Incubation rhythm and behaviour of a Dotterel *Charadrius morinellus* nesting in Norway

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A male Dotterel was watched at its nest for a total of 150 h during incubation and hatching. The timing of absences from the nest was recorded, as was all behaviour whilst on the nest.

Attentiveness averaged 87.5 % but varied both within and between days. Four elements of this variation are described: (1) the short-term hunger urge and its suppression during times of stress; (2) total daily feeding time; (3) a 24 h rhythm in feeding activity, related to air temperature; (4) relative changes in absence frequency and mean absence duration. The frequency of resettling also followed a 24 h rhythm, which lags 4—6 h behind attentiveness.

The temporal relationships of resettling and nest absence with various incubation behaviours were investigated. Their relationships with nest-building and preening were different from those previously observed in gulls, suggesting that models of incubation behaviour in gulls are not applicable to waders.

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Introduction

Although the breeding biology of boreal waders has attracted great interest over recent years, there is still relatively little known about the organization of behaviour during the incubation period. More information is required on this critical stage of the breeding cycle if we are to understand the physiological pressures faced by nesting waders (Ashkenazie & Safriel 1979) and the wide variety of breeding systems that have evolved (Pitelka et al. 1974, Hildén 1975). Perhaps the most fundamental division of breeding systems is between those in which one sex incubates and those in which both do so. Most boreal waders share incubation, with the obvious advantage that the eggs can be covered continuously. The Dotterel is one of the minority of species in which one sex (in this case the male) usually incubates alone (Pulliainen 1970, Nethersole-Thompson 1973). Being relatively easy to watch, in terms of geographical accessibility, confiding habits, size, coloration and use of open nesting terrain, it provides a good model for the study of single-sex incubation in waders.

This paper reports some results of a prolonged man-watch of a single Dotterel nest made during a visit to the Hardangervidda, south Norway by the Cambridge Norwegian Expedition 1978. Particular emphasis is placed here on the rhythm of incubation and incubation behaviour; information on other aspects of the work may be found in the Expedition's report (Wilkie 1980).

Methods

Nest observation. The nest chosen, near Dyranut (60°22′N, 7°30′E), was on typical mid-alpine heath habitat at an altitude of 1310 m; it had an incomplete clutch when first found. The task of watching the nest was divided amongst seven members of the Expedition, usually working in 4 h shifts. Observations were made from a distance of 60 m, except in thick cloud or at night, when points down to 10 m had to be used. This did not appear to alter the bird's behaviour. All behaviour was entered in a log book and timed to the nearest minute.

Analysis of data. As both weather and hatching are known to affect incubation behaviour (Drent 1970), the observations were divided into three separate blocks for analysis:

A: fine weather during the incubation period (sun, light winds, little precipitation) — 82 h.

B: bad weather during the incubation period (frequent precipitation or strong winds) — 28 h 23 min.

C: hatching and post-hatching period — 36 h 17 min.

Altogether, the nest was watched for just under 150 h; a general diary of events is given in Table 1.

TABLE 1. Diary of observations on the study nest. Block A = fine weather; B = bad weather; C = after hatching. After nest departure, daily position of brood is given relative to nest site.

Date	Time	Block	Notes
17/6	17.00	—	♀ sitting, 2 eggs
	19.00	—	Eggs cold
19	11.19	—	♂ sitting, 3 eggs
29	12.30—14.35	B	
	16.21—19.00	B	
30	06.45—13.38	B	
	16.15—17.20	B	
1/7	15.38—16.20	B	
	17.50—19.44	B	
2	08.17—18.00	B	
6	10.50—19.50	A	
9	14.20—16.00	A	11.00 1 egg chipping
10	08.30—20.00	A	
11	04.40—24.00	A	21.04 1 egg chipping
12	00.00—24.00	A	05.38 3 eggs chipping
13	00.00—16.30	A	
	16.30—19.42	B	18.47 none hatched
	19.42—21.27	C	
14	05.00—23.21	C	05.00, 19.15 2 hatched
15	02.11—18.22	C	00.10 3rd hatched, wet 12.37 nest departure 18.22 55 m SE of nest
16	12.07	—	3 chicks, 150 m W
17	13.00	—	3 chicks, 75 m W
18	12.15	—	3 chicks, 75 m E
19	13.00	—	2 older chicks, 60 m S
20	12.00	—	Adult and chicks disappeared

Analysis of the incubation rhythm follows the nomenclature and methods of Drent (1970) and Norton (1972). Uninterrupted periods of incubation (= sitting spells) were broken either by the bird rising and immediately sitting down again (= resettling) or by its leaving the nest to feed (= absence). Periods of incubation between successive absences are termed shifts, and the attentiveness is the percentage of time occupied by shifts. On a few occasions the bird ran off the nest either to perform sideways-throwing (Harrison 1967) or in response to a predator. These are excluded from the analysis of absences which is intended to examine the feeding rhythm.

