Dotterel populations and spacing on three Scottish areas in 1967–86

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An area over schist held a higher mean spring density of Dotterel *Charadrius morinellus* than two areas over granite. Spring density varied little between years. Density was highest on ground dominated by *Juncus trifidus* or *Carex bigelowii*, especially where there were ridges, terraces, hummocks or boulders, and was low on *Nardus stricta* or heath. Most clutches with fresh eggs hatched. After losses of clutches or broods up to mid July, some pairs formed, clutches were laid in a few days and some late young fledged. Most chick losses occurred before two weeks. Breeding success varied much. It was associated positively with July temperature and negatively with July precipitation. Birds over granite bred more poorly than over schist. On each area, flocks after arrival and before departure favoured the upper parts of the largest block of favoured habitat. Early spring flocks did not comprise pairs, but later spring flocks did. On each study area the spring sex ratio was close to 1:1. Nearly all agonistic encounters involved birds in flocks. and pairs close together on snow-free patches. On the area over schist, more birds were seen after arrival than just before egg laying. When snow lay late on high parts, pairs there waited to nest late after the thaw. Nearly all incubating birds, and all birds attending dependent young, were cocks.

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Introduction

Much study has been done on the reversed sexual roles of Dotterel *Charadrius morinellus*, where cocks do most of the incubation and chick rearing (Nethersole-Thompson 1973, Cramp 1983, Kålås & Byrkjedal 1984a, Kålås 1988). However, hardly any long-term work has been published on Dotterel populations, although sex ratio and breeding success are important for understanding the bird's reversed sexual roles. Little has been published on the bird's spacing behaviour (Kålås & Byrkjedal 1984a, Kålås 1988), especially when the young are big. A study on three Scottish areas in 1967–86 showed that greater human impact following easier access did not reduce density or breeding success (Watson 1988). Below, I use data from the same areas to tackle demographic questions, especially (a) do densities vary within and between areas, and between different habitats, (b) do sex ratios vary, and (c) what accounts for varying breeding success? The second part of the paper is mostly about spacing behaviour in spring and autumn, and the sex of adults tending eggs and young. The main weakness of the study was that it was done largely in my spare time, so I did not have time to find many nests or mark adults; many inferences are therefore tentative. The main strength was the long run of data.

Study areas and methods

The study areas were on hills west of Aberdeen in Scotland — area A at Cairn Gorm, area B nearby in the east Cairngorms range, and C in the Mounth range 20 km to the south. They covered 11.9, 3.5, and 1.1 km^2, at 1000–1300, 900–1200, and 950–1100 m altitude. Dotterel nested throughout these altitude ranges. Granite underlies A and B, and C is over Dalradian schist. Similar ground at the same altitudes on A and B has broadly similar vegetation cover, but C has more continuous vegetation than at the same altitudes on A and B, and has deeper, richer soils. Area C was a minor part of a big tract of Dotterel habitat; this applied less to B, and area A formed most of the birds' habitat on that hill.

Hen Dotterel are bigger and more brightly coloured than cocks, as quantified by Kålås (1988). On my areas a paired cock and hen seldom (<2%) looked the same size, and never when hens were displaying

Table 1. Number of settled pairs in spring, number of big young in late summer per ten adults in spring, and number of cocks attending dependent big young in late summer (as a percentage of the number of spring cocks), on areas A, B and C.

	Pairs			Young*			Cocks with young*	
	Part of A	Part of B	C	A	B	C	A	C
1967	–	–	–	1.6	1.6	8.3	19	83
1968	8	6	5	0.6	0.9	5.0	6	60
1969	9	6	5	1.6	0.9	8.0	19	80
1970	9	5	6	1.6	0.9	8.3	19	83
1971	9,10[x]	7	6	3.7	1.6	7.5	44	83
1972	9	–	7	2.5	–	7.9	31	71
1973	9	–	6	5.9	–	5.8	25	67
1974	9,10	–	5	1.3	–	3.0	25	60
1975	9	7	6	3.1	5.5	9.2	37	83
1976	10	–	5	4.7	4.4	3.0	50	40
1977	10,11	5,6	6	1.6	1.3	10.0	25	67
1978	10	–	6	1.5	1.6	2.5	29	33
1979	9	5	6	1.6	1.4	5.0	19	50
1980	8,9	7,8	6	1.6	–	2.5	19	33
1981	8,7	–	5	1.9	–	2.0	25	40
1982	9	–	5	1.3	–	4.0	19	40
1983	8.9	–	6	2.5	1.9	12.5	25	50
1984	10	7	6	2.4	1.3	3.3	24	33
1985	9	–	6	0.9	–	2.5	13	33
1986	11	–	7	1.8	–	10.7	29	86

* To calculate this for years when spring pairs were counted on only part of an area, I used the mean of the annual values in springs when counts were done on all of the area (16 pairs on A, and B, and 6 pairs on C); this seemed reasonable because spring numbers varied so little between years.

[x] Values separated by a comma show cock and hen numbers where these differed; to judge from the anxious behaviour of the extra hen or cock, an overlooked cock or hen was on eggs nearby.

Counts on all of A showed 16 pairs in 1971, 1975, 1976 and 1979, and 17 in 1978, 1984 and 1986. Counts on all of B showed 14 cocks and 15 hens in 1975 and 1979, 15 pairs in 1977, 15 cocks and 16 hens in 1971, 16 pairs in 1984, and 16 cocks and 17 hens in 1980.

The value for young on C in 1965 and in 1966 was 7.5.

with feathers puffed out. Hens about to lay appeared very big and had distended bellies with a bulge behind the legs. In late April – early May, hens were in or well into summer plumage, but a few cocks still retained much of their winter dress. Nearly all hens were in summer dress by 20 May, but <1% of cocks had some winter feathers till 31 May. Most hens showed a few pale winter feathers on the belly and upper parts by 20 July, and many such feathers by 1 August, but most cocks and an occasional hen showed few winter feathers until 10 August.

Dotterel with eggs or small chicks are harder to count accurately than many wader species because the attendant cocks sit still when a man comes near, and so are easily overlooked (Kålås & Byrkjedal 1984a, b, Watson & Rae 1987). I concentrated on spring counts before breeding, and on breeding success in late summer when the young were big.

Watson (1988) described methods for counting pairs in spring, and discussed their consistency and accuracy. For several days before egg laying, each pair usually stayed well apart from other pairs and was settled in location, being seen in approximately the same place at different times on the same day and on successive days. I often found that birds nested soon afterwards in these places.

For A and C, the data in Table 1 are based on at least two spring counts and at least two late-summer counts per area each year, but for B only one of each type in most years. Cold, fine weather allowed all spring counts to be completed before nesting began in most years. However, during three counts in warm weather I found a cock warming an egg or a hen laying an egg, although nearly all birds were in pairs. In several other counts, the anxious behaviour of an extra hen suggested that an overlooked cock was on eggs nearby (Table 1).

