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Breeding of South Island pied oystercatchers (*Haematopus ostralegus finschi*) on farmland in mid-Canterbury, New Zealand

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Abstract Breeding of South Island pied oystercatchers (*Haematopus ostralegus finschi*) on farmland in mid-Canterbury was studied from 1987 to 1997. Each year birds returned to breeding territories from early June; females arrived about six days earlier than males. Laying dates extended from early August to mid-November and were similar in all years. Most first clutches were laid from late August to mid-September. Up to two replacement clutches were laid. Clutch size averaged 2.29 (range 1-3 eggs) and declined through the breeding season, but was consistent from year to year. Mean first clutch sizes were larger than replacement clutches. On average, 47% of eggs hatched and 59% of these chicks survived to fledge. Both hatching and fledging rates declined through the season. On average, 52% of pairs which laid in any year failed to rear a fledgling. Hatching success was greater in cultivated sites than pasture sites, but fledging success was similar at both sites. Trampling by stock, farming activities, and unknown causes were the main causes of egg loss.

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INTRODUCTION

Since human colonisation of New Zealand, the proportion of the total land area in grassland has risen from about 5% to over 50% (Taylor & Smith 1997). In 1993, some 36% of the total land area was in improved grassland, with less than 1% each attributed to arable crops, fodder crops, and fallow land (Taylor & Smith 1997). Among the main land issues associated with this conversion to farmland are the decline in ecological processes and biodiversity caused by habitat fragmentation (Taylor & Smith 1997).

Oystercatchers (family Haematopodidae) are large and conspicuous waders comprising about 21 forms in a single genus (Cramp *et al.* 1983). One species, *Haematopus ostralegus*, is almost cosmopolitan, occurring throughout Europe and being represented in New Zealand by the South Island pied oystercatcher (*Haematopus ostralegus finschi*), hereafter referred to as pied oystercatcher. In New Zealand, this is one species to benefit from the conversion to agricultural land. Although this species bred inland on shingle riverbeds, since about 1950 it has spread onto arable land and high country tussock grasslands (Turbott 1969; Baker 1974). After the breeding season, all birds migrate to non-breeding grounds which are usually in coastal areas (Baker 1974; Sagar & Geddes 1999).

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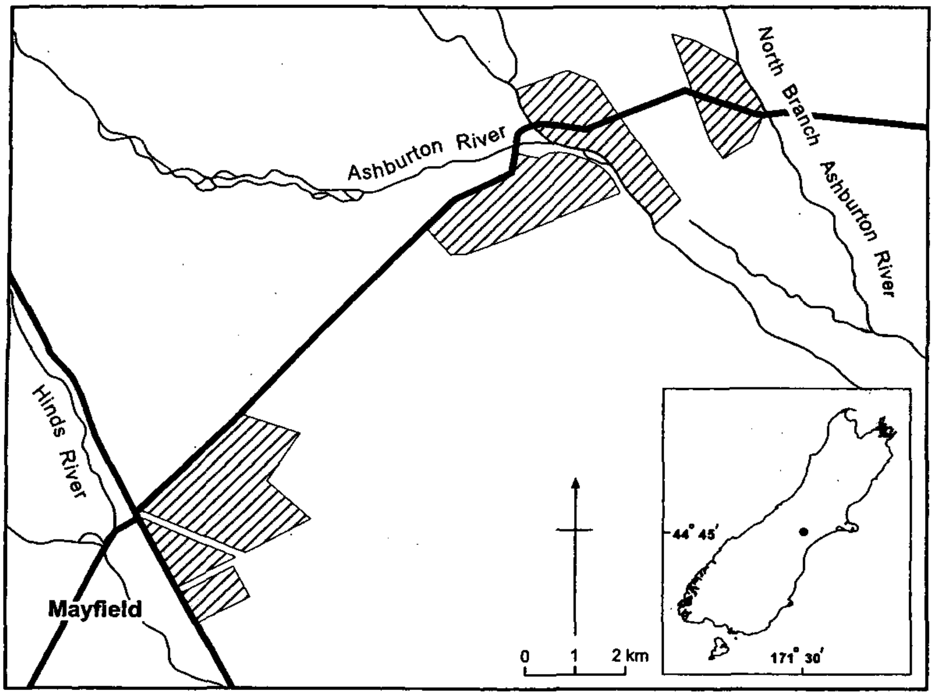

Fig. 1 Location of study area in mid-Canterbury. Hatched areas show the approximate location of study farms.

Over the period 1870 to 1940 the numbers of pied oystercatchers declined, but this trend was reversed following legislation in 1940 which prohibited shooting of shorebirds (Sibson 1966). In fact, a spectacular increase of the species has occurred, particularly in the numbers of birds wintering at coastal sites in the northern North Island (Sibson 1966; Baker 1973; Sagar *et al.* 1999). The population increase has continued, with numbers rising from an estimated 49,000 in 1970-71 (Baker 1973) to an estimated 112,000 in the period 1984-1994 (Sagar *et al.* 1999).

