

Incubation behaviour of the Dotterel *Charadrius morinellus* in Finland

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Abstract. Incubation behaviour of the Dotterel *Charadrius morinellus* was studied in Finnish Lapland (67°44'N, 29°37'E) particularly in 1969 and 1971 during 75.6 days. The total amount of absences was approx. 19.0% of the time. When both the male and the female incubated, the nest was occupied for about 95% of the time; in nests with only the male, this figure ranged between 70 and 90%. In one unsuccessful nest, this was below 65%. The duration of periods off were on average 5.3 min. in the nest incubated by two birds, between 8.7 and 34.6 min. in the rest. In the morning the ground temperature has to exceed 8°C on average before the birds are prepared to spend 20% of their time off eggs. The mean length of periods off decreased significantly with advancing incubation, but not the total time off the eggs. Our results differed in many respects from those observed in south Norway (e.g. daily rhythm and the lengths of periods off). This is probably best explained by a lower availability of food and smaller predation pressure in our study area. **Key-words:** Constancy of incubation, male/female incubation, daily rhythm

Introduction

The incubation behaviour of the Dotterel *Charadrius morinellus* has been generally described by e.g. Nethersole-Thompson (1973), Glutz von Blotzheim, Bauer and Bezzel (1975), and Cramp and Simmons (1983). Quantitative data were provided by Wilkie (1981) and Kälås (1986). At the Värriö Subarctic Research Station (67°44'N, 29°37'E) breeding biology of the Dotterel has been studied since 1968 (Pulliainen 1970, Pulliainen and Saari 1992a). Intensive nest watches were carried out mainly in 1969-1971. Part of this material has already been treated (Pulliainen and Saari, manuscript). In this paper we present the study on incubation constancy at different nests relating it to the stage of incubation and ambient temperature. As the incubation period, we consider the time from the completion of the clutch until the chicks left the nest. In our study area, the sun is continually above the horizon during the Dotterel breeding season, and

in this respect, our results are supposed to differ from those published elsewhere. Predation pressure is low in our study area (Pulliainen and Saari 1992a) and the physical condition of breeding Dotterel is poor (Pulliainen and Saari 1992b), which both may be reflected in the incubation constancy and diurnal rhythm (Kälås 1986).

Material and methods

In 1969, five nests were watched continuously from a hide for a variable amount of time (see Pulliainen 1970).

Nest I/69: Between 26 June and 5 July, intensive nest watches for 10,738 min. Hatching started on 5 July. Male mass was 110 g on 15 June, and 100 g on 3 July. Three chicks hatched.

Nest II/69: Between 19 and 27 June, intensive nest watches for 8,500 min. Male mass was 118.5 g on 15 June, and 100 g on 3 July. Two chicks hatched on 8 July.

Nest III/69: Between 26 June and 5 July, nest watches for 10,420 min. Male mass was 101 g on 15 June, and 85 g on 3 July. Three chicks hatched on 5 July.

Nest IV/69: Watched for 1,020 min. on 27 June. Male mass was 105 g on 26 June, and 102 g on 3 July. Three chicks hatched on 11 July.

Nest V/69: Watched for 3,297 min. between 3 and 6 July. Three chicks hatched on 6 July. Both parents incubated. Male mass was 132 g on 2 July, female mass was 120 g on 3 July.

In 1969, the nest watches were concentrated between about 06 and 21 hrs and thus the longer absences during the "day" are overrepresented. Therefore we calculated the percentage of absence for both the whole observation period and the hourly mean of absences, which better illustrates the intensity of incubation. In four of these nests, only the male incubated, in one, both sexes shared the incubation duties. The absences were assigned to the hour when the incubating bird left the nest, and thus the absences sometimes extended to the next hour(s), too.

In 1970 three nests were watched intensively during the incubation period. The results have been treated elsewhere (Pulliainen and Saari, manuscript)

Nest	Obs. min.	Min. off	%	Daily X± SD	N	Corr. X	Periods off min.	
							X	(N)
I/69	10 738	2 973	27.7	28.4± 6.3	(10)	21.8	17.1	(174)
II/69	8 500	3 052	35.9	34.8±22.3	(9)	30.4	23.3	(131)
III/69	10 390	2 791	26.9	27.7± 12.8	(10)	22.1	10.7	(260)
IV/69	1 020	373	36.6	36.6± 0	(1)	-	8.7	(43)
V/69	3 397	237	7.0	7.2± 5.3	(4)	(4.5)	5.3	(45)
I/71	36 000	5 380	14.9	14.9± 7.3	(25)	14.9	12.5	(432)
II/71	37 440	4 981	13.3	13.3± 5.3	(26)	13.3	12.3	(401)
I/88	1 440	519	36.0	36.0± 0	(1)	36.0	34.6	(15)
Total	108 925	20 657	19.0					

Table 1. Incubation constancy at eight Dotterel nests at Värriö. The number of minutes of intensive observations, the number of minutes off the nest during these, the percentage of time off the nest (overall mean, daily mean and corrected daily mean) and the duration of the periods off are shown. For details see text.

and are only used here for comparison.