Temperature data were obtained from the reports of *Det Norske Meteorologiske Institutt* for 1972—1975. The nearest weather station to the survey area is at Finse (60°36′N, 7°31′E), about 25 km away, and the curve of diurnal temperature variation was derived by fitting the more comprehensive data for Oslo, corrected for longitude, to that for Finse by a least squares method.

The data were also examined to determine whether resettling and nest absence were associated with increases or decreases in different types of incubation behaviour (e.g. preening, nest-building). First, a 'basal' activity *B* for the behaviour was calculated from all sitting spell periods separated on both sides by more than 10 min from the nearest resettling or nest absence, and therefore hopefully unaffected by them. Separate values for blocks A and B were derived, to be combined in the final calculation (this controls for the effects of weather on the magnitude of the behaviour). Next, the average frequency *F* of the behaviour in the 10 min immediately preceding or following every resettling or nest absence was computed. All such 10 min periods were included, provided that another resettling or nest absence did not occur within 21 min of the first — i.e., no period was included twice in the calculation. For clarification, Fig. 1 gives an example of a period of incubation and how it was analysed. The frequency relative to the basal level was then obtained by the formula:

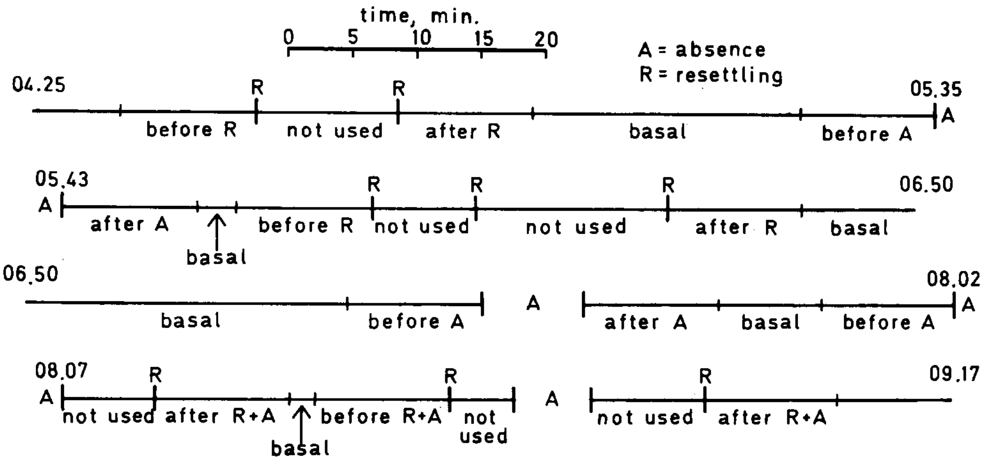

FIG. 1. An example of nest activity over a 5 h period (on 12 July) showing, above the line, the times of resettling (R) and nest absence (A), and, below the line, how the time was divided up in the behaviour analysis.

$$\text{relative frequency} = \frac{N_A F_A{:}B_A + N_B F_B{:}B_B}{N_A + N_B}$$

where N is the number of 10 min periods, the subscripts refer to blocks A and B, and B and F are defined above.

Rhythm of incubation

Rhythm in fine weather. Fig. 2 shows the diurnal variations in resettling frequency, absence frequency, mean absence duration and attentiveness in fine weather (block A data). The mean values are 1.32/h, 1.18/h, 6.54 min and 87.2 %, respectively, and the mean shift duration was 47.6 min. Attentiveness is lowest during the afternoon (~ 80 %) and highest during the early morning: the two longest shifts recorded (01.42—05.35 and 01.14—04.43) occurred on the two days (12 and 13 July) that the nest was watched during the latter period. The morning fall in attentiveness results from increases in both absence frequency and absence duration, whereas the evening rise is due to a decrease in absence duration alone. Resettling frequency also has a diurnal cycle, which correlates significantly with attentiveness only when the resettling rhythm is shifted 6 h forward ($r = -0.60$, $df = 10$, $P < 0.05$) or 4 h back ($r = +0.72$, $df = 10$, $P < 0.01$) — i.e. the resettling rhythm lags 4—6 h behind attentiveness. The tendency for activity to fall off in the evening is in every case reversed in the period 22.00—23.59; individually none of these changes is significant, but together they suggest a burst of activity before the long early morning shift.