Watson (1988) defined breeding success as the number of big young reared per adult in late summer. "Big" young were well-feathered but not fully grown; they still had some down on the body and were in separate, dependent broods, each with its attendant adult cock. (Independent, fully grown juveniles which either had no down or else retained only traces of down above the bill or on the crown and nape, and which had no attendant adult cock looking after them, were ignored, as they might have flown from elsewhere). The inclusion of late-summer adult numbers in Watson's (1988) measure is not ideal, because by that time many hens are missing and also some cocks that were seen earlier without young. Hence a better measure of success is the number of big young in dependent broods during late summer per ten adults in settled pairs before egg laying. I use this measure below. It was strongly correlated with the index which Watson (1988) used (r_s=0.76 on A and 0.75 on C, n=20 and 22), but only weakly on B (r_s=0.33) where there were only 12 years of data (P not given as the two measures were not independent).

Weather data came from Braemar village at 330 m (Monthly Weather Report of the Meteorological Office at Bracknell), in a valley between the mountain study areas. I could see area B from near my house, and when fresh snow lay there I estimated its extent visually on A, B and C.

Probability values given below are two-tailed.

Results

Spring sex ratio, density, and habitat

The sex ratio when pairs had settled in spring was near 1:1 on each area in all years, and also on each part of an area (Table 1). The spring density of settled pairs was highest on the rich area C, intermediate on B, and lowest on A (Table 1). It varied little between years. Some parts of the areas had a higher spring density than other parts (Table 2). The overall density on the granite area A was lower than on granite area B. This was partly because large boulder fields held no birds regularly; A had large boulder fields, but B and C none. Also, birds usually avoided slopes steeper than 15°, and A had some of these, whereas B and C had none.

Table 2. Density of settled pairs per km² in spring on different habitats.

Study area		Size (ha)	Habitat dominated by	Mean density in pairs/km² (95% confidence limits)	n (years)
A, part	a	90	Jt	6.1 (0.3)	20
	b	61	Jt	6.2 (0.4)	20
	c	214	Ns	0.6 (0.1)	11
	d	430	Rl-Jt	0.7 (0)	10
	e	131	Boulders	0 (0)	20
	f	50	Jt-Rl	4.0 (0)	14
	all	1187		1.4 (0)	7
B, part	a	96	Jt	5.4 (0.7)	9
	b	121	Jt	5.4 (0.7)	9
	c	70	Jt	5.1 (0.7)	5
	d	65	Cv	1.7 (0.3)	9
	all	352		2.3 (0.1)	6
C, part	a	42	Cbt	10.5 (0.5)	19
	b	65	Cb	1.8 (0.3)	19
	all	107		5.2 (0.2)	19

Jt *Juncus trifidus* tussocks among rock granules and stones
Ns *Nardus stricta*, but most birds were on small tracts dominated by *Juncus trifidus*.
Rl-Jt *Racomitrium lanuginosum* with much *Juncus trifidus*
Jt-Rl *Juncus trifidus* with much *Racomitrium lanuginosum*
Cv Prostrate, lichen-rich *Calluna vulgaris* with some *Juncus trifidus*
Cbt *Carex bigelowii* on ground broken by terraces and stony patches
Cb *Carex bigelowii* on smooth flattish ground

Not all individual parts of A are shown.

Spring densities were highest on ground dominated by *Juncus trifidus* on A and B, and by *Carex bigelowii* on C where *Juncus trifidus* was scarce (Table 2). Densities were lower on ground dominated by *Racomitrium lanuginosum* or prostrate *Calluna vulgaris*, and lower still on gravelly tracts with little vegetation and on ground dominated by *Nardus stricta* or *Vaccinium myrtillus* — *Empetrum hermaphroditum* heath.

The highest densities on the above favoured vegetation on each area were on ground broken by either ridges, terraces and earth hummocks, or patches with rock granules, pebbles, cobbles and boulders. Feeding birds preferred such broken ground, and all 61 nests found and most broods were there. Observers found it hard to see birds there, so predators may also find this. Resting and sleeping birds tended to use more heavily broken ground, especially stony patches where they were even harder to see. They sat or stood facing the wind, and in strong winds each bird was in the lee of a tussock or cobble. Resting birds often crouched until a person came within 4–5 m before they flew. Shortly after arriving in spring, resting and sleeping birds were twice seen during afternoons on 35° stony slopes below C. Birds were also found roosting at night on these slopes and sometimes flew there when escaping from raptors. Although Cramp (1983) stated "Lifestyle virtually omits relation to fresh or salt water", on four days in May I saw several adults bathing in pools on a vehicle track and in streams.

Adult numbers over the summer

When cocks were sitting on incomplete clutches I saw more hens than cocks, probably because cocks on eggs were silent and motionless. This made them much harder to find than hens, which often called and moved conspicuously when not laying. By contrast, counts in the incubation period and in the period with small chicks revealed only a small proportion of the number of hens seen earlier; I assumed that most of them were absent from the study areas for most of the time. However, a high proportion of the number of hens seen in spring was occasionally seen in a single flock of hens in July, such as 11 on 21 July 1977 on A and nine on 28 July 1968 on B, so probably they were still visiting the areas at times.

The percentage loss of hens between spring and late July exceeded that of cocks in all 13 years when the percentages for cocks and hens differed on A (sign test, $P<0.002$), and in 13 out of the 14 years when they differed on C ($P=0.002$).

The number of cocks in late summer was usually lower than it had been in spring, and the number of hens much lower. In late July on A, the mean number of cocks was 24% lower than it had been in spring, but the mean for hens was 53% lower. On C the mean value for cocks was 6% lower, but for hens 36% lower. Annual values for the late-summer number of adult hens per ten cocks varied from 0 to 10 on both A and C, with means of only 6.7 and 6.2. Values for the last summer counts fell even lower, to 0–2 on A (mean 0.2) and to 0 on C. The last birds in September were usually cocks with late young. Presumably the lower numbers of adults in late summer were a result of birds leaving, perhaps on migration. Such large losses were unlikely to be due to mortality, which in any case appeared to be low. The only mortality of fully grown birds seen was that Peregrine Falcons *Falco peregrinus* killed two adults in August, on A in 1975 and on C in 1967, and a juvenile on A in 1972.

Cock numbers in late summer were not always lower than in spring. In four years on A and five years on C, 1–2 more cocks with dependent big young were on the study areas in late summer than had been seen in spring. Some such birds might have arrived late, after the rest had started to nest. There was another possible explanation in each of two late summers on C; the number of cocks with big, non-flying young was greater by two than the number seen a week earlier, suggesting that birds had walked uphill on to the study area from adjacent ground.

Clutch size, robbing, desertion and hatching

All 61 nests found had three eggs, except one with four eggs on A in 1968 (Nethersole-Thompson 1973) which maybe involved two hens. Out of 50 nests whose fate was followed, six were deserted after snowstorms on A, and Crows *Corvus corone* robbed two on A. Seven of the 50 nests involved presumed repeat clutches and three more had clutches delayed by late thaws; all ten hatched after 20 July. These ten late nests all had three eggs, so clutch size did not decline with date. All 30 late eggs hatched. Each of four nests after hatching contained an unhatched egg with a dead embryo; two had died in the first few days of development and two were fully formed but had not got out of the egg shells.

Out of the above 50 nests, 18 had fresh eggs when first found, with 54 fresh eggs. Out of 10 such nests on A, one was robbed by a Crow and two were deserted after snowstorms. At the 15 such nests that were not robbed or deserted, the 45 fresh eggs produced 44 hatched chicks. In addition, a day-old chick on C died in the nest.

