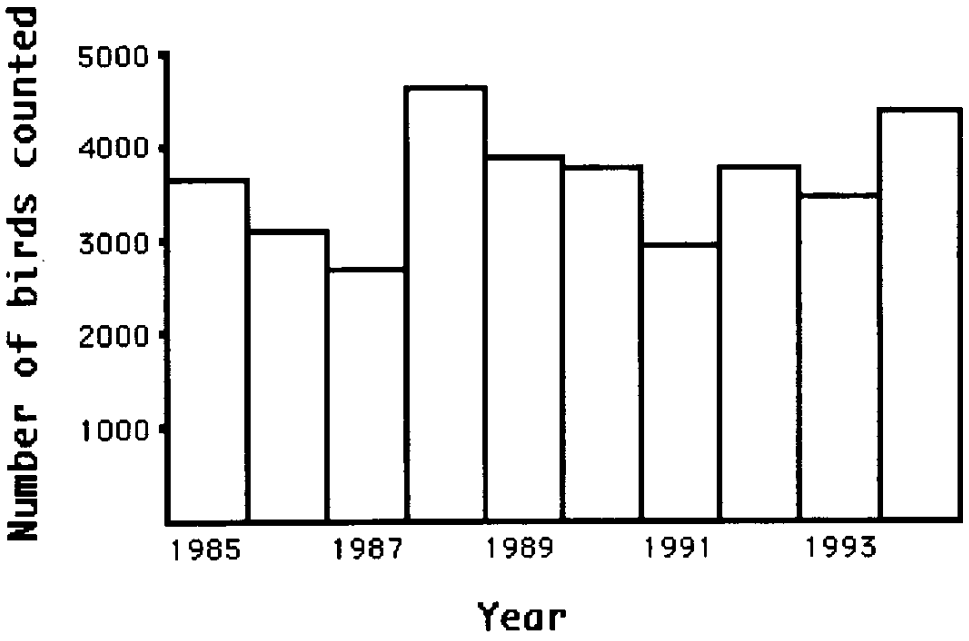

FIGURE 3 – Year to year variation in the national winter (June) counts of Wrybills.

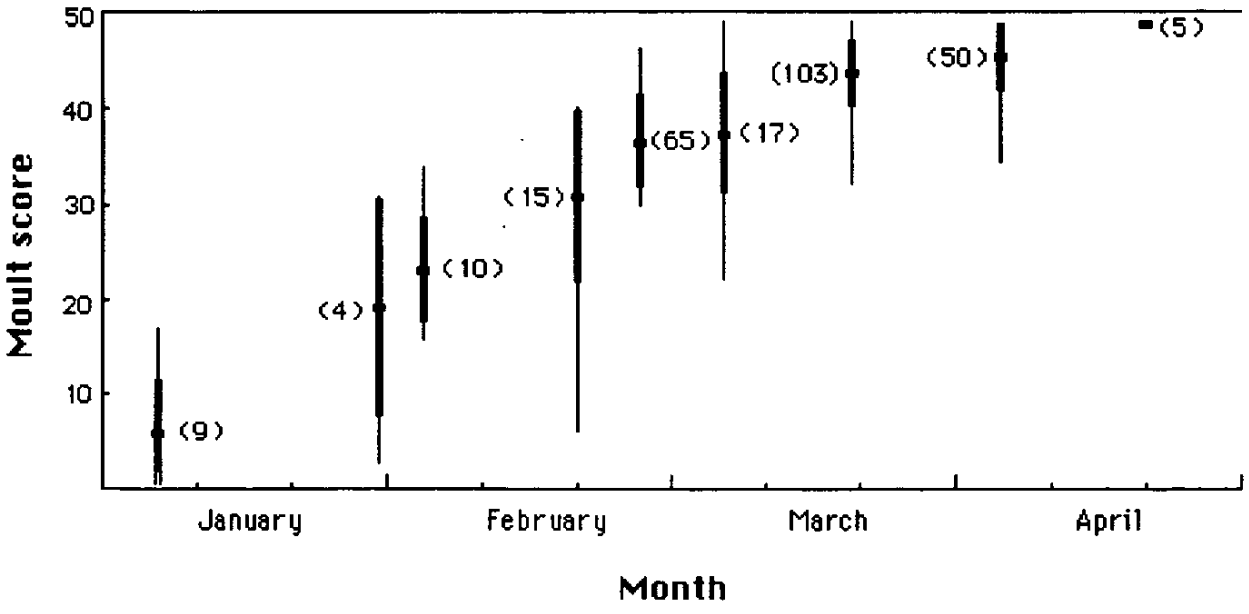

FIGURE 4 –Seasonal dynamics of moult in Wrybills. The thick segments show one S.D.; the thin lines indicate the range. Sample sizes are given in parentheses.

