BREEDING CHRONOLOGY AND MATING SYSTEM OF THE EURASIAN DOTTEREL (*CHARADRIUS MORINELLUS*)

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ABSTRACT.—We studied and color-banded a population of Eurasian Dotterel on a middle alpine breeding ground in southern Norway over 4 yr. Birds arrived paired in mid-May, dispersed onto nesting sites in late May to early June, when 75% of the ground was still covered by snow, and began to lay eggs a few days later. The egg-laying season of the population was long, up to 1½ months. After completion of the earliest clutches, females started to perform display flights, apparently to seek males. The female displaying period lasted until the second week in July, when the females began to form flocks and prebasic molt was in progress. The display period thus covered most of the egg-laying period of the population. Females had a low site tenacity during the season, and evidence for territoriality was found in neither of the sexes. We argue that sequential polyandry is common in this dotterel population. *Received 20 September 1983, accepted 4 March 1984.*

POLYANDRY is not common. Among mammals, Eisenberg (1966) found no good case. Less than 1% of the species of birds studied to date are polyandrous (Jenni 1974), and all have precocial young. Most of the documented cases are found in the orders Gruiformes and Charadriiformes (Jenni 1974).

In Eurasian Dotterel (*Charadrius morinellus*), cases of sequential polyandry have been documented (Franke 1953, Pulliainen 1971, Nethersole-Thompson 1973). Because of the reversal of sexual roles and the fact that the male alone cares for the young, the species holds a great potential for the regular occurrence of polyandry. We report here the breeding-season schedule of a dotterel population in southern Norway and discuss the patterns in relation to the mating system.

STUDY AREA AND METHODS

The study area was a 6-km^2, north-facing, sloping plot (1,170–1,350 m) in the middle alpine region at Steinbuheii (60°23'N, 07°38'E), Hardangervidda, southern Norway. The vegetation is a mosaic of meadows and small bogs, the former characterized by grasses (*Anthoxanthum odoratum, Deschampsia flexuosa, Nardus stricta*), *Carex* spp., *Juncus trifidus, Empetrum hermaphroditum* and lichens, and the latter by *Eriophorum* spp. The monthly mean temperatures for June and July are 4.7 and 8.0°C, respectively. Total snow-cover usually extends from October until the beginning of June. Even in the middle of the summer, however, snow-fall is not uncommon, and cold spells with temperatures below 0°C may last for several days. In the middle of the summer there is only a 3.5-h dark period. [For more information on climate, see Skartvit et al. (1975).] The most common mammalian and avian predators in the area are red foxes (*Vulpes vulpes*), Common Ravens (*Corvus corax*), and Mew Gulls (*Larus canus*) (Byrkjedal 1980a), all potential predators on dotterel adults, chicks, and eggs.

The fieldwork was carried out from mid-May to early August 1978–1981. Dotterel are abundant on Hardangervidda (Kålås and Byrkjedal 1981), and each year 11–28 nests and/or broods were found on the study plot (Fig. 1). The breeding season was divided into the following periods: (1) Arrival—from arrival on the breeding ground until the birds disperse from the hill-tops to the area where the nests are placed; (2) Pre-laying—from the time a pair is present on the nesting ground until the first egg is laid (also including new matings by males from destroyed nests); (3) Egg laying—from the time the first egg is laid until the clutch is completed; and (4) Incubation—from the time the clutch is completed until the last chick is hatched.

Censuses of all the dotterel in the study area were done in May and early June, before and just after dispersal downhill to the breeding sites in 1979 and 1980. During subsequent daily fieldwork, however, all observations of dotterel were recorded and mapped. We found nests by walking at random and flushing birds from their nests or by watching birds return to their nests. The entire area was searched many times each season. Snow-melting was monitored by photographing the area from a fixed point, usually once a week.

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We determined the dates of egg laying by exact observations, by back-dating from hatching date (using a 25-day incubation period), or from chick weights ($y = 3.2x + 10$, where y = age in days, and x = chick weight in grams; based on 32 weighings of 14 chicks). Eggs that sank during a water test were regarded as newly laid.

