

BREEDING AND SOCIAL PATTERNS OF BANDED DOTTERELS (*Charadrius bicinctus*) AT CASS RIVER

By R.J. PIERCE

ABSTRACT

The breeding of Banded Dotterels was studied in 1977-1987 at Cass River Delta, Lake Tekapo. Most birds first nested as 1-year-olds, but 1-year-olds arrived later on the breeding grounds than experienced adults. Nest site fidelity between years was high for experienced males but less for experienced females. Natal site fidelity was lower in females, which nested up to 31 km from the natal site. The birds were monogamous and usually retained the same mate for repeat clutches within a season, but most changed mates between years. Family members parted at about the time the young could fly. Sight recoveries of juveniles indicated that those which had fledged early or midway through the season subsequently migrated to Australia but late-fledging juveniles were non-migratory.

INTRODUCTION

Members of the cosmopolitan plover genus *Charadrius* are fairly homogeneous in morphology, breeding displays and voice (e.g. Cramp & Simmons 1983, Bomford 1986). They are, however, diverse in their patterns of nesting biology, particularly mating systems and fidelity to the nest site (e.g. Lessels 1984). Breeding patterns of Northern Hemisphere plovers are generally well known, but those of others, including the Banded Dotterel, have been little studied.

This paper gives details of arrival times, mate and site fidelities, post-breeding flocking and local wintering at Cass River Delta, Lake Tekapo. It is based on observations of colour-banded birds from 1977 to 1987.

STUDY AREA AND METHODS

The main study area, described previously (Pierce 1983), was the mainly stable shingle beds of the Cass River Delta (700-730 m a.s.l.). I checked for dispersing Cass Delta birds and did further banding on the middle and upper reaches of the Cass River, the Godley and Macaulay River Valleys (20 km to the north) and Tekapo River (>20 km to the south). In 1985 and 1986 several people helped me check and band dotterels throughout the MacKenzie Basin.

Dotterel nests were found mainly by watching the adult birds from a vehicle used on the many access tracks on the riverbed. I marked each nest-site with a small (<100 mm high) stone cairn about 10 m from the nest, and this was a recognisable landmark the following season. I captured adults at the nest by means of a netting drop-trap, which the bird sprang as it returned to the nest. Each bird was taken 20-30 m away from the nest site to be sexed, weighed, measured and banded. Sexes were distinguished by

markings on the breast and especially the head, which are darkest in males. Each bird was given an individual colour combination: a numbered stainless steel band (size B) and 1-4 coloured PVC bands, placed on the tarsi. For example, M-RY is metal on the left and red over yellow on the right. This work disrupted nesting dotterels for no longer than 30 minutes.

Throughout the year I made frequent counts on the Cass Delta and checked all birds seen for colour bands. In the late winter and spring of four years (1979, 1983, 1984, and 1985), I spent a few hours searching for returned migrants every 2-3 days. As the dotterels tended to be in local concentrations in winter and early spring, they were easy to check for new arrivals. Even so, I would have missed many birds, especially late in the season. Because of this problem, any birds that were already nesting when I saw them first and any birds first seen after October are excluded from the analyses of arrival times of different age and sex groups.

RESULTS

Return of migrants

The earliest returning colour-banded migrants were recorded in the second half of July (Table 1). Mean arrival times of experienced birds (2+ years old) were the first week of September in 1979, 1983, and 1984, but in the second half of August in 1985. There was no significant difference in arrival times between experienced males and experienced females. One-year-old birds arrived later than experienced adults in all years.

TABLE 1 — Arrival dates of migrants in four years

Year	Earliest Arrival Date	Mean Arrival Dates		
		Experienced Males	Experienced Females	One-year-olds
1979	21 July ¹	1 Sep (n = 20) ²		1 Oct ³ (14)
1983	No July data	5 Sep (14)	4 Sep (28)	18 Sep ³ (12)
1984	17 July	6 Sep (17)	2 Sep (23)	Few Data
1985	19 July	18 Aug (27)	25 Aug (49)	31 Aug (13)

Notes: 1. Returned from Australia (Dann & Pierce 1979).