Although prohibition of shooting was considered the main reason for the initial rise in oystercatcher numbers (Sibson 1966), the recent colonisation of agricultural land has provided an increasing proportion of the species with an extensive area of habitat for feeding and breeding, thereby possibly contributing to the population increase. In this paper, we describe annual variation in the breeding of pied oystercatchers on agricultural land. The main aims of this study were to determine: (1) the onset and duration of the breeding season; (2) seasonal and interannual variations in clutch size and breeding success; and (3) causes of egg failure.

STUDY AREA

Observations were made in the Valetta and Mayfield areas (44°45'S, 171°30'E) of mid-Canterbury in farmland lying between the north branch of the Ashburton River and the Hinds River (Fig. 1). Here, the land is predominantly flat and forms part of the Canterbury Plains. The 11 study farms covered an area of about 1473 ha: the main land uses were pasture for grazing by sheep, and cultivated land for cereal crops or winter feed for stock.

METHODS

Observations of the breeding activity of pied oystercatchers were made from September to November 1987 and then during the period early August to at least late November each year from 1988 to 1997. Breeding birds were caught using a netting drop trap, which the birds activated when they returned to their nests (Mills & Ryder 1979). During trapping operations, we replaced each clutch with artificial eggs to avoid the possibility of captured birds trampling eggs before they were removed from the trap; the birds' clutch was returned at the end of trapping at that nest, usually within 30 minutes. The sex of each adult caught for banding was determined by bill measurements, following the criteria reported by Baker (1974b). By the end of the 1988 season at least one bird, usually both, of each pair was individually colour banded for identification. From 1 June to 7 August in both 1988 and 1989 daily observations over part of the study area were made of the date of first sighting of colour banded birds. Additional observations on the return of birds were made in 1997 when known breeding territories were checked every two or three days from 7 July to 31 August.

Nests were found by observing adult birds at the nest. Each nest was then marked with a stone cairn, placed about 5 m from the nest. The nest location was marked on a large scale map and described as pasture or cultivated land. In this study we defined pasture as established grassland, and cultivated as soil that was loose and bare or was recently sown. While some land started as pasture and then became cultivated during the season, none started a season as cultivated and became pasture. Although some paddocks were always in pasture, there was a general increase in the area under cultivation throughout the study period.

Most cultivated land was sown in autumn and spring with cereal crops (wheat *Triticum* spp., barley *Hordeum* spp., and oats *Avena* spp.) or fodder crops. All nests and pairs of pied oystercatchers were monitored every 6 - 10 days. The fate of eggs lost or destroyed was recorded as trampling by stock, the result of other farm activities, predation, desertion, or disappearance. After hatching, the survival and fledging of chicks was monitored by observing families or parental behaviour. Chicks older than about 21 days were banded with a stainless steel band and one colour band to denote year class. Failure at the chick stage was recorded, but usually no cause was attributed as most chicks just disappeared.

Date of laying was the date on which the first egg was laid, and was used only if it could be estimated to within five days. Laying dates were estimated where clutches were incomplete when first located, or by back-calculation from known hatching dates. Clutch size was recorded where there was no change in the number of eggs between nest visits and there was no indication of egg remains in the nest. Clutch size was not recorded if the nest was visited only once before it failed or observations began after the eggs had hatched. Incubation in pied oystercatchers begins after the last egg is laid (Baker 1969), so the incubation period was taken at the period between the laying and hatching of the last egg. Hatching was considered successful if chicks were observed with parents or if parental behaviour indicated the presence of chicks. The latter usually involved an increase in the intensity of distraction display compared with that exhibited during the egg stage.

Hatching success was calculated as the number of eggs that hatched compared with the number that were previously observed. As some eggs would have been lost before being observed, hatching sucess is likely to have been overestimated. However, this effect is likely to have been small because it was usual for whole clutches rather than single eggs to disappear and the presence of broken shell or dried yolk in the nest or on the other eggs usually indicated whether an egg had been broken. Fledging was considered successful for chicks aged 21 days. This procedure may have tended to bias success rates upward because some chicks may have subsequently died before flying at about 30 days of age. Charadriiform chicks are, however, notoriously difficult to locate because of their cryptic colouration and behaviour. Our observations indicated that few chicks older than 10 days died, and so any bias introduced should be very small. The fledging period was taken as the period between hatching and first flight of a chick.

In 1987, observations began about a month after laying began, and so analyses of data from that season were used only for descriptions of overall clutch size. Thus sample size varies with the type of analysis being undertaken.

Daily failure rates during incubation were calculated using the Mayfield (1961, 1975) method. The fate of eggs that did not hatch was based upon observations of the type of damage to eggs and nests. For example, vehicle tracks left the most obvious signs, while trampling by stock was indicated by the flattened remains of eggs in the nest or scattered nearby and disturbance of the nest material. Clutch destruction by cultivation was an important cause of nest failure and the signs of this were obvious –complete disappearance of the nest as the ground was ploughed, harrowed, or drilled. Likewise, the nest and contents were completely flattened when a paddock was rolled. We assumed predation had occurred only in the few instances where egg remains were found with obvious beak or tooth marks. Where eggs did not hatch despite full incubation, infertility or early embryo death was indicated by the mobility of the egg contents.