Captured birds were weighed and measured. Their physical condition was calculated by using the formula:

$$\text{Condition} = [\text{Body weight (g)}/\text{Wing length (mm)} \times 100].$$

We also recorded the prebasic molt of birds captured for color-banding. Only the primaries were considered, and they were scored according to Snow (1967), i.e. each feather was given a score from 0 (old) to 5 (new, fully grown). In addition, newly molted primaries found in the study area were collected. When estimating the molt score of the birds that had molted these feathers, we identified the feather found and gave it a score of 1, the proximate primary next to this a score of 3, and any other proximate primaries a score of 5 (cf. Blanken et al. 1981).

Color-banding started in 1979, and the adults were marked individually (70% of the males and 20% of the females each year), whereas chicks were given only year codes. Most adults were captured on their nests; only a few were mist-netted before egg laying. In 1981, 3 males and 1 female were radio-marked and followed for a total of 19⅓ bird-days.

The flight display of the females ("winnow-glide" display flight; Nethersole-Thompson 1973) is characterized by quick rhythmic sequences of the basic *peep* call. The frequency of female display flight was expressed as the number of females displaying per hour of observation, including any displaying female recorded, not only those under observation during the activity-observation bouts. Thus, the data consist of the number of flights performed by an unknown number of females. Only those days with more than 5 h of observations were included.

The time spent feeding was calculated from a combination of "focal animal sampling" and "instantaneous sampling" (Altman 1974). The activities of a male and female were recorded simultaneously once each minute. Only sampling periods when the birds were watched continuously for more than 30 min during the arrival period and 60 min during the prelaying periods were used. Observations were made at different times of the day and on different pairs. Sampling of feeding activity was never undertaken during rainy or foggy weather.

RESULTS

NESTING CHRONOLOGY

Arrival.—The birds arrive in the study area in mid-May. In 1980, the birds were first observed on 17 May; in 1981, the birds had arrived on 18 May but were not present on 13 May. Data from the post-dispersal censuses in 1979 and 1980 (8 males/11 females and 4 males/5 females, respectively) indicate that initially there is no skewed sex-ratio in favor of males.

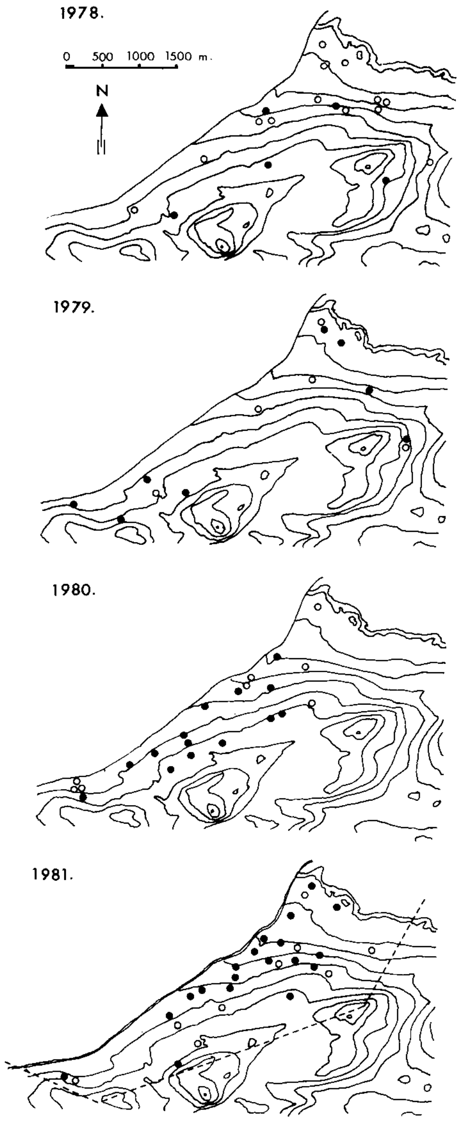

Fig. 1. Spacing of dotterel nests and different broods in four breeding seasons at Hardangervidda study area. Height contours in 20-m intervals. (● = nest found; ○ = chicks found but nest site unknown; dashed line = border of study area.)

