

DIFFERENCES IN SUSCEPTIBILITY TO PREDATION DURING NESTING BETWEEN PIED AND BLACK STILTS (*HIMANTOPUS* SPP.)

RAYMOND J. PIERCE¹

Department of Zoology, University of Otago, Dunedin, New Zealand

ABSTRACT.—The nesting success of the Pied Stilt (*Himantopus himantopus leucocephalus*) and the endangered Black Stilt (*H. novaezealandiae*) was studied for three consecutive breeding seasons (1977–1979) in New Zealand. Black Stilts had a breeding success of less than 1%, compared with over 8% for Pied Stilts. Predation by feral mammals was the main cause of nest failure for both species, but the impact was greater on Black Stilts. Direct and indirect evidence (including trapping predators) suggests that these introduced ground predators kill many chicks. Several factors made Black Stilts vulnerable, particularly their nesting along stream banks that were often frequented by predators; Pied Stilts nested in swamps where predators were few. Black Stilt chicks took up to 2 weeks longer to fledge and their foraging patterns made them more vulnerable than Pied Stilt chicks. Other factors that possibly increased predation risk of Black Stilts include nesting at times of high predator activity, solitary nesting, high site fidelity, ineffective distraction displays, and lack of a disruptive camouflage pattern in adults. Introduced ground predators probably have contributed greatly to the decline of Black Stilts. Pied Stilts have not been affected similarly, because their evolutionary past has included long exposure to ground predators. Received 27 February 1984, accepted 1 July 1985.

Two species of stilts (Recurvirostridae) occur in New Zealand: the endemic Black Stilt (*Himantopus novaezealandiae*) and the Pied Stilt (*H. himantopus leucocephalus*), which is the Australasian race of the widespread Black-winged Stilt. The Black Stilt probably has occurred in New Zealand for many thousands of years, but the Pied Stilt is a more recent immigrant, probably having arrived in the late 18th or early 19th century (Fleming 1962, Pierce 1984a). During the 19th century Black Stilts were widespread in New Zealand riverbeds and nested at least as far north as central North Island, but they declined rapidly. Since the 1950's a small breeding population has remained only in central South Island (Pierce 1984a). By contrast, Pied Stilts have expanded recently and are now common in most types of wetland throughout New Zealand.

Stilts are ground nesters and are therefore vulnerable to predation by mammals. The introduction of carnivorous mammals in the 19th century often is claimed to have had a deleterious effect on New Zealand wildlife, particularly forest birds (e.g. see Moors 1983), but good

data for most species are lacking. In this study of stilt ecology in South Canterbury, I examined the nesting success of Pied and Black stilts and compared their susceptibility to predation.

STUDY AREA AND METHODS

Most data were collected during three field seasons (1977–1978, 1978–1979, and 1979–1980) in the lower 15 km of the Cass River Valley, Lake Tekapo at 710–850 m (Fig. 1).

The study site is a glaciated valley flanked by mountains, with tussocks (*Festuca* spp., *Poa* spp., and *Chionochloa* spp.) and other grasses and small shrubs on the lower slopes. Stilts of both species nested in four habitats: riverbed, side streams, ponds, and swamps. The riverbed consisted of bare shingle and had braided channels with widely varying flows (mean annual flow was about 10 m³/s). The side streams had relatively constant flows, and a variety of grasses and other small plants grew on their banks. Muddy ponds were surrounded by grassland and usually contained water all year. The swamps were small (<10 ha), and the dominant plants were *Juncus* spp. and *Carex* spp. I previously described some physical and biological aspects of these habitats and the seasonal use of each habitat by stilts and other charadriiform species (Pierce 1983). Supplementary data on Black Stilts were collected in the Cass River Valley from 1970 to 1982 and in the neighboring Godley River Valley from 1977 to 1979.

¹ Present address: P.O. Box 69, Lake Tekapo, South Island, New Zealand.

