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ON THE TIMING OF FORAGING FLIGHTS BY OYSTERCATCHERS, HAEMATOPUS OSTRALEGUS, ON TIDAL MUDFLATS

by

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1. INTRODUCTION: DIURNAL BIRDS WITH TIDAL FOOD

Most creatures on our planet live in an 24-hour environment. Their foods and risks vary through the day with predictable variations. Endogenous circadian clocks have developed to cope with this periodic world. For some animals, food recurs periodically but in intervals different from 24 hours. Most prominently affected are those fish and wading birds which exploit the riches of the intertidal. Their food sources are locked away once every tide, as though in a gigantic circadian food schedule experiment.

The crop is usually abundant on estuarine tidal mudflats, but it is shared by dense populations of harvesters—each species with its own specialization—and its availability varies with time. The incoming tide covers the mudflats which the preceding ebb had exposed to the exploitation by waders. During low tide systematic temporal changes affect the availability of prey (VADER, 1964; EVANS, 1979). On dry flats lugworms often remain undetectable after the last defecation, ca one hour after the water runs off. Mussels close their valves, thus avoiding desiccation and predation. While food is rich for a wader, time for its exploitation is restricted. Moreover, the time of food availability is delayed
every successive day. Optimum exploitation may require the fine tuning of a wader’s temporal program to the movement of the tides. How is this accomplished; by endogenous timers or by direct observation of and response to the tidal flow? In the oystercatcher we have obtained field evidence suggesting that this bird can employ an internal timing mechanism for its tidal foraging flights. We have also performed some cage experiments trying to sort out which type of mechanism is likely to be responsible. These experiments, though inconclusive in the final analysis, allow us to at least define more clearly the general issues involved in distinguishing circatidal and circadian systems. Since they were finished, each of us has become absorbed by different ventures. We decided to document the evidence without in any way claiming the problems solved.

Acknowledgements.—The field work was done in 1975 to 1976 on the Dutch Wadden islands Texel and Schiermonnikoog, partly in collaboration with two undergraduate course groups. We acknowledge the countless counts made by these students, particularly Wibe Altenburg, Adrie Verkaik and Marc van den Berg. For help with cage and recording facilities, and for supply of captive oystercatchers we are grateful to our colleague Dr J. B. Hulscher and to the Netherlands Institute for Sea Research and its officers C. Swennen, P. Duiven and H. Boekel.

2. METHODS

The fieldwork was distributed over three episodes, referred to as “Texel 1975” (observations 6 to 22 October 1975), “Schier 1976” (observations 4 to 31 May 1976) and “Texel 1976” (observations 21 September to 5 October, 12 to 25 October, 4 to 18 November 1976).

On both islands the study areas included two different parts, separated by a high dike forming a visual barrier between the two areas. The observers were stationed on top of the dike and did their work from a hide or in the open air. The inland part existed on Texel of pastures and arable fields (Fig. 1), while on Schiermonnikoog only pastures were present. During high tide the oystercatchers formed roosting gatherings on these inland parts. They occasionally used the pastures as an additional feeding ground for earthworms. On the seaside, mudflats were exposed during low tide with scattered musselbeds.

We established tidal movements to and from the musselbeds by counting the numbers on both sides. The counting methods varied between observation periods. In Texel 1975 the number of oystercatchers preening, resting and foraging on the roostings and on the mudflats were counted every 5 minutes, and so were the numbers of oystercatchers
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flying over the dike between counts. These observations usually covered
the entire daylight period. In Schier 1976 only the number of birds
flying over the dike were counted every 5 minutes during several hours

around the receding tide. In Texel 1976 the number of foraging and
non-foraging oystercatchers on the roostings and on the mudflats were
counted once per 15 minutes, across the whole period of low tide.

To estimate the central tendency of moving from roost to mudflat we
had to use different parameters. For the Texel data we used the time at
which half of the oystercatchers had left the roost (the median roost-
leaver, R), for the Schiermonnikoog data the midpoint of the 30-minute
interval during which most birds flew over the dike, was taken (the
modal flyer, F). Times of high water (H) were collected from the pre-
dicted high waters from tidetables, while the exposure of the mudflats
was estimated by the first exposure of a point of reference, which was the
level with the highest mussels on the mudflat.