The earliest brood found was on C in 1978; the fledged young had the last traces of down on 11 July. The latest, on A that same year, was like this on 12 September. The latest fresh eggs seen were two being warmed by a cock on 11 July 1979 on A; the anxious hen nearby was thought to have an egg still to lay.

First hatch dates coincided on A and C in a few years, and median hatch dates too (Table 3), but both were usually later on A, which had wider snow cover left from the winter and more frequent spring snow-

Table 3. Hatch dates in days after 31 May, calculated from estimated ages of chicks or known from 48 observed hatch dates.

	Areas		
	A	C	P[+]
1967	31, 33, 33, 34	22, 31, 33	
1968	30, 30, 31, 61	30, 30, 31	
1969	31, 41, 41, 53, 57	22, 31, 33	0.072
1970	28, 29, 31, 33	28, 29, 31	
1971	31, 35, 41, 42, 52, 62, 65	16, 16, 16, 18	0.006
1972	38, 40, 42, 42, 49, 62, 62	36, 37, 39	0.034
1973	25, 25, 45, 45, 45, 45, 48, 49	25, 25	0.044
1974	39, 39, 41	38, 39, 41	
1975	26, 31, 31, 31, 41, 43, 58	23, 31, 31, 31, 31	0.030
1976	24, 28, 31, 31, 34, 39	24, 30, 33, 34	
1977	51, 55, 59, 61	32, 32, 36	0.056
1978	24, 25, 30, 31, 57, 58, 58, 74	13, 20, 42, 45	
1979	32, 54, 62, 70	25, 47, 58	
1980	30, 33, 35, 46, 56	15, 32, 33, 40	
1981	22, 22, 22, 26, 28, 28, 33, 62, 63	14, 25, 31, 35	
1982	56, 61, 66	32, 33, 34	0.10
1983	47, 55, 57, 58, 58	35, 45, 51	0.072
1984	26, 27, 30, 33, 65, 69	26, 27, 33, 37	
1985	23, 28, 50, 57	22, 23, 44, 44	
1986	38, 39, 51	27, 27, 28, 29, 29	0.036

[+] Mann-Whitney tests for A vs. C within years; blank spaces indicate P>0.1. For A vs. C in all years: medians and first dates, P<0.02; ranges and last dates, P<0.002.

Chick ages were estimated from the appearance of chicks of known age from nests that were isolated either geographically or through being very early or very late, and from a few colour-ringed broods on C.

falls. The last hatches on A were later than on C in nearly all years, so the range in hatch dates on A was usually greater too. Hatch dates on A tended to be bimodally distributed in most years, with a gap between presumed first clutches and presumed replacements. In five years with a unimodal distribution of hatch dates on A (1974, 1977, 1982, 1983 and 1986), deep winter snow and fresh snowfalls in May and June delayed first clutches. However, in 1970 and 1976, when far less winter snow remained in May and June, the unimodal distribution of hatch dates on A resulted from presumed first clutches. Samples on C were small, but suggested a unimodal distribution of hatch dates in all but three years, reflecting a predominance of presumed first clutches.

First hatch dates for each year on A and on C were related only weakly (r_s=–0.39, P<0.1) to the May daily mean air temperature at Braemar village, and median hatch dates even more weakly (P>0.1). This was not surprising, as extensive snow left from snowy winters delayed breeding even in warm Mays.

Late broods, and brood size at different ages

"Late" broods hatched after 20 July (Table 4). In 1977, 1982 and 1983 they were from first clutches which had been delayed by late thaws. In other years they were presumed to be from repeat clutches; some new clutches were certainly laid a few days after summer snowfalls when a high proportion of cocks deserted their nests or lost their chicks (Table 5). "Repeat" means that the unsuccessful cock was given a fresh clutch, not that the same hen laid a repeat.

Late broods suffered heavy losses, but in a few years they succeeded better than earlier attempts. In 1968, which had very heavy rainfall in July, the only young reared on A were in a late brood that probably came from a repeat. In 1978, which had the worst July snowstorms during the whole study, only three young were reared from all first attempts on A, but two young were reared from four presumed repeats. In the 15 years with late hatches on A in Tables 3 and 4, 28 young were reared from at least 35 presumed repeats, and only 62 from 210 presumed first attempts (esti-

Table 4. Losses in late broods followed up on area A.

	Hatch date (see Table 3 title)	Number of young at 1 day	2 days	1 week	3 weeks	4 weeks
1968	31 Jul.	–	–	–	2	2
1969	23	3	–	–	3	3
1971	22	3	–	–	1	1
	1 Aug.	–	–	–	2	2
	4	–	–	–	2	2
1972	1	3	3	–	0	0
		3	3	–	0	0
1975	28 Jul.	3	–	1	0	0
1977	25	–	–	–	1	1
	29	–	–	1	1	1
	31	–	–	2	2	2
1978	27	3	3	2	1	1
	28	3	–	2	0	0
		3	–	2	0	0
	13 Aug.	3	–	2	1	1
1980	26 Jul.	–	–	–	1	1
1981	1 Aug.	2	2	–	2	2
1982	26 Jul.	3	–	3	2	2
	5 Aug.	–	–	–	1	1
1983	28 Jul.	3	–	–	2	2
1984	4 Aug.	3	–	–	1	1
1985	27 Jul.	–	–	–	2	2
1986	21 Jul.	3	–	–	1	1

There were two late broods on area C: a 12-day chick on 2 August 1983 survived to full grown; in addition, a late nesting in 1979 (Table 3) produced no big young. The only two late broods seen on B hatched on 23 and 26 July 1971; one chick in each brood survived to a week old but their fate was not followed later. Twelve late-hatched broods on A in Table 3 are not in Table 4 because they all failed in the first week.

Table 5. Estimated number of days until a cock was given a first new egg after his clutch or brood was lost from snowstorms or robbing.

Year	Area	Loss of	Date of loss from snowstorm (robbing)	Estimated no. of days until cock was given a first new egg*
1971	A	clutch	18 June	6
	B			7
				10
1972	A		(29 June)	5
1974			9 June	8
1978		brood	2 July	0+
				0+
				0+
1981		clutch	(1 July)	5+o
1985			5 June	6
			13 June	7
1986		clutch	10 June	4o
				5

* Assuming an egg laid per day and incubation starting with the third egg and lasting 26 days.

\+ Heavy snow fell on 2–5 July and snow showers on 6 July, with cold weather until 8 July. Egg-laying and incubation could not have exceeded 25–26 days (see also Table 4); incubation may be shorter in late nests, as Galbraith (1988) found in Lapwings *Vanellus vanellus*.

o Fresh clutch found nearby.

mated from Table 1, assuming that all settled pairs in spring did nest there). In the five years without late hatches on A, 48 young were reared from an estimated 72 attempts. As my visits were often infrequent, other late clutches which were not found might have hatched and the chicks might have died before my next visit. Hence the losses in Table 4 and the rest of the 35 presumed repeats above are a minimum, and their apparent success may be too high.

The late broods listed in Table 4 could be followed as there were so few in any one area and year, and as nearly all first nestings on that area in that year had failed. A different question was whether, among probable first clutches, early clutches in any one year produced more young than later clutches. I could not tackle this, because early layers were too numerous to follow individually without marked birds and because some cocks with young probably moved into the areas from outside (see Adult numbers over the summer).