2. Sample sizes are given in parentheses. Male and female data pooled for 1979.

3. Significantly later mean arrival dates than those of experienced birds in the same year ($p < 0.05$, Student's t-test).

There was no evidence that experienced breeders missed breeding seasons: on only 11 (3%) occasions were birds missed one year but seen in a later year ($n = 382$ "bird years"), and these may just have been birds I missed. Not all 1-year-old birds were found on the breeding grounds (Table 2). Of surviving chicks, the return rate (76%) at 1-year old is significantly less than the χ^2 expected value of 100% ($\chi^2 = 4.9$, 1 d. f., $p < 0.05$, $n = 89$). Proportionately more colour-banded males than females were seen as 1-year-olds on the Cass Delta ($\chi^2 = 4.62$, 1 d.f., $p < 0.05$, $n = 86$). All returning 1-year-olds that were closely monitored did nest or attempt to nest during that season.

TABLE 2 — Age at which birds colour-banded as chicks were first recorded back at Cass Delta.

Sex	N	Age in years				
		1	2	3	4	5
Male	54	41	9	1	0	3
Female	32	25	5	2	0	0
Unknown	3	2	0	1	0	0
Total	89	68	14	4	0	3

Dispersal for nesting

Arriving migrants in July and August joined the groups of birds that had overwintered. During cold periods and while snow was lying, the birds foraged mostly on lakeshore mud or along river channels, where some individuals maintained small feeding territories up to 40 m in length and for up to 5 weeks at a time. In milder weather, most birds foraged on short-turfed pasture, particularly in wet areas. Included among these delta concentrations were several birds whose nesting areas were up to 10 km further upstream in the Cass Valley. During August and September, increasing numbers of birds began to visit and eventually occupied the breeding grounds, which mainly comprised regenerating herbfields on or adjacent to the riverbed.

Usually the males occupied the breeding grounds first, establishing territories often in the absence of females. The females tended to continue foraging on the pasture or on the mudflats, giving rise to local variations in the sex ratio. During snowfalls and ensuing snow-cover, prebreeding birds or failed nesters often returned to the lakeshore or river edges. While nesting, off-duty dotterels usually foraged within 200 m of the nest site, but many (and failed nesters) returned to the pasture where they foraged in loose flocks up to 2 km from their nest sites.

Possibly the highest density of nesting pairs seen on the riverbed was in November 1985: on the central part of the north bed of the delta I found 17 pairs nesting in an area measuring 180 × 700 m, giving an overall density of 1.35 pairs per hectare. Adults did some (probably most) of their feeding in those territories.

Mate fidelity

Banded Dotterels are monogamous. On rare occasions, additional males (Oreti River 1985, M. Barlow, pers. comm.; Waipawa River 1986, pers. obs.) or females (Ruamahanga River 1987, pers. obs.) share nest duties.

At Cass River there were 18 colour-banded pairs in which both members were known to be alive the following year. Eight of these pairs renested together, and ten nested separately. For repeat clutches within a season, however, the pair bond was usually retained (Table 3a). In most cases in which interseasonal bonds were broken, the female had settled farther away from the previous season's nest site than the male had (Table 3b).

TABLE 3 — Pair bond retention and corresponding shifts in rest sites

A. Pair bond retention

	Number Examined	Number Retained	Number Separated
Interyear	18	8	10
Repeat clutches	10	8	2

B. Distances of nest-site shifts between years by birds of known pair bonds

	Number Measured	Average Shift (m)	Range (m)
Retained pairs	6	51	18 - 120
Males in separated pairs	8	44	5 - 200
Females in separated pairs	8	270	45 - 400

Nesting site fidelity

Experienced nesters had a very high site fidelity. Of 360 bird-years, in only two had birds shifted more than 1 km from the previous season's nest site. Precise distances between interyear nest sites were found for a random sample of 62 adults (Table 4). For experienced males this distance averaged 42 m, but for females it averaged more than 5 times this value. The value for females is increased greatly by one that shifted 6.2 km to the middle reaches of the Cass Valley three seasons after if had been banded. (This bird was recaptured to confirm its identity from the band number.) Even with this exceptional record excluded, the average shift (126 m) of females is still significantly greater.