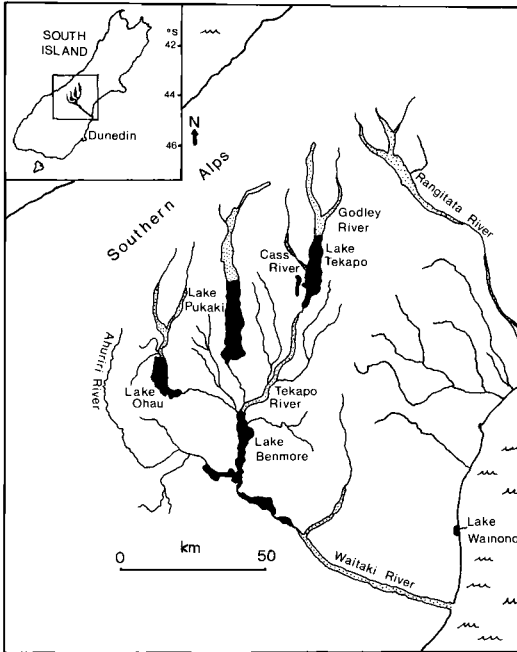


Fig. 1. Location of study areas. The main study area was in the Cass River Valley.

On every sixth day of the breeding season I walked the wetland nesting grounds to check whether individual pairs were laying, incubating, or guarding chicks. Other data collected were habitat, substrate, distance to water (all after the eggs had hatched), and proximity of other nesting stilts. Inevitably some nests would have been abandoned before I found them, so I used the Mayfield (1975) method for calculating breeding success. Because nest checks were frequent, I used the midpoint assumption rather than the Mayfield - 40% method (Miller and Johnson 1978, Johnson 1979). Failed nests were examined for evidence of the cause of failure. I identified nest predators as (1) ferret (*Mustela furo*), 13 nests in which the eggs were taken whole (no eggshell left), 10 of which had ferret footprints leading to or from the nest and 4 of which had ferret faeces at the nest; (2) feral cat (*Felis catus*), 11 nests in which 4-6 large and many small eggshell fragments were in or near the nest, 6 of which had cat footprints and 5 of which had cat faeces nearby; (3) Norway rat (*Rattus norvegicus*), 14 nests in which very small shell fragments were scattered in and around the nest, 3 of which had rat footprints and 2 of which had rat faeces nearby; or (4) Australasian Harrier (*Circus approximans*), 2 nests in which more than half of each eggshell remained in or near the nest, each shell with one or two puncture marks; 1 nest also had a harrier pellet present. I identified mammal signs from the guide of Lawrence and Brown (1973) or with help from staff of the New Zealand

TABLE 1. Breeding success of Pied and Black stilts.

	Pied Stilt	Black Stilt	
		Unprotected	Protected
Total nests	125	27	23
Nest days (N)	1,374	305.5	353
Total failed nests (F)	49	19	12
Total eggs hatched ^a	260	33	40
Total fledged young	69	2	13
Probability of nest surviving to hatching ^b (A)	0.349	0.155	0.367
Probability of egg hatching in a surviving nest ^c (B)	0.903	0.971	0.909
Probability of chick surviving to fledging (C)	0.265	0.061	0.325
Breeding success ^d	0.084	0.009	0.108

^a Mean clutch size of Pied Stilts was 3.8 (range 3-4); mean clutch size of Black Stilts was 4.0 (range 3-6).

^b $(1 - F/N)^{29}$. The duration of egg-laying and incubation was 29 days for both species.

^c The remaining eggs were infertile or addled.

^d Probability of egg producing flying young ($= A \times B \times C$).

Wildlife Service. I found no evidence of mammals scavenging on deserted stilt eggs. Deserted eggs of stilts (3 clutches) and of other charadriiform species were usually still intact two weeks after having been abandoned.

To test the hypothesis that breeding success would increase if predator numbers were reduced near nests, I set traps around 23 randomly selected Black Stilt territories. Gin or Fenn traps were set at intervals of 40-90 m (average 60 m) and no closer than 30 m to nests. Each trap was placed under a *Discaria* bush or covered with a wooden tunnel 30-45 cm long \times 20-24 cm wide \times 16-20 cm high. The traps were baited with rabbit flesh and checked every second day. The success of these "protected" Black Stilt nests was compared with 27 Black Stilt nests without traps ("unprotected"). In case predators followed my scent to nests (Bart 1977), I visited only those nests that could be approached through water. When I was within 10 m of these nests I recorded the reactions of the adult birds to my presence, as well as their nesting stage. Nocturnal observations of breeding behavior were made using an NVC night vision system with 500-mm lens from a hide or tent 60-200 m away.