Mean brood size was the number of young per dependent brood, omitting adults without young. If one considers only the late broods (Table 4), losses were at least a third in the first week, at least a further half in the next two weeks, and then negligible. If one considers all broods combined, only a crude analysis was possible, as sample sizes differed between years and data were missing for certain ages of young in some years. Moreover, losses in this crude analysis were minima; adults which had been seen earlier with small chicks but which later lost all of them would obviously not appear in the later counts of adults with broods. The results for all broods combined showed that mean brood size in the first day after hatching was 2.9 (SD=0.3) on both A and C (n=20 and 11). By 2–3 weeks, it was down to 1.8 on both A and C (SD=0.8 and 0.7, n=13 and 6), and then stayed similar up to the stage of fully grown young per dependent brood (means 1.76, SD=0.77, n=55) on A and 2.00 (SD=0.82, n=31) on C.

Table 6. Kendall rank correlations coefficients from comparisons of breeding success (number of big young in late summer per ten adults in spring) with July weather at Braemar.

Comparisons with	Area	Years	Coefficient	P+
Mean temperature	A	20	0.48	0.01
	B	12	0.42	0.10
	C	22	0.15	
Precipitation	A	20	−0.22	
	B	12	−0.13	
	C	22	−0.20	
Mean temperature, keeping precipitation constant	A	20	0.44	0.01
	B	12	0.36	
	C	22	0.11	

+ Blank spaces indicate P>0.1.

Breeding success between years and areas

Breeding success on a given area varied greatly from year to year (Table 1). It was not related to median hatch dates (Table 3) on A or C. It was associated positively with the July daily mean air temperature at Braemar, and negatively, although not significantly, with July precipitation (Table 6). On A, only the relationship with temperature was significant; this still held when a partial correlation analysis was used, keeping precipitation constant. Breeding success on B was almost as strongly related to July temperature as on A, but not significantly because there were fewer years with data. On C the association with July temperature was very weak, probably because the early chick period on C in some years was late June, not July (Table 3).

One might expect summer snowfalls to reduce breeding success. For B and C there were too few years with both summer snowfalls and breeding data to justify analysis. Birds on A bred worse in years when summer snowfalls lay there during the nesting and chick periods in these particular years (1971, 1972, 1974, 1978, 1981, 1985, 1986) than in years without such snowfalls, but not significantly so (Mann-Whitney test, n=7 & 13, P>0.1).

The old measure of breeding success (the number of big young in dependent broods per adult in late summer) on C exceeded that on A or B; it was slightly higher on B than on A, although not significantly so (Watson 1988). Annual values for the new measure (the number of big young in dependent broods in late summer per ten adults in settled pairs in spring) on C also exceeded those on A (Mann-Whitney test, n=20, P<0.002) and on B (n=12, P<0.002). They were slightly higher on A than on B, although not significantly so (n=12, P=0.1). Summer snowfalls cannot account for the overall poorer breeding success on A. Snowfalls lay on A during the nesting and chick periods in seven years (see previous paragraph), but on C only in 1980. However, even with these years excluded, breeding success on C still greatly exceeded that on A (P<0.002).

Mean breeding success with the new measure was similar on A (2.2) and B (1.9) in the 12 years with data from both areas, and was 6.9 on C in these years. In the 20 years with data from A and C in the same year, it was 2.19 on A and 6.05 on C.

The generally better breeding success on C than on A was not the result of birds tending to breed earlier on C. In the five years when median hatch dates on A and C coincided (Table 3), breeding success was better on C in four years and worse in only one. Out of the nine years when median hatch dates were the same or within two days on A and C, breeding success on C exceeded that on A in eight years and the annual values on C exceeded those on A (Mann-Whitney test, P<0.02). The main reason for breeding success being better on C than on A was that a far higher percentage of cocks on C had dependent big young (Table 1, Mann-Whitney test, P<0.002).

Breeding success in summer i was not related to change in adult numbers from spring i to spring i+1 on that part of A with enough years of data for analysis (in Table 1), or on C. Hence numbers on each area could not have been a closed population.

Annual values for the old measure of breeding success (the number of big young per late-summer adult) were not significantly related on A, B, or C to annual mean densities of people seen per count there or to densities of dogs seen with these people (Watson 1988). Using the new measure (the number of big young per ten adults in settled pairs in spring) does not affect these conclusions. A different point is that Watson (1988) wondered whether breeding on C might have been poorer in 1974–86 than in 1965–73, but this does not hold with the new measure (Mann-Whitney test, n=9 & 13, P>0.1).

Arrival, spring spacing and snow cover

First sightings were quite early in some years (Table 7), despite wide snow cover and wintry weather in a few of them, such as in 1977, 1985 and 1986. First sightings on A and C were at broadly similar dates

Table 7. First and last sightings on areas A and C.

	First, in days after 10 April		Last, in days after 31 July	
	A	C	A	C
1967	–	–	18	–1*
1968	46	–1*	28	–18
1969	35	–4	20	–4
1970	25	–1	24	–1
1971	34	+1	35	–12
1972	30	+1	29	–6
1973	9	+1	24	–13
1974	30	+1	22	–4
1975	38	–2	9	–6
1976	25	+1	17	–17
1977	26	+2	38	–28
1978	41	–3	43	–32
1979	32	+3	29	–14
1980	31	+1	10	–1
1981	23	–1	23	–23
1982	29	–1	32	–31
1983	32	–1	27	–6
1984	19	–1	19	–8
1985	27	+4	17	–6
1986	24	+1	11	–2

* –1 means a day earlier, and +1 a day later, than on A. Differences of up to four days were within the variation expected from my visits to A and C having to be in reasonably good weather on different days.

Last sightings on C in 1965 and 1966 were on days 8 and 14.

Table 8. Number of Dotterel seen during spring in relation to snow cover, after the birds had arrived on the study areas.

Number seen, as a % of the number seen later, just before egg-laying	% of ground under continuous deep snow	n
100	0–80	14
25, 100	90	2
100	95	1
0	96	1
0	98	4
one 16, others 0	99	7
0	100	4

within years, and data from B fitted this. After arrival, birds on each study area concentrated on the upper parts of the largest block of favoured habitat that was snow-free and had thawed, drained surface soils. They avoided snowfields and frozen snow-free ground, but occasionally ate invertebrates stranded on snow within 0.5 m of the snow edge.

When birds arrived, the amount of continuous deep snow left from the winter varied greatly between years, and between different parts of an area in any one year (Table 8). Early birds in late April or the beginning of May mostly congregated in flocks, even when snow cover was only 5% and when the snow-free ground had thawed and drained. If fresh deep snow gave 100% cover over entire study areas after the birds arrived, flocks and pairs were absent. For instance, I saw none on C when snow covered all of it on 8 and 15 May 1977, but isolated pairs were feeding at snow-free streams on steep snow-covered hillsides down to 800 m in places where no birds with nests or chicks have been seen. When fresh snowfalls covered only the higher parts of the study areas, all birds were concentrated on less snowy parts lower down. However, pairs in warm weather remained on the higher parts despite 90–95% snow cover, if the snow-free patches exceeded 0.5 ha each. On three occasions I saw a pair on a 10 × 10 m patch, but birds usually avoided patches as small as that and also long strips only 2–3 m wide; during thaws, such ground was usually still frozen.