Fig. 2 shows, by way of example, the bird counts inland and on the
mudflats in the course of the entire observation period Texel 1975.
Counts inland during high tide were consistently higher than counts on
the mudflat during low tide, since the birds tended to disperse partly out
of view during low tide. While the time of presence on the tidal flat was
determined by the rise and fall of the sea level, presence on the inland
roost had a clear diel component. In the evening, just before dark, all
oystercatchers left the inland roost for a night roost on a small dike near
the water (see Fig. 1). Partitioning of activities by the oystercatchers on
the roost and the mudflat is illustrated by way of example in Fig. 3. The
time spent foraging on the roost decreased steadily towards the ex-
pected time of exposure of the mudflats (Fig. 3a). The total number of

---

Fig. 1. Map of the study area on Texel with cross section showing the inland roost (B),
the observation hide on the dike (■) and the mudflat (shaded).
birds on the roost was fairly constant (at ca 85) until 13.30 h. The median roostleaver (43 birds present) departed at an estimated time of 13.47 h (Fig. 3a). The modal flyer crossed the dike at 13.45 h (Fig. 3b). These two estimates are very close indeed for most of our data. A sharp increase of oystercatchers on the mudflats (Fig. 3c) accompanies the decrease numbers on the roost. On the mudflat many birds initially were either preening or resting (Fig. 3c). Foraging gradually took over when more of the musselbed was exposed and reduced oystercatcher density enhanced foraging return (Koene & Drent, 1981).

To answer the question how timing of roost departure was affected by variation in tidal flat exposure, we had to make a critical selection of our data. We used tidal migrations which met the following criteria: (a) at least 50 birds on the roost; (b) not later than one hour before sunset (such that we can be certain to exclude departures for the night roost); (c) less than one hour between the maximum number of roosters present and the median roostleaver (or modal flyer). These criteria excluded 7 of the 82 observations. There remained 75 observations (Texel 1975: 15, Schier 1976: 22 and Texel 1976: 38) for an analysis of the timing of foraging flights in oystercatchers.
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3. TEMPORAL CONSTRAINTS ON FORAGING

The importance of accurate timing of foraging flights to the tidal mudflats can be appropriately illustrated by an analysis of the effects of the duration of low tide on food intake and foraging behaviour. We will discuss separately the effects on total intake on the mudflats and on foraging behaviour inland during the subsequent high tide period.

Fig. 4 demonstrates some of the characteristics and consequences of low tides of short (ca 4 h), medium (ca 5 h) and long (ca 6 h) duration. Short low tides obviously occur when mean water levels are relatively high (Fig. 4a) mainly related to westerly winds sweeping the water into the Wadden Sea. During such short low tides, less surface area of the mudflat is exposed (Fig. 4b) although the usable area of the musselbank (the area covered by 1 to 8 cm of sea water; cf. Koene & Drent, 1981) attains the same maximum extension (Fig. 4c). The numbers of oystercatchers present on the bank (Fig. 4d) runs parallel to the usable area. In long tides there is a bimodality in the curve, suggesting that around the time of low water some oystercatchers left the observation area, probably in search of other musselbanks outside. With short low tides a lower maximum number of oystercatchers is observed. We have evidence (Fig. 7) that in such conditions some birds remain inland. The density of oystercatchers (per ha) is lowest around LW (Fig. 4e), due to the maximum extension of exposed mudflat at that time. Following ebb tide, there is a progressive increase in the fraction of birds engaged in
foraging activities (Fig. 4f) such that this fraction culminates at 80 to 90% ca ½ hour after LW, about the time when oystercatchers density is lowest. We assume that these figures can be treated as estimates of individual frequency of foraging, except during the initial increase phase and during the terminal decrease phase of the mudflat oystercatcher population. At these initial and terminal phases part of the population was inland and hence not foraging on the mudflat. If we take into account the rising and falling slopes of the curves in Fig. 4d, foraging frequency counts (Fig. 4f) lead to estimates of individual foraging ac-
tivity (Fig. 4h). The yield of foraging was obtained by translating the fraction of birds handling prey in all counts into capture rates, using average handling times per prey. Yield was then expressed in gram ashfree dry weight per minute of foraging. This could be done as prey size selection and dry prey weights were known for the same situation (Koene & Drent, 1981). There are neither conspicuous variations in the course of the tide nor important differences in yield between tides of different duration (Fig. 4g). For translation of individual foraging frequency (Fig. 4h) into overall intake rate we have therefore used a constant yield of 105 mg per minute foraging (Fig. 4h, inserted scale).