Dispersal onto nesting grounds and agonistic behavior.—When the birds arrive, the study area

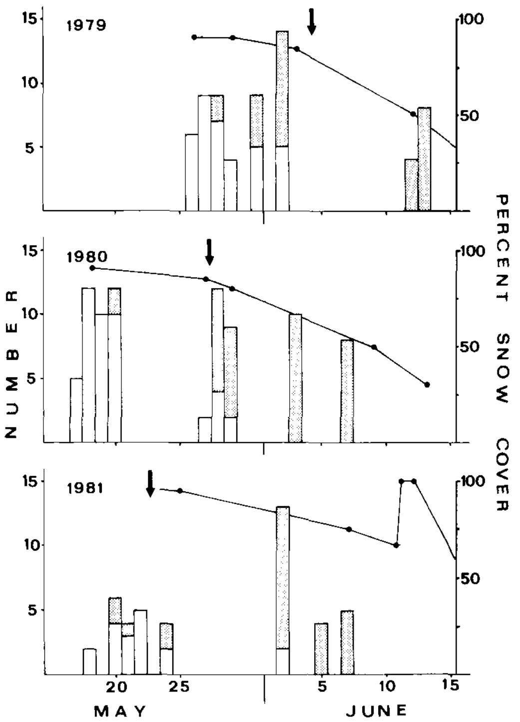

Fig. 2. Dispersal of birds from hill tops onto nesting ground in different years. (Open = observations on hill tops; shaded = observations on nesting ground.) Solid line illustrates snow cover; arrows indicate start of egg laying of the first nest in the study area.

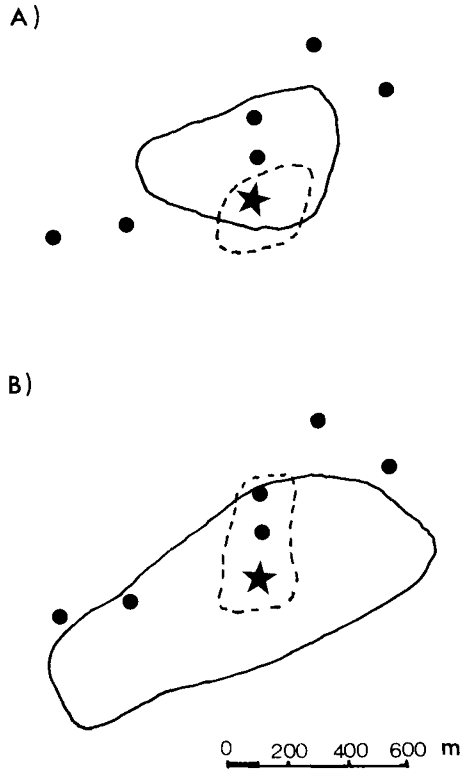

Fig. 3. Home-range of pair 3/81 at different times of the season in 1981 (from observations of the color-banded male and the radio-tracked and color-banded female). (Star = nest 3/81, dots = other dotterel nests.) (A) Solid line = pre-laying home range of male and female; dashed line = egg-laying home range of male and female. (B) Solid line = home range of the female during incubation; dashed line = home range of the male during incubation.

is nearly totally covered by snow. From the very first day of observation, the birds are paired and spend most of the time feeding on snow-free patches on higher ground. As soon as snow-free areas emerge on the slopes, the pairs disperse downhill and start their pre-laying activities. Time spent on the hilltops depends on the progression of snow-melting (Fig. 2). When the snow-cover is about 75%, all birds have dispersed onto their nesting grounds.

The dotterel does not defend any defined area during the pre-laying period. During 75 h of scheduled observation of six different pairs, we never saw flight displays that could be interpreted as territorial demarcation. In 32 cases, one pair encountered other pairs, which came as close as about 10 m before aggression was elicted. These encounters occurred more or less randomly, not along specific territory boundaries. During the pre-laying period, the home range of pair 3/81 was 0.22 km^2, and, as can be seen from Fig. 3, at least two other nests were located in the pre-laying home range of this pair after they had completed their own nests. Each of these nests was used by a different female. The nest-spacing mechanisms seem rather weak, as the distances between nests may be short (Fig. 1). Most of these close nests are known to be used by different females. During egg laying, the home range (0.06 km^2) of pair 3/81 was smaller than during the pre-laying period, and the birds usually stayed within a few hundred meters of the nest (Fig. 3). At this nest, the female took part in incubation, but she had a much larger home range than the