The density of pairs on snow-free patches decreased as the amount of snow-free ground increased with the thaw. For example, the only Dotterel found on a 147-ha part of A on 21 May 1978 were five pairs on 8 ha, on three patches of closely adjacent snow-free ground; the nearest two pairs were 90 m apart. On 28 May, five pairs were again found, further apart on the snow-free ground, which had now spread to 27 ha. A week later, five pairs were again found, spread well over the 147 ha area, which had by now mostly cleared; the nearest two pairs were 500 m apart. Birds were not found nesting on A until after that date.

The sex ratio in all spring flocks combined for a whole study area was near 1:1 (Tables 9 & 10). However, when early flocks were seen in April and up to 6 May, the sex ratio for each individual small flock varied considerably. For example, four early small flocks on A in 1984 had cock:hen numbers of 2:4, 4:5, 2:2 and 4:1, and four on C in 1973 had 2:6, 4:5, 8:6 and 6:3. Early flocks that were larger (>15 birds) tended to have sex ratios nearer 1:1. By contrast, 14 out of 17 later small flocks between 14 May and egg-laying (not in Table 9) had 1:1 sex ratios, and the remaining three flocks had only one bird out on either side (e.g. 5 cocks and 6 hens, or 6 cocks and 5 hens).

Table 9. Sex ratio in spring flocks totalled for a whole study area or other large area (excluding data in Table 10).

Year	Study area	♂	♀	Year	Other areas	♂	♀
1970	A	6	5	1971	West Cairngorms	5	5
1971	A	12	13	1972	East Mounth	14	14
1972	A	7	7	1973		3	3
1974	A	14	14	1976		6	6
	B	15	14	1981		2	2
	C	8	8		Monadh Liath	4	4
1975	B	21	20	1982	East Cairngorms	13	12
	C	7	7	1983	East Mounth	12	13
1976	A	6	6		East Cairngorms	9	9
	C	3	3	1984	West Cairngorms	6	6
1977	A	4	4		East Mounth	2	2
1978	A	3	3	1985		15	15
1979	C	3	4			3	3
1981	A	3	3			2	2
	C	10	10	1986		7	6
1982	A	3	3			8	8
1983	A	7	7			3	2
	C	6	5				
1986	A	15	15				
	C	21	21				
Total		174	172			114	112

Out of 32 individual flocks in April and up to 6 May, none consisted of pairs; one could see this when the flocks loosened at times during feeding. In 38 individual flocks on 7–13 May, most birds were still not in pairs. After 14 May, however, 26 individual flocks consisted of 104 pairs, plus seven mixed-sex trios and a single cock.

In mild weather during early May, birds were in flocks or in widely spaced, settled pairs. Often the flocks temporarily became loose amalgamations of pairs, singletons, and mixed-sex trios. After fresh snowfalls the flocks became compact, and birds which had been found as pairs far apart earlier that day were seen flying to join the flocks. Numbers on C soon after the birds' arrival often exceeded numbers just before egg laying (Table 10). After the flocks finally broke up, some extra pairs were seen in new places on C, but were not consistently in these places on later days; they tended to flush further from me than closely settled pairs. In 1982 such extra pairs occurred for a longer time and in larger numbers on C, but were not found there just before egg laying. The number of pairs just before egg laying on C was very similar to that of settled pairs seen earlier. On A I saw no such extra birds before nesting.

Table 10. Numbers on area C in early May, and later (just before egg laying).

	Most of time							
	in flocks				in settled pairs			
	Early		Later		Early		Later	
	♂	♀	♂	♀	♂	♀	♂	♀
1972	2	2	0	0	7	7	7	7
1978	8	8	0	0	5	5	6	6
1980	4	4	0	0	6	6	6	6
1982	11	11	0	0	5	5	5	5
1984	13	14	0	0	6	6	6	6
1985	5	5	0	0	6	6	6	6

Deep snow sometimes delayed the onset of snow-free conditions in June. If the snow cover was not total, however, much the same number of pairs was seen on every visit until the snow melted and the ground thawed and drained; only then did they nest. In 1977, for instance, when deep snow covered most of a high part of A, the only birds seen there on 22 June were four pairs well apart. On the snowiest section of this high part, a pair still displayed on 3 July, and eggs in a nest there hatched on 31 July. Yet breeding birds were as abundant on this high part in 1977 as in years when little or no snow lay there in June. Also, birds in 1977 were no more numerous than usual on low parts which held birds each summer and which were snow-free by mid June every year. Hence birds on high snowy parts waited to nest there.

Spring agonistic encounters

These often occurred in flocks (see Kålås 1988), and between pairs which were only 5–10 m apart on small snow-free areas. One bird would jump at another which ran or fluttered away, or two jumped up and down for a second or two, partly fluttering. Some left the flock as a pair or mixed-sex trio in high flights, and alighted together. Ground chases for a few seconds were common in flocks, and within a few minutes the chases could involve a cock chasing after a cock, a cock after a hen, a hen after a hen, and a hen after a cock. In four independent cases I saw a cock chase a cock, in four a cock chase a hen, in 12 a hen chase a cock, and in 16 a hen chase a hen. Thus, hens had most encounters, and this was especially the case with fights. Pairs undisturbed by me often raised one or both wings while in a flock; I noted eight independent cases of cocks doing so, and 20 of hens. Encounters became frequent within a few minutes when a flock loosened, as pairs, singletons and trios broke off. Calling reached a peak when flocks broke up in May, especially in evenings and early mornings.

An unusual incident on 24 May 1979 on C involved three pairs which were spaced roughly at the corners of a triangle. After hen Y sang on the ground, hen X left her cock to walk 200 m to Y; hen Z sang and walked 150 m to Y, followed by her cock 5–10 m behind. The three hens then displayed at one another before joining their cocks in pairs which moved apart again.

Lone hens often made wide-ranging song flights (see Kålås & Byrkjedal 1984a) when other hens were in spring flocks and pairs. When such flights were seen to end, the singer alighted to join a lone cock.

Spacing during the egg-laying and chick-rearing periods

During the egg-laying period I saw agonistic encounters in mixed-sex flocks, but not involving a pair, except when an extra hen appeared near the pair; if so, the paired hen drove the intruder away from her cock. A hen on a hill near area A spent an hour chasing two others from the cock whom she accompanied (M. Marquiss, pers. comm.).

When laying and immediately after laying her first egg or later eggs, each hen became anxious when I approached within 100 m of her nest. Some laying hens led me away, walking conspicuously and calling; meanwhile, on two occasions a silent cock walked inconspicuously to sit on an egg. Two cocks which had been paired with laying hens were seen to join mixed-sex flocks when their hens were laying, but both cocks left the flocks to brood the eggs as soon as the hens had laid. When a cock went to brood an egg, the hen sometimes joined a nearby flock. Not all pairs were at the same stage of the breeding cycle. For instance, in 1971 and 1973 a few cocks were found sitting on 1–3 eggs while some other birds in pairs were still in flocks that later broke into settled pairs. Copulation was noted from 9 May until 16 July; I often saw copulation by pairs just before and during egg-laying, but not by cocks brooding completed clutches or attending chicks.

When most or all cocks were brooding full clutches, agonistic encounters and calling still occurred in hen flocks. Single hens made frequent, wide-ranging song flights as late as 13 July on A. In early-mid July, I often heard one or more birds at a time calling at dusk, during the night, and at dawn, sometimes on the ground and sometimes in flight. A few cases at dusk involved a pair which I had seen just before dusk, and other cases involved presumed single hens singing. On two occasions I heard a single presumed hen flying 3.3 km at dusk in a straight line from the main part of A to Dotterel habitat further north-east, crossing steep slopes where no birds were ever seen on the ground.