In 1971 two nests were watched continuously for the entire incubation period. Nest I/71 for 36,000 min. between 6 and 30 June (the chicks left the nest on 1 July) and nest II/71 for 37,440 min. between 5 June 12.00 hrs and 1 July 12.00 hrs (when the chicks had left the nest). In addition the nest III/71 was visited 279 times between 6 and 30 June. This material is included since the male was the same as in the nest I/69 and I/70 and thus we were able to compare the behaviour of the same male in different seasons. The male mass was 138 g on 4 June at nest I/71 and 140 g on 5 June at nest II/71. Three chicks hatched in both nests.

In 1988, one nest later deserted was watched continuously for 24 h beginning on 21 July at 07 hrs. Several other nests were also visited numerous times but only if the results differ markedly from the nests studied intensively these are mentioned.

During the watches at several nests, the meteorological data were collected at 15 min. intervals. The most important data was the ground temperature (in the shade if possible; in bright sunshine sometimes impossible to obtain without disturbing the bird), wind speed and direction, cloudiness and sometimes also humidity. Other important weather data were also recorded: showers of rain/sleet/snow, depth of snow on the ground etc. Fig. 1 shows the mean hourly temperatures (at full hours) at the nest I/71 between 5 June at 16.00 hrs and 1 July at 11.00 hrs. When relating the incubation constancy to the mean daily temperature the data for the period between 6 and 30 June was used. The time referred to in this study is always Finnish solar time.

This study concentrated on documenting the number and lengths of the periods off but all other behaviour was also recorded. Since this behaviour was not studied according to any standardized formula these results are semi-quantitative (different observers probably recording the various behavioural traits somewhat differently). Consequently this part of the study is mostly descriptive, but we try to describe the behaviour we consider typical. Spearman rank correlations were used to test the dependencies throughout the study.

Results

Constancy of incubation

The constancy of incubation (= attentiveness) at eight nests watched continuously for a varying amount of time is shown in Table 1. These nests were watched intensively during a total of 108,925 min. (i.e. about 75.6 days). The total amount of absences was 20,657 min., i.e. 19.0% of the time. Owing to the way some of the data were collected (nest watches concentrated to the "day" in 1969), this figure is a slight overestimation. The corrected means for three nests in 1969 were 21.8-30.4%, whereas the daily means were higher, i.e. 27.7-34.8%. The corrected mean was calculated as the mean of the hourly means, thus overcoming the bias introduced by an uneven sampling during the day. There seemed to be great annual variations in the constancy of incubation. In 1969, the absences were great, exceeding 30% in the uncorrected sample, whereas it was below 15% in the 1971 nests (Table 1). When both parents incubated the absences were few, only 7.2% (nest V/69). The corrected mean for this nest was 4.5% assuming no absences during the night hours (00-06; a reasonable assumption since the nest was continuously occupied from 20 to 07 hrs during the hours the nest was watched, Table 2). The mean length of absences also varied considerably at different nests: between 8.7 and 34.6 min. in nests with only the male incubating and 5.3 min. in the nest with both the parents incubating.

At some of the nests a few long periods off were recorded. These are shown in the tabulation below.

Nest Longest periods off

I/69	79, 82, 141, and 202 min.
II/69	102, at least 120, 240, 418, and 627 min.
III/69	184, and 265 min.
I/71	125, 138, 142, 148, 161, 178, 180 and 190 min.
II/72	82, 85, 102, 127, 140, 143, 169, and 173 min.
I/88	at least 162, and 198 min.

These periods usually seemed to occur during the first part of incubation (cf. Table 3). At some other nests,