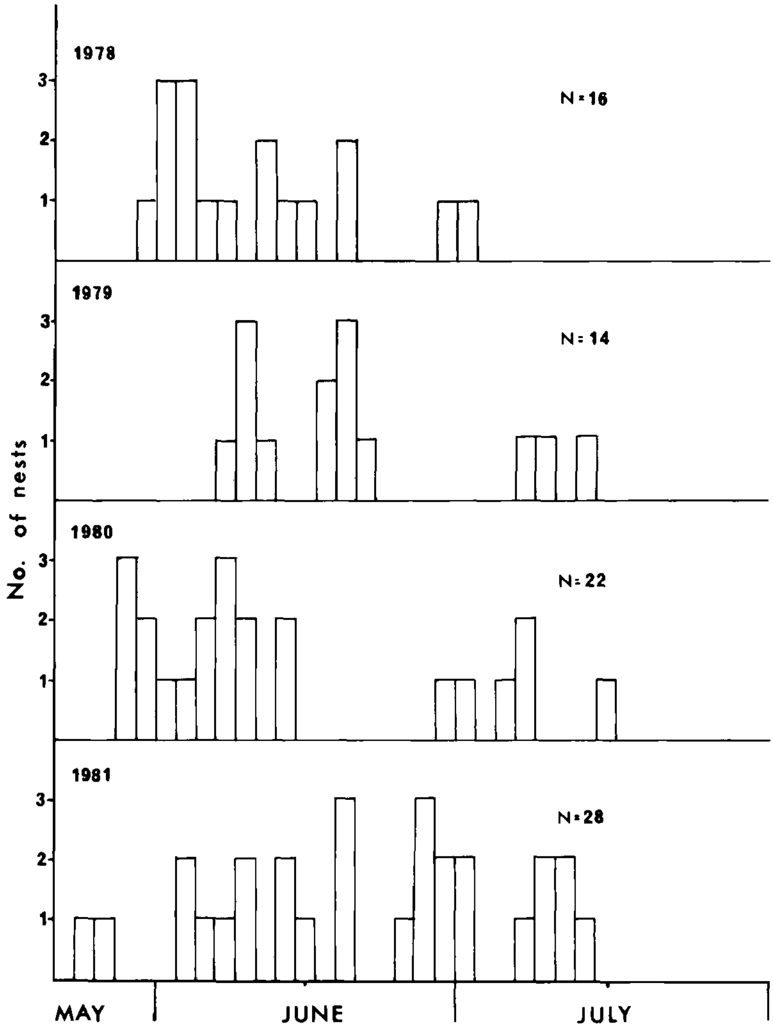

Fig. 4. Completed clutches of dotterel (2-day intervals) in different years.

male did during the incubation period (0.57 km^2 and 0.09 km^2, respectively; Fig. 3).

Egg laying.—Egg laying starts only a few days after the birds have dispersed from the hill tops (Fig. 2). The length of the egg-laying season varies from year to year (Fig. 4) but usually starts the last week of May. The latest clutches are finished in mid-July. During egg laying, the birds continue to copulate. All but one nest contained three eggs ($n = 52$). The average interval recorded between the laying of individual eggs was 30.8 h ± 2.1 (SD) ($n = 7$).

Little information on the number of nests produced per female each year was obtained. Dissection of the ovaries of two females (following the procedure given by Parmelee and Payne 1973) indicated that each had laid at least two clutches. If the first nest is destroyed, the male will accept a second one. In two cases, the distance between the first and the second clutch of the same incubating male was 250 and 400 m. Color-banded males sat on five other nests, which were eventually robbed through predation. The predation took place after mid-July, so new nestings could not be expected in these cases, and the males were not seen again. In

TABLE 1. Percentage of nests in which the male dotterel incubated alone and in which both male and female incubated.

	Time of egg laying		
	Before 15 June	15–30 June	After 30 June
Number of nests	7	10	10
Percentage of nests in which the male incubated alone	100	60	50
Percentage of nests in which both male and female incubated	0	40	50

one case a male accepted a new clutch of eggs after the loss of his 4-day-old chicks.

