

# PLUMAGE, MORPHOLOGY AND HYBRIDISATION OF NEW ZEALAND STILTS *Himantopus* spp.

By R. J. PIERCE

## ABSTRACT

New Zealand has experienced two invasions of stilts, the first giving rise to the endemic Black Stilt (*Himantopus novaeseelandiae*) and the second being that of the Pied Stilt (*H. himantopus leucocephalus*). The geographical separation of these forms was of insufficient duration for reproductive isolation to become complete, and introgressive hybridisation has occurred. Hybrids are usually intermediate in plumage and morphology between their parents and are distinguishable from immature Black Stilts. There was no evidence of hybrid infertility or lack of vigour. Through hybridisation, the Pied Stilt has become distinguishable from the Australian population of Pied Stilts by several characteristics, including shorter tarsus, longer tail, and variable plumage markings. Selective mating and a different wintering area have helped keep the small remnant population of Black Stilts from being absorbed into the much larger Pied Stilt population. On the basis of aspects of its morphology, ecology and behaviour, the Black Stilt merits its status as a full species.

## INTRODUCTION

Repeated invasions of an ancestral form are a feature of island systems, the descendants of an early invasion adapting with time to the new environment and further invasions occurring much later (Mayr 1970). In New Zealand, double invasions have been postulated to account for the occurrence of closely related species of rails, oystercatchers, stilts and flycatchers (Fleming 1962, Heather 1966, Baker 1975). The first stilt invasion gave rise to the Black Stilt (*H. novaeseelandiae*), while the second invasion — that of the Pied Stilt (*H. h. leucocephalus*) may have occurred as late as the early 19th century. Since the mid-19th century the Pied Stilt has greatly increased in numbers and range, but the Black Stilt is now an endangered species, the remaining 10-15 pairs breeding entirely in the Upper Waitaki River Basin (Pierce 1984).

In addition to its entirely black plumage, the Black Stilt has long been known to differ morphologically from the Pied Stilt by a longer bill and shorter tarsus. How far the two stilts differ in these and other morphological features, however, has not been shown conclusively. Consequently the Black Stilt has been variously considered as, for example, a "seasonally dimorphic species" (Buller 1882), a "mutant form of the White-headed (Pied) Stilt" (Oliver 1930), a "subspecies" (Mayr & Short 1970), and a "full species" (Potts 1869, Kinsky 1970).

Moreover, birds in various intermediate plumages have caused much confusion in the literature. In the 19th century, birds exhibiting unusual plumages were often placed in separate species: since 1841 no fewer than ten species names have been applied to New Zealand stilts in attempts to account for several common plumage forms. The situation was well summed up by Buller's (1875a) comment that the stilts are "probably the most puzzling group of birds we have in New Zealand . . ." In the 20th century, birds in intermediate plumage have continued to cause confusion and still do. Three terms, "hybrid" (Hutton & Drummond 1905, Oliver 1930, 1955), "intermediate" (Stead 1932) and, more lastingly, "smudgy" (Stead 1932, OSNZ Recording Scheme) were commonly used to embrace all those birds that did not fit the known plumage forms.

In this paper I shall describe from field observations the plumage patterns of birds of known parentage, compare morphological features and breeding behaviour of Pied, Black and hybrid Stilts, and review the early literature.

## METHODS

Plumage characters and the timing and duration of moult were observed for colour-banded birds in the Cass River Valley (see Pierce 1983) and in several other parts of South Canterbury from 1977 to 1982. During the last two weeks of the fledgling period, several young were captured and given individual combinations on the tarsi of coloured plastic bands and numbered stainless steel band (size Y) issued by the Wildlife Service. For biometric data, nesting adults were trapped with a self-release drop trap with a wire frame and nylon netting. To avoid nest desertions, adults were trapped only at nests in which young were hatching or about to hatch. All adult birds seen in the field were classified into one of ten plumage nodes. See Fig. 4. Birds in nodes A-C ("Pied Stilts") and birds in node J ("Black Stilts") have formed the basis for other studies (e.g. Pierce 1983). Stilt skins were examined at the Otago, Canterbury, National and Auckland Museums, using the procedures outlined by Heather (1966). Equivalent measurements of Pied and Black Stilts were provided by the British, Australian and Bishop Museums, the National Museum of Victoria, the American Museum of Natural History and the CSIRO Museum in Canberra.

## BLACK AND PIED STILTS

### *Plumages*

*Nestling:* Nestlings closely resemble those of other forms of *Himantopus* (Bent 1927, Cramp & Simmons 1983). The forehead is buff with one or two black spots on the midline. Upper parts are pale grey, buff or fawn (and usually darker in Black Stilts), interrupted by black spots, smaller on the crown. The spots are in four to six longitudinal lines with the middle two having the

largest spots, which sometimes overlap. A horizontal black line extends from the base of the upper mandible through the eye to the hind neck. The under surface is white or off-white, except for a dark grey patch on the thigh, larger in Black Stilts. In nestlings of both species, the iris is brownish; bill black or brownish black, often with a paler base; tibia bluish grey to brownish grey; tarsus and toes bluish grey to orange-grey, the soles of the toes orange.

*Juvenile Pied:* At fledging, Pied Stilts have a white forehead and forecrown, off-white to grey cheeks and grey over the eye. Most birds have a grey or dark grey hind crown, paling to light grey on the nape, hind neck and forepart of the mantle. Exceptional birds have no dark markings anterior to the mantle. The feathers of the hind mantle and wings are greyish black, tipped with pale grey to buff, giving a spotted appearance. The rump and tail are off-white, and the tail has a broad (5-30 mm) terminal band of grey or brownish grey. The underparts, except for the tail band, are white. About 2-4 weeks after flying, the pale tips to the wing- and back-feathers are lost, leaving those parts uniform greyish black. The iris is brownish; bill greyish black with a fleshy base, legs pale pink.

*Juvenile Black:* At fledging, Black Stilts are mainly dark above and white below. The forehead is white, the cheeks are grey, and the crown is dark grey to greyish black, which usually extends in a paler vertical band to and encircling the eye (Fig. 1a). The hind crown and nape are off-white with variable amounts of grey flecking, becoming more continuous grey on the hind neck and forepart of the mantle (Fig. 2). The wings and hind part of the mantle are smooth greyish black with variable greenish gloss, lacking the pale feather-tips of Pied Stilt juveniles. The rump and tail are white with a broad (20-50 mm) dark grey terminal band on the tail. The underparts, except for the tail band, are white. Iris and bill are as for Pied Stilt juvenile, but the legs are reddish pink.

*First-winter Pied:* This plumage resembles that of juvenile Pied, except that the nape, foreneck and hind crown are darker. Iris brownish red, bill black, and legs pink.

*First-winter Black:* Early-flying birds (November-December) began to develop greyish black blotches or streaks on the sides in late December. By late March or April, visible moult (which lasted 8-14 weeks per bird) had ceased and these markings had extended over much of the sides and flanks. Very rarely were these side and flank markings laterally symmetrical and there was great variation between individuals, including siblings (Fig. 1b, 1c). Of ten birds studied, two had small greyish black markings extending forward to the breast, but in all others the breast was white. In all birds a dark, fragmented band, usually incomplete, extended from the flank to the cloacal region, giving the impression of linking the two flanks (Fig. 3). The legs were darker than in juveniles.