TABLE 4 — Annual shifts in nest site location

Age Group	Distance Shifted (m)			T-Test (all $p < 0.05$)
	N	Mean	Range	
1. Experienced males	13	42	5 - 200	With 2: $t = 2.62$
2. Experienced females	49	245	0 - 6200	
3. Total experienced	62	202	0 - 6200	
4. One-year males	24	1170	75 - 6100	With 5: $t = 2.22$
5. One-year females	16	5150	100 - 30700	
6. Total one-year-olds	40	2030	75 - 30700	

For repeat clutches, the distance from first nest to second nest ranged from 0 m (once in same nest) to 15 km (a 1-year-old female renesting in the Godley Valley). Excluding the two greatest shifts (15 km and 2.16 km), all shifts were less than 110 m ($n = 9$ for males and females combined).

Natal site fidelity

One-year-old birds nested on average 2.03 km from their natal sites ($n = 40$ for males and females combined). Only three of these 40 birds nested within 150 m of their natal sites, one of which was a female nesting with her male parent of the previous season. As in experienced birds, male 1-year-olds were more philopatric than females, males returning on average 4-5 times closer to their natal area (Table 4). Some 1-year females nested considerable distances away, including three on other riverbeds up to 31 km away (Fig. 1). A fourth 1-year-old female was found on the bed of the Macaulay River (19 km to the north) during the breeding season, but it was not nesting at that time. Once a 1-year-old chose an area for nesting, however, it returned to that vicinity in subsequent years.