It would be interesting to relate these cycles to variations in temperature and daylight. Unfortunately, measurements were not made in the field, so the temperature curve shown in Fig. 2 is the average for July 1972—1975 at Finse, calculated as described in Methods. Attentiveness appears to be more closely related to temperature than to daylight, confirming the subjective impression obtained in the field.

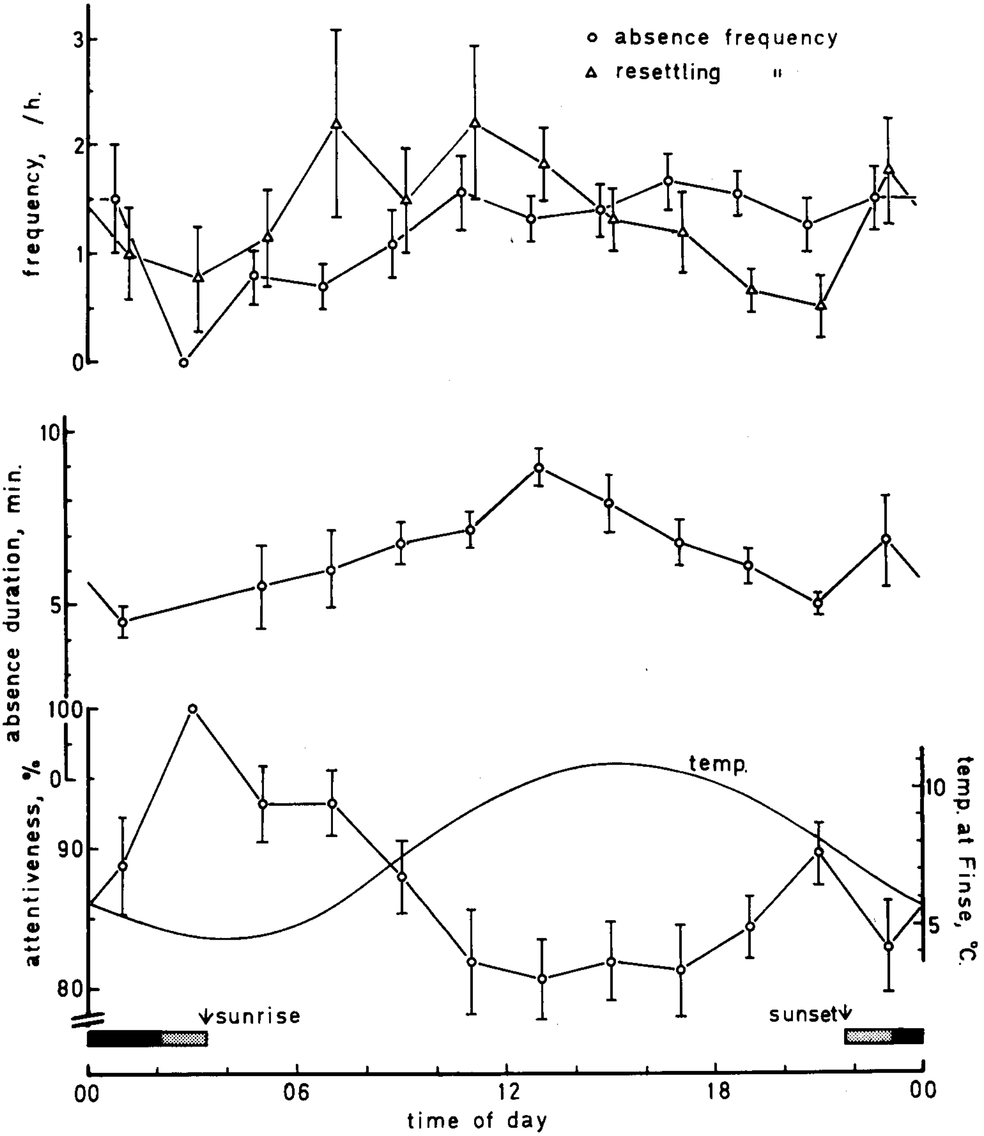

FIG. 2. Diurnal rhythms of (top) resettling frequency and absence frequency, (middle) mean absence duration and (bottom) attentiveness. All points are mean ± SEM for 2 h blocks. Only fine weather (block A) data were used. For comparison are shown the July temperature variation at Finse (mean for 1972—1975) and the periods of twilight (stippled) and darkness (black) on July 10.