Some cocks which were brooding eggs when fresh snow covered the vegetation were seen flying to feed below A and C on steep snow-free slopes at 900–1000 m, where no birds were seen feeding on days when A and C were snow-free. Most broods were far apart but occasionally two came within 50 m. On three occasions two broods were only 10 m apart in flushes; both cocks showed distraction display when I approached either brood.

After summer snowstorms, many cocks on A and B were found to have deserted their nests or lost their chicks. Pairs were seen again (Fig. 1), which called frequently and showed conspicuous display typical of pairing behaviour in May. The same behaviour occurred after eggs were robbed by predators. In these

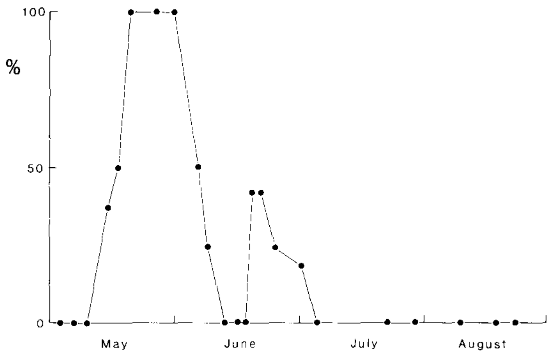

Fig. 1. The percentage of adults seen as pairs on area A in 1971. In mid May – beginning of June, a total of 32 birds was found. Percentages are based on that total, although many hens were thought to have left by late summer. On the first three observation dates, birds had not arrived. The later peak came immediately after cocks deserted clutches in a severe June snowfall, and was followed by laying of fresh clutches.

cases, some fresh clutches were laid within a few days (Table 5). Although nearly all of these freshly formed pairs were seen in nest-scraping displays, some pairs disappeared shortly after, and not all were thought to have attained egg laying.

Sex of adults with eggs and young

At 61 nests with incubated clutches, all birds that were brooding when the nest was first found were cocks. Only two hens were subsequently seen on completed clutches in daylight, and each was seen only once, compared with five and eight occasions for the cocks at these nests. Both these hens were on C. One had a late clutch in July (see Kålås & Byrkjedal 1984a), and the other had a clutch of average date.

The oldest chicks which I saw being brooded were two weeks old, on late evenings with cold wind and rain. I saw no hen brooding or attending chicks, but many cocks doing so. Each dependent brood plus its attendant adult cock formed a unit; when I came near, he did not leave except in distraction display, and he returned to the chicks as soon as I had gone away 150 m. Most observations were in daylight, but in the hour after sunset I saw cocks attending 12 broods which varied from one to seven days old. No brood was seen being attended by a hen alone. When a cock on A called in distraction display beside a day-old brood on 29 July, a hen appeared and walked to within 50 m of me before flying away. When another cock on A called in distraction display beside two 2.5 week-old chicks on 30 June, a hen appeared and walked to 20 m from me. A hen on C once walked to 30 m from me when a cock showed distraction display from day-old chicks in early June.

Each dependent brood and its attendant cock stayed separated from other broods or adults until the chicks were 2.5 weeks old. I saw only five cases where an attendant cock with young aged from three weeks up to near fledging associated with 1–3 other adult cocks or hens. However, when a man, dog or raptor came near, the other adults walked or flew away from the family and did not return. In all but these five cases, each brood stayed separate with its attendant adult cock until the young became fully fledged.

Independent juveniles, either singly or in flocks, were often seen with or without varying numbers of adult cock and hen Dotterel, sometimes with Golden Plover *Pluvialis apricaria*, a few times with Dunlin *Calidris alpina*, and once with a juvenile Purple Sandpiper *Calidris maritima*. Frequently, one or more juvenile Dotterel left a Dotterel flock by walking or flying spontaneously, without any adult staying with them, and joined other flocks or singletons, or became singletons themselves.

Departure and autumn spacing

Flocks of >40 birds at a time occurred on A, B, and C during August in some years. Flocks were seen in all 20 autumns on A, in 11 out of 12 on B, and in 21 out of 22 on C. Last sightings on A all came later than on C in the same year (Table 7, Mann-Whitney test, $P<0.002$). Some of the later departures on A resulted from the much higher proportion of late broods on A than on C, but other late birds were cocks without young, and independent juveniles. Moreover, birds stayed late on A in years with no late broods, such as in 1976, when all the young had become juveniles by 5 August, yet 41 adults and juveniles remained on 15 August and 17 birds on 17 August. Late broods on C hatched after 20 July in only two years, but some birds were seen late even in years when all the young became independent much earlier. For instance, all young in 1967 on C were independent by 31 July, yet 4, 4 and 6 birds occurred on 2, 6 and 17 August. All young in 1972 on C were independent by 6 August, but I saw 17, 19 and 4 on 10, 12 and 20 August. By contrast, in 1976 on C, young and their attendant cocks disappeared shortly after each brood fledged.

Nethersole-Thompson (1973) wrote that young Dotterel sometimes stay behind after the others have gone, and mentioned two observations of mine in 1967. One was a juvenile seen by me on C on 11 August, but an adult cock was only 1 km away that day, and my father saw six adults on C on 17 August. The other case involved a juvenile seen on B on 13 August, but we might well have overlooked birds when searching the remaining half of the area, because of thick fog coming down.

Birds seldom departed all together. Typical examples on A were that I saw 28, 17, 7 and 5 birds on 12, 15, 21 and 24 August 1973, and 15, three and two birds on 14 August, 28 August, and 1 September 1982.

Far fewer encounters were seen in autumn flocks than in spring flocks. Usually one bird would briefly displace another; this occurred often when my movement concentrated them, but seldom when I watched from afar. Flocks in late August showed unusually frequent calling for the autumn, and many spontaneous flights. For instance, birds in a flock on 15 August 1976 called much on the ground, and often one or two flew and called high up before returning in a few minutes; none was seen four days later. On 29 August 1979, three adults and a juvenile flushed unusually far from me, called frequently, and made several high flights; none was seen three hours later.

Discussion

Although Dotterel in Scotland are at one edge of their Eurasian range, population density on the three study areas was quite high on favoured habitat and was fairly steady over the years. Also, the birds bred quite well, especially on C. No data on breeding success from defined areas over a long run of years have been published from other countries. In a set of data lumped from seven years in Norway, half the eggs were robbed (Byrkjedal 1987). Kålås & Byrkjedal (1984a) showed data for each year in 1979–81, when 16% to 67% of nests were robbed (mean 37%). Egg predation on the three Scottish areas was much lower. Cocks in Norway accept fresh clutches after nest robbing (Kålås & Byrkjedal 1984a), but Scotland provides a longer summer for birds to renest after losing their clutches or broods. Future observations on density and breeding success over a number of years from Fennoscandia or the USSR would allow the Scottish results to be compared with data from the main part of the bird's range. At the moment, the preliminary indications are that conditions on the Scottish study areas are quite good, not marginal.

It is possible that some Scottish areas are more marginal than the three study areas, perhaps on small tracts of habitat or on hills at low altitudes. One might expect spring densities there to vary more between years, and breeding success to be poorer. This remains to be checked.