RESULTS

Return to breeding territories

In 1988 and 1989, the first bird was observed on 8 June, the second on 26 June, and birds returned almost daily from 2 July. The date of return of females of a pair ($\bar{x}$ = 18 July, SD = 14 days; range, 8 June-7 August; n = 40) was significantly earlier (t = 2.211, df = 78, $P < 0.05$) than that of males of a pair ($\bar{x}$ = 24 July, SD = 10 days, range, 4 July-7 August; n = 40). In the three years where detailed observations were made (1988, 1989, 1997) females returned to territories before males (Table 1). This territory occupation was significantly different from the sexes returning at random (χ^2 = 19.56, df = 1, n = 43, $P <$ 0.001).

It is possible that pairs returned together and that males were less visible than females. However, the female bias in return to the breeding territories was also supported by anecdotal observations. In 1997, three definite male-female pairs formed between banded birds where the male was subsequently deposed from the pair by the original male from the previous year. Additionally, four pairs formed between banded females and unbanded birds. These pairs could not be confirmed as male-female pairs as sexing birds in the field is extremely difficult. However, the unbanded birds were subsequently displaced by banded males which had been territory holders the previous year.

Laying dates

Laying dates of first clutches were similar in all years (Kruskal-Wallis non-parametric ANOVA, H = 4.05, df = 8, $P > 0.75$). Most of the first clutches were initiated between the third week of August and the second week of September (Fig. 2). Although not significantly different, laying dates of first clutches in 1992 were later than in all other years, probably because a snow storm on 27-28 August blanketed the study area in snow drifts up to 0.5 m deep, and so delayed breeding. Before the storm, the breeding season that year began as in all other years. There was a second small peak of laying during the second week of October which corresponds with the initiation of first- or second-replacement clutches (Fig. 2). Of all clutches, 18.7% (56/299) were initiated from the third week of September and 76.8% (43/56) of these were confirmed as replacement clutches.

Laying dates were similar in cultivated and pasture sites, although usually a smaller proportion of clutches was laid in cultivated sites from late September (Fig. 3). Pied oystercatchers nest in open-country and require uninterrupted views from the nest. Therefore, while in August and early September cultivated sites comprised bare ground or the seedlings of crops and provided suitable nesting habitat, by late September most cultivated sites were unsuitable for nesting because the growth of most crops interrupted the views of incubating birds.

Clutch size

The mean clutch size for all years (1987-1997) combined was 2.29 (mode = 2, range 1-3, Table 2). Kruskal-Wallis ANOVA showed no significant difference between the years (H = 3.583, df = 10, $P > 0.90$). The size of first clutches declined slightly through the season, particularly from the third week in September, but the size of first replacement clutches remained relatively constant throughout the season (Fig. 4). There were insufficient second replacement clutches to plot against time of season. First clutches ($\bar{x}$ = 2.31, SD = 0.52, n = 291) were not significantly larger than first replacement clutches ($\bar{x}$ = 2.16, SD = 0.53, n = 78; Wilcoxon z = 1.53, $P > 0.05$), but were significantly larger than second replacement clutches ($\bar{x}$ = 1.75, SD = 0.43, n = 9; Wilcoxon z = 2.37, $P < 0.05$). First replacement clutches were not significantly larger than second replacement clutches (Wilcoxon z = 1.65, $P > 0.05$).

Table 1 Sex of first bird of pairs of South Island pied oystercatchers (*Haematopus ostralegus finschi*) returning to the breeding territory at the start of the season.

Sex of bird returning first	1988	1989	1997	Total
Female	7	13	16	36
Male	0	4	3	7
No difference observed	4	7	5	16

Table 2 Mean sizes of South Island pied oystercatcher clutches in mid-Canterbury, 1987-1997.

Year	Mean	SD	*n*
1987	2.25	0.52	24
1988	2.28	0.45	39
1989	2.27	0.52	26
1990	2.43	0.50	28
1991	2.31	0.59	45
1992	2.40	0.58	42
1993	2.27	0.51	30
1994	2.17	0.50	36
1995	2.22	0.42	27
1996	2.09	0.50	47
1997	2.38	0.49	34
All years	2.29	0.51	378

Incubation and fledgling periods

The incubation period was determined at 14 nests and averaged 28.2 days (SD = 1.3 days, range 25-30 days). Fledging periods of three chicks were 30, 33, and 37 days.

Breeding success

Breeding success varied little in the study area during the period 1988-1997 (Table 3). On average, about 47% of

Table 3 Breeding success (%) and productivity of South Island pied oystercatchers nesting inland, mid-Canterbury, 1988-1997. E, eggs laid; C, chicks hatched; F, fledglings. Figures for 1988-97 are $\bar{x}\pm$ SD.