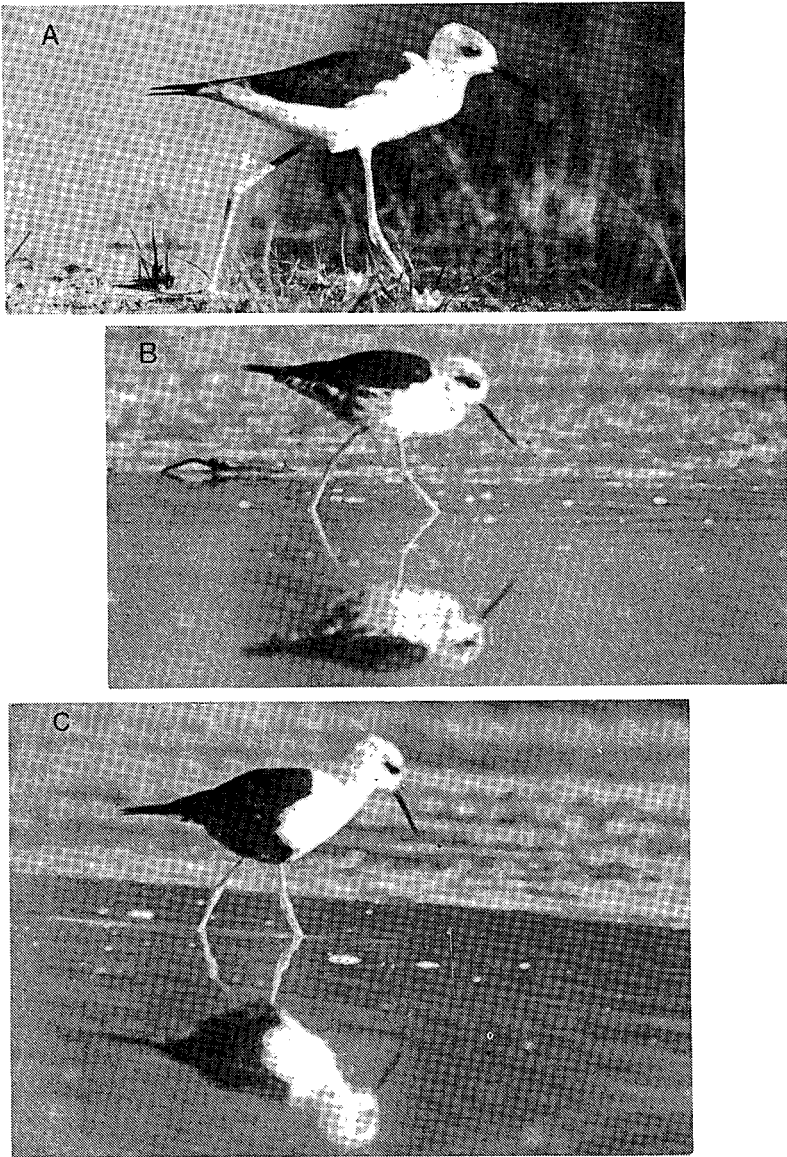
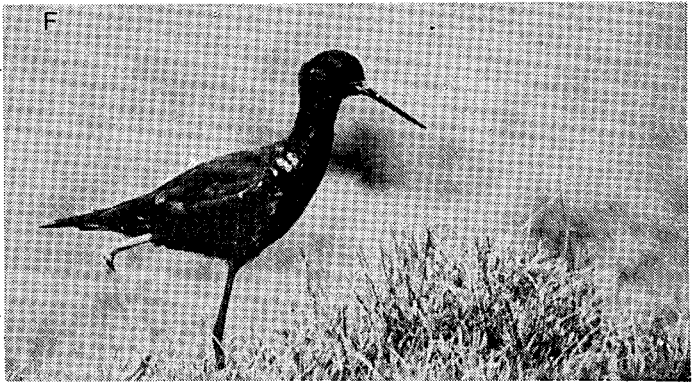
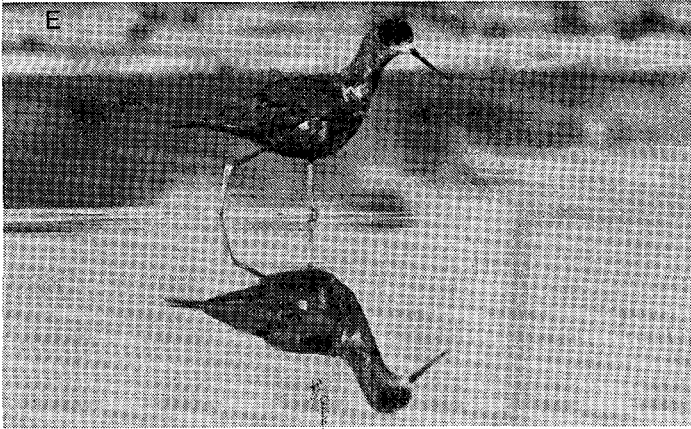
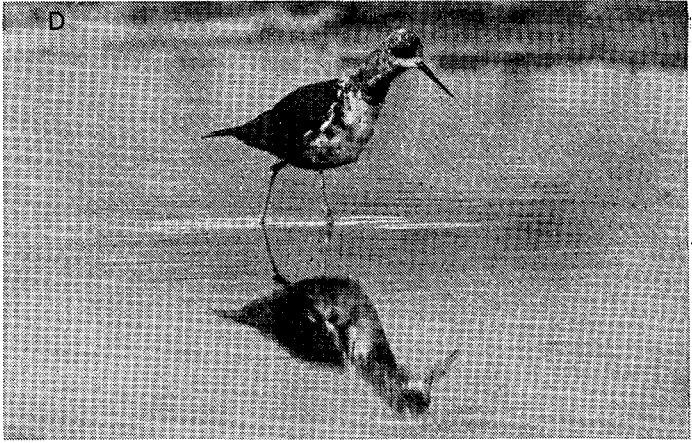


FIGURE 1 — Immature plumages of Black Stilts. A: Juvenile, December. B, C: First winter, June (siblings). D: Second-summer moult, September. E: Second-summer moult, October. F: Second-summer plumage, January



*Second-summer Pied:* Some birds were indistinguishable from adults, but the hind neck of most retained a small amount of fine flecking, and there were greyish markings about the ear coverts.

*Second-summer Black:* The second summer moult of Black Stilts occurred from late June to October, lasting 8-12 weeks per bird. Early in this moult the crown and hind neck developed scattered greyish black blotches followed by uniform darkening of the areas between the blotches. After nearly one month, this pattern had extended to the foreneck (Fig. 1d), and finally, after a further month, to the breast and sides (Fig. 1e). The largest patches of white in the second summer plumage were on the abdomen and undertail, with smaller patches on the breast, foreneck, sides of neck, chin and forehead (Fig. 1f). Iris crimson, bill black, legs crimson.

*Second-winter (adult) Pied:* Adult plumage was mainly white with black hind neck, nape, mantle and wings. The black areas of the male in particular had a greenish gloss. A narrow white mantle band, often with black mottling, usually separated the black of the nape from the black of the mantle. The boundary between black and



FIGURE 2 — Juvenile Black Stilt, January

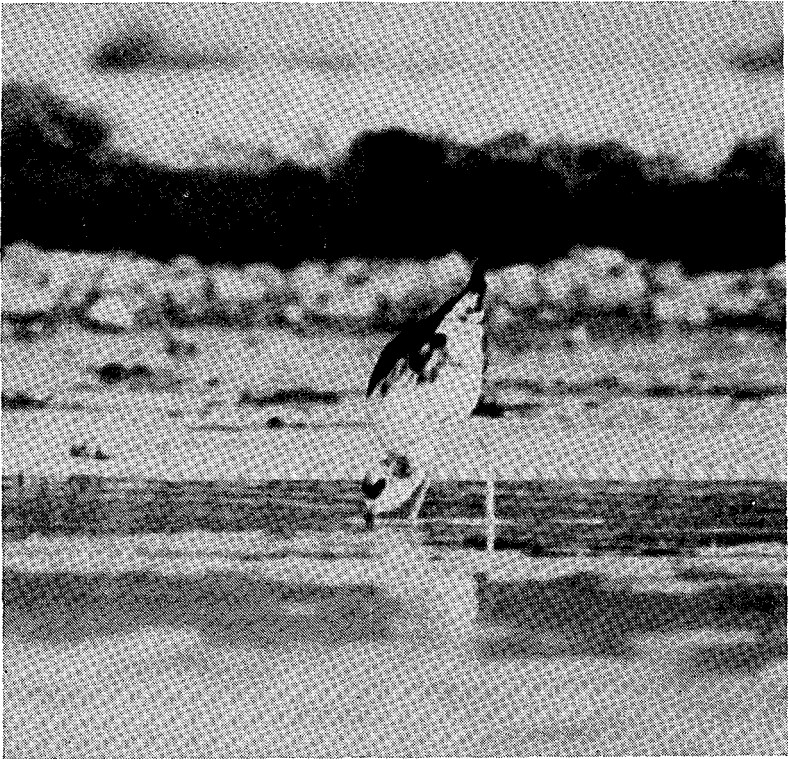


FIGURE 3 — Underparts of a first-winter Black Stilt, July

white on the sides of the neck was very variable in both position and extent of black mottling. On the tail of all birds was a terminal band of light grey to greyish brown, sometimes extending 50 mm up the tail.