Timing of absences. Between 10.00 and 01.59 the absence frequency remains approximately constant with a mean of 1.46/h (Fig. 2). If the timing of the bird's absences during this period were randomly determined, one would expect the occurrence of different (integral) hourly absence frequencies to follow the Poisson frequency distribution. In fact (Fig. 3), the actual distribution differs significantly from this expected form ($\chi^2 = 15.63$, $df = 3$, $P < 0.005$), indicating that absences are not randomly timed.

Influence of weather. The block B data were analysed in a similar manner to determine the effect of bad weather on the bird's behaviour. The only significant change observed was a decrease in resettling frequency (to 0.74/h: $\chi^2 = 9.19$, $df = 1$, $P < 0.005$). There were slight decreases in absence frequency and duration, raising the attentiveness for blocks A and B combined to 87.5 %. Wind direction was found to influence orientation on the nest: the bird tended to face into the wind and this tendency increased with increasing wind force. The mean angle of incidence with the wind decreased from 78° at Force 1 to 21° at Force 5.

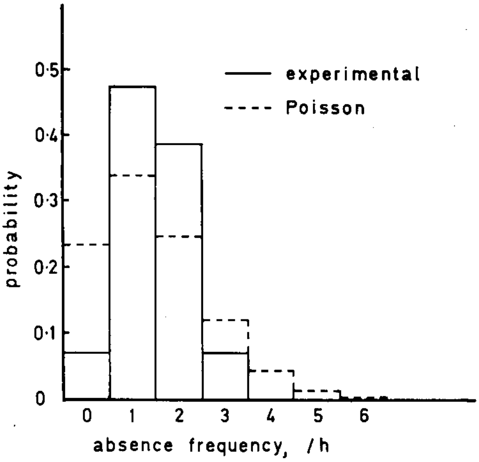

Fig. 3. Probability distribution of hourly absence frequencies for the period 10.00—01.59. Solid lines show the observed proportions, dashed lines the equivalent Poisson probabilities ($\mu = 1.46$).

Changes in rhythm during incubation and hatching. Fig. 4 shows the variations in resettling and absence frequency, mean absence duration and attentiveness as incubation proceeds, for the period 11.00—17.59 on all days for which coverage of this period was complete. No consistent trends are shown, but an interesting finding is that absence frequency and absence duration are negatively correlated when whole days are compared ($r = -0.82$, $df = 4$, $P < 0.05$). Since the changes in absence frequency are proportionately the greater, this is the dominant factor determining attentiveness. This situation contrasts (Fig. 2) with the weak positive correlation between absence frequency and absence duration at different times within a single day ($r = +0.21$, $df = 9$, N.S.).

The evening of 13 July was marked by two events (Table 1): hatching of the first chick and a rapid deterioration in the weather, with low cloud, strong winds, rain and snow, which continued over the next few days. The adult began to resettle much more frequently (57 times in 105 min at one stage), and an elevated resettling rate continued whilst the chicks were in the nest (average for 14 and 15 July: 3.7/h). The changes in absence frequency, absence duration and attentiveness on 14 and 15 July are illustrated in Fig. 5. On 14 July (when one egg remained unhatched), time spent by the adult away from the nest fell by 61 %, but it had returned to near normal the