To establish chick survival, observations of brood size were made with a telescope about every 10 days for 9 protected Black Stilt broods and 6 unprotected Black Stilt nests over 3 yr. I abandoned similar attempts with Pied Stilt chicks, because family groups

were usually closely spaced and therefore easy to confuse. It was not until juvenile Pied Stilts were flying (and less wary) that family sizes could be established. Adult Pied Stilts were individually recognizable all season by their plumage markings (Pierce 1984b), and many were also banded with individual color combinations. Family parties with flying young usually stayed near the nesting area for a few days at least. To be certain that the correct number of young was established, however, I made more visits than usual to pairs about to fledge young.

RESULTS

BREEDING SUCCESS AND CAUSES OF FAILURE

The breeding success of Black Stilts was much lower than that of Pied Stilts (Table 1). The probability that an egg present at the beginning of incubation would produce a fledgling was 0.084 for Pied Stilts and 0.009 for unprotected Black Stilts. Eggs in protected Black Stilt nests had a much higher probability of producing a fledgling (0.108) than those in unprotected nests.

Predation by mammals and birds accounted for 49% of Pied Stilt failures and 64% of Black Stilt failures for which the cause was established (Table 2). The impact of predation was more severe on Black Stilts. At least 41% of the unprotected nests were preyed upon, compared with only 19% in Pied Stilts ($\chi^2 = 7.37$, $P < 0.01$). Even protected Black Stilt nests were preyed on, but proportionately fewer (22%) than for unprotected nests. Ferrets, feral cats, Norway rats, and harriers all ate eggs (Table 3). Three other potential predators in the study area were stoats (*Mustela erminea*) and weasels (*M. nivalis*), both of which were uncommon, and hedgehogs (*Erinaceus europaeus*), which were common.

Except in severe conditions, Black Stilt nests were not very susceptible to flooding because the birds tended to nest in stable situations where food density was high.

No nests were known to be deserted after light snowfalls (up to 10 cm of snow), but in late October 1982, a heavy snowfall of 25–35 cm caused almost all Pied and Black stilts to desert their eggs.

Because stilts are nidifugous, it is very difficult to establish even by indirect means how chicks die. Except during two heavy snowfalls, there was no correlation between bad weather

TABLE 2. Cause of nest failure of Pied and Black stilts.

	Side stream	River	Pond	Swamp	Total
Pied Stilt					
Total nests	16	24	15	70	125
Preyed on	5	2	6	11	24
Flooded	0	13	0	3	16
Other ^a	3	2	0	4	9
Black Stilt unprotected					
Total nests	15	2	3	7	27
Preyed on	7	0	3	1	11
Flooded	1	0	0	0	1
Other ^a	4	1	0	2	7
Black Stilt protected					
Total nests	13	0	6	4	23
Preyed on	3	0	2	0	5
Flooded	3	0	0	0	3
Other ^a	2	0	1	1	4

^a "Other" includes desertion, damage by stock and wind, and unknown causes, some of which could have been predation.

and chick mortality. I had no direct evidence of predators taking Pied Stilt chicks but found two cases in which Black Stilt chicks were taken by a ferret and a cat.

Indirect evidence of the impact of predators on Black Stilt chicks came from using two predator-proof exclosures (Pierce 1982). Before these sites were fenced, four nesting attempts by Black Stilts were unsuccessful. Mammals took eggs and chicks in 1977, 1978, and 1979. Of the 30 chicks that have hatched in these exclosures since 1980, about 60% have flown. This high productivity contrasts with a fledging rate of only 7% at unprotected Black Stilt nests that hatched eggs (Table 1).

POSTBREEDING MORTALITY

Thirteen of 15 young Black Stilts survived until the end of winter (August), when the family units split up. This represents a mortality rate for flying young of 13% for 6 months, or 0.5% per week.

The longevity of Black and Pied stilts is unknown, but an adult female Black Stilt (2+ yr old) banded at its nest in December 1973 (R. J. Nilsson pers. comm.) was still alive and nesting in November 1983 at the age of over 12 yr. This bird is probably an exception, however, as several banded Black Stilts disappeared at an age of 2–3 yr, indicating that the potential life span may rarely be realized. Of 10 color-banded Black

TABLE 3. Predation on Pied and Black stilts in the Cass Valley, 1977-1979. Figures in parentheses are from the Godley Valley.