*Second-winter Black:* The second-winter moult occurred between December and April. After moult, birds were black above with a greenish gloss to the hind neck, mantle and wings. The underparts were dark brownish black. In some birds a small amount of white mottling on the abdomen was retained until the next summer moult, beginning about June, at the age of 17-20 months. This white was usually less clearly defined than the white of nodes H or I hybrids (Fig. 4).

*Third-summer (adult) Black:* As for second-winter Black, but without white abdominal markings. During periods of moult, adults may have grey to off-white forehead and chin.

TABLE 1 — Comparative morphology of adult Pied and Black Stilts

Measurement	Sex	n			$\bar{x}$			sd			P <sup>1</sup>		$\bar{x}_{PA}/\bar{x}_{PNZ}$	$\bar{x}_B/\bar{x}_{PNZ}$
		PA	PNZ	B	PA	PNZ	B	PA	PNZ	B	PA	B		
Bill length (mm)	M	18	42	3	62.1	62.0	66.6	2.3	2.7	0.8	NS	-	1.00	1.07
	F	14	31	7	60.7	61.3	65.7	3.0	2.4	1.8	NS	-	0.99	1.07
	M + F	32	73	27	61.5	61.7	66.2	2.8	2.5	2.5	NS	+++	1.00	1.07
Bill width (mm)	M + F	34	34	34	6.0	6.1	6.8	0.7	0.5	0.5	NS	+++	0.98	1.11
Bill depth (mm)	M + F	..	35	15	..	6.7	6.9	..	0.6	0.5	-	NS	..	1.03
Tarsal length (mm)	M	19	47	4	114.3	100.3	90.8	6.3	6.4	2.3	+++	-	1.14	0.91
	F	15	45	9	109.0	93.0	85.6	7.8	3.8	5.8	+++	++	1.17	0.92
	M + F	34	92	32	112.0	96.6	88.1	6.7	8.5	4.9	+++	+++	1.16	0.91
Tail length (mm)	M	19	40	4	72.9	76.9	79.8	2.7	3.4	2.5	+++	-	0.96	1.04
	F	15	37	8	73.4	75.1	78.6	5.4	3.5	4.8	NS	+	0.98	1.05
	M + F	34	77	33	73.1	76.0	78.5	4.1	3.4	4.3	+++	++	0.96	1.03
Wing length (mm)	M	19	44	4	228.6	230.3	235.5	8.4	12.1	3.7	NS	-	0.99	1.02
	F	15	39	9	220.1	220.5	237.5	6.7	13.3	8.7	NS	+++	1.00	1.07
	M + F	34	83	37	224.8	225.5	236.3	8.7	13.5	11.0	NS	+++	1.00	1.05
Fresh weight (g)	M	6	15	2	176	193	219	12.4	10.2	-	-	-	-	-
	F	12	14	2	176	192	227	20.8	18.2	-	-	-	-	-
	M + F	18	29	4	176	193	223	18.0	20.9	8.3	-	-	0.91	1.16

## NOTES:

<sup>1</sup> t - test with New Zealand Pied Stilts, NS = not significant; +, ++, +++ significant at the p = 0.05, 0.01 and 0.001 levels respectively; - = not tested.

PA = Australian Pied Stilts, PNZ = N.Z. Pied Stilts, B = Black Stilts; M + F includes some unsexed specimens; Except for weight, measurements are of dried specimens



*Morphology of Pied and Black Stilts*

Table 1 compares Black Stilts, New Zealand Pied Stilts and Australian Pied Stilts. Black Stilts differed from New Zealand Pied Stilts by having longer bills ( $p < 0.001$ ), broader bills ( $p < 0.001$ ), shorter tarsi ( $p < 0.01$  for females,  $p < 0.001$  for sexes combined), longer tails ( $p < 0.01$  for sexes combined), and longer wings ( $p < 0.001$ ). New Zealand Pied Stilts differed from Australian Pied Stilts mainly by having shorter tarsi ( $p < 0.001$ ), by being heavier ( $p < 0.01$ ) in an equivalent season's comparison, and by having longer tails ( $p < 0.001$  for sexes combined) as well as by having variable plumage markings.

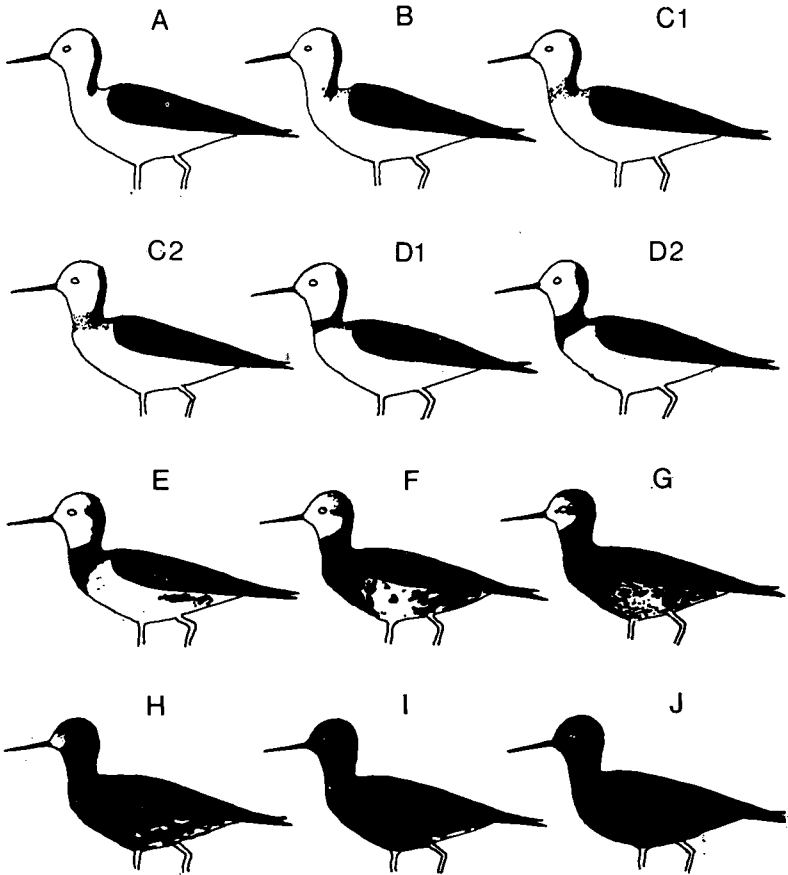


FIGURE 4 — Plumage classification of adults. Not all birds fitted into one node exactly, but each was allocated to whichever node it most closely resembled

## HYBRIDS

*Plumages and morphology*

The categories or nodes of adult plumage are shown in Figure 4. The validity of using these particular nodes lay in an approximately linear relationship between lengths of appendages and proportion of black and white on the underparts. For example, tarsal lengths decreased linearly with increasing blackness of the birds. Table 2 presents plumage forms of offspring from various pairings. Pairs of node A birds ("pure" Pied Stilts) produced node A offspring (n=2), and pairs of node J birds ("pure" Black Stilts) produced node J offspring (n=10). The offspring from backcrossing intermediate nodes with "pure" nodes, however, were generally intermediate in markings between their parents. Some variations occurred within each category of backcrossing, but no throwbacks to either parental phenotype (nodes A or J) were found and there was no evidence of sex linkage. The two 'approximate' F1 hybrids (nodes B x J) observed both had node E plumage. The plumage markings of individual adult stilts were approximately similar from year to year. Only one bird changed nodes (from being node H at 2 and 3 years to being node I at 4 years).