Incubation.—The incubation period is 24.6 ± 0.6 (SD) days ($n = 6$). The male starts incubating during egg laying. We observed no sexual behavior on the part of incubating males after egg laying at their nests was finished. In early nests, the male is in sole charge of the incubation, but, in nests started later than mid-June, the female frequently assists (Table 1). Females were never found incubating alone.

Female flight displays and excess female groups.—The occurrence of flight displays in the study area varied from day to day, but there was a distinct seasonal pattern (Fig. 5). We observed some birds displaying just after their arrival, but there was a drastic increase after completion of the first nests. The frequency then fluctuated at a high level until it dropped in early July. Of 17 occasions upon which the displaying bird was seen well enough for sexing, all were females. Display flights were long, often over several kilometers, and they seldom ended at the starting point (Fig. 6). In fact, none of the color-banded females was seen in the study area after egg laying, except four that were incubating late clutches (see below). Presumably the display flights take the females over large distances.

Groups with excess females (most often 1 pair + 1–3 females) occurred through the egg-laying season, especially in the latter part, and there was an increase in the relative number of single females toward the last week in June (Fig. 7). In 13 of the 16 observed groups with excess females, aggression between the group members was seen. The six pairs held under systematic observation were joined by a female on seven occasions, all of which resulted in aggression from both pair members toward the newcomer.

Female flocks.—The females start flocking at the beginning of July. At first, the flocks con-

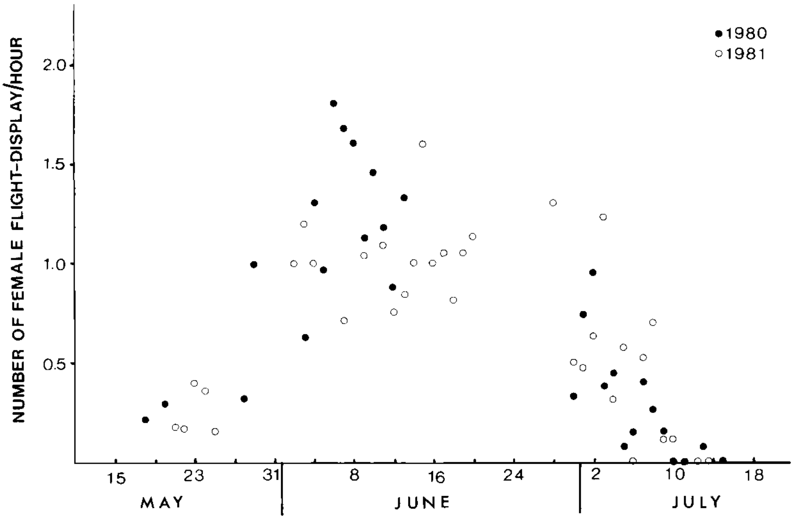

Fig. 5. Intensity of female flight-display during the breeding season.

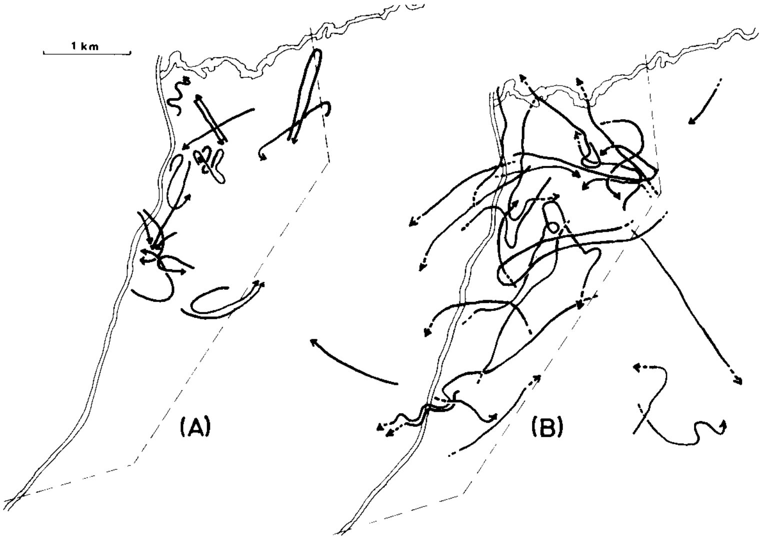

Fig. 6. Flight paths (arrows) of displaying dotterels within and adjacent to the study area as far as the bird could be followed with 8 × 30 binoculars. (A) Start and finish of the flight seen; (B) start or finish not seen (dotted end of arrow indicates which).

sist of only a few females, but, by mid-July, they may contain 30–40 individuals. At the end of July, males and fledged young also join the flocks. Incubating males have never been observed in these flocks, but all four color-banded incubating females were seen in the female flocks when they were off the nest.