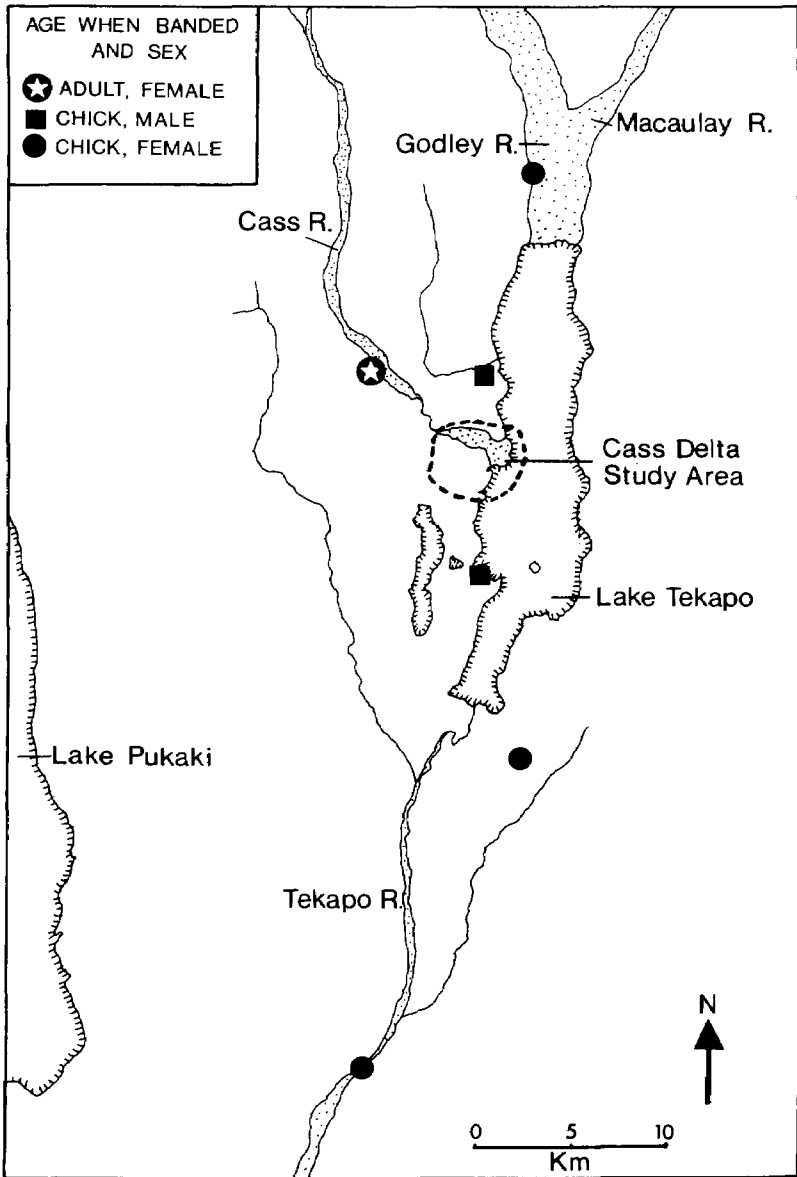


FIGURE 1 — Location of study area and of nest sites of birds which have left the delta

With their wide dispersal from their natal areas, 1-year-olds are colonisers of new areas. For example, stabilisation of the south bed in 1979 and subsequent colonisation by mat plants (Pierce 1983) has improved conditions

for dotterels there. To date (1987 season), four of the five colour-banded dotterels that have colonised this bed have been 1-year-olds. (In any given year 1-year-olds account for less than 20% of colour-banded birds on the Cass Delta.)

Nesting period and renesting

Laying extended from early September to December, and Bomford (1988) found one nest in August. In the cold early spring of 1986, nesting pairs were concentrated along the main river channels where mayflies were abundant. Included among these pairs were a few colour-banded 1-year-olds nesting or attempting to nest for the first time, as well as many experienced birds which usually nested on the adjacent herbfields. The nests of these regular river-flanking pairs were closer to water than in the previous spring (\bar{x} = c.120 m in 1985, \bar{x} = 22 m in 1986, n = 5 pairs).

Late-nesting adults in all years were often moulting, the earliest being recorded on 13 November 1987. Wing moult was recorded in 9 (12%) of 73 incubating adults (both sexes) in November, 4 out of 9 adults in December and 2 out of 2 in January.

If a pair of dotterels lost eggs or downy chicks, they usually renested within a month. One female produced four unsuccessful clutches in one season (each of three eggs), but most pairs were successful with the first or second clutch. Renesting after the loss of older chicks was recorded for several pairs after a heavy snowfall in October 1982 (Pierce 1983). In 1984 I recorded one case of apparent double brooding: on 15 September female WYR-M was incubating three eggs, two of which hatched between 9 and 13 October (the third egg being infertile), and one juvenile was flying by 21 November: on 10 December WYR-M was found with another three-egg nest, but this was preyed on between 18 and 24 December. I do not know whether the same male was at both nests.

Chicks

Although they are mobile within a few hours of hatching, chicks usually stayed within 200 m of their natal site until they could fly. Of 76 recaptures of chicks from known nests, only five were more than 500 m from the nest site. On two of these occasions, the chicks were nearly flying and had apparently been abandoned by their parents, a not unusual event on the Cass Delta, especially late in the season. As with adults, invertebrates were the main food, but in good fruiting years, berries of *Muehlenbeckia*, *Coprosma pumila* and *Pimelea* sp. were also taken.

Post-breeding dispersal

Family members appeared to part company usually within 2 weeks of the young flying. Colour-banded members of a family (including siblings) were subsequently never seen together again that season. They joined loose daytime flocks of up to 150 dotterels and foraged on the riverbed (especially near the channels of water) and also at drying-up ponds which had been little used by dotterels during the breeding period. Riverbed flocks comprised almost entirely adults, whereas flocks at flooded pasture and pools contained

high proportions of juveniles (Table 5). This habitat partitioning was also noted in other parts of the MacKenzie Basin and in coastal South Canterbury.