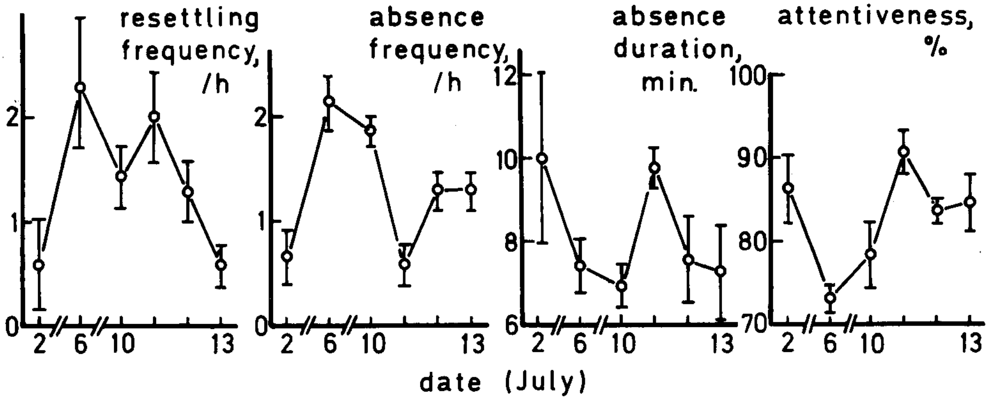

FIG. 4. Changes in resettling frequency, absence frequency, mean absence duration and attentiveness towards the end of incubation. All points are for the period 11.00—17.59.

next day, when absence frequency had increased and mean absence duration had decreased, each by a factor of 3—4 compared with the incubation values.

Behavioural interrelationships

Characteristically, periods of quiet incubation were interspersed with bouts of active behaviour, including nest-building (hereafter called 'building'), preening, head-bobbing and periods when the head was raised alertly ('head-up'). Previous work on gulls has shown that building and preening may be closely related in time to resettling and nest absence (Beer 1963, Baerends et al. 1970). The patterns of these temporal relationships have been used to propose a 'model' of incubation behaviour in the Herring Gull *Larus argentatus* (Baerends 1959, 1970). The behaviour of the Dotterel was examined to see if it would fit this model: increases or decreases in a particular behaviour associated with resettling or nest absence were detected by calculating their frequency in the adjacent 10 min period, relative to a 'basal' activity (see Methods). The basal activities of the behaviours studied are shown in Table 2: there was an insignificant increase in building in bad weather, with significant decreases in preening and head-up.

Table 3 shows the 10 min relative frequencies obtained. With the exception of head bobbing, the tendency is for all types of behaviour to increase in frequency before resettling and nest absence, and to decrease below basal immediately after resettling and nest absence. However, the exact pattern varies with the type of behaviour: most notably, building and preening increase significantly before resettling, but not before nest absence, whereas the converse is true of head-up. Head-bobbing increases in all cases, but most dramatically before and after nest absence.

Discussion

Organization of feeding rhythm in single-sex incubation. The only previous studies on single-sex incubation in boreal waders have been those of Norton (1972) on the female Pectoral Sandpiper *Calidris melanotos* and Parmelee (1970) on a male Sanderling *Calidris alba.* The attentiveness values reported were 85.0 % and 81 % respectively, and 70—80 % has been estimated for the female White-rumped Sandpiper *Calidris fuscicollis* (Drury 1961, Parmelee et al. 1968). These compare well with the figure of 87.5 % for the Dotterel. Both Norton (1972) and Parmelee (1970) found that attentiveness was 95 % or greater at night, falling to 65—75 % during the day; mean absence durations were 5—10 min and absence frequencies 1—2/h. All these values are similar to those in the present study, and begin to suggest that waders incubating alone share a common strategy for organizing their behaviour. However, Nethersole-Thompson (1973) in 23 h 10 min of observations at three Dotterel nests in Scotland, recorded only seven absences, whose mean duration (19.7 min) was greater than the longest of the 138 absences recorded for the Norwegian bird (17 min). This shows that incubation strategies do vary: probable factors are geography, temperature, food availability and size differences between species, in addition to which different birds (of one species) within

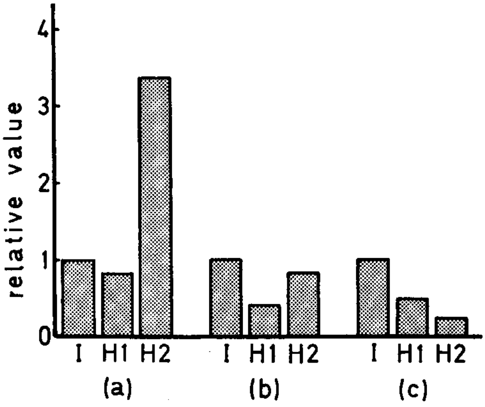

FIG. 5. Feeding activity of the adult on the first (H1 = 14 July) and second (H2 = 15 July) days after hatching of the first two chicks, relative to block A incubation (I) values (= 1). (a) absence frequency; (b) total time off nest; (c) mean absence duration.