	Ferret	Feral cat	Norway rat	HARRIER	Unknown	Total
Pied Stilt						
Adult	0	1	0	0	1	2
Eggs	4	5	12	2	1	24
Chicks	0	0	0	0	0	0
Black Stilt						
Adult	0	2	0	0	1	3
Eggs	8 (1)	4 (2)	2	0	6 (2)	20 (5)
Chicks	1	1	0	0	0	2

Stilt fledglings in 1977-1979, only 4 survived to 3 yr of age and 1 to 4 yr.

Nesting was a vulnerable period for adult Black Stilts, with 5 of 7 known deaths occurring then. Three of these birds were taken with their eggs by mammals. Two birds disappeared during the fledging period of their young in 1980, but the cause of death was not established. In two cases following the death of one member of a pair, the nesting area was not used for nesting by Black Stilts again, despite unchanged food supplies and nest sites.

SOURCES OF BLACK STILT VULNERABILITY

Nesting habitat.—In the Cass Valley Pied Stilts nested mainly in swamps, whereas Black Stilts preferred the banks of side streams. Overall choice was significantly different between the species ($\chi^2 = 52.29$, 3 df, $P < 0.001$). Few predators were trapped in the swamps, but many were trapped at the side streams (Fig. 2). This concentration of predators exerted a high predation pressure on all stilts nesting at side streams: 31% of Pied Stilt nests and 47% of unprotected Black Stilt nests found at the streams were preyed on (Table 2). The effects of interhabitat differences in prey availability on chick survivorship are not known.

Antipredator behavior.—When I was within 10 m of a Pied Stilt nest, the adults usually performed distraction displays, often several birds together. The birds displayed at almost all nests being incubated and also at some during the laying period (Fig. 3). Black Stilts often used the aggressive flight (dive-bombing) method and less often distraction displays, but there was considerable variation among pairs. Ten

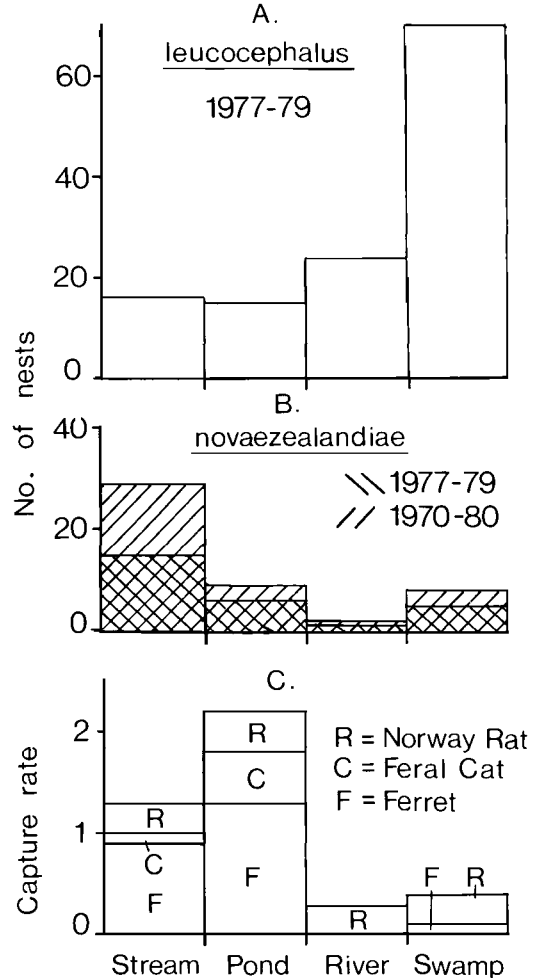


Fig. 2. Nesting habitats of Pied (A) and Black (B) stilts, and the trapping frequencies of predators in those habitats (C). Capture rates of predators are expressed as number caught per 100 trap nights, where "number of trap nights" is defined as "number of traps \times number of nights of trapping."

reactions (4 by Pied Stilts, 6 by Black Stilts) to ferrets and cats followed similar trends.