TABLE 6 - Body mass (g) changes in Wrybills during the non-breeding season near Auckland, North Island.

	January	February	March	April	July
Adults					
Mean	55.4	53.4	54.9	51.4	57.1
S.D.	2.1	3.0	2.8	2.2	4.4
Range	52-59	48-64	48-62	43-58	48-68
Sample size	15	92	101	109	83
First year birds					
Mean	48.4	52.8	54.1	52.8	52.9
S.D.	2.7	2.6	3.4	2.3	3.1
Range	44-51	46-56	48-60	51-57	46-58
Sample size	5	14	20	6	28

DISCUSSION

Wintering

Hay (1984) suggested that adults fly directly to wintering sites from the breeding area in mid-January. Counts and observations of individually marked birds showed that many adults arrive at wintering sites several weeks earlier than this. Also, some adults must have commenced their primary moult on the wintering grounds in early January (see later).

Adults are usually faithful to their past wintering sites (Hay 1984, Davies 1991), but a minority have been recorded as using more than one site. Recaptures of individuals between January and April of a single season, as well as counts, indicate that adults remain at the same place during their moult. The data showed that adults leave Jordan's Farm when they complete their primary moult. (Some birds stay at Jordan's Farm after May. Since many of these over-summer, they are likely to be first-years.) Presumably these adults move to the Firth of Thames or Manukau Harbour to spend several months before migrating south in August. That is, these birds use two sites during the winter season. This hypothesis is consistent with the April-May influx of Wrybills in the Firth of Thames and Manukau Harbour recorded in censuses (Veitch 1978). Winter counts of Wrybills in the Firth of Thames are 66% higher in early April than in early March (C.R. Veitch, unpublished).

If Jordan's Farm is typical, it may be that northerly sites are used by adult Wrybills only for moulting between January and April, whereas the large number of birds that moult in the Firth of Thames and Manukau Harbour remain there throughout the winter.

Population size

Flocks of thousands of Wrybills were recorded in the late nineteenth century (Buller 1905), but the species had become rare by 1940. Groups totalling 213 on Muriwai Beach on 27 April 1941 were at first thought to comprise the bulk of the population (Sibson 1990) but a further thousand were discovered in the Firth of Thames later in the year (Sibson 1943, 1963). There are no counts to substantiate the estimate of Johnsgard (1981 - no source cited) of 5,000 in the early 1940s. Given that the vast majority of birds gather during winter at a small number of sites that have been known and visited regularly since 1941, the higher counts of subsequent years indicated a genuine increase in

the size of the population. Totals rose to about 1,500-2,000 birds by 1950 and to more than 4,000 by 1960 (Sibson 1963). The population probably was stable in the 20 years following 1960 (Hughey 1985), at around 5,000. Hay (1984) estimated the total in 1975-1977 at slightly more than 5,000; Johnsgard (1981 - no source cited) suggested a total of 6,000 for the late 1970s. Hayman *et al.* (1986) cited a population estimated at 5,000-7,000 for the early 1980s, but gave no source of this information.

Since flooding is the main cause of losses to eggs and chicks (Pierce 1979, Hay 1984, Hughey 1985), the increase has been attributed to low rainfall in the breeding area in 1940-1960 (Hughey 1985). High rainfall is also beneficial, however, since regular flooding is needed to keep the breeding areas clear of plants, especially the introduced lupin (*Lupinus arboreus*), which has degraded much traditional breeding habitat in recent years (Hay 1984, Hughey 1985).

The overall distribution of Wrybills on 29 May 1994 was consistent with earlier observations (Sibson 1963, Hay 1984). The total of 4,278 in the Ornithological Society of New Zealand's 1994 mid-winter shorebird count was 20% lower than that of the earlier, more thorough census. If this underestimation applied in earlier years, the totals in Figure 3 suggest that the population has rarely exceeded 5,000 since 1985.