Year	Number pairs	Number eggs	Hatched (E:C)	Fledged (C:F)	Overall success (E:F)	Chicks fledged per pair	Chicks fledged per successful pair
1988	32	95	41.1	53.8	22.1	0.66	1.40
1989	31	79	51.9	70.7	36.7	0.94	1.45
1990	31	77	48.1	73.0	35.1	0.87	1.60
1991	37	107	49.5	62.3	30.8	0.89	1.65
1992	30	111	36.0	50.0	18.0	0.67	1.67
1993	32	78	50.0	71.8	35.9	0.88	1.87
1994	26	78	47.4	51.4	24.4	0.73	1.73
1995	24	56	69.6	48.7	33.9	0.79	1.46
1996	37	100	49.0	53.1	26.0	0.70	1.63
1997	20	67	26.9	55.6	14.9	0.50	1.42
1988-97	30.0±5.0	84.8±16.9	46.9±10.6	59.0±9.1	27.8±7.4	0.76±0.13	1.58±0.15

Table 4 Breeding success parameters of South Island pied oystercatchers nesting in inland mid-Canterbury, 1988-1997. Total clutch failures = no.of nests in which all eggs were lost; total brood failures = no. broods where all chicks were lost. [95% binomial confidence interval] from Pearson & Hartley (1969).

Nest site Clutch	No. of nests	No. (%) of total clutch failures	No. of eggs laid	No. (%) of eggs hatched	No. (%) of total blood failures	Minimum no. (%) of chicks fledged
Pasture						
First clutch	219	116 (53) [41-63]	490	206 (42) [35-52]	21 (20) [13-27]	130 (63) [58-72]
First replacement	62	37 (60) [45-75]	133	51 (38) [23-55]	9 (36) [7-63]	22 (44) [20-68]
Second replacement	7	4 (57)	11	5 (45)	3 (100)	0 (0)
Cultivated						
First clutch	80	27 (34) [19-43]	180	110 (61) [53-75]	13 (25) [3-47]	65 (59) [36-80]
First replacement	13	6 (46) [9-58]	33	18 (54) [45-89]	2 (29) [0-82]	11 (61) [21-100]
Second replacement	2	2 (100)	4	0 (0)	-	0 (0)
Both sites						
First clutch	299	143 (48) [38-54]	670	316 (47) [42-56]	34 (22) [24-30]	195 (62) [54-70]
First replacement	75	43(57) [42-70]	166	69 (43) [29-50]	11 (34) [9-59]	33 (48) [27-69]
Second replacement	9	6 (63)	15	5 (33)	3 (100)	0 (0)
All clutches	383	192 (50) [39-53]	851	390 (46) [42-54]	48 (25) [17-33]	228 (58) [52-66]

Table 5 Causes of egg failure in pied oystercatchers breeding on farmland in mid-Canterbury, 1987-1997. *n*, number of clutches used in the analysis.

		Percentage						
Nest site	Numbers of eggs lost	Stock	Human activities	Predation	Weather	Infertile	Died at hatching	Unknown
Pasture (*n*=262)	326	47.0	7.9	0.7	3.1	4.8	1.8	34.7
Cultivated (*n*=87)	67	0	49.9	0	11.1	2.8	0	36.3

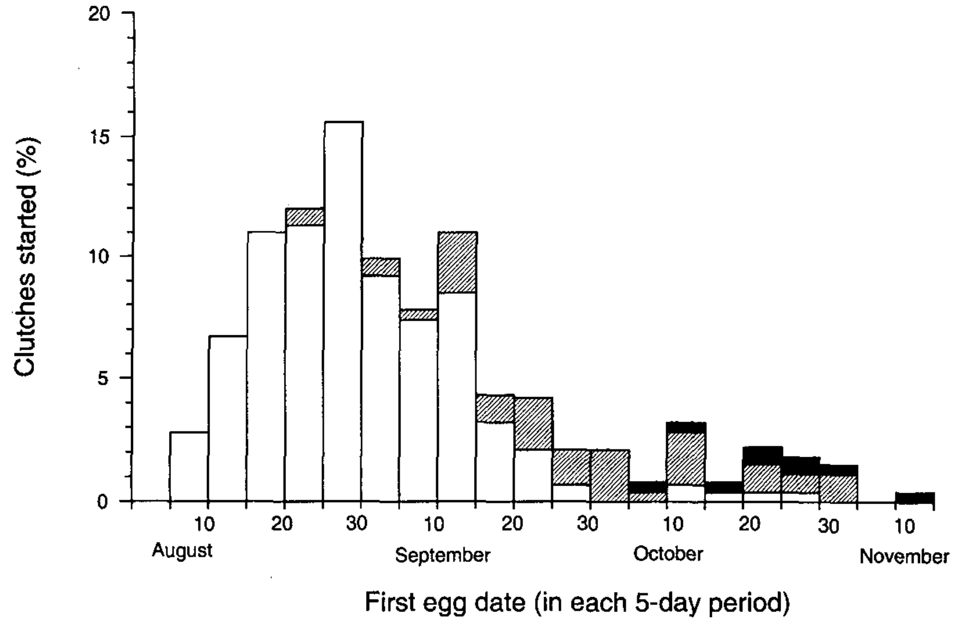

Fig. 2 Proportion (%) of clutches of pied oystercatchers started in each 5-day period, 1988-1997: open, 1st clutch (n = 250; hatched, 1st replacement (n = 50); filled, 2nd replacement (n = 9).