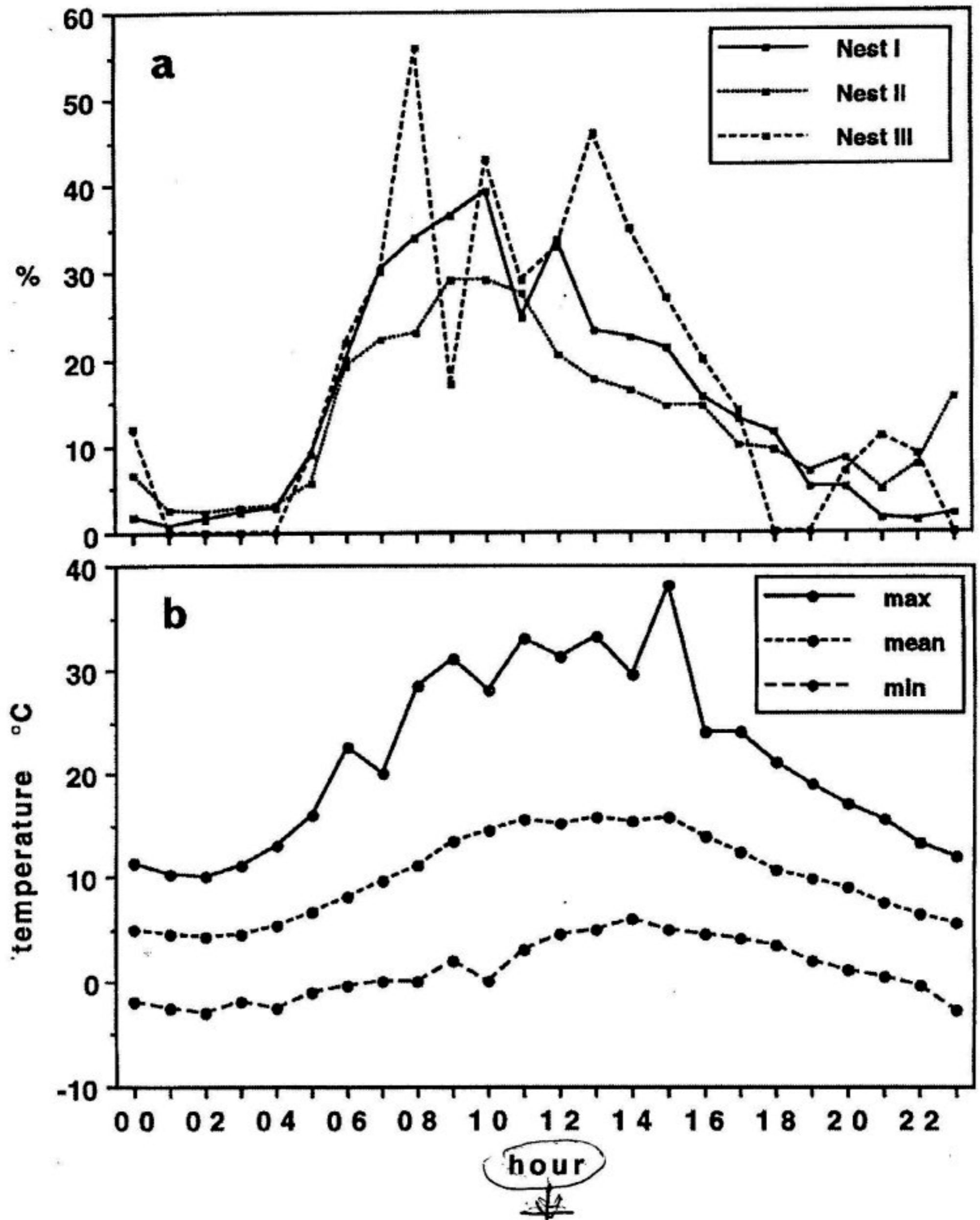


Fig. 1. **a.** Hourly absences of the male Dotterel in three nests in 1971 (% of time in nest I/71 and II/71, % of visits in nest III/71). The nest I/71 was observed for 1,500 min. each hour, the nest II/71 for 1,560 min. The minutes of absence are given correctly for each hour, i.e. if a period off extended to the next hour(s) the period was divided between these. The nest III/71 was visited 279 times during the incubation period. **b.** Hourly maximum, mean and minimum temperatures (°C, at full hours) at nest I/71 between 5 June 16 hrs and 1 July 11 hrs. N=26 measurements, except between 12 and 15 hrs when n=25.