On areas where birds breed well, such as C, one would expect a net export of birds to areas where breeding is poorer, such as A and B. This could be studied only with marked birds. I predict that rich areas such as C should export colonists to poorer areas. However, the difference in conditions for breeding was only relative, as birds on A bred better than on C in two years and almost as well in a third. Thus, one might expect a net loss from richer areas, but not necessarily a loss every year.

Watson et al. (1970) attributed the higher density and better breeding success on C than on A to the richer rocks and soils at C, leading perhaps to more invertebrates as food for Dotterel chicks. One might expect not only total invertebrate abundance to be greater on ground with richer soils, but also the number of species. The hill range at C is also a rich site for Ptarmigan *Lagopus mutus*, Red Grouse *Lagopus lagopus* and Mountain Hares *Lepus timidus*, in association with their main food plants being higher in nutritive value than the same plant species at A (Watson 1979).

Using some data from A, including Nethersole-Thompson's (1973) past observations, Watson & Parr (1973) noted that more young tended to be reared per old Dotterel when July was warm, but there were not nearly enough years of data to check this properly. A much longer run was available from the present study. Breeding success was found to be associated with July weather, but most of the variation remained unaccounted for. The analysis was crude, as the weather station lay in a valley far below the birds' habitat. Moreover, the three study areas had obvious differences in climate. All summer snowfalls came with northerly winds, so the more northerly area A had heavier falls than B, area B had heavier falls than the more southerly C, and even the southern parts of A and B got far less snow than the northern parts of the same areas. Rain in thunderstorms varied even more. Fog varied between and within areas, and led to water drops on grass, which can make Dotterel chicks wet. Such local weather data were unavailable. A weather station is now on area A, so breeding success could be compared with mountain weather in future.

The better breeding success on C than on A and B cannot be attributed to less predation on eggs and chicks. Few eggs were robbed on any of the areas. Crows occurred each summer in small numbers on A (Watson 1979), but were absent on B where Dotterel bred no better than on A. Crows were much scarcer on the hill range at C than at A, and in most years were absent. Common Gulls *Larus canus* and Black-headed Gulls *L. ridibundus* were in small numbers on A but not B, and were much more abundant on C than on A, in association with visually obvious greater numbers of the craneflies (Tipulidae) that they mainly fed on there. A Snowy Owl *Nyctea scandiaca* was on A in a few summers, but not in most years. Peregrine Falcons, Kestrels *Falco tinnunculus* and Golden Eagles *Aquila chrysaetos* were seen much more frequently on C than on A or B.

Breeding was delayed by deep snow cover from the winter and by fresh spring snowfalls. However, Dotterel did not nest as soon as the ground became clear of snow. Snow-free patches were at first waterlogged by thaw water, and this could not drain away because of the frozen ground underneath and because snow downhill was damming up the water. The birds did not nest until the ground surface had drained. Another result of wide snow cover from the winter and of spring snowfalls was that they also delayed the main emergence of the invertebrates which provide chick food. Hence lateness did not necessarily mean poorer food conditions. Moreover, large snow patches which lasted into July and August resulted in the main invertebrate emergence being further extended. Dotterel should be able to find abundant invertebrates by taking their chicks to thawed, drained ground near these patches.

Fewer hens than cocks were seen on the study areas during the incubation and chick-rearing periods, although hens during these periods were much more conspicuous than cocks that were tending eggs and chicks. However, a high proportion of the number of hens seen in spring was occasionally seen in a conspicuous hen flock in June and July. This suggested that most hens were still visiting the areas, even if not present there enough of the time to be observed as often as cocks. Another piece of evidence backing this suggestion is that many cocks which had lost their eggs or young from snowstorms were paired on the first day of the subsequent thaw. It seems likely that considerable numbers of hens remained near the areas, and were then available to pair again quickly and provide unsuccessful cocks with fresh clutches.

Birds arrived earlier in some years than in others. Two very early arrivals in 1973 and 1984 coincided with several days of hot south winds from western North Africa, which produced maximum air temperatures of 21–25°C in lowland northern Scotland and rapid thawing of snow on the study areas. African winds that stopped short of Scotland might cause birds to move north from Africa, but Dotterel arrivals on the study areas did not occur until large patches of snow-free, drained ground were available there for feeding.

In a few springs after long snowy winters, there was little or no snow-free ground when the birds returned. If so, they probably waited on lower hills, including low moorland where Dotterel do not nest; in late April and early May I saw birds temporarily on lower hills and moors on several occasions when the study areas were under 100% snow cover. However, unusually early clearance of snow from the study areas sometimes occurred for a week or more without Dotterel being present. For example, in 1971 the main habitats on C and even on the higher A had mostly cleared of snow and were drained dry in 2–7 May, yet no Dotterel were present until late in the next week. In 1981 the ground was like this by 17 April — an exceptionally early clearance of snow — but Dotterel were not back till 2–3 May. To sum up, I suggest that hot southerly winds from North Africa after mid April may be necessary for the birds to move north, but not sufficient for their arrival on the Scottish or other breeding areas unless large snow-free patches of breeding habitat are available. The reason why birds do not appear in warm weather even earlier, in early April or March, may be the much greater risk of being caught by snow lying on lower hills and lowland farmland, let alone on the breeding grounds.

Birds in Norway arrived on snow-free hilltops above snow-covered slopes, and moved down as snow-free ground spread; most nested downhill (Kålås & Byrkjedal 1984a). On arrival in Scotland, by contrast, they favoured the upper parts of the largest block of favoured habitat on each area, unless deep snow covered it. They did this even when most of the Dotterel habitat downhill was snow-free, so their preference for upper parts could not have been because these were the only snow-free places. Birds also favoured upper parts in late July–August, when all snow on the main habitats had long melted.

Nethersole-Thompson (1973) stated that Dotterel were territorial in Scotland, mostly describing birds attacking others coming near their mates, nests, or chicks. Kålås & Byrkjedal (1984a) wrote that they were not territorial in Norway. Birds on my areas did not defend territorial boundaries, but the possibility that Dotterel show dominance in relation to overlapping home ranges cannot be excluded.

The number of spring pairs changed little between years. This might suggest that behaviour may limit numbers, perhaps between the times when extra pairs were present and when they were not, as on C. However, I saw no such extra birds on A, yet spring numbers on A also varied little between years. A related suggestion is that non-breeding may limit numbers. Nethersole-Thompson (1973) wrote of non-breeding cocks and hens, but his evidence did not distinguish between non-breeding, nesting and then failing, and nesting late. I found no evidence of non-breeding birds.

The extra birds seen on the rich area C in spring but not on the poorer area A might suggest a greater competition to settle on the rich area, and would be worth looking for on rich areas elsewhere. The question arises, what happens to the extra birds? The possibility that they nested at lower altitudes on the same hill seems unlikely, because flocks, pairs and breeding birds at high density were seen every year on the lower slopes too, and on nearby rich hills 1–2 km away. A second possibility, that they went to poorer areas such as A also seems unlikely, because numbers on A were already at their usual level during the period when the extra birds were seen on C, and did not increase just before nesting began on A. A third possibility, that the extra birds moved to more marginal lower hills in Scotland, could be checked in future if birds on such a marginal area were studied for several years. However, my own casual observations from lower hills indicated that birds were already paired there at the same time as on C. A fourth possibility is that they moved on to other countries such as Norway; marked birds would help elucidate this.