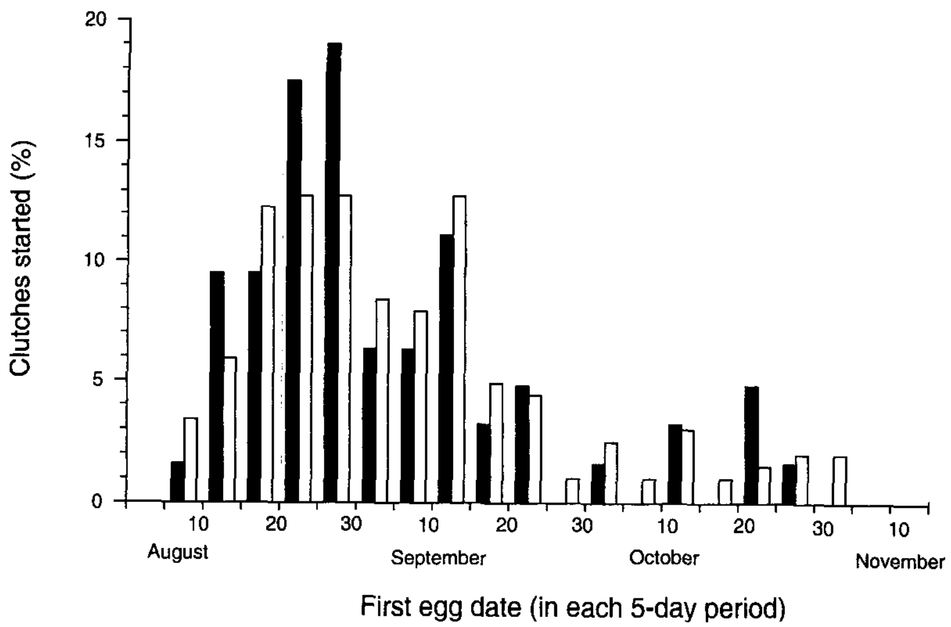

Fig. 3 Proportion (%) of clutches of pied oystercatchers started in each 5-day period for cultivated (n = 63) and pasture (n = 203) sites, 1988-1997: filled, cultivated; open, pasture.

eggs laid hatched and about 58% of these chicks survived to fledge. Thus, the overall breeding success was about 28%. Lowest breeding success occurred in 1992 (18%) and was mainly attributable to the low hatching success resulting from a snow storm during late August that year, and in 1997 (14.9%) when changes in farming were implemented. The number of fledglings raised by each pair per year ranged from 0 to 3, with 52% of pairs which laid failing to rear a fledgling (Table 3).

When plotted against the estimated dates of laying of the clutch, hatching and fledging success exhibited similar trends throughout the breeding season, but the timing of each varied (Fig. 5). Hatching success fluctuated around 50% for those clutches laid until the middle of October and then decreased rapidly. However, fledging success of chicks only remained above 50% for those clutches laid before the end of September.

During the study, 383 nests were found during incubation (Table 4). Of the 299 first clutches found, 177 resulted in total failure at the egg or chick stage and 75 of these (42.4%) resulted in a replacement clutch being laid. A second-replacement clutch was produced on 16.7% (9/54) of occasions where the first replacement clutch or resulting brood was also lost. There was no record of a