Longevity and survival

In Europe, the oldest known Ringed Plover (*C. hiaticula*), which is a plover similar in size to the Wrybill, is 10 years (Cramp & Simmons 1982). By comparison, the older Wrybills are long-lived. Some other New Zealand waders are similar. A Shore Plover (*Thinornis novaeseelandiae*) has been recorded at 20+ years (Dilks & O'Donnell 1993), while the maximum known age for a Variable Oystercatcher (*Haematopus unicolor*) was 27 and, for a New Zealand Dotterel, was 21 years (John Dowding, pers. comm.). In general, survival is higher in populations of island endemics than in those of similar mainland species or long-distance migrants (MacArthur & Wilson 1967). In the Shore Plover, 14% of non-juveniles were 13 years or older in 1993. A similar pattern might be anticipated for Wrybills.

If the catch of 19 March 1995 was typical, about 32% of Wrybills are at least 5 years of age. This percentage is consistent with Hay's (1984) figure of an annual mortality of 17% for non-juvenile Wrybills, according to which 39% of second-years should survive for a further five years. By comparison, the annual mortality of Ringed Plovers in Europe is 42.0 ± 5.48% (61% for first-years) (Cramp & Simmons 1982).

In 1975-77, each pair of Wrybills averaged 0.8 fledglings annually (Hay 1984). If all fledglings survived to the end of December, they should account for 28% of the population. At 9.3%, the percentage of birds aged as first-years at the first time of capture by NZWSG is much lower. Assuming that breeding productivity in 1987-1995 was similar to that in 1975-1977, this figure indicated that many first-years do not survive the six months that follow fledging. No doubt the first migration to the wintering grounds, as well as the hardships of the early days of independence, account for many deaths.

Counts of over-summering Wrybills in the North Island also provided indirect evidence of mortality and survival during the first year. According to Hay (1984), about half of the total of first-year birds remain in the North Island after September. The mean number of

Wrybills noted in the North Island in the Ornithological Society of New Zealand's national summer (November) shorebird censuses of 1983-1993 was 110 (S.D. = 80, range = 40-271). These figures corresponded to less than 4% of the national summer population (Veitch 1978), suggesting that less than 10% of the population at this time are first-year birds.

Morphometrics and moult

The discrepancy between NZWSG's method A and others' results in measuring the tarsus can be attributed to differences in the techniques of measurement, but it is surprising that NZWSG's method B results differed from those of others using the same technique.

The differences between body masses in Wrybills recorded by NZWSG and others (Table 5) are probably attributable to seasonal changes. Many of Hay's (1984) data were collected on the breeding grounds, whereas NZWSG's were taken in autumn and winter. Apparently Wrybills are heavier when breeding. Both water and air temperature often are lower or more extreme in the breeding area in August-December than in wintering areas in January-July; birds tend to carry more fat in colder conditions.

The lighter body mass of first-year birds recorded by NZWSG in January might suggest that they are less able than adults to cope with the rigours of migration. On 6 January 1996, when first-years and adults had only recently arrived in the wintering area, there was a significant difference between adults (11 birds) and first-years (5 birds) in body mass (t_{14} = 5.67, P<0.0002). The increase in the mean body mass of adults in July was a consequence of fat deposition in preparation for migration. First-years showed no similar increase at this time because their departure was not imminent. Adults leave the wintering area in August, while those first-years that migrate south do so a month or more later.

From a subset of the data presented here, Marchant & Higgins (1993) calculated that the moult of individual birds lasted about 100 days. The same duration was given by them for the unsuspended moult of Ringed Plover, which is a related species. The moult of New Zealand Dotterel also has been calculated at 100 days (John Dowding, pers. comm.).

According to Hay (1984), adults undergo a prebasic (body) moult in early January on the breeding grounds; most leave the South Island about mid-January and begin their primary moult as soon as they arrive on the northern wintering areas, completing by late April. These observations were confirmed by NZWSG, except that a number of adults were trapped in a condition indicating that their moult commenced prior to mid-January, while several others were unlikely to complete their moult until early May. (NZWSG has not trapped Wrybills in May, so none have been examined for late moult.) If primary moult takes about 100 days, the majority of adults that complete the moult before late April must begin prior to mid-January.

NZWSG's moult data implied that some second-years begin their moult in December. Either these second-years remain on, or return prematurely to, non-breeding areas. This moult strategy is consistent with patterns shown by other waders in the area. NZWSG's data have indicated that the onset of primary moult in over-wintering second-year Lesser Knots (*Calidris canutus*) and Bar-tailed Godwits (*Limosa lapponica*) precedes the

main arrivals of older birds from the north. In the endemic Shore Plover, second-years were more advanced early in primary moult than adults (Dowding & Kennedy 1993). The same applies to the New Zealand Dotterel (John Dowding, pers. comm.).

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