The curves of individual intake rates (Fig. 4h) are obviously different for tides of different duration. Shorter tides allow for less intake, not only because the total time available is less, but also because maximum foraging frequency is reduced. The latter effect is due mainly to increased oystercatcher density on the bank in short tides which leads via predator interference to a smaller fraction of birds engaged in foraging (Goss-Custard, 1980; Koene & Drent, 1981). Thus the duration of tidal flat exposures has two cumulative effects on food intake of oystercatchers, via total area and hence prey available, and via duration of its availability. The added effects (Table I) indicate that considerable variation in total food intake is induced by variation on the length of the tides. We should not expect that such degree of variation is characteristic of the total amount of daily food intake in freeliving birds. There is evidence that this variation is compensated to some extent by foraging behaviour inland. On the island of Texel, the population of oystercatchers studied customarily foraged in meadows behind the dike, around the tidal roost (see Fig. 1). This was rule rather than exception especially in the first 2 hours and the last 2 hours of the daylight (Fig. 5).

<table>
<thead>
<tr>
<th>Parameters (units)</th>
<th>Duration of low tide (h):</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.5-3.5</td>
</tr>
<tr>
<td>Number of tides</td>
<td>2</td>
</tr>
<tr>
<td>Number of 15 min bird counts</td>
<td>23</td>
</tr>
<tr>
<td>Mean number (birds)</td>
<td>23.6</td>
</tr>
<tr>
<td>Mean density (birds·ha⁻¹)</td>
<td>258</td>
</tr>
<tr>
<td>Mean foraging frequency (% birds)</td>
<td>73.8</td>
</tr>
<tr>
<td>Mean foraging yield (mg·min⁻¹)</td>
<td>99</td>
</tr>
<tr>
<td>Mean foraging activity (% time)</td>
<td>38.4</td>
</tr>
<tr>
<td>Total food intake (ADW·tide⁻¹)</td>
<td>6.9</td>
</tr>
</tbody>
</table>
Foraging in early morning was only infrequent when a nocturnal low tide had just preceded dawn. These patterns suggest that foraging inland near the roost was an exclusively diurnal affair, whereas mussel-banks at low tide may have been exploited both day and night. We have not been able to quantify the food intake inland as we did on the mussel-banks. The birds probably ate mainly earthworms here, but yields of foraging remain unknown. If they have been generally as constant as on the musselbank (Fig. 4g) then fractions of foraging birds would be proportional to intake rates per high water period per individual. The average fraction of oystercatchers foraging inland steeply declines with increasing duration of the preceding low tide (Fig. 6). This correlation strongly suggests that at least the short low tides were insufficient to supply the birds with their total daily needs, and that additional foraging inland was necessary under such circumstances.

In extremely short low tides some birds even don’t take the trouble at all to fly out, but remain inland instead. This was seen for instance in the afternoon of October 7, 1975 (Figs. 2 and 5). In such circumstances the fraction of foraging birds around the roost again was elevated (Fig. 7).

![Diagram](image-url)

fig. 5. Foraging activity on the inland roost as a function of time of day; Texel 1975. Indicated are the percentage of oystercatchers engaged in foraging on the pastures inland (black) and absence of birds inland (white). Bottom bar gives the overall foraging frequency inland.
4. ANTICIATION OF LOW TIDE: IN THE FIELD

The data discussed above indicate that the duration of foraging on the musselbanks may be of critical importance for the oystercatchers. Obviously, accurate timing of tidal migration seaward and landward would contribute to maximum exploitation of the low tide. Coming too late would encroach on the total intake on the mudflat during low tide. Coming too early would force them to return inland as there would be

Fig. 6. Fraction of oystercatchers foraging on the inland roost during high tide (%) as a function of the duration of the preceding low tide (hours). High tides were restricted to hours of no exposure of the mudflat and to tides when at least two complete hours of data (24 counts) were collected; Texel 1975. Line shows linear regression \( Y = 86.39 - 8.57 X; r = -0.71; p < 0.01 \).