Colonial vs. solitary nesting.—In the Cass Valley Pied Stilts nested in loose groups or small (average of 5 nests) colonies and 117 of the 125 nests were less than 100 m (average 18 m, $n = 55$) from nests of other Pied Stilts. The other 8 nests were of "solitary" pairs. In contrast, Black Stilts nested more than 100 m from other stilts (Black or Pied) on 20 of 27 occasions. At Pied Stilt colonies the first bird to detect a predator would fly into the air, gaining height quickly and often uttering alarm calls. This behavior

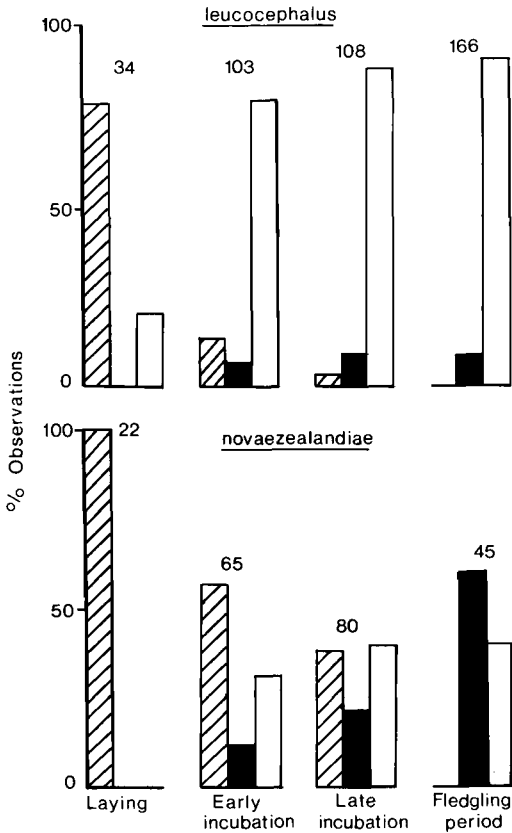


Fig. 3. Reaction of nesting stilts to a human intruder. Pied Stilts (top) usually performed distraction displays (open bars) such as false brooding and feigning injury; Black Stilts (bottom) usually flew about (shaded bars) or flew aggressively at the intruder (black bars).

immediately alerted all other birds, and they grouped together to attack the predator or lure it away with distraction displays. Black Stilts, being mostly solitary, seldom had this advantage.

Of 14 individually known pairs of Pied Stilts that renested, only 5 did so within 100 m of the old site. Of 15 pairs of renesting Black Stilts, however, 10 renested within 100 m of the old site.

Timing of and duration of nesting.—Black Stilts began nesting earlier than Pied Stilts (Fig. 4). In all three years no first nests (mid-September to early October) of Black Stilts were successful, and only one survived to hatching. This high level of predation may have resulted from a shortage of alternative food for predators (R. Pierce unpubl. data). Pied Stilts had a low rate

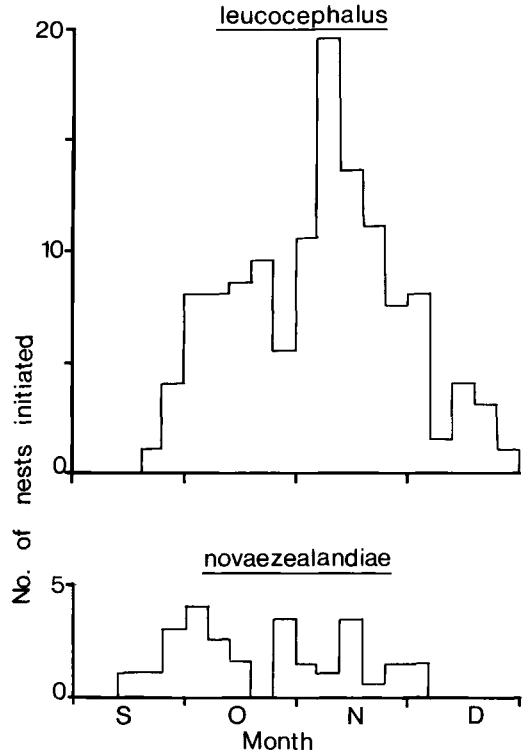


Fig. 4. Nest initiation by Pied (top) and Black (bottom) stilts in the Cass Valley.

of success early and late in the season (Fig. 5A); late-nesting birds had to contend with increased predator densities (Fig. 5B) resulting from influxes of adult predators and especially kittens.

Chick behavior.—During the night, especially on calm, moonlit nights, 4-7-week-old Black Stilt chicks foraged up to 100 m apart and up to 150 m from the guarding parent. Pied Stilt chicks foraged and called at night also, but they seldom ventured even 40-50 m from their parents. The wide-ranging activity of Black Stilt chicks probably made them more vulnerable, although I never saw predation actually occur.