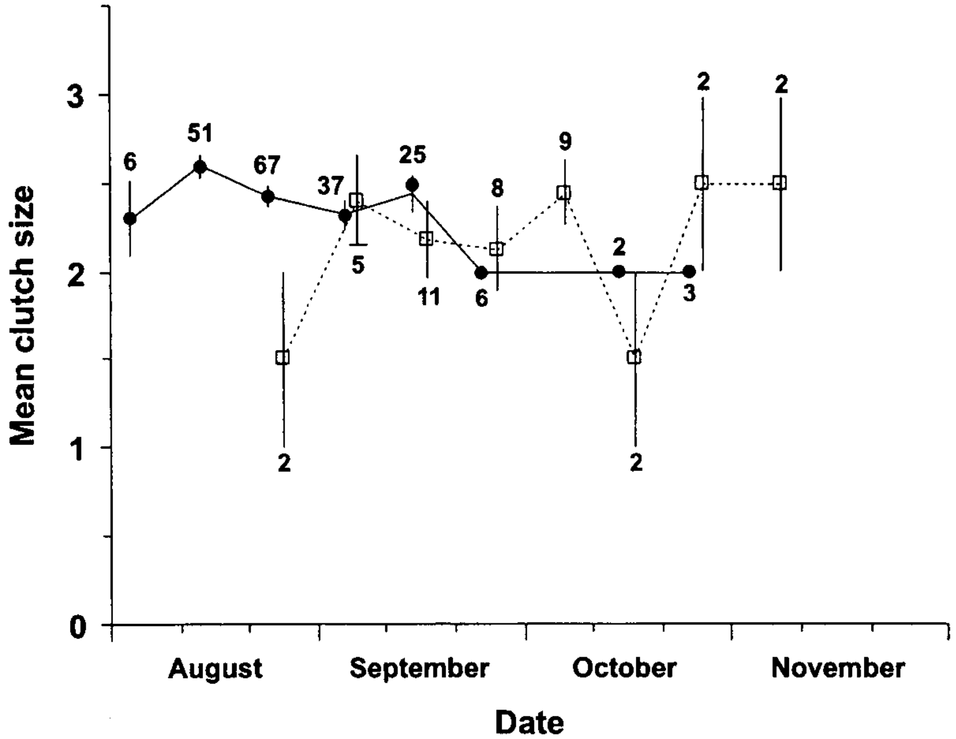

Fig. 4 Mean (± 1 $SE_{\bar{x}}$) size of first (n = 197) and first-replacement (n = 41) clutches of pied oystercatchers, by 10-day periods, 1988-1997. Numbers above (first) and below (first-replacement) represent the clutches started in each period.

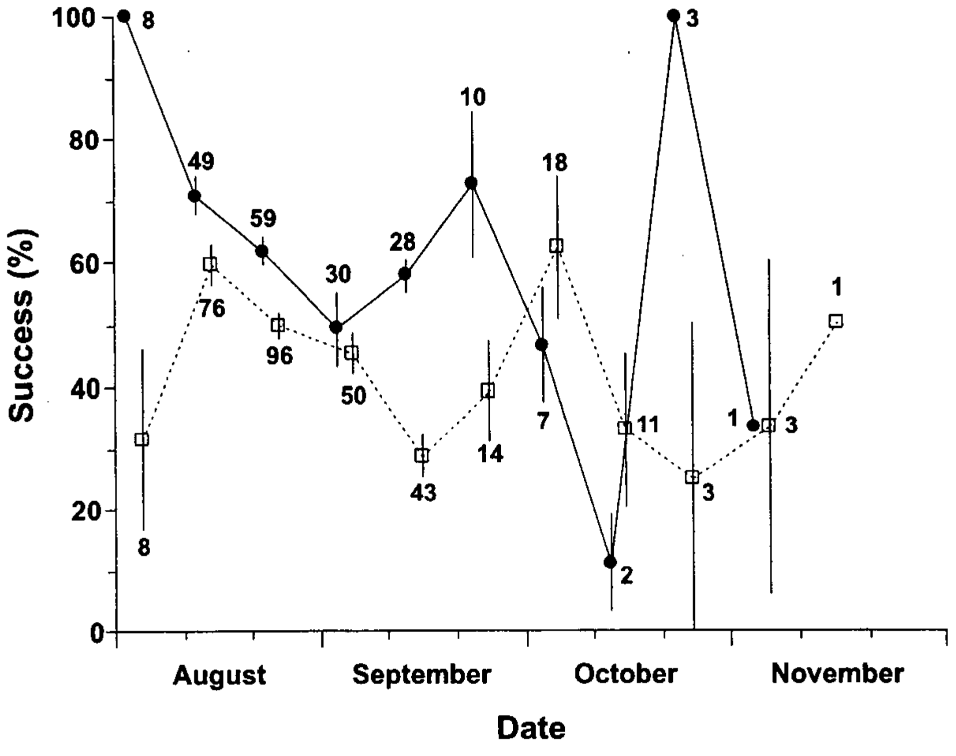

Fig. 5 Mean (± 1 $SE_{\bar{x}}$) hatching (open squares) and fledging success (closed circles) of pied oystercatchers, by 10-day periods, 1988-1997. The numbers of eggs hatched and chicks fledged are given above and below, respectively, each time period.

pair renesting after successfully fledging chicks, even from a first clutch.

Overall, hatching success was similar for first and first-replacement clutches (all χ^2 values calculated with Yates' correction, χ^2 = 1.12, df = 1, P > 0.25). However, the first clutches had a greater fledging success than first-replacement clutches (χ^2 = 4.26, df = 1, P < 0.05). When assessed by nest site, hatching success between first clutches and first-replacement clutches was not significantly different (pasture sites: χ^2 = 0.40, df = 1, P > 0.50; cultivated sites: χ^2 = 0.13, df = 1, P > 0.0.50). Fledging success was significantly greater for first clutches than first replacement clutches laid in pasture (χ^2 = 6.31, df = 1, P < 0.025), but not for clutches laid in cultivated sites (χ^2 = 0.20, df = 1, P > 0.50). When the outcomes of first and first-replacement clutches were combined, hatching success was significantly higher for clutches on the cultivated sites than the pasture sites ($\chi^2 = 27.62$, df = 1, $P < 0.001$). Thus, about 54% of clutches laid on pasture sites were lost compared with 37% of clutches on cultivated sites (Table 4). However, the fledging success was similar ($\chi^2 = 0.001$, df = 1, $P > 0.90$), with chick survival (minimum number of chicks fledged compared with number of eggs hatched) averaging 58% and 59% at pasture and cultivated sites, respectively.