Bivariate plotting of morphological features revealed that Pied and Black Stilts could best be distinguished from hybrids by tarsal and bill analyses and by tarsal and wing analyses. See Fig. 5. The continuous variation between extremes of plumage and body measurements, however, indicates that inheritance of these traits is controlled by several genes (Anderson 1953). In a simple two-gene system, back-crossing of an F1 hybrid with a parental phenotype, for example, would give a plumage ratio of 1 parent : 1 F1 hybrid : 2 intermediates. But of 20 progeny recovered so far from various hybrid backcrosses, 19 have been intermediate, and one similar to the hybrid parent.

The immature plumages of hybrids were not easily followed because few were resident in the Upper Waitaki River Basin. I had

TABLE 2 — Plumage nodes of mature offspring resulting from matings between pure stilts and various hybrids. Number of birds in parentheses

Node of one parent	—Pied—			Hybrids					Black	
	A	B	C	D	E	F	G	H	I	J
Node of other parent										
Pied A	A(2)	B(1)	C(2)	C(3)	D(1)					
Pied B		B(4)	B(1)	C(1)	D(2)			E(2)		
					E(1)					
Black J		E(2)			I(1)	G(1)		I(1)		J(10)
						H(4)				

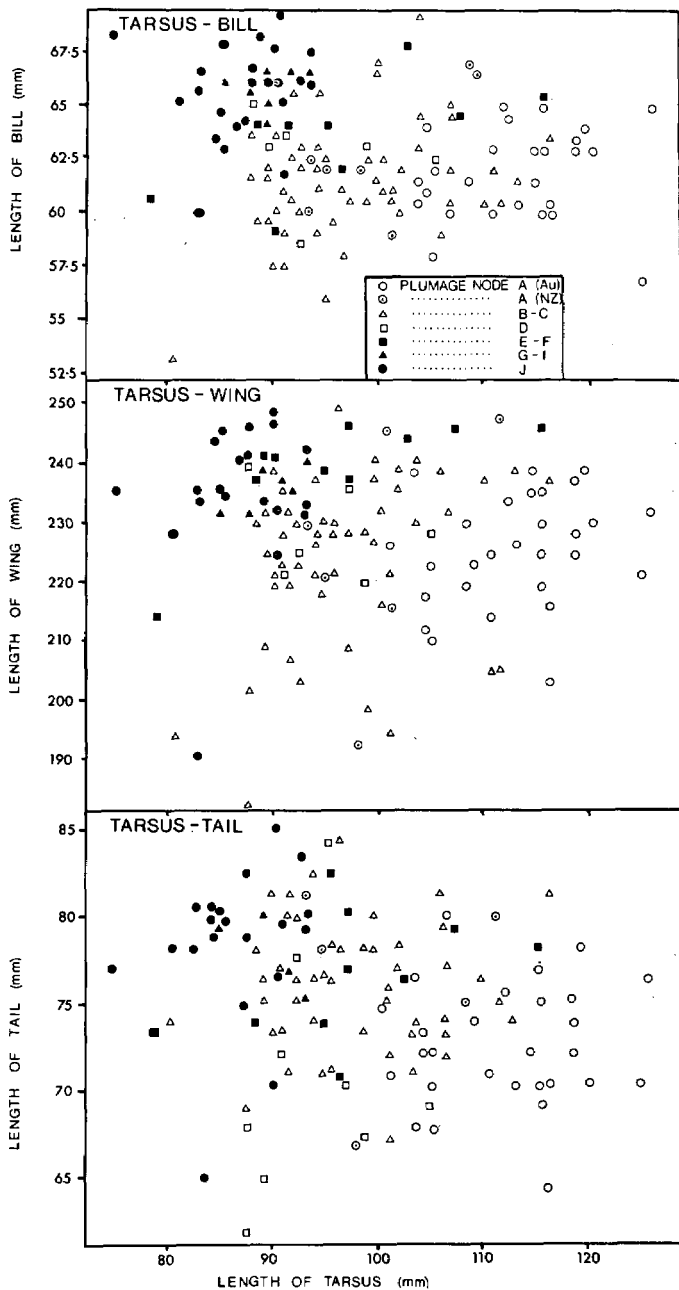


FIGURE 5 — Morphology of New Zealand and Australian stilts. Bivariate plots of tarsal length against lengths of bill, wing and tail for birds in different plumage nodes

complete observations of nodes D, E (four) G and H (two) birds. The juvenile plumage of these birds was similar to that of juvenile Black Stilts. In first-winter plumage, however, the flank and side markings of all hybrids except one of the node H birds were not as extensive or as dark as those of Black Stilts in first-winter plumage, the markings on the node E birds being particularly faint. In second-summer plumage, the flank, side, and abdominal markings of all hybrids reached their maximum extent, but the nape, hind neck, sides of the neck and much of the foreneck were mainly black with greyish streaking. These streakings (indicative of immatures) were lost during the second-winter moult. Immature Black Stilts were, therefore, best distinguished from immature hybrids by more extensive body markings both in first-winter plumage and in second-summer plumage. The variation among immature Black Stilts, however, means that it is probably not possible to distinguish safely between second-summer Blacks and second-summer nodes H and I birds. The identification of juvenile and first-winter plumages of Black Stilts is simplified by the fact that family parties remain associated for the duration of these plumages.

Although I regarded node A and node J birds as "pure" Pied Stilts and "pure" Black Stilts respectively, they need not necessarily be genetically pure. Four out of seven node A birds had tarsal lengths below the range of Australian Pied Stilts (Fig. 5), indicating that there may be very few genetically pure Pied Stilts in New Zealand. Thus, true F1 hybrids are unlikely to occur, and some node J birds may not be genetically pure. In view of this it would be just as legitimate to regard nodes H and I birds as Black Stilts as to regard only node J birds as Black Stilts. To date I have had no recoveries of offspring of H x J or I x J pairings, which would shed some light on this problem.

#### *Frequency and distribution of hybrids*

During each breeding season the stilt population of the Cass River Valley and the Upper Waitaki River Basin as a whole was dominated by birds in nodes B and C plumage and not node A plumage (Fig. 6A). The distribution of hybrids was centred on the Upper Waitaki River Basin (Fig. 6B) where they accounted for 17.5% of adult stilts in 1980-81 ( $n=1372$ ). Away from this area, per cent frequency of hybrids was consistently lower, including 3.4% ( $n=442$ ) in coastal Otago. Lake Wainono was the coastal locality with the highest hybrid frequency (14.9%,  $n=295$ ), which was consistent with that area being used as a feeding ground by at least some stilts from the Upper Waitaki River Basin (Pierce 1983).