Hatching and fledging.—The time lapse in hatching between the first and the third chick was found to be 24.3 h ± 5.5 (SD) ($n = 11$). Females were never observed attending chicks. Young from two clutches were observed flying at the ages of 24 and 26 days, respectively.

Molt.—The molt of primaries starts at the beginning of July (Fig. 8). There are no significant differences in the molt progression between males attending chicks and incubating males. We have no data on the molting of the outermost primaries, but Fig. 8 suggests that the molt of primaries is finished before the birds' departure from the breeding grounds.

FEEDING ACTIVITY

During the first days after arrival, nearly 90% of the daylight time is spent feeding (Table 2). There is a significant decrease in the time spent feeding between the arrival and pre-laying periods (χ^2 test, $P < 0.001$) but no significant difference in time spent feeding between the early pre-laying (I; early June) and late pre-laying (II; early July) periods. This does not indicate a food shortage during the egg-laying season.

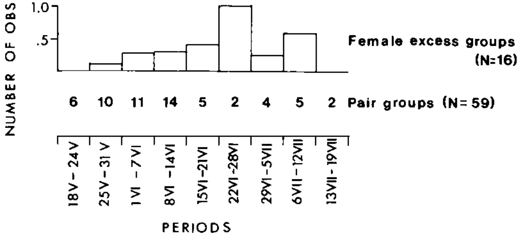

Fig. 7. Seasonal distribution of single birds and groups in the study area in relation to the number of observed pair groups. "Pair groups" consisted of more than one pair in only four cases. Birds having nest or young and postbreeding female flocks are not included.

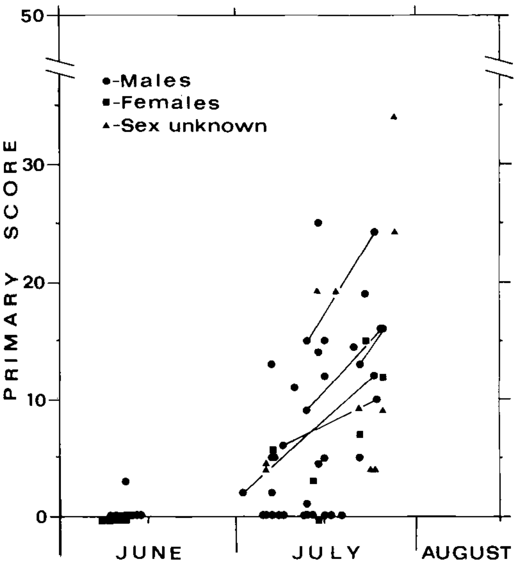

Fig. 8. Molt of primaries of dotterel. (Lines join the same individuals.)

The sexes did not differ significantly in the proportion of time spent feeding in any of the three periods.

Physical Condition of Incubating Males

There was a significant decrease in the ratio of wing length to weight (a measure of physical condition) of incubating males during the incubation period ($r = -0.50$, $P < 0.001$), but the decrease was slight (Fig. 9). From the regression, the average decrease during the whole incubation period was estimated to be 8.8%. Birds weighed both early and late in the incubation period had a daily weight decrease of 0.39 g ± 0.32 (SD) ($n = 6$), which means a total weight decrease of 6.9% through the incubation period. Thus, incubation does not imply a serious physical taxation upon the males.