The difference in hatching rates between clutches in pasture and cultivated sites is reflected in the daily failure rates of clutches which, during incubation, were 0.025 ($SE_{\bar{x}} = 0.0004$, $n = 278$) in pasture and 0.016 ($SE_{\bar{x}} = 0.0015$, $n = 88$) in cultivated sites; the difference being significantly different ($z = 5.81$, $P < 0.01$).

Causes of egg loss

Causes of breeding failure were identified only during the egg stage, when trampling by stock, unknown causes, and human activities associated with farming were the main causes of loss (Table 5). Other factors were of relatively minor importance. The role of predation is likely to have been underestimated because we classified the disappearance of eggs as an unknown cause of egg loss, but in many instances their disappearance possibly resulted from the activities of introduced mammals such as cats (*Felis catus*), ferrets (*Mustela furo*), stoats (*M. erminea*) and hedgehogs (*Erinaceus europaeus*), and native birds such as Australasian harriers (*Circus approximans*) and black-backed gulls (*Larus dominicanus*). Snow up to 0.5 m deep during 26-28 August 1992 was responsible for the loss of all 19 eggs attributable to weather. In all instances of weather loss, the clutches were found intact but abandoned.

Comparison of losses between nests sited in pasture and cultivated land showed that losses attributable to trampling by stock occurred only in nests sited in pasture (Table 5). In contrast, losses attributable to human activities (e.g., use of machinery) were significantly greater (χ^2 with Yates' correction = 32.57, df = 1, $P < 0.001$) in cultivated land than in pasture.

Losses from causes other than stock or human activities were similar between the two nest site categories.

DISCUSSION

Comparison with other studies

Despite being the most abundant wader in New Zealand (Sagar *et al.* 1999) there has been relatively little information available about the breeding of pied oystercatchers, and this study of their breeding is the first to be carried out in farmland habitat. Baker (1969, 1974) studied 11 pairs of pied oystercatchers nesting on the Ashley River, about 90 km north east of our study area, and a comparison of the breeding of the species on riverbed and farmland territories shows several similarities and differences.

There are distinct habitat-related differences in the timing and gender of birds returning to breeding territories. Baker (1969) reported a peak of arrivals on the Ashley River in August, and that both birds of a pair arrived together; and Pierce (1983) reported similar observations for pied oystercatchers returning to the Cass River in a high-country valley. On the Ashley River, the first pair arrived in the first week of August, with most birds returning by the end of August (Baker 1969). These dates contrast with the results of our study, where most birds had arrived back by the third week in July, and females arrived earlier than males. The earlier return of birds to farmland compared to riverbed territories may result from differences in habitat, especially the availability of food organisms during the chick stage, as in most bird species chicks hatch and are fed at times of greatest food abundance (Lack 1954).

Oystercatchers on wet coastal fields ate grass grub beetle (*Costelytra zelandica*) larvae (Baker 1974). In mid-Canterbury, large, third instar larvae of grass grubs were available for starlings (*Sturnus vulgaris*) during winter and early spring, but the ensuing prepupal and pupal stages were smaller and not eaten (East & Pottinger 1975). Also, earthworms were abundant on mid-Canterbury farmland during July when there was usually an excess of soil moisture (Lobb & Wood 1971), and so these may be preyed upon by the oystercatchers, as they are in Europe (Heppleston 1972). Consequently, if grass grub larvae and earthworms are major items in the diet of oystercatchers breeding on farmland, then the breeding success of these birds may be influenced by the availability of these prey. Alternatively, the population increase of pied oystercatchers since Baker's (1969) study may have resulted in greater competition for territories in riverbeds and farmland, so birds return earlier to defend territories used previously.

The earlier return to farmland of female compared to male pied oystercatchers is unusual and contrasts with many other charadriiform species where the male precedes the female sometimes by several weeks (Baker 1969). In Europe, Harris (1967) reported that it was unusual to see only one oystercatcher in a territory at the start of the breeding season, so it was impossible to ascertain which sex was responsible for taking up the territory. Whatever the mechanism determining the timing of return and despite the 3-4 month difference between the start date of the first and last clutches within a breeding season, the breeding season is remarkably fixed and the range of laying dates was consistent between years, a similar situation to that reported in a range of studies of oystercatcher breeding in Europe (Ens *et al.* 1996).