TABLE 5 — Number and percentage of juveniles in post-breeding dotterel flocks in the three preferred habitats on the Cass Delta

Date	Herbfield		Riverbed		Ponds and Saturated Pasture		χ^2 Value, (all $p < 0.001$)
	N	J	N	J	N	J	
20 Jan 1986	54	6 (11)	65	5 (8)	34	31 (91)	64.8
08 Jan 1987	56	5 (9)	65	6 (9)	59	54 (92)	78.4
19 Feb 1987	32	1 (3)	140	10 (14)	26	18 (69)	61.1

Note: N = number of dotterels seen; J = number of juveniles, percentage in parentheses.

From December to at least late February, most Cass adults (which were moulting) and many juveniles were in flocks within 10 km of the Cass Delta. Compared with prebreeding flocks, the flocks of post-breeding birds were more widespread and departure was very protracted, extending from December to at least late March. During this period some adults, and especially juveniles, were found in other parts of the MacKenzie Basin (up to 65 km from the Cass Delta) and at several coastal areas around the South Island.

Overwintering

Despite marked differences in the severity of winters, numbers of birds wintering around the shores of Lake Tekapo were fairly similar (100-200) from year to year, although counts during the 1980s tended to be higher than those of the 1970s. About equal numbers of males and females overwintered around Lake Tekapo. Once a juvenile had wintered in the Tekapo area, it would do the same in successive years, and the very cold winter in 1986 did not deter regular winterers (Table 6).

TABLE 6 — Wintering of Cass River birds at Lake Tekapo

Bird	Breeding Season in Which Banded	Age	Sex	Year and Mean Winter Temp. ($^{\circ}$ C)			
				1984	1985	1986	1987
				3.7	2.9	2.2	-
WM-R	1983	Ad	F	C	C	C	C
WM-RY	1983	Ad	F	C	C	C	x
WM-WR	1983	Ad	M	C	C	C	C
BM-YRW	1983	Juv	F	C	C	x	x
RYB-M	1984	Ad	F	-	G	x	x
MW-WB	1984	Juv	M	-	G	G	C
MW-YG	1984	Juv	F	-	C	C	-

Note: C = Cass Delta, G = Godley Delta, x = not seen, "mean winter temp." = mean daily air temperatures for June-August at Lake Tekapo.

Whether a bird was sedentary or became migratory seemed to depend on when it fledged (Fig. 2). Thus, all winter sightings of chicks which had fledged in November-December were in Australia (the main destination of MacKenzie Basin birds, unpub. data), whereas late-fledging chicks wintered locally ($x^2 = 13.1$, $p < 0.01$, sedentary behaviour by month). There was only one post-breeding sighting of offspring from these regular winterers: the November 1983 offspring of WM-R was found by K.F. Hughey at Clutha

Lagoon in coastal Otago in February and March 1985. We did not find its wintering area, although I am certain it did not winter at Lake Tekapo.