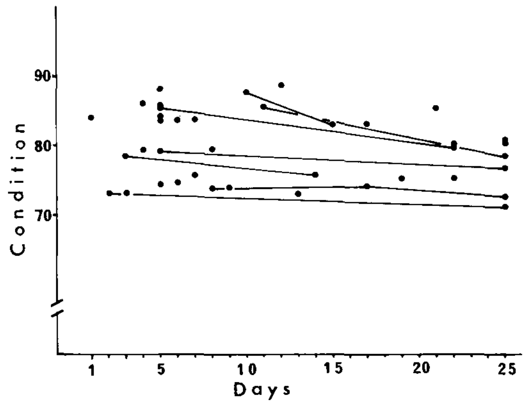

Fig. 9. Variation in the physical condition [(wing length/weight) × 100] of dotterel males during the incubation period. (Lines join the same individuals.)

Predation

Predation on adult birds was never recorded. During incubation, however, there was severe but highly variable predation on eggs. Table 3 indicates that the predation on nests (calculated according to Mayfield 1975) varied between 22% and 67% during the years 1979–1981, with an average of 48%. Predation on chicks occurs but could not be quantified.

Discussion

The breeding schedule of the dotterel on Hardangervidda is schematically summarized

Table 2. Percentage of daylight time (0400–2300) spent feeding by dotterel on Hardangervidda.

Period	Sex	Number of sampling periods	Number of different pairs	χ^2 test of homogeneity between sampling periods	Total sample size (min)	Percentage of time feeding
Arrival	♂	20	5	$\chi^2_{19} = 4.89$	942	89.4
(17–20 May)	♀	20	5	$\chi^2_{19} = 5.67$	942	88.4
Pre-laying (I)	♂	9	4	$\chi^2_{8} = 9.77$	731	58.7
(29 May–6 June)	♀	9	4	$\chi^2_{8} = 11.55$	770	57.1
Pre-laying (II)	♂	6	3	$\chi^2_{5} = 9.19$	382	53.7
(2–6 July)	♀	6	3	$\chi^2_{5} = 1.61$	363	54.5

TABLE 3. Predation on dotterel nests in different years on Hardangervidda.

Year	1979	1980	1981
Number of nests	7	12	19
Number destroyed	2	8	3
Percentage predation	29	67	16
Percentage predation estimated according to Mayfield (1975)	56	67	22

in Fig. 10. The most striking difference from the other shorebird species in the area [Greater Golden-Plover (*Pluvialis apricaria*), Dunlin (*Calidris alpina*), Purple Sandpiper (*Calidris maritima*), Temminck's Stint (*Calidris temminckii*)] is that the egg-laying season is 30% longer in dotterel (Byrkjedal 1978, Breiehagen pers. comm., pers. obs.). From indirect evidence, we find this most likely to be explained by a high incidence of polyandry in this dotterel population. Cases of polyandry have previously been documented in other dotterel populations (Franke 1953, Pulliainen 1971, Nethersole-Thompson 1973), but the species was regarded as monogamous by Jenni (1974) and Wittenberger (1979).

There are several aspects of dotterel that strongly favor polyandry. (1) The females are emancipated once the eggs are laid, and the males take on all parental duties (the few cases of females sharing incubation with males are commented upon below). (2) Unaided incubation seems to have a minor influence on the males' physical condition. (3) Food [mainly larvae and adult Tipulidae, Coleoptera, and *Mitopus morio* (Byrkjedal unpubl. data)] is available over a large part of the the summer (Hofsvang 1974, Byrkjedal 1980b), thus facilitating a long breeding season. (4) Males are available throughout the season because of nest predation, which may be severe (on average 48%). (5) Eggs are relatively small, and a full clutch consists of only three eggs, so the cost of egg production should be relatively low. The indications that polyandry does occur frequently are summarized as follows.

(a) The females apparently seek new mates during a large part of the season by the display flights. These flights are not considered to be territorial flights, because they appear not to be confined to specific areas. Rather, the females seem to make advertisement flights over large areas, in a similar manner as the male Eurasian Woodcock (*Scolopax rusticola*) (Hirons 1980). The lack of subsequent sightings of color-banded females also indicates a low within-season site tenacity. Moreover, the flights start to appear in the population after the completion of the first nests, not in connection with the earlier dispersal downhill to the nesting sites, as would be expected if the flights were territorial demarcations. Observed encounters between displaying and other birds have only been seen at some distance, but, instead of resulting in a chase, the encounters ended with both birds soon alighting together. These cases looked more like encounters between displaying females and unattached males than like those between territorial opponents. Because the flight starts after the earliest clutches in the popula-