About 90% of the Black Stilt population winters in the Upper Waitaki River Basin. Most hybrid stilts, however, followed the Pied Stilt migration pattern, leaving the Upper Waitaki River Basin after nesting and moving northwards. Regular wintering grounds include

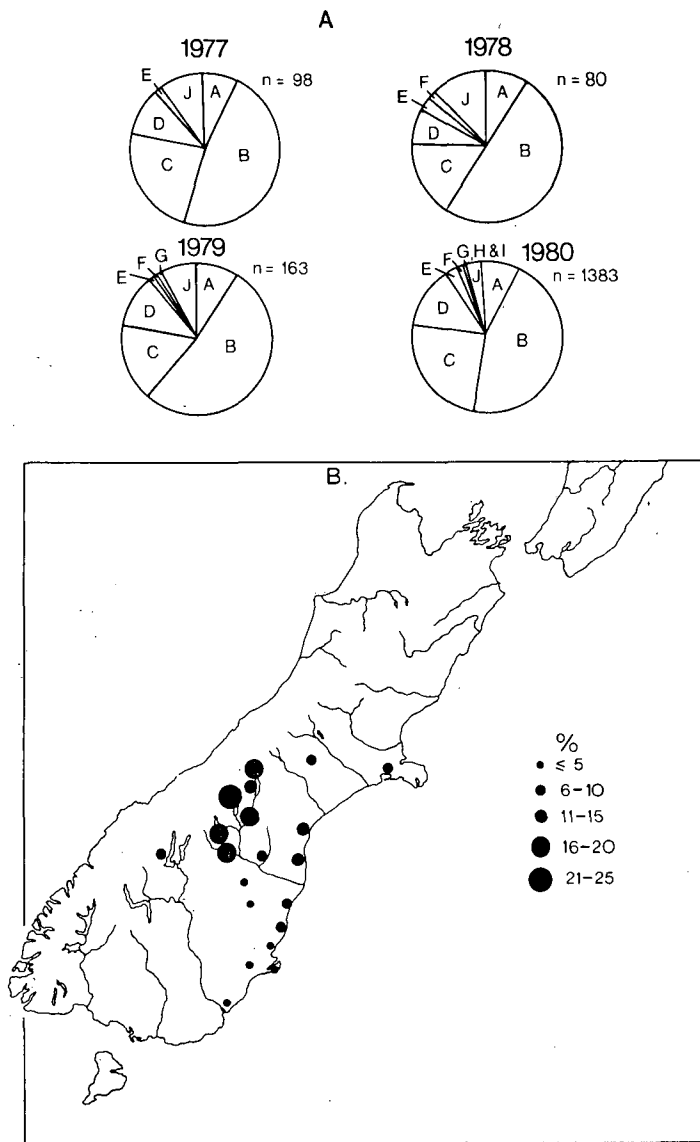


FIGURE 6 — Frequency and distribution of hybrids.

A. Percent frequency of plumage nodes (Fig. 4) of stilts in the Cass River Valley in 1977, 1978 and 1979, and in the Upper Waitaki River Basin as a whole in 1980

B. Frequency occurrence of hybrid stilts (nodes D-I) as percent total stilts, Nov 1980 to Jan 1981, in some Canterbury and Otago sites

Kawhia and Manukau Harbours, where associations with Black Stilts are often noted (OSNZ Recording Scheme; B. H. Seddon, pers. comm.). One node I bird, colour-banded as a juvenile on the Cass River Delta on 8 January 1980, was seen in the Manukau Harbour on 7 October 1981 (C. R. Veitch, pers. comm.) and returned to the Cass River Valley to breed in the 1982-83 season. Small numbers of hybrids overwintered in the high country, particularly at Lake Benmore: approximately 50% of these hybrids were apparently paired to Black Stilts, some of which were accompanied by young.

Hybrids returned early to the Cass River Valley, at a date corresponding to the general period of arrival of Black Stilts. In August of each year hybrids accounted for 28-37% of the stilt population in the valley, but by December, when Pied Stilts had become common, they accounted for about 11% of the population. Hybrids not only arrived early like Black Stilts but also, like Black Stilts, had the ability to probe for aquatic invertebrates which were hidden beneath the stones during periods of low water temperature. Nodes F to I hybrids used the lateral probing of Black Stilts (Pierce, in prep.) and so were able to maintain consistently high feeding rates during the morning. Birds in nodes D and E plumage had variable feeding patterns: all early arrivals used lateral probing extensively, but many later arriving birds used this method very little or not at all, like Pied Stilts.

#### *Breeding biology and behaviour of mixed pairs*

The formation of pair bonds involving at least one Black Stilt was seen on ten occasions in the Cass River Valley (Table 3), nine of them between late July and October. All ten pairings included a male Black Stilt, four of them when unmated female Black Stilts were in the valley, and Black-Black pair bonds were formed in three of the four cases. In the other six pairings, no unmated females were available locally: each male was approached on separate occasions by female Pied Stilts and/or hybrids. The females attempted contact by assuming the soliciting posture (e.g. Goriup 1982, Cramp & Simmons 1983), thus inviting the attention of the Black males. Five of the six males eventually mated with hybrids in nodes D-G plumage.

The preference of Black Stilts for black or near-black birds concurred with pairing choices throughout the Upper Waitaki River Basin. Although Black Stilts comprised only 3% of the stilts in this area (Fig. 6A), 70% of them occurred in Black-Black pair bonds (Table 4). This positive assortative mating was highly significant ( $\chi^2=222.5$ , 1 df,  $p<0.001$ ,  $n=24$  pairs). In addition, Black Stilts preferred hybrid mates to Pied Stilt mates ( $\chi^2=29.5$ , 1 df,  $p<0.001$ ,  $n=11$ ). Similarly, hybrids preferred hybrid or Black Stilt mates more than Pied Stilt mates ( $\chi^2=52.4$ , 1 df,  $p<0.001$ ,  $n=57$ ).

In the Cass River Valley, 10 nests of Black Stilt x hybrid or Black x Pied pairings were found in the five seasons 1977-81. Except

TABLE 3 — Pairing by ten male Black Stilts

Bird	Month	Plumage node of potential mates <sup>1</sup>								Partner chosen
		A-C	D	E	F	G	H	I	J	
1	Aug. 1978	2	0	1	0	0	0	0	0	E
2	Aug-Sep 1978	3-4	0	1	0	0	0	0	0	E
3	July-Aug 1979	2+	4	0	0	1	0	0	1	J
4	Aug 1979	2-3	4	0	0	1 <sup>3</sup>	0	0	1 <sup>4</sup>	D
5	July-Aug 1979	2-3	4	0	0	1	0	0	1 <sup>4</sup>	G <sup>2</sup>
6	Aug 1980	..	..	..	..	..	..	..	1	J
7	Oct 1981	..	..	..	..	..	..	..	1	J
8	Feb 1982	..	..	..	..	1	..	..	1	G
9	Aug 1983	0	0	0	1	0	0	0	0	F
10	Aug-Sep 1983	2+	0	0	0	0	0	0	0	C

Notes: <sup>1</sup> Potential mates refer to female stilts at the same locality in the study area.

<sup>2</sup> Bird 5 was with a node G bird on 31 July and 1 August, but on 9 August it was with a node A bird. It eventually mated and nested with the node G bird.

<sup>3</sup> The node G bird was already forming a pair bond with bird 5, and so it was not readily available to bird 4.

<sup>4</sup> The node J potential mate was already forming a pair bond with bird 3, and so it was not readily available to birds 4 or 5.

.. = no data

TABLE 4 — Pair composition of Black Stilts in the Upper Waitaki River Valley, November to December 1979

Plumages of pair	JxJ	JxI	JxH	JxG	JxF	JxE	JxD	JxC	JxB	JxA
No. of occurrences	13	1	0	2	3	1	2	1	1	0

for one of the 1979 pairs, all mixed matings involved male Black Stilts. None of the pairs occurred in the study area for two consecutive years, and at least two pair bonds were broken after unsuccessful nesting and each bird remated with a new bird the following year. One pair (including the only female Black Stilt) kept their pair bond for at least three seasons, nesting at Lake McGregor (5 km south of Cass River) in 1977 and 1978 and on the Cass River Delta in 1979. The scarcity of Black Stilt females may have been caused by their susceptibility to predation (Pierce, in prep.) because several were preyed on during the incubation period (along with the eggs) and during the chick-rearing stage. The selection of nesting habitat by mixed pairs was in three cases strongly influenced by the Black Stilt partner: in 1977, 1978 and 1980, pairs consisting of Black Stilt males and nodes E, D and C females respectively were found along streams in the middle reaches of the valley where Black Stilts, but not Pied Stilts, nested regularly. Reverse examples were a Black Stilt male and a node C Pied Stilt in 1978 and a Black Stilt female and a node F male in 1979 nesting in Pied Stilt colonies.