Fledging period.—The fledging period of 17 Pied Stilts (\bar{x} = 34 days, range 30-37) was significantly shorter than for 14 Black Stilts (\bar{x} = 46 days, range 39-55; $P < 0.001$; all data recorded between November and January). No between-habitat differences in fledging period were found. The differences were a result of slower growth rates in Black Stilts (Fig. 6). The onset of rapid growth of the chick occurred at about 2 weeks in Pied Stilts, but not until after

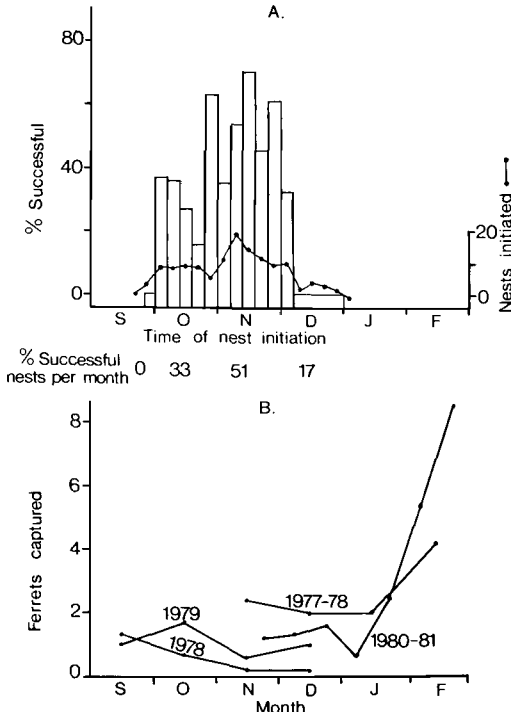


Fig. 5. Success of Pied Stilt nests in relation to time of initiation (A) and the number of predators trapped (B).

about 3 weeks in Black Stilts. During the very warm 1983 season chicks of both species grew more rapidly than usual, with some Black Stilt young flying at 35–37 days.

Most deaths of Black Stilt chicks occurred in the first 2 weeks of the fledging period (Fig. 7), but several Black Stilt chicks disappeared when they were over 5 weeks old, an age at which most Pied Stilt chicks had fledged.

DISCUSSION

Before carnivorous mammals were introduced to New Zealand, mainly in the 19th century (Thompson 1922, Wodzicki 1950), Black Stilts had few major predators. Native birds known to prey on the eggs or young of other birds are the Weka (*Gallirallus australis*), Pukeko (*Porphyrio porphyrio melanotus*), Australasian Harrier, and gulls (*Larus* spp.), while the New Zealand Falcon (*Falco novaeseelandiae*) and harrier sometimes prey on stilt-size adult birds (Oliver 1955, Baker-Gabb 1981).

The breeding success of Pied Stilts approximates the breeding success reported for several

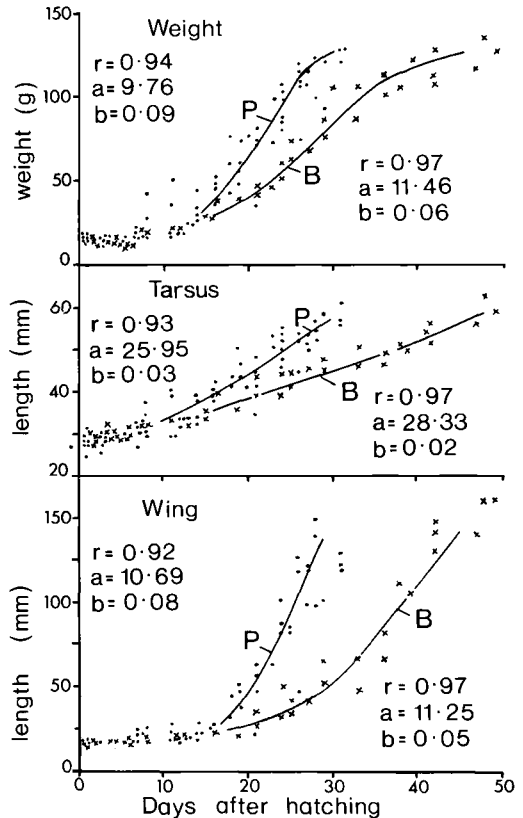


Fig. 6. Growth of stilt chicks. Each point (Pied Stilt) and cross (Black Stilt) represents one chick of known age. The exponential curve $y = ae^{bx}$ was of best fit, probably because growth continued beyond the date of first flight, after which no measurements could be taken. P = Pied Stilt, B = Black Stilt.