Nethersole-Thompson (1973) stated that birds in Scotland paired from "mating flocks", but Kålås & Byrkjedal (1984a) wrote that birds were paired on arrival in Norway. On my areas, each individual small flock in April and the beginning of May did not comprise pairs or equal numbers of both sexes, whereas flocks later in May did; this was consistent with Nethersole-Thompson's statement. It is possible that birds pair in Scotland on their way to Norway, which might account for the observation that they arrive in Norway already paired, but not in Scotland.

Spring sex ratios in flocks were near 1:1 when the flocks were totalled for each study area as a whole, even just after the birds' arrival (see also Watson & Rae 1987, Watson 1988). Strongly uneven sex ratios on a whole study area occurred only after hens started laying and some cocks were brooding, or when cocks had dependent young and many hens were absent. Any cases where appreciably uneven sex ratios (particularly an excess of hens) are reported should therefore be considered with caution, and examined to ensure that the data are free from the above bias.

If waders were to nest on small, snow-free patches, predators would be expected to find the nests easily (Byrkjedal 1980). On my areas the favoured habitats were mostly snow-free in early or mid May in some years, but Dotterel did not lay until the surface soils had thawed and drained. On frozen or waterlogged ground, eggs would cool faster and food would be less available; also, predation on brooding birds would be more likely on snow-free patches than on larger areas.

Nethersole-Thompson & Nethersole-Thompson (1986) wrote that a cock with chicks often accepts a hen's "presence when chicks are older and stronger", and "quite regularly does so when they are able to fly". After chicks were 2.5 weeks old, I occasionally saw a cock and dependent young along with one or more adult cocks or hens, and often saw this when dependent young could fly strongly. However, unlike the attendant cock, the others did not stay with the young after disturbance. Clearly the presence of such birds with a cock and dependent young indicated temporary flocking, not parental behaviour.

My results suggest that hens on the study areas played little or no role in rearing chicks. Having no parental duties might help hens replace lost eggs or "lay a second clutch for a spare mate" (Nethersole-Thompson 1973). I saw no hen on eggs repeatedly, and none attending young repeatedly. Moreover, some hens laid only a few days after cocks lost clutches or broods. Many eggs and chicks are lost in bad weather, and summers are too short for a long delay before cocks are given replacement eggs. There is some evidence that incubating cocks balance their incubation attendance against losing weight (Kålås & Byrkjedal 1984a, Kålås 1986, Kålås & Løfaldli 1987). So, hens that share incubation with cocks might be less able to lay fresh clutches for other cocks, or replacement clutches a few days after clutches or broods have been lost.

The present study ended in 1986, and has become greatly enlarged into a full-time, five-year study by a team (Thompson 1986) on A, C and other areas, including the marking of many birds and measurements of invertebrate abundance.

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Selostus: **Keräkurmitsapopulaatioiden ekologiaa Skotlannissa vuosina 1967–86**

Kirjoittaja tutki kolmella alueella vaihteleeko keräkurmitsapopulaatioiden koko alueiden sisällä ja välillä, vaihteleeko sukupuolten lukusuhde ja mitkä tekijät vaikuttavat pesimämenestykseen. Keräkurmitsa on mielenkiintoinen tutkimuskohde, sillä sukupuolten roolit ovat vaihtuneet: koiraat vastaavat melkein yksinään pesyeen haudonnasta ja poikasten hoivaamisesta.

Keräkurmitsapopulaatio oli liuskealueilla tiheämpi kuin graniittialueilla. Niityt, erityisesti jos niitä elävöittivät harjanteet tai kivikot, olivat suositumpia asuinalueita kuin nummet. Keväinen populaatiokoko ei juuri vaihdellut vuosien välillä. Munapesien selviytyvyys oli hyvä. Poikaset menestyivät parin ensimmäisen kriittisen viikon aikana parhaiten, jos heinäkuu oli lämmin ja sateeton.

Kaikilla kolmella tutkimusalueella muutoparvet suosivat mieliympäristönsä korkeimpia alueita. Jos lintujen välille kehkeytyi nahistelua, oli aina kyse parvista tai liian lähellä toisiaan olevista pareista. Keväällä sukupuolten lukusuhde oli kaikkialla tasainen. Jos lumi suli myöhään, parit odottivat niiden suosimien ylänköalueiden vapautumista lumesta. Jokseenkin kaikki hautovat tai poikasia hoivaavat linnut olivat koiraita.

References

Byrkjedal, I. 1980: Nest predation in relation to snow-cover — a possible factor influencing the start of breeding in shorebirds. — Ornis Scand. 11:249–252.

Byrkjedal, I. 1987: Antipredator behaviour and breeding success in greater golden-plover and Eurasian dotterel. — Condor 89:40–47.

Cramp, S. (ed.) 1983: Handbook of the birds of Europe, the Middle East and North Africa, 3. — Oxford Univ. Press, Oxford.

Galbraith, H. 1988: Effects of egg size and composition on the size, quality and survival of lapwing Vanellus vanellus chicks. — J. Zool., Lond. 214:383–398.

Kålås, J. A. 1986: Incubation schedules in different parental care systems in the Dotterel Charadrius morinellus. — Ardea 74:185–190.

Kålås, J. A. 1988: Sexual dimorphism in size and plumage of the polyandrous Dotterel (Charadrius morinellus): sex roles and constraints on sexual selection. — Can. J. Zool. 66:1334–1341.

Kålås, J. A. & Byrkjedal, I. 1984a: Breeding chronology and mating system of the Eurasian Dotterel (Charadrius morinellus). — Auk 101:838–847.

Kålås, J. A. & Byrkjedal, I. 1984b: Line transects of waders in an alpine area: a methodological study. — Ann. Zool. Fennici 21:399–402.

Kålås, J. A. & Løfaldli, L. 1987: Clutch size in the Dotterel Charadrius morinellus: an adaptation to parental incubation behaviour? — Ornis Scand. 18:316–319.

Nethersole-Thompson, D. 1973: The Dotterel. — Collins, London.

Nethersole-Thompson, D. & Nethersole-Thompson, M. 1986: Waders. — Poyser, Calton.

Thompson, D. 1986: Conflict on the high tops. -- Scott. Bird News 4:6–7.

Watson, A. 1979: Bird and mammal numbers in relation to human impact at ski lifts on Scottish hills. — J. appl. Ecol. 16:753–764.

Watson, A. 1988: Dotterel Charadrius morinellus numbers in relation to human impact in Scotland. — Biol. Conserv. 43:245–256.

Watson, A., Bayfield, N. G. & Moyes, S. M. 1970: Research on human pressures on Scottish mountain tundra, soils and animals. — In: Fuller, W. A. & Kevan, P. G. (eds.), Productivity and conservation in northern circumpolar lands, pp. 256–266. IUCN Publns, New Ser. 16, Morges, Switzerland.

Watson, A. & Parr, R. 1973: Timing of reproduction in dotterel and ptarmigan. — In: Nethersole-Thompson, D., The Dotterel, pp. 78–88. Collins, London.

Watson, A. & Rae, R. 1987: Dotterel numbers, habitats and breeding success in Scotland. — Scott. Birds 14:191–198.

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