Eight of the above ten nests of mixed pairs contained 3-4 fertile eggs out of a clutch of 4, but the other two clutches were preyed on, one by a ferret (*Mustela furo*) and one by a Norway rat (*Rattus norvegicus*). Seven of 16 clutches of hybrids x Pied Stilt pairs contained fertile eggs, but the rest were preyed on or, more often, flooded. The limited data on nesting success of hybrids suggest that those nesting with Pied Stilts fared better (17% of 64 eggs produced flying young) than those nesting with Black Stilts in which 3 (11%) of 32 eggs produced flying young. This can be attributed to several life history patterns of Pied Stilts, such as colonial nesting in swamps and effective distraction displays, which alleviate the potentially heavy predation that affects the Black Stilt (Pierce, in prep.). The fledgling period of hybrid juveniles seemed to be intermediate (35-43 days,  $\bar{x}=39$ ,  $n=3$ ) between those of Pied Stilts (30-37 days,  $\bar{x}=34$ ,  $n=17$ ) and Black Stilts (41-55 days,  $\bar{x}=47$ ,  $n=12$ ).

#### PREVIOUS INTERPRETATIONS OF STILT PLUMAGES

Table 5 summaries interpretations of stilt plumages over the last 140 years. Black Stilts were described as species in 1841 by Gould (1841) and by Hombroën & Jacquinet (1841) with the names of *H. novaezealandiae* and *H. melas* respectively, the former eventually being retained on grounds of priority. Australian Pied Stilts had meanwhile been described as *H. leucocephalus* (Gould 1837) and this name was applied, after some dissent (Ellman 1861), to New Zealand specimens also (Buller 1865). Most of the confusion in the early literature was caused by the enigmatic hybrid and immature plumages. Hutton (1871) recognised correctly that birds with very



pale hind necks were juveniles, but he recognised three species, *H. leucocephalus* (Pied Stilts), *H. melas* (Black Stilts) and *H. novaezealandiae* (probably intermediate nodes). Hutton's main error was to regard first-winter Black Stilts as the young of his *novaezealandiae*, but this was later corrected (Hutton & Drummond 1905). Potts (1872) added a fourth species, *H. spicatus*, from Canterbury, which was a hybrid in node E plumage, but this was later incorporated into the species *H. picatus* (Buller 1905, Hutton & Drummond 1905), which included nodes C-F birds.

Hutton's fundamentally correct views on stilt plumages were opposed by Buller and others, who had a rather more complex interpretation. From 1875 to 1905 Buller believed that at least three species of stilt were in New Zealand, *H. leucocephalus* (adult Pied Stilt), the seasonally dimorphic *H. novaezealandiae* (adult Black Stilt, hybrids, some juveniles, and first-winter Black Stilts), and *H. albicollis*

TABLE 5 — Nomenclature of stilts in New Zealand, 1841-1970

Author	Adult Pied	Adult Hybrid (Nodes D-F)	Juvenile	First-winter Black	Adult Black
Gould 1841					<i>novae</i>
Hornbroon & Jacquinot 1841					<i>novae</i>
Elliman 1861	<i>albus</i> <sup>1</sup>	<i>picatus</i> ? <sup>1</sup>		<i>picatus</i> ? <sup>1</sup>	<i>melas niger</i> <sup>1</sup>
Gray 1862			<i>melas</i>		<i>melas</i> & <i>syn.</i>
Buller 1865	<i>novae</i>				<i>novae</i>
Buller 1868	<i>leuco</i>				<i>novae</i>
Finsch 1868	<i>novae</i> ?			<i>novae</i>	<i>novae</i>
Potts 1869	<i>novae</i>				<i>melas</i>
Travers 1871	<i>novae</i>				<i>melas</i>
Hutton 1871	<i>leuco</i>	<i>novae</i> ?	<i>spp.</i>	<i>novae</i> <sup>2</sup>	<i>melas</i>
Potts 1872	<i>leuco</i>	<i>spicatus (varius)</i>			<i>melas (novae)</i>
Finsch 1872	<i>leuco</i>				<i>melas (novae)</i>
Buller 1873	<i>leuco</i>				<i>novae</i> <sup>5</sup>
Buller 1875a		<i>novae</i> <sup>4</sup>	<i>albicollis</i> B		<i>novae</i> <sup>5</sup>
Buller 1875b			<i>novae</i> B <sup>3</sup>		<i>novae</i> <sup>5</sup>
Buller 1878	<i>leuco</i>				<i>novae</i> <sup>5</sup>
Buller 1882	<i>leuco</i>	<i>novae</i> ? <sup>4</sup>	<i>novae</i> B	<i>novae</i> ? <sup>4</sup>	<i>novae</i> <sup>5</sup>
Buller 1882 (contd)			<i>albicollis</i> P		<i>novae</i> <sup>5</sup>
Buller 1888	<i>leuco</i>	<i>novae</i>	<i>novae</i> B	<i>novae</i>	<i>novae</i> <sup>6</sup>
Buller 1891 & 1892					<i>novae</i> <sup>6</sup>
Buller 1905	<i>leuco</i>	<i>picatus</i>	<i>albicollis</i>		<i>melas</i>
Hutton & Drummond 1905	<i>leuco</i>	<i>picatus</i> <sup>7</sup>	<i>spp.</i>	<i>melas</i>	<i>melas</i>
Matthews & Iredale 1913	<i>albus</i> <sup>1</sup>	<i>picatus</i> <sup>1</sup>			<i>novae</i> <sup>1</sup>
Stead 1927	<i>leuco</i>				<i>melas</i>
Oliver 1930	<i>leuco albus</i>	"hybrids"		"hybrids"	<i>novae</i>
Stead 1932	<i>leuco albus</i>	"intermediates"		"intermediates"	<i>novae</i>
Peters 1934	<i>him leuco</i>	"mutants"		"mutants"	<i>him novae</i>
Fleming 1953	<i>him leuco</i>				<i>novae</i>
Oliver 1955	<i>leuco</i>	"hybrids"		"hybrids"	<i>novae</i>
Kinsky 1970	<i>him leuco</i>				<i>novae</i>

Notes: *leuco* = *leucocephalus*; *novae* = *novaezealandiae*; *him* = *himantopus*;  
 B = Black Stilt; P = Pied Stilt; *spp.* = juveniles of unknown parentage;  
 ? the descriptions given by the author are insufficient to enable a positive identification;  
 & *syn.* = synonyms given also

1 of the genus *Hypsibates*

2 Hutton considered this to be the young of his *novaezealandiae* which was a category possibly of

3 The specimen was a partial albino

4 Buller considered this to be the winter plumage of Black Stilts

5 Buller considered this to be the summer plumage of Black Stilts

6 Includes specimens in second summer plumage

7 Hutton and Drummond considered Potts' (1872) *spicatus* to be a variety of *picatus* and that both *spicatus* and *picatus* ought to be conspecific with *leucocephalus*.

(very pale juveniles). Buller's *H. novaezealandiae* was supposedly black in summer plumage and black and white in winter plumage, while the juveniles were pale with dark crown, mantle and wings (Buller 1882, 1888). His description of winter adults was sooty black crown, sides of head, hind neck and abdomen, glossy greenish-black wings and tail, and mainly white underparts: this description may correspond to adult hybrids, but the abdominal markings and lack of greenish gloss on the hind neck suggest first-winter Black Stilt. This plumage was later (Buller 1905) noted as being very variable. It is very likely that many of these "adult winter Blacks" were in fact first-winter Black Stilts, which would also account for Buller's interpretation of a seasonally dimorphic adult plumage. Adult hybrids, by contrast, would have been in "winter" plumage throughout the year and so would not have fitted the seasonal pattern. Buller's allotting of some juveniles to species status is not altogether surprising because he relied heavily on specimens received by the Colonial Museum, rather than on field observations.