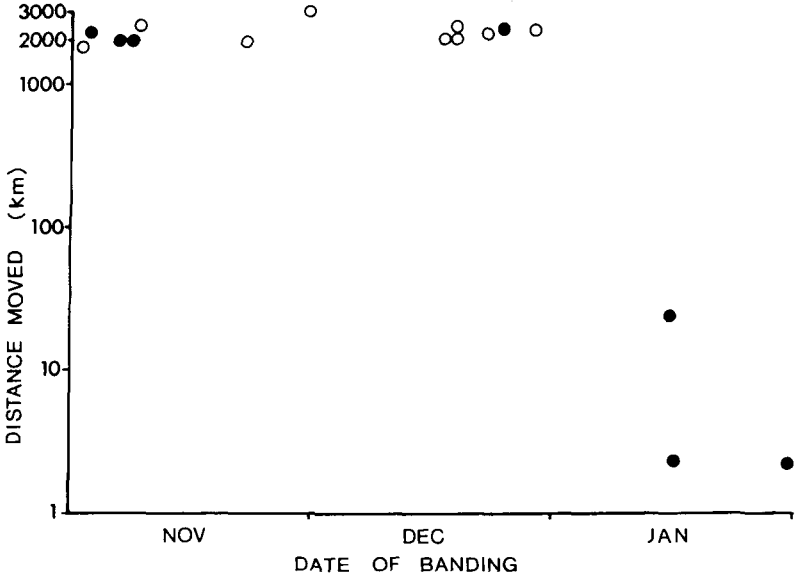


FIGURE 2 — The relationship between dates of banding of juvenile dotterels on the Cass Delta and the distances they moved to the wintering grounds. Closed circles represent sightings in their first year (\pm subsequent years); open circles represent sightings in second or later years only.

DISCUSSION

First breeding and migration

The age of first breeding in species of small plover varies from one to two or more years (Cramp & Simmons 1983). Breeding by most Banded Dotterels in their first year is in keeping with their relatively high productivity and low life expectancy (in prep.)

The late arrival of 1-year-olds at the breeding grounds concurs with observations on the Banded Dotterel wintering grounds in south-eastern Australia, where juveniles deposit premigratory fat later than adults do (Barter & Minton 1987). The latest sighting in any year of a colour-banded bird in Australia was of a 1-year-old Godley River bird in south-eastern Tasmania on 21 September 1986 (E. Woehler, pers. comm.). Very few Banded Dotterels spend the summer in Australia, however. My not finding some colour-banded birds in their first breeding season may be due to their brief appearances at the breeding grounds in their first season, rather than their not having returned at all.

Migratory and sedentary behaviour among partial migrants is thought to be under genetic control (e.g. Berthold 1984). It seems, however, that this genetic base can be modified by other factors, including the timing of fledging. Thus, late-fledging passerines (e.g. Adriaensen 1987) and Eurasian

Golden Plovers (*Pluvialis apricaria*) (Townshend 1975) migrated farther than early fledglings. The reverse was true for Cass River dotterels, in which late-fledging birds were sedentary. The development of migratory behaviour seems to depend on the time available for juvenile dotterels to deposit the fat they need for migration, late-fledging birds apparently not having enough time.

In the Golden Plover study, early-fledging birds were sedentary because they could use the prime local feeding areas, where they became dominants, thereby forcing the late-fledging birds to migrate (Townshend 1985). An important difference between the Golden Plover and Banded Dotterel studies is that the Golden Plover had dependable food locally, whereas at Lake Tekapo the food supply was undependable, fluctuating greatly between seasons and years (Pierce 1983, unpub. data). In addition, the dispersing Golden Plover were able to travel in "leap-frog" fashion along a semicontinuous coastline, food being available at frequent intervals, whereas the trans-Tasman migration of dotterels has to be a single flight of about 2000 km.

At present I cannot say whether one of the two wintering alternatives of Banded Dotterels is more adaptive, although survival data indicate a trend towards early-fledging juveniles having highest survival (unpub. data). Age-related migration patterns are currently being examined for Banded Dotterels in other parts of New Zealand.

Site fidelity

In the MacKenzie Basin, Banded Dotterels avoid inbreeding by the young birds (especially females) having low site fidelity. Males nest closer to their natal sites than females do and return earlier and nearer to the previous season's nest site. The early return of males to the breeding ground is usual for migratory species (Gauthreaux 1978). Greenwood (1980) proposed that the avian tendency for males to be more site specific than females is caused by the advantage of site familiarity, which in most species is more important to males than females. The dominant role of male Banded Dotterels in establishing and maintaining territories (e.g. Bomford 1988) is consistent with Greenwood's hypothesis. One wader species in which females are known to have greater site fidelity than males is the polyandrous Spotted Sandpiper (*Tringa macularia*), in which many of the roles of the sexes are reversed (Oring & Lank 1982).