Hour	Nest I/69		Nest II/69		Nest III/69		Nest IV/69		Nest V/69	
00	1.0±	0 (1)	6.0±	0 (1)	11.0±	0 (1)
01	0		0		6.0±	0 (1)
02	0		0		4.0±	0 (1)
03	0		0		4.0±	1.4 (2)
04	0		5.0±	0 (1)	8.0±	0 (1)
05	8.2±	3.8 (5)	7.0±	4.5 (4)	7.0±	3.5 (3)
06	19.3±	15.2 (6)	92.8±	162.5 (6)	8.0±	2.9 (9)	0	0	0	0
07	18.3±	23.2 (10)	113.9±	222.8 (8)	10.4±	7.3 (19)	3.5±	2.1 (2)	5.7±	2.1 (3)
08	14.9±	5.8 (16)	51.4±	54.8 (5)	32.3±	70.3 (13)	4.7±	2.3 (3)	9.5±	0.7 (2)
09	37.0±	55.7 (12)	25.3±	20.8 (3)	10.6±	4.9 (16)	4.7±	4.6 (2)	3.3±	1.9 (4)
10	27.8±	35.1 (13)	18.5±	10.2 (4)	9.9±	7.8 (21)	5.0±	2.8 (4)	4.0±	4.2 (2)
11	17.9±	8.3 (11)	14.5±	12.3 (6)	12.4±	7.0 (17)	11.0±	7.9 (4)	3.0±	0 (1)
12	15.0±	7.0 (15)	11.2±	7.4 (9)	11.0±	9.5 (18)	9.0±	4.4 (3)	6.5±	4.2 (6)
13	18.4±	7.4 (16)	17.5±	18.7 (8)	11.3±	6.3 (20)	12.0±	1.4 (2)	8.0±	4.2 (5)
14	12.3±	9.0 (17)	14.1±	10.0 (12)	16.3±	36.8 (23)	10.0±	7.8 (3)	6.8±	3.5 (4)
15	18.2±	12.4 (11)	13.6±	5.9 (8)	8.9±	7.0 (15)	9.7±	0.6 (3)	4.4±	4.7 (7)
16	12.6±	6.9 (16)	13.1±	6.5 (12)	9.3±	9.6 (18)	10.0±	1.7 (3)	5.5±	0.7 (2)
17	11.4±	5.2 (9)	10.9±	5.2 (10)	7.2±	2.2 (15)	10.0±	0 (2)	3.8±	0.8 (5)
18	10.2±	4.3 (5)	9.7±	3.7 (11)	4.4±	2.4 (20)	9.0±	4.2 (9)	2.0±	1.7 (3)
19	11.0±	5.7 (5)	7.0±	2.8 (9)	5.3±	1.3 (9)	5.8±	3.9 (4)	4.0±	0 (1)
20	10.3±	0.6 (3)	7.8±	2.3 (5)	5.0±	2.4 (6)	21.0±	7.1 (2)	0	0
21	7.3±	2.3 (3)	6.5±	0.6 (4)	6.0±	3.3 (6)	13.5±	10.6 (2)	0	0
22	0		6.8±	1.0 (4)	9.8±	9.0 (4)	4.0±	0 (1)	0	0
23	0		4.0±	0 (1)	4.0±	1.4 (2)	0	0

Table 2. Mean length of periods off the nest at different clutches in 1969. Note that the absence was assigned to the hour it started: thus some hours have long mean periods off.