Hutton & Drummond (1905) produced an accurate assessment of stilt plumages, reducing the number of species to three: *H. leucocephalus* (adult and juvenile Pied Stilts), *H. melas* (adult, juvenile and first-winter Black Stilts) and *H. picatus* (nodes C-E birds), and they further suggested that *H. leucocephalus* and *H. picatus* might be conspecific. Surprisingly, authors in the mid-20th century did not distinguish between plumages of hybrids and first-winter Black Stilts. For example, Oliver (1930, 1955) stated "Stilts having their plumage intermediate in colour between the Black and the Pied species are undoubtedly hybrids", and Peters (1934), in his checklist of world birds, considered that stilts in New Zealand have "a tendency to melanism resulting in the production of a certain proportion of melanistic mutants of varying intensity". Oliver and Peters were either unaware of, or doubted, the precise descriptions given by Hutton & Drummond (1905). Stead (1932) on the other hand, was aware of hybrid juveniles and first-winter plumages, as is shown by his correct labelling of museum skins.

## DISCUSSION

The extent of hybridisation in the 19th century is hard to assess. Node D or E hybrids were recorded by Hutton (1871), Potts (1872), Buller (1875a, 1888), and possibly by Ellmann (1861). In about 1880, A. Reischek collected a node D bird from Mt Selwyn, Canterbury, and this specimen is in the Vienna Museum (K. E. Westerskov, pers. comm.). Buller (1888) found that Pied Stilts varied considerably in size. Of 24 pre-1900 Pied Stilt skins in the British, Canterbury, Otago and Auckland Museums, seven only are in node A plumage. Despite these records, actual instances of interbreeding between Pied and Black Stilts may have been relatively few. For example, Potts (1869) stated ". . . we have never once found the two species breeding together or using the same or even similar


situations for their nesting place," and Buller (1882, 1888) endorsed Potts' observations.

Records in the 20th century suggested that the interbreeding increased wherever Black Stilts were rare or on the edge of their main range. On the bed of the Waipara River (North Canterbury) in 1904, Stead found several pairs of "pure Pied Stilts," along with several pairs of Black Stilts, one Pied x Black pair and several "intermediates," one of which was a "Potts type" bird (node D or E) nesting with a Pied Stilt. In 1907, Stead found no Black Stilts on the Waipara River bed, but in other parts of Canterbury he observed hybrids and "several instances of Blacks breeding with Pied mates" (Stead 1932). Stead suggested that Black Stilts interbred with Pied Stilts owing to a shortage of potential mates. This opinion is supported by my observations of selective mating at Lake Tekapo, where male Black Stilts greatly outnumbered females. Similar observations to Stead's are available for the Marawhenua River in North Otago, where M. Keioller (pers. comm.) found several pairs of Pied Stilts and several pairs of Black Stilts in the 1950s. In later years, Mr Keioller found only Pied Stilts and "smudgies" nesting at the river. In recent years some mixed pairs have been found nesting outside the normal Black Stilt breeding range, including the Routeburn River in 1958 (M. F. Soper, pers. comm.), near Hawea in 1966 (P. Child, pers. comm.), and along the Hakataramea River in 1971 and at Lake Wainono in 1979 (pers. obs.).

Interbreeding is currently contributing to the decline of Black Stilts. Introgression alone, however, could not have been responsible for the dramatic decline of Black Stilts in the late 19th and early 20th centuries. In the mid-19th century, Black Stilts were widespread and common in New Zealand, whereas Pied Stilts were uncommon and may have arrived only recently from Australia. Reproductive isolation would have remained largely intact during this period owing to selective mating by Black Stilts. Moreover, had a total breakdown in reproductive isolation occurred, it would have resulted in the then-rarer Pied Stilt being incorporated into the large Black Stilt population.

In my opinion the Black Stilt declined because it could not adapt to man-induced changes in the environment, particularly increased predation pressure and habitat alteration (Pierce 1982). However, the Black Stilt has maintained a very small population for about the last 25 years without being absorbed into the large Pied Stilt population. In part, at least, this has probably been helped by separate wintering grounds and habits, by which Black Stilts form pair bonds before Pied Stilts return inland. Pied Stilts were very rare in the Upper Waitaki River Basin in winter and early spring, when unpaired resident Black Stilts were usually forming pair bonds. If all Black Stilts had wintered alongside Pied Stilts in scattered coastal localities, mixed pairings would have been more likely than they are.

TABLE 6 — Plumage and biometric comparisons within the genus *Himantopus*

Form	<i>novaezealandiae</i> <sup>1</sup>	<i>leucocephalus</i> <sup>2</sup> (N.Z.)	<i>leucocephalus</i> <sup>3</sup> (Aust.)	<i>himantopus</i> <sup>4</sup>	<i>ceylonensis</i> <sup>5</sup>	<i>meridionalis</i> <sup>6</sup>	<i>mexicanus</i> <sup>7</sup>	<i>knudseni</i> <sup>8</sup>	<i>melanurus</i> <sup>9</sup>
Plumage M									
F	Similar	Similar	Similar	Back brown	Back brownish	Back brownish	Back brown	Back browner	Similar
Plumage variability	Moderate Head, abdomen	High Neck, collar crown	Low -	High Crown hind neck	..	..	High Crown	High Neck	High Crown, collar
Bill length n	27	73	32	63	..	14	36	36	28
(mm) $\bar{x}$	66.2	61.7	61.5	63.6	..	63.5	64.4	74.11	62.0
sd	2.5	2.8	..	..	..	..	..	..	2.9
Tarsus M n	4	47	19	43	4	14	18	43	13
(mm) $\bar{x}$	90.8	101.3	114.3	124.7	117	115	113	123.9	114.5
sd	2.3	6.4	6.3	..	..	..	6.0	6.1	6.0
Tarsus F n	9	45	15	32	3	..	21	45	16
(mm) $\bar{x}$	85.6	93.0	109.0	111.8	113.5	..	103.2	116.9	107.6
sd	5.8	5.2	7.8	..	..	..	4.1	5.9	6.9
Wing n	37	83	34	76	7	14	39	88	29
(mm) $\bar{x}$	236.3	225.5	224.9	237.5	239.5	226	219.5	235.0	220.5
sd	11.0	3.3	..	..	..	..	..	..	13.0
Tail n	33	77	34	..	7	14	39	88	29
(mm) $\bar{x}$	78.5	76.0	73.1	..	79	80.9	67.7	76.1	76.2
sd	4.3	3.4	..	..	..	..	..	..	4.4
Weight n	4	29	18	..	..	..	18	85	..
(g) $\bar{x}$	223.1	192.7	176.4	..	..	..	166	202.6	..
sd	..	19.9	..	..	..	..	..	..	..

Notes: .. = no data; M = male, F = female

Source of data: 1 British, Auckland, National, Canterbury and Otago Museums: field data  
2 As for *novaezealandiae* with the addition of data from B.F. McConkey (pers.comm).  
3 Australian Museum, National Museum of Victoria, CSIRO

4 Prater *et al.* (1977), Goriup (1982)  
5 Ali & Ripley 1980 ( $\bar{x}$  = mid point of range)  
6 McLachlan & Liversidge (1972). Tarsal measurements are for male and female combined.  
7 Hamilton (1975), Prater *et al.* (1977)  
8 Coleman (1981)  
9 American Museum of Natural History

For geographical ranges of individual taxa see Fig 7

As a result of introgressive hybridisation, Pied Stilt plumages throughout New Zealand are highly variable. Node A birds accounted for only about 9% of the stilt population in the Upper Waitaki River Basin, and in the North Island, McConkey (1971) found that only 18 (13%) of 140 stilts had the white mantle band of node A birds. In addition, the tail of most node A birds in New Zealand is tipped grey to dark grey, whereas the tail of Australian birds is tipped light grey.