For information regarding laying dates and clutch size, Baker (1969) does not distinguish between that recorded for his Ashley River study population and information obtained from an analysis of nest record cards of the Ornithological Society of New Zealand. However, when comparing laying dates and clutch size, we assume that most of the information came from birds breeding on riverbeds. Despite the difference in the timing of their return, laying by birds in both riverbed and farmland began in the second week of August and extended to early December (Baker 1969; this study). However, peak egg production occurred earlier on farmland; late August as against the first half of September on riverbeds (Baker 1969). Clutch sizes were similar in both studies, with modes of 2 eggs and means of 2.3 (Baker 1969) and 2.26 (this study). The main difference was the occurrence of two 4-egg clutches in the 55 clutches analysed by Baker (1969): in our study clutch size was 1-3 eggs.

There was a small decrease in clutch size over the season in six studies of oystercatchers in Europe (Ens *et al.* 1996). Likewise, in New Zealand, Baker (1969) found that mean clutch size of pied oystercatchers decreased as the breeding season progressed. We found that mean clutch size decreased, mainly as a result of the smaller size of replacement clutches compared to first clutches, although the size of first clutches laid after the third week in September also declined. A seasonal decline in clutch size among a population of oystercatchers in Britain was attributed to older birds breeding earlier in the season (Harris 1967). In contrast, Baker (1969) argued that the seasonal decline probably resulted from older birds being more efficient feeders, therefore reached breeding condition earlier than first-time breeders. Such an interpretation fits with Lack's (1947) hypothesis that birds breeding for the first time are probably less efficient at food gathering and adjust by breeding later and laying smaller clutches. Subsequently, Drent & Daan (1980) studied the date of laying of the first egg and clutch size in European oystercatchers and proposed that natural variations existed because individuals in good nutritional circumstances laid earlier and produced larger clutches. As the mean size of first and replacement clutches declined with season, our study indicates that the availability of food may also have declined with season, resulting in smaller clutches from both experienced and inexperienced birds.

Decreases in hatching and fledging success over the season (this study) are consistent with the results of studies of pied oystercatchers nesting in Europe (reviewed by Ens *et al.* 1996), although the situation varies with habitat. Thus, in coastal sites hatching success did not change over the season, but fledging success declined steeply. At an inland site, in contrast, a decline in hatching success rather than fledging success caused fledgling production to decline with season. Whereas at sites where birds fed both inland and on the coast, hatching and fledging success declined with season. Consequently, all these studies indicate that the probability that an egg will result in a fledgling declines over the season.

No previous studies have reported the breeding success of pied oystercatchers in New Zealand. Our calculated values of hatching (46.9%) and fledging (59.0%) success are generally higher than comparable data from four inland and coastal nesting migratory populations studied in Europe, where hatching and fledging success ranged from 31.8% to 56.5% and 20.4% to 55.5%, respectively (Goss-Custard *et al.* 1995).

Our results show that hatching success was greater for pairs which nested in cultivated rather than pasture sites. In part, this was because of the behaviour of individual farmers, some of whom saw the nests as they cultivated a paddock, and so either worked around the nest or moved the eggs to one side, cultivated the ground, then replaced the eggs in a hand-made nest scrape.

It was not surprising to find that survival of chicks hatched from clutches laid at pasture and cultivated sites was similar. Charadriiform chicks leave the nest shortly after hatching and move to adjacent areas to feed. In all years of this study, many chicks left their natal cultivated paddock and moved to nearby pasture, particularly when the growth of crops prevented the parents from having uninterrupted views. Consequently, chicks hatched from clutches laid on cultivated and pasture sites were raised in similar habitats, hence the similarity in their survival rates. In our study, the proximity of pasture to cultivated nesting sites may have contributed to the survival of chicks. In a study of the effects of agriculture on breeding lapwings (*Vanellus vanellus*), Galbraith (1988) found that survival of chicks hatched in cereal fields with direct access to pasture was much higher than that of chicks which had to cross intervening cereal or hay fields. This led him to conclude that accessibility of short-grass pasture was a major determinant of the breeding success of lapwings that nested on cultivated land.

Causes of nest loss

Hatching success at cultivated and pasture sites was influenced primarily by farming activities. For birds nesting on cultivated sites, the start of laying usually coincided with that of cultivation, so this was the major cause of egg loss. Such losses could be moderated by weather patterns during June and July; warm, dry conditions allowed cultivation to be completed before the laying started. Peak laying also coincided with the onset of lambing at pasture sites. From about mid-August, ewes were usually moved to paddocks on which they subsequently gave birth, so oystercatchers nesting there suffered heavy egg loss from trampling by higher densities of stock.

Despite such losses, this study shows that farmland provides a suitable habitat for breeding pied oystercatchers. Whether the productivity of birds breeding in this highly modified habitat has been the main cause of the observed increase in numbers since the 1940s has not yet been determined. Studies of the comparative breeding success of birds nesting on riverbeds and farmland, and better knowledge of the population dynamics of riverbed and farmland nesting birds will contribute towards an understanding of the processes driving the overall population growth.

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