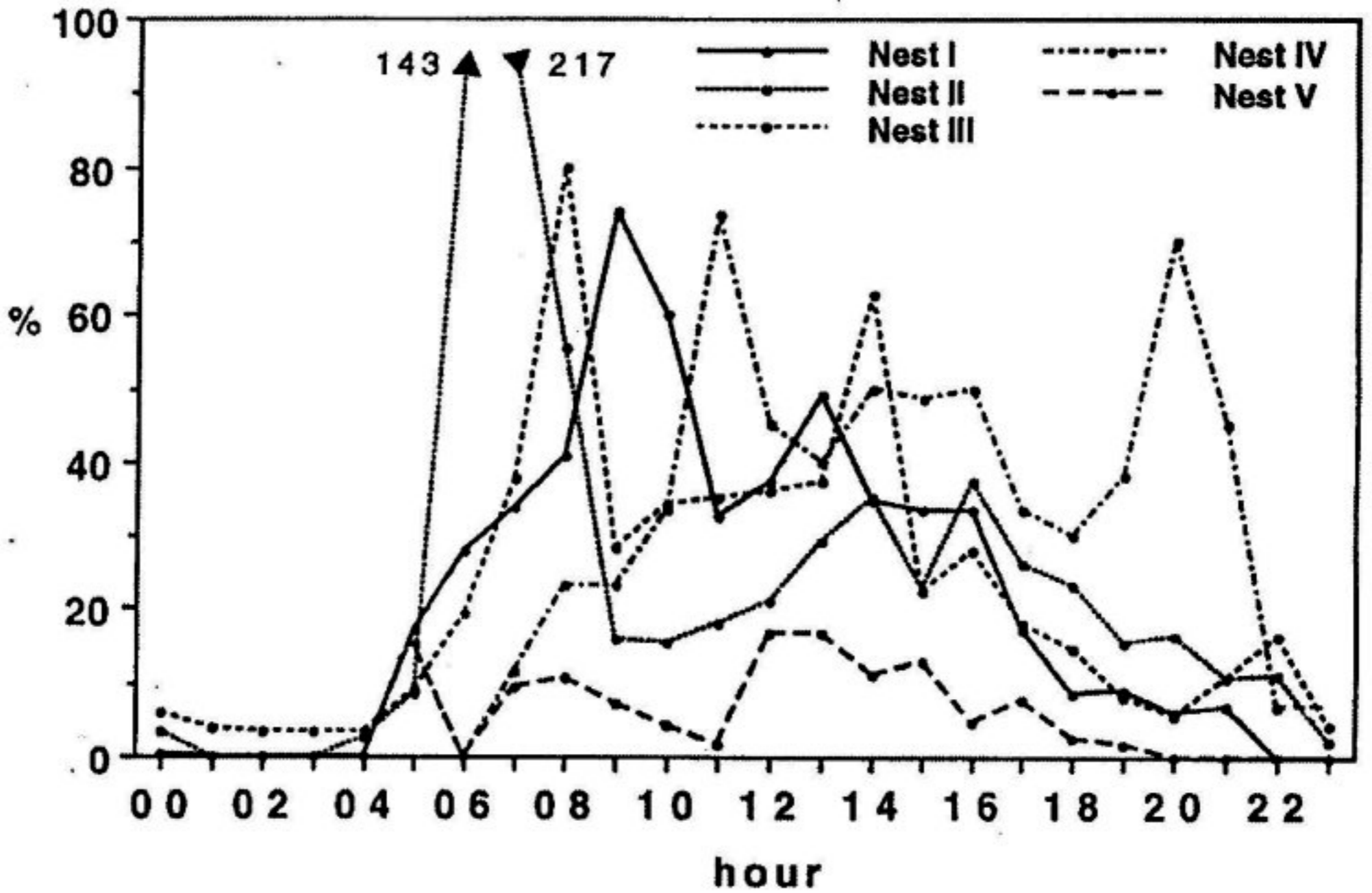


Fig. 2. The time off (in %) per each hour of the clutches in 1969. As the periods off were assigned to the hour they commenced some hours with starts of very long periods off have a percentage exceeding 100.

Date	Nest I/71	Nest II/71	Mean temperature at Nest I/71 (°C)
5.VI		7.7± 5.0 (3)	
6.VI	9.8± 7.5 (5)	63.8±52.1 (5)	4.3
7.VI	22.9±37.6 (10)	15.3±14.5 (12)	4.7
8.VI	32.3±28.0 (3)	12.7± 9.3 (6)	1.9
9.VI	22.6±36.1 (5)	29.9±40.5 (8)	2.5
10.VI	50.0±58.3 (5)	67.3±88.3 (3)	4.0
11.VI	29.1±57.4 (10)	24.4±41.1 (10)	8.4
12.VI	24.9±48.4 (10)	34.9±52.6 (11)	9.5
13.VI	26.5±47.4 (13)	24.1±32.7 (10)	11.5
14.VI	12.0± 8.0 (18)	11.0± 8.3 (12)	13.0
15.VI	19.0±28.5 (21)	12.5± 4.6 (21)	15.9
16.VI	24.5±47.0 (13)	14.3±12.5 (24)	14.4
17.VI	15.6± 8.6 (22)	8.7± 3.6 (22)	17.9
18.VI	15.4±26.5 (27)	11.3± 5.7 (22)	17.8
19.VI	9.0± 4.9 (26)	8.4± 5.0 (19)	18.7
20.VI	9.7± 6.0 (24)	7.9± 4.9 (23)	19.6
21.VI	8.6± 5.3 (25)	9.0± 5.5 (21)	16.0
22.VI	6.8± 2.6 (12)	6.1± 3.5 (13)	6.4
23.VI	9.5± 4.7 (15)	8.7± 4.4 (15)	4.4
24.VI	8.5± 3.4 (15)	8.1± 2.3 (17)	5.1
25.VI	10.9± 5.6 (22)	7.3± 2.2 (18)	5.1
26.VI	6.2± 2.6 (9)	11.0± 1.5 (7)	3.4
27.VI	10.5± 3.2 (23)	9.3± 3.0 (22)	6.1
28.VI	8.7± 3.4 (30)	8.8± 3.3 (22)	12.9
29.VI	7.7± 5.9 (21)	8.2± 3.6 (25)	14.2
30.VI	2.4± 1.8 (30)	6.2± 2.3 (25)	13.0
1.VII	2.0± 1.5 (18)	4.0± 2.4 (5)	
Mean	12.5 (432)	12.3 (401)	

Table 3. Mean length of periods off at the nests I/71 and II/71. Temperature at nest I/71 is the mean of 24 hourly measurements.

however, no long periods off were recorded. For instance at nest V/69 with both parents incubating, the longest period off was 14 min., but also at nest IV/69 no absence exceeded 26 min., but this nest was watched only for one day.

At hatching, the periods off the nest were very short; usually the bird rushed for only one or a few minutes off the nest, many periods off were even less than one minute. The bird then ran hurriedly some tens of metres with for instance an eggshell fragment in its bill and returned immediately to warm the chick(s) and/or unhatched egg(s). On returning, the male sometimes snapped a few food items, but feeding seemed highly inefficient and it seemed very improbable that the energy losses could be compensated for.