TABLE 2. Basal levels (proportion of minutes with activity) of building (b), preening (p), head-up (hu) and head-bobbing (hb) in good (block A) and bad (block B) weather. Probabilities were calculated by χ^2 test.

	b	p	hu	hb
Block A (1074 min)	0.035	0.054	0.067	0.001
Block B (494 min)	0.043	0.022	0.026	0.001
P of difference	N.S.	0.02	0.002	—

TABLE 3. Frequency of four incubation activities in the 10 min immediately before and after resettling (R) and nest absence (A), relative to their basal levels (= 1). R+A indicates that an absence occurred within 10 min of resettling (see Fig. 1). Significance of difference from basal level was calculated by χ^2-test: $^*0.05>P>0.025$, $^{**}0.025>P>0.01$, $^{***}P<0.01$. Sample sizes are given in brackets.

	Before			After		
	R(32)	R+A(11)	A(56)	R(23)	R+A(8)	A(65)
Building	1.69*	3.35***	1.11	0.56	1.61	0.80
Preening	3.40***	3.21***	1.03	1.10	1.05	0.41**
Head-up	1.38	2.04**	2.99***	0.94	0.51	0.69
Head bobbing	4.65		21.1***	7.92		17.3***

a single population may have their own, individualistic incubation rhythms (Pulliainen 1971, Norton 1972).

Ashkenazie & Safriel (1979) estimated the breeding season energy balance of the Semipalmated Sandpiper *Calidris pusilla,* in which both sexes incubate. They calculated that during the incubation period the birds replaced only one third of their energy utilization (representing a net daily loss of ∿ 100 kJ), even though each member of the pair had to incubate for only 50 % of the time and spent about 40 % of its time feeding. This estimate is impossibly pessimistic (a 25 g bird losing 100 kJ/d would rapidly die), but does serve to emphasize the even greater energetic problems faced by birds incubating alone: these can feed for only 10—20 % of their time and must incubate for the remaining 80—90 %, yet the risk of egg chilling is still greater than with shared incubation, in which attendance is almost 100 % (Norton 1972). The behaviour of this Dotterel illustrates several of the ways in which a bird incubating alone can vary its time-energy allocation, the optimization of which is clearly under heavy selective pressure.

(1) The non-random distribution of absence frequencies (Fig. 3), with lower proportions of low (0/h) and high ($\geq$3/h) frequencies than expected, strongly suggests that the primary determinant of spacing of feeding trips was the short-term need to satisfy the hunger urge. This was suppressed when outweighed by danger to eggs or chicks (e.g. at night or on hatching) and sometimes perhaps enhanced also (the burst of activity before the long early morning shift, Fig. 2).

(2) The daily total time spent feeding varied over a three-fold range during the incubation period (Fig. 4), perhaps depending on the ease of catching food or ambient temperature. On the day after hatching, a critical period for chick survival, the adult fed for 61 % less time than normal (Fig. 5), probably incurring a temporary energy deficit. It should be noted that the hatching spread (20—27 h) was unusually long for the Dotterel (Pulliainen 1970).

(3) There was a marked diurnal rhythm in feeding activity which appeared to be more closely related to temperature than to daylight (Fig. 2). This was probably determined by the need to protect the eggs from chilling, but variations in food availability (certainly important for the Snow Bunting *Plectrophenax nivalis* and Wheatear *Oenanthe oenanthe* in Greenland, Asbirk & Franzmann 1978 a, b) and predator avoidance are also possibilities.

(4) There are two independent controls on feeding time: absence frequency and absence duration. The 24 h rhythm of attentiveness resulted from concerted variations in both of these, but the differences in total feeding time between days were effected solely through changes in absence frequency — mean absence duration actually partly counteracting these (Fig. 4). After hatching, absences tended to be shorter but more numerous (Fig. 5), a feature also noted by Norton (1972).

The adaptive explanation of the Dotterel's single-sex (male only) incubation strategy remains mysterious, for it is not (except in occasional cases of polyandry, Nethersole-Thompson 1973) the inevitable consequence of its breeding system, as would be true for species in which polygamy or lekking was usual or each pair had two nests (reviewed by Pitelka et al. 1974, Hildén 1975). Since the female puts no energetic investment into incubation, it is particularly surprising that its investment in eggs (the clutch size being three) is lower than in most other waders.