other shorebirds (Boyd 1962, Hale 1980). Breeding success for unprotected Black Stilts is exceptionally low, with predation by mammals being the main cause. The breeding success of other recurvirostrids is considerably higher than that for Black Stilts (Lippens et al. 1966, Cadbury and Olney 1978). The low annual production of Black Stilts, together with the existence of much unoccupied habitat (Pierce 1982), suggests that predation has contributed considerably to the overall population decline. In addition, low population recruitment facilitates the formation of mixed pair bonds (Pied × Black Stilt) with subsequent hybridization (Pierce 1984b).

Several features of its biology suggest that the Black Stilt has not developed antipredator behavior toward mammals. Dive-bombing, an

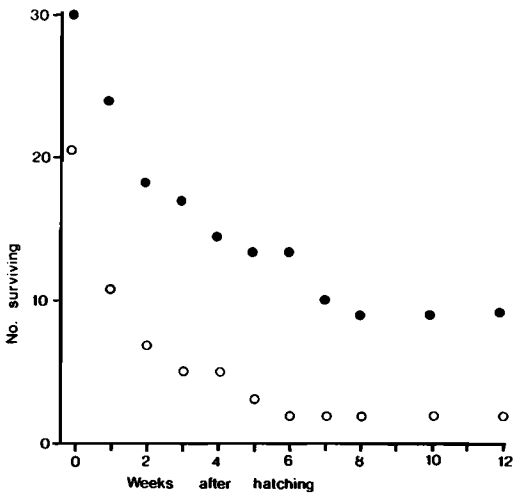


Fig. 7. Survivorship of protected (closed circles) and unprotected (open circles) Black Stilt chicks.

effective deterrent of avian predators (Kruuk 1964, Sordahl 1981), was used frequently by Black Stilts but was infrequently used by Pied Stilts. The Black Stilt shows strong nest-site fidelity, rather than shifting to a new nest site after nest loss (e.g. see Furrer 1979), and this probably increases the chances of double failure. High chick-adult distances in Black Stilt families probably reduce the energy cost of vigilance by the parents (e.g. Walters 1982) but at the same time increase the risk of chick predation.

Wide spacing between nests is generally considered to be an adaptation against predation (Tinbergen et al. 1967, Page et al. 1983). It is likely that spacing of Pied Stilt nests was sufficiently wide that a predator would not be attracted to the area, yet also sufficiently close for group distraction displays to be performed. Solitary-nesting stilts (mostly Black Stilts) were dependent entirely on their own ability to detect and repel predators, although in some cases Banded Dotterels or other species may have provided early warnings of approaching predators. Eight solitary-nesting pairs of Pied Stilts had a breeding success of only 5%, similar to the success rate of Black Stilts. Conversely, 6 Black Stilt nests in or near Pied Stilt colonies had an average success of 8% compared with about 1% for unprotected solitary nests. These differences, however, were not significant. Goransson et al. (1975) and Dyrz et al. (1981) found that, when "timid" species, including



Fig. 8. Incubating stilts, showing the disruptive camouflage pattern of a Pied Stilt (top) and the more conspicuous Black Stilt plumage (bottom).

shorebirds, nested close to "bold" species, they suffered less from predation than did isolated breeders.

With Black Stilts, their side-stream nesting habitat, high site fidelity, solitary nesting, poor distraction displays, high chick-adult distances, and slow growth rates in chicks all increase their susceptibility to mammalian predation. The conspicuous black plumage itself (Fig. 8) may assist predators in locating nests or young. These features probably reflect the absence of predatory mammals from New Zealand until the 19th century. Nesting on the dry banks of streams and ponds, having a high site fidelity, wide-roaming of chicks, and using dive-bombing on harriers would have imposed little predation risk. The Pied Stilt exhibits alternative features in its breeding biology, probably because of a different evolutionary past that involved exposure to many types of native ground predators in Australia. In New Zealand the Pied Stilt retained many of its predator-avoidance features, enabling it to deal with the introduced carnivorous mammals.

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