Site fidelity is high in many other *Charadrius* plovers, including Ringed Plovers (*C. hiaticula*) (Laven 1940, Bub 1962), Kentish Plovers (*C. a. alexandrinus*) (Rittinghaus 1956), Mountain Plovers (*C. montanus*) (Graul 1973), Kildeers (*C. vociferus*) (Lenington & Mace 1975), and Piping Plovers (*C. melodus*). As with Banded Dotterels, male Piping Plovers have a higher site fidelity than females (Wilcox 1959). Two notable exceptions are the Eurasian Dotterel (*C. morinellus*) (Cramp & Simmons 1983) and Little Ringed Plover (*C. dubius*). In the latter species, Glutz *et al.* (1975) found that first-time breeders settled up to 250 km (mean 33.2 km) from the natal area (in Germany), and that adults settled up to 102 km (mean 5.5 km) from the previous season's site.

On the Cass River, the maximum distance found between the natal area of Banded Dotterels and their area of first nesting was only 31 km. Recent work by the Banded Dotterel Study Group has revealed several instances of 1-year-olds and experienced birds nesting up to 23.5 km from their original banding sites. The two greatest shifts have been of experienced birds banded near Alexandra in Central Otago: a 1985 male renesting the same season 23.5 km away on the summit of Old Man Range; and a 1985 or 1986 female nesting 22 km away near Cromwell in 1987 (M. Child, pers. comm). Most of the shifts have been from small pockets of changing habitat, including areas in which the growth of tall grass sometimes prevents nesting. By contrast, dotterel habitat on the Cass Delta is extensive and mainly stable from year to year, and so the dotterels do not need to make major changes in nest location. If strong site fidelity is usual throughout New Zealand, the Banded Dotterel may well vary morphologically on the mainland. This aspect is currently being examined.

Mating systems and pair bonds

The genus *Charadrius* has a wide range of mating patterns, from multiple clutches reared separately by the male and female in the Mountain Plover (Graul 1973), through frequent sequential polyandry in the Kentish Plover (Lessels 1984) and the Eurasian Dotterel (Nethersole-Thompson 1973), to monogamy with or without multiple brooding in the Ringed Plover (Pienkowski 1984), the Piping Plover (Cairns 1982) and the Kildeer (Lenington 1980). Banded Dotterels are in the last category, being mainly monogamous and single brooded.

Nest "helpers", seen on three New Zealand rivers, have been recorded in several *Charadrius* species (Cramp & Simmons 1983). In the apparent double brooding by the female M-WYR, the males at the two nests were not banded and so may not have been the same bird. Polyandry seems unlikely because, in the polyandrous Kentish Plover, the female deserts the brood soon after it hatches (Lessels 1984). Female M-WYR attended the chick from the first brood until it could fly and then renested, and so the incident was probably genuine double brooding.

A feature of all *Charadrius* plovers studied is that the pair bond is kept for the breeding season only. Usually each bird has a new mate the following year. Exceptionally, Ringed and Kentish Plovers may keep their pair bonds for several years, especially in unchanging habitats (Cramp & Simmons 1983). Banded Dotterels have kept their pair bonds for at least three seasons on pasture near Mayfield (D. Geddes, pers. comm.) and on the ocean beach at the mouth of the Rakaia River (K. Hughey, pers. comm.), but at the Cass Delta mate retention is low. This is surprising because the habitat changes little and males move little between sites from year to year. However, if many unmated, territorial males are spread over a large area (as is usual at the Cass Delta), competition for female partners would be high. Thus a male is likely to have the same mate in successive seasons only by chance, depending largely on how soon the female arrives after the male's initial displays on territory. Some useful comparisons could be made with areas containing fewer dotterels than the Cass Delta and in areas where habitat changes markedly from year to year.

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RAY PIERCE, P.O. Box 5521, Auckland