Behavioural interrelationships and their significance. The temporal relationships between building, preening, resettling and nest absence in Charadriiformes have been examined for a few species. Increased building activity both before and after resettling was reported for the Herring Gull (Baerends et al. 1970) and Black-headed Gull *Larus ridibundus* (Beer 1963), but in the Black-tailed Godwit *Limosa limosa* building increased only before resettling (Lind 1961). Baerends et al. (1970) also noted that the Herring Gull preened before, but not after resettling, and that the ratio of building to preening activities ('building/preening ratio') declined over the course of a shift. Baerends (1959, 1970), deriving a 'model' for incubation behaviour in the Herring Gull, concluded that the patterns of occurrence of building and preening during incubation were fundamentally different and so assigned these behaviours to separate 'systems', related to the incubating/resettling and escaping urges, respectively.

In this Dotterel, by contrast, building and preening were very similar in their associations with resettling and nest absence (Table 3). Although in some cases these associations resembled those in gulls (e.g., preening increased before, but not after resettling), the building-resettling relation clearly differed from that in gulls but resembled that in the Black-tailed Godwit (Lind 1961). Also, there was no consistent trend in the building/preening ratio over the course of a shift (the values for the four successive quarters being 1.38, 0.84, 1.17 and 1.42), whereas the progressive decline found in the Herring Gull was an important feature of Baerend's (1970) model. So far it appears that waders have patterns of incubation behaviour different from those in gulls, which limits the usefulness of any incubation 'model' or adaptive explanation of these relationships. Clearly it would be interesting to investigate this further in other Dotterels and waders.

Various other features of the Dotterel's behaviour deserve comment. The analysis of behavioural associations was extended to include head-up and head bobbing (Table 3). Head-up (alert) movements could occur at any stage of a sitting spell but were most frequent immediately before nest absence and least so after returning to the nest, possibly because their main function is to look for predators. In marked contrast, head bobbing was intimately associated with the actions of standing or settling at the nest, hardly occurring otherwise — however, its function is unknown. The 24 h rhythm in resettling frequency (Fig. 2) is also difficult to explain, since it cannot be correlated adaptively with an environmental variable. Its lack of phase with attentiveness, also noted by Norton (1972), may be an indirect result of the apparent inhibition of resettling after returning to the nest (A. O. M. Wilkie, unpublished results); alternatively, it could reflect an endogenous circadian activity rhythm.

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Selostus: Keräkurmitsan hautomisrytmistä ja käyttäytymisestä Norjassa

Etelä-Norjassa tarkkailtiin kesällä 1978 yhtä keräkurmitsakoirasta kaikkiaan 150 tuntia haudonnan ja poikasten kuoriutumisen aikana. Haudonta- ja poissaolojaksot kirjattiin, samoin kaikki havainnot linnun käyttäytymisestä. Taulukossa 1 on esitetty havaintojaksot sekä tietoja muninnasta ja poikasten kuoriutumisesta.

Lintu hautoi keskimäärin 87.5 % tarkkailuajasta, mutta haudontarytmi vaihteli sekä saman vuorokauden aikana että eri päivinä. Vaihteluun vaikutti neljä tekijää: (1) hetkellinen tarve nälän tyydyttämiseen ja sen estyminen munien ja poikasten ollessa alttiina vaaroille; (2) päivittäinen ruokailuun käytetty kokonaisaika, joka vaihteli ilmeisesti ruokailun tehokkuuden mukaan; (3) vuorokautinen ruokailurytmi, joka oli riippuvainen lämpötilasta; (4) muutokset poissaolojen yleisyydessä ja kestossa. Kuva 2 esittää poissaolojen yleisyyttä (ylh.), kestoa (kesk.) ja haudonnan %-osuutta (alh.) vuorokauden aikana hyvällä säällä. Keskimäärin lintu poistui pesästä 1.18 kertaa tunnissa ja viipyi poissa 6.54 min.; se hautoi innokkaimmin aamupuolella ja käytti eniten aikaa ruokailuun iltapäivällä, mikä lienee yhteydessä lämpötilaan ja ravintohyönteisten esiintymiseen. Hautomisrytmin muutokset kuvassa 4.

Pesään asettumisen ja siitä poistumisen vaikutusta haudonnan aikaiseen käyttäytymiseen tutkittiin (taulukot 2 ja 3). Pesänrakentamisen ja puhdistautumisen osalta se poikkesi lokeilla aikaisemmin todetusta, minkä perusteella lokkien hautomiskäyttäytymisen mallia ei voida soveltaa kahlaajiin.

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