During the day the amount of time off varied considerably in the nests followed through the entire breeding season (Fig. 1, see also Fig. 2). This daily rhythm is best explained by the ambient temperature (Fig. 1). There was a strong correlation in both these nests between the hourly percentage of time off and the hourly mean ambient temperature ($r_s=0.817$ and 0.758 $n=24$, for nest I/71 and II/71 respectively. One-tailed, since according to expectation, $P<0.01$ for both). Thus

the periods off are concentrated to the time of day when the ambient temperature is highest. In the morning, the temperature has to exceed 8°C on average before the birds are prepared to spend c. 20% of their time off the eggs. In the evening, the activity drops at a higher ambient temperature; around 9°C only slightly more than 5% of the time is spent off the nest. The higher activity at lower temperatures in the morning is probably due to hunger after a long night's rest.

Less clear relationships were recorded between the daily mean temperature and the daily percentage of time off nest. At nest I/71, there was a significant positive correlation ($r_s=0.515$, $n=25$, two-tailed $P<0.02$), but not at nest II/71 ($r_s=0.244$, $n=25$).

The mean length of periods off decreased with advancing incubation in both nest I/71 and II/71: $r_s=-0.792$ and $r_s=-0.803$, respectively ($n=25$, two-tailed $P<0.02$ for both, cf. Table 3). However, the total amount of time off did not decrease significantly with advancing incubation in nest I/71 ($r_s=-0.130$, $n=25$), but did almost so in nest II/71 ($r_s=-0.399$, $n=25$, two-tailed $P<0.10$). Thus the males spend shorter times off the eggs with an advancing incubation period, but do not necessarily sit more tightly on the eggs.

There was a negative correlation between the mean daily temperature and the mean length of the periods off, but this was not significant (nest I/71: $r_s=-0.189$, $n=25$) or only nearly significant (nest II/71: $r_s=-0.381$, $n=25$, two-tailed $P<0.10$).

Feeding

The absences were predominantly feeding absences. Before leaving the nest, the bird usually stretched its neck, scanned the surroundings and walked a few metres before flying further. The bird seldom flew directly from the nest. The distance flown varied, often the bird remained within some tens of metres of the nest, but it could also fly up to 200 m, exceptionally 400 m, and sometimes even disappear from sight. It also could run a few metres, snatch a food item and return to the nest within less than one minute. No regular feeding sites were recognized, the birds were utilizing the nest surroundings quite evenly.

The incubating bird usually seemed to be in a hurry when feeding. It ran fast a few metres, stopped, picked some food item and ran again. After feeding, it usually flew within about 10 m of the nest, running the last metres, sometimes still feeding. On some occasions, it ran all the way to the nest in a zig-zag like fashion.

In 1969, the feeding areas of the nests I-V were described. The birds were feeding on the almost treeless alpine heath. A few small Scots Pines *Pinus sylvestris* were recorded within four of the feeding areas (1-15 ex; in one area, the pines were 2-4 m high and 30 m apart). In two of the areas there were 1-3 small Norway Spruces *Picea abies*. Mountain Birches *Betula tortuosa* were found in three of the areas (in one 2.5-3.0 m high), usually 10-20 m apart. In one of the areas, no birches were recorded even though the nest was only 20 m above the *regio subalpina*. Some small Junipers *Juniperus communis* (<1.0 m) were found in all the feeding areas (in one only 2 ex.; in the others, the Junipers were appr. 5-20 m apart). The ground was covered by lichens and mosses,

sometimes also by grasses (*Festuca* sp.). The lichens were small and worn due to overgrazing by semi-domestic Reindeer *Rangifer tarandus*. The coverage of stone fields varied from scattered stones up to 40% of the ground surface.

The most abundant dwarf shrub was *Empetrum nigrum* (in all the areas, up to 60%). Other dwarf shrubs were *Arctostaphylos uva-ursi* (all areas, up to 30%), *A. alpina* (all areas, up to 20%) and *Vaccinium myrtillus* (three areas, up to 40%). In three of the areas, there were also some *V. vitis-idaea* (up to 5%), once also *V. uliginosum* and twice *Lycopodium* sp.

The birds were seen feeding on berries of *Empetrum nigrum*, blossoms of *Trientalis europaea* and *Vaccinium myrtillus*, and on *Coleoptera*, *Diptera* and *Lepidoptera* (Pulliainen 1970). Once it was noticed that the Dotterel had difficulties in tearing the blossoms off *V. myrtillus* plants.

In one case, a Dotterel had fed upon something unsuitable which it tried to remove from the throat by coughing and head shaking. When not successful it applied the foot resulting that the wind overturned the bird several times when standing on one foot. The scratching resulted in a wound in the left corner of the mouth. Finally, it was able to swallow the item and it resumed feeding.