Fig. 7. a. Numbers of oystercatchers on the inland roost during low tides (hours) durations of 3, 4, 5 and 6 hours. b. Fraction of birds engaged in foraging on the inland roost during the low tides of different duration. Texel 1976.
no place to land. How do oystercatchers “know” when the tide is out? Do they have and directly use information on the water movement itself? Or is some endogenous timing system involved?

We can extract part of the answer by comparing the birds’ behaviour under spontaneous natural variations in tidal exposure of the mussel-beds. Depending on meteorological conditions and resulting water level, relative times of exposure of the musselbanks vary considerably: The tip of the musselbank may appear (at time E) from 1 till 5 hours after tabulated high water (H). With very early exposure—as on Oc-

![Diagram](image_url)

Fig. 8. Times of exposure of the mudflat (E to C) and median departure time of oystercatchers of the roost (R; ●) in relation to tabulated times of high (H; ▲) and low water (L; ▼). Texel 1975.

tober 11 and 12, 1975 (Fig. 8)—the oystercatchers may arrive 2 to 3 hours after E on the musselbank. With late exposure the modal bird (F) crosses the dike already before there is any place to fly to (October 7). This trend, of relatively late migration when the flat is exposed early, is supported in all three series of observations (Fig. 9a, b and c). It is statistically not significant in the data of Texel 1975 (shown in Fig. 8), but highly significant in the other two series (Fig. 9b and c). It suggests that the oystercatchers did not use incidental variations in water level to adjust their flying times directly. However, this conclusion is not really convincing since we are comparing $y = (D-E)$ with $x = (E-H)$ and any error in $E$ determination would result in a negative correlation between $x$ and $y$. This casts some doubts on the applicability of the rank correlation test we used.
A better statistical approach is suggested if we rephrase the question asked: Is the median departure time (R) predicted better by tabulated high water (H) than by the realized musselbank exposure (E)? To answer this question we have to take into account that times of high water shift across the day with variable speed (Fig. 8). Thus, we compare the day-to-day shift in the medium departure time (ΔD) with the daily shifts in H and E (ΔH and ΔE, respectively; see Fig. 10).

It turns out that ΔD is significantly positively correlated with ΔH (Fig. 10a), but not so with ΔE (Fig. 10b). Keeping the other variable constant in multiple regression analysis has no effect on this outcome (Table II). ΔD is further negatively correlated, but not significantly, with ΔC, the daily shift in the time at which the mudflat was previously covered by the incoming tide (Fig. 10c).

These data, in our opinion, strongly support the view that oystercatch-
er movements are more accurately predicted by local tide tabulations than by the actually realized times of exposure of the mudflat. Although there would be many possible cues to inform the birds about tidal water movements—such as smell of the exposed mudflats, movements of gulls dropping mussels on the tarmac surfaces of the dike, etcetera—we have to conclude that none of these actually trigger tidal migration. If the tide is early, the oystercatchers remain idly on the inland roost while their main food source goes unexploited. If the tide is late, many fly seaward long before the mussels can be harvested and have to return unrewarded. Usually, the variations are small and only little harm is done indeed. The birds’ behaviour in responses to them, however, illuminates how they time their foraging flights and thus achieve maximum exploitation of the average length of the low tide.

Fig. 10. Daily shifts in departure time (ΔD) plotted against daily shifts in various tidal parameters: a. high water (ΔH); b. mudflat exposure (ΔE); c. mudflat coverage (ΔC). Solid lines are simple linear regressions (all data; dashed line in a. indicates partial regression for ΔE constant; dashed line in b. indicates partial regression with ΔH constant; for regression statistics see Table II).
TABLE II
Dependence of the daily shift in departure times (ΔD) on the daily shifts in various parameters of tidal movements (ΔH shift in tabulated high tide; ΔE shifts in mudflat exposure time, ΔC shift in mudflat coverage time as in Fig. 10a to c).

<table>
<thead>
<tr>
<th>Lines</th>
<th>Pearsons product-moment correlation</