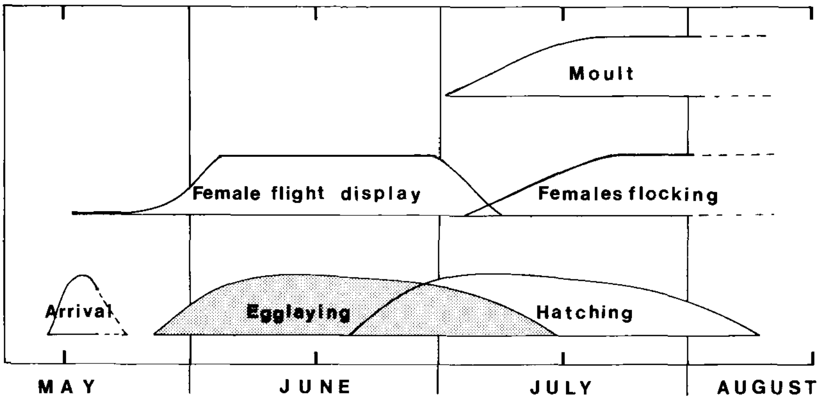

Fig. 10. Summary of the breeding schedule of the dotterel at Hardangervidda.

tion have been completed, it is likely that at least some of the displaying females have already laid a clutch. Considering the low site tenacity and the high frequency of displays it is likely that many different females are involved.

(b) As female flocks do not start to form before the end of the egg-laying season, it is likely that most of the females are involved in seeking mates and laying eggs over most of the egg-laying season.

(c) That there is frequent aggression between members of groups with excess females strongly indicates that competition between females for males occurs throughout the season and seems, indeed, to increase toward the end of the season in accordance with a decreasing number of available males [cf. Byrkjedal (1980a) on seasonality of nest predation] and a possible increase in the number of emancipated females.

(d) We have shown that females lay two clutches in one season and that males accept new clutches after nest predation. These may, admittedly, be cases of replacement clutches (i.e. a second nesting by the same pair). As the emancipation of females follows immediately after clutch completion, however, and as the emancipated females seem to roam far and wide, we find it unlikely that they come into contact with their former mates for a second (replacement) clutch.

The system outlined above is in contrast to that seen in Scotland. It seems that female advertisement flights are less frequent there than on Hardangervidda, and monogamy is considered to be the rule (Nethersole-Thompson 1973). In Scotland the dotterel is also reported to be territorial; not only are there pre-laying hostilities, but incubating males drive off other dotterels from the vicinity around the nest, and the nests are usually spaced at least 200–250 m apart (Nethersole-Thompson 1973). On Hardangervidda, we have never observed such behavior by incubating dotterel males. In fact, on two occasions, we saw an incubating dotterel (two different nests) squat flat in the presence of other dotterels a few meters from the nest. This was also seen by Wilkie (1981) at a nest on Hardangervidda. Probably in accordance with the lack of territories, spacing of nests on Hardangervidda seems to be less developed than in Scotland. The pre-laying fights seen on Hardangervidda are not confined to specific territory boundaries, and they are elicited only at short distances. Thus, we consider them as having to do with mate guarding rather than territorial defense.

Female participation in incubation has also been reported by Hildén (1966), Pulliainen (1970), and Nethersole-Thompson (1973). The occurrence of this phenomenon only in the late clutches indicates that, as the prospects for further matings and successfully raising broods decrease late in the season, females may increase investments in late clutches by taking part in the incubation instead of continuing to seek mates. Female participation in brood rearing has been observed once, a case in which a male and a female were seen to divide a brood between them (D.B.A. and P. S. Thompson in Cramp and Simmons 1983). Several instances of females showing up near males with chicks have been interpreted as the returning of females to their mates after the chicks have hatched (Franke 1953, Rittinghaus 1962, Pulliainen 1970, Nethersole-Thompson 1973). Such females were often met with aggression from males (Cramp and Simmons 1983), and we rather assume they were strange females prospecting for mates.

Apparently the breeding system of the dotterel may differ between populations. A comparative study of its breeding ecology in Norway and Scotland, involving large-scale color banding, would hold great promise.

ACKNOWLEDGMENTS

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