Other behaviour at the nest

Usually, when sitting on the eggs, the male side-threw small objects. At some nests, this behaviour was very conspicuous. It also pecked the nest bowl and the rim of the nest or cleaned the immediate vicinity of the nest. At least, when it was cold and windy, it preferred to face the wind. Other comfort movements included preening which could be quite intensive and scratching for instance the incubation patch. It also often turned around in the nest facing different directions, sometimes it kept turning repeatedly before finding a satisfactory one. Sometimes the bird turned its eggs. It also frequently shook its head when otherwise incubating calmly. Sometimes the whole bird shook in the nest and sometimes it shook its body in order to get the eggs in a better position.

During the night, the bird was incubating in a very low position with the neck indrawn and feathers fluffed, sometimes yawning and shutting the eyes for a while. Sometimes the bird even slept with the beak underneath the wing. Sometimes the bird was seen making comfort movements even beside the nest; stretching, shaking, fluttering the wings and calling.

The incubating Dotterel is renowned for its tameness at nest. At least at the end of the incubation period, the bird will sometimes allow an approach within some dm from the nest. When leaving the nest, it injury feigns intensively. Individual differences exists as some birds may leave the nest when the observer is tens of metres away, sometimes even when 100 m (twice) and 200 m (once) apart. Birds ringed on the nest may leave the nest earlier on the next visit. On the other hand at least one male seemed to rush to the nest if absent when it saw the research workers approaching the nest.

Often when settling on the eggs, the bird called "tjupp, tjupp". This was described as soft and to resemble the call of the Thrush Nightingale *Luscinia*.

luscinia. It also called "dipp, dipp" when arriving at the nest. Other calls heard were "plytt" and "tsiur". "Peep"-calls were also heard but not as often as during the laying period. When leaving the nest, the male was recorded uttering "brr, brr" and "tsjurr".

When the temperature was high (maximum ground temperature recorded 48.2°C!), the bird often panted (already at c. 20-25°C) and stood repeatedly for some time in the nest shading the eggs. Sometimes only the bill was kept slightly open and swallowing movements were made. In heavy rain, the incubating bird shook the raindrops off the plumage. In one case, an empty bottle was hanging in a nearby tree (8 m from the nest). Every time the wind blew in the bottle and the bird heard the sound of it the bird shook its head. When snowing the bird incubated without moving for about 15 h. after which it took a long absence (148 min.). The snow may accumulate against the incubating bird so that there is a snowpile of up to 5 cm against it. During the summer snowstorm of 1977 (Pulliainen 1978), Dotterel nests were not watched and thus we do not have data on the behaviour of Dotterel in extreme weather conditions. Anyhow, even in normal conditions the incubating Dotterel may face a temperature amplitude exceeding 50°C.

At nest V/69 both parents incubated. The off duty bird was seen sneaking inconspicuously to the nest before the nest shift was made. When the female of this nest was off duty, its behaviour was followed for c. 1 h. on 5 July around 10 hrs. It was mostly standing, only occasionally eating, flying away but when relocated mostly standing and walking slowly before flying away again. It did not seem to be in a hurry as the males incubating alone. The body mass of the birds sharing the incubation duties was much higher than of those males incubating alone, indicating that if both birds incubate there is enough time to feed.

Behaviour at hatching and nest leaving

The first cracks in the eggshells may appear at least 3 days prior to hatching. One day later the chicks commonly call from within the eggs. When the chicks begin to hatch out the male sits attentively on the eggs. Exceptionally the male may be absent from the nest when the first chick hatches out (33 min. absence at nest III/69, thereafter none exceeding 9 min.). Usually, however, the absences are about one minute or even less until the chicks leave the nest. The male takes some eggshell fragments, runs or flies about 20 m, drops the eggshell and runs back to the nest. It may even snap some food item while returning. About half a dozen trips with eggshell fragments off the nests seems normal. The male III/69 arriving to the nest with a newly hatched chick was seen pecking the empty eggshell.

When the chick hatches, the yolk sac can often be seen, but in a few hours it is drawn within the body (e.g. once within 1 h 40 min.). The chicks dry usually within about 3 h. After a few hours, the oldest chick makes some very short excursions from the nest but it is usually called back by the male. A little later the next one to hatch gets out for short spells and it becomes increasingly difficult to keep the brood together under the brooding male. Sometimes after the first short trips outside the nest the oldest chick starts pecking at different objects in the immediate

vicinity of the nest. The excursions by the two oldest chicks become increasingly frequent and finally the male decides to leave the nest. The youngest chick may still have great difficulties in following the rest of the family. Nest leaving is probably a compromise between the interests of the older and youngest chicks. When the male is unable to keep the older siblings together, it has to leave the nest and the youngest is forced to follow the rest of the family in the best possible way.

In the tabulation below the events around hatching and nest leaving are shown for one nest (I/69):

1st egg hatched	5 July 19.06 hrs
1st chick dry	5 July 21.08 hrs
2nd chick hatched	5 July 23.45 hrs (± 45 min.)
3rd chick hatched	6 July 04.30 hrs
1st chick out	6 July 07.12 hrs
1st chick feeding	6 July 07.44 hrs
2nd chick out	6 July 10.20 hrs (first attempt 10.14)
3rd chick out	6 July 14.21 hrs
Chicks left finally	6 July 15.16 hrs
The brood 125 m from nest	6 July 21.05 hrs

Discussion

According to Kålås (1986) the incubating Dotterel faces the following conflicting problems: 1) thermal requirements of the embryo for development, 2) metabolic requirements for self-maintenance, 3) predation on the eggs, and 4) predation risk for itself. The south Norwegian rhythm is not to leave the nest during dawn and dusk, and many short periods away from the nest during rest of the day. This incubation schedule satisfies the points 1, 2 and 4, but not entirely 3 as there is a high predation on eggs (Kålås 1986).

In Lapland, the "night" (the sun is there continuously above the horizon) is spent on the eggs, contrary to south Norway where feeding is intensive during the dark period. As it ought to be energetically the best alternative to sit on eggs when the ambient temperature is lowest (as in Lapland), there must be some disadvantages of doing so in south Norway, which probably somehow is related to predation pressure. Kålås (1986) suggested these predators to be mammalian, which are most active during dawn and dusk. At Värriö, the mammalian predators are scarce on the alpine heath during the Dotterel incubation period (Pulliainen and Saari, manuscript). The incubation rhythm in Lapland seems to satisfy the above points quite well. However, even if most of the males at Värriö are able to successfully incubate their clutches alone, this seems to be at the expense of their own physical condition, as many males are at the end of the incubation period in a poor physical condition according to Norwegian standards (Kålås and Byrkjedal 1984, Pulliainen and Saari 1992b). Sometimes the Dotterel apparently is not able to complete the incubation owing to the demands for self-maintenance (Pulliainen and Saari manuscript, nest I/88 in this study). The males incubating alone seem to be in a great hurry in Lapland when feeding during the time off the eggs, whereas the female sharing the incubation with her mate moved leisurely on the fell. The physical condition of both members of the pair incu-

bating was good compared with the males incubating alone (Pulliainen and Saari 1992b), indicating a great physiological stress to incubate alone.

Another difference with south Norway was in the incubation constancy (or attentiveness). Despite different regimes in Norway (only male, both male and female, and experimentally only female), the attentiveness was in each case close to 90% (Kålås 1986) and the reduction of mass was slow during incubation: 7% during the whole period in contrast to 25% in Lapland (Kålås and Byrkjedal 1984, Pulliainen and Saari 1992b). In our study area the pair incubating together sat for about 95% of the time (corrected value), whereas in the nests incubated by the male alone, the attentiveness was around 85% in 1971 and between about 70 and 80% (corrected values) in 1969. The chicks may thus hatch from eggs which are incubated slightly below 70% of the time, but when the attentiveness drops to about 65% the nest may be at risk (nest I/88).

In the nest studied by Wilkie (1981) in southern Norway, the attentiveness was on average 87.5%, or about the same as in our nests in 1971. In his study, the attentiveness was highest at the coldest part of the day, as at Värriö. However, peaks in attentiveness were recorded both around the sunrise and sunset (Wilkie 1981).

The mean length of absence in different nests studied by Kålås (1986) was between 8.1 and 9.7 min., in the nest studied by Wilkie (1981) 6.5 min. In our study area, in the nest incubated by both birds, the length of the periods off averaged 5.3 min, in the other nests, the mean was only once within the range given by Kålås (1986), in the rest between 10.7 and 34.6 min. Probably a poorer availability of food forces the birds to stay longer off the nest in Lapland. The developing embryos in the eggs seem to tolerate this pretty well.

At Värriö the mean length of periods off decreased with advancing incubation, but not the total time off the eggs. Thus the birds only left their nests more often in the latter part of the incubation period, except around hatching, when both the periods off were short and the absences relatively few. Around hatching the needs of the chicks seemed to get priority over those of the male. The longer absences at Värriö, yet the poorer physical condition with advancing breeding season points at a low availability of food and difficulties to satisfy the immediate hunger urge. However, despite a harsh and unproductive environment and consequently a poor physical condition, the Dotterel is able to successfully raise chicks at Värriö, the advantages of this environment probably being scarcity of predators compared with for instance the South Norwegian breeding areas.

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