The introgression has contributed not only to plumage variations, but probably also to a shortening of the tarsus in Pied Stilts. Two of three measurements given in the early literature (Hutton 1871, Buller 1888, Hutton & Drummond 1905) list nodes A or B Pied Stilts as having tarsi of 4.5 inches (about 115 mm) in length. (The same authors list 90-95 mm for Black Stilt tarsi, consistent with this study). The Pied Stilt tarsal measurement is within the range of Australian birds, but outside the present-day range of New Zealand stilts. Of 195 stilt tarsi measured in New Zealand since 1970, only one of 115 mm, a male measured by B. F. McConkey (pers. comm.), has been of similar length to birds of the same sex in Australia. In addition, the tail is longer in New Zealand Pied Stilts than it is in Australian birds (Table 1). It is apparent that these variations in plumage and morphology began while Pied Stilts were still expanding their population in New Zealand.

The morphological differences between New Zealand and Australian Pied Stilts are comparable to those used to distinguish several world taxa of *Himantopus* (Table 6). Recent workers (Cramp & Simmons 1983), however, have considered that subspecific recognition of *meridionalis* and *ceylonensis* is not warranted and that the other forms, except perhaps the species *H. novaezealandiae*, are only subspecies of *Himantopus himantopus*. Nevertheless, the present morphological divergence of Pied Stilts in New Zealand may indicate a transitional stage in the speciation process, but it is too early to speculate on the outcome of this process. In South America, hybridisation between *H. h. mexicanus* and *H. h. melanurus* has given rise to variations in plumage (Blake 1977).

Black Stilt morphology has not changed noticeably since the 19th century, probably because the positive assortative mating of the original large population continued during the 20th century, even as the population declined. But now that they are rare and have a very low rate of population recruitment, they are very likely to acquire some Pied Stilt traits through interbreeding.

The presence of two forms of stilts in New Zealand probably represents a double invasion from Australia, but speciation of the Black Stilt was not complete when reinvasion occurred. The nomenclature of the Black Stilt is therefore not straightforward. Pied and Black Stilts exhibit a combination of specific and subspecific characteristics (Table 7), which places them in the "semispecies" category

TABLE 7 — Characters which (A) promote reproductive isolation and (B) reduce reproductive isolation between Pied and Black Stilts

	A. Isolating mechanisms	B. Unifying mechanisms
Morphology	Plumage and lengths of appendages differ	
Behaviour	Selective mating	Precopulatory behaviour and copulation alike
Voice	Black Stilt higher pitched	Responsive to pre-copulatory calls
Physiology	Chick growth rate differs	
Ecology	Mainly sedentary versus migratory; habitat partitioning; feeding differences	High overlap in habitat and foraging at certain times
Genetic		Hybrids are viable and fertile and so introgression occurs
Abundance		When rare Black Stilts cannot find Black mates

of some authors (Short 1969, Mayr 1970). In the literature, semi-species have been treated taxonomically as either species or subspecies. The apparently high level of interbreeding between Pied and Black Stilts suggests conspecificity (L. L. Short, pers. comm.). In some recent studies of interbreeding in birds, however, the criterion for species status has been the proportion of mixed pairs in the zone of contact, which may bring about reversal in nomenclatural decisions (E. Mayr, pers. comm.). Black Stilts show positive assortative mating, most breeding birds being paired Black-Black. The proportion of mixed pairs is clearly made higher by Black Stilts being locally and totally rare, one of several factors which encourage interbreeding between different species (Mayr 1970). The chances of a Black Stilt finding a suitable Black Stilt mate become less as the population decreases, and the potential for reproductive isolation between the two species also decreases. Because Black Stilts select other Black Stilts for breeding if they can, and because of their morphological and ecological differences from Pied Stilts (Pierce, in prep.), I recommend that Black Stilts retain their full specific status.

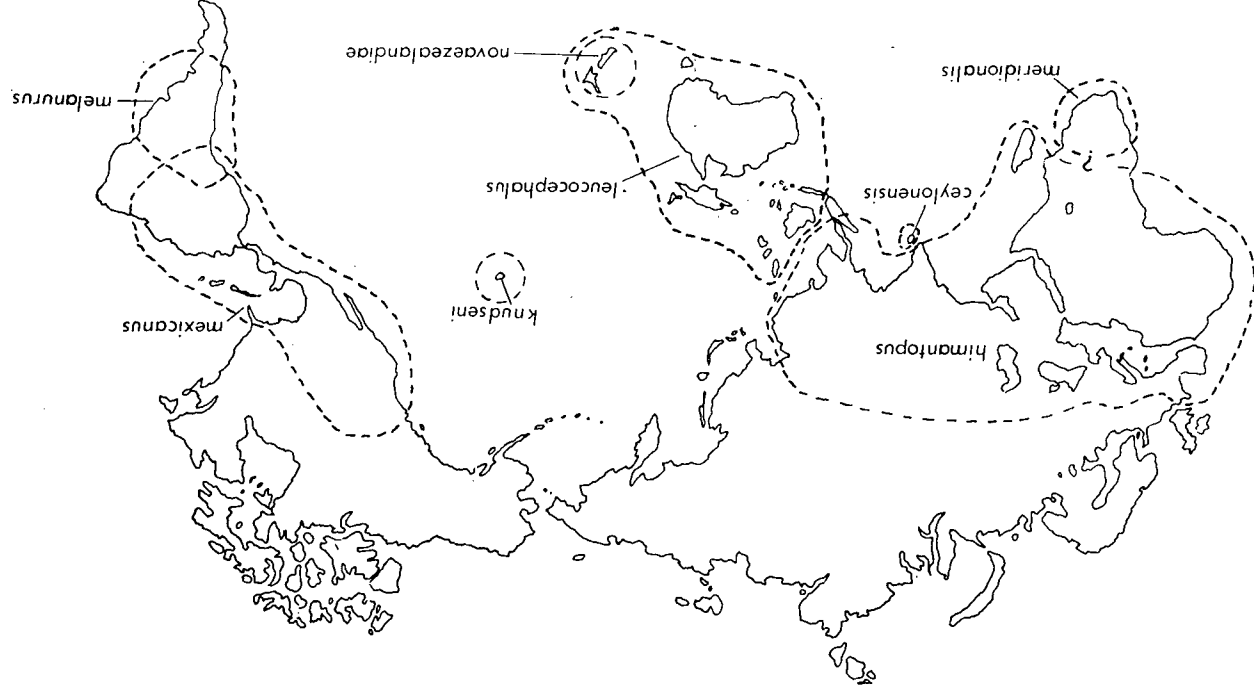


FIGURE 7 — World distribution of the genus *Himantopus*. Data from the references cited in Table 6. Most forms are considered to be subspecies of *H. himantopus* (e.g. Cramp & Simmons 1983), but the American Ornithologists' Union recognises *knudseni*, *mexicanus* and *melanurus* as subspecies of *H. mexicanus* (Coleman 1981), and the New Zealand checklist (Kinsky 1970) recognises *H. novaezealandiae* as a full species.

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R. J. PIERCE, *Department of Zoology, University of Otago, Dunedin*



## SHORT NOTE

### CORRECTION: NORTH ATLANTIC SHEARWATER TO PINK-FOOTED SHEARWATER

**First sightings of the North Atlantic (Cory's) Shearwater *Calonectris diomedea* (Scopoli, 1769) in Australasian seas (*Notornis* 29: 85-91, 1982).**

Overseas correspondence I have received in response to my report on the sightings of Cory's (North Atlantic) Shearwater, *Calonectris diomedea*, off the east coast of the South Island, has convinced me that my identification was incorrect. Indisputable evidence has been presented in support of Pink-footed Shearwater, *Puffinus creatopus*.

In May 1983 the OSNZ Rare Birds Committee met and reappraised the colour transparencies which featured as Figures 1, 2 and 3 in *Notornis* 29: 85-91 (1982). The Committee sent colour prints of the transparencies to Professor R. Schlatter, Universidad Austral de Chile, and Dr F. Roux, Museum of Natural History, Paris; both confirmed the birds in the photographs as Pink-footed Shearwater.

This is the first record of Pink-footed Shearwater in New Zealand.

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G. A. TUNNICLIFFE, *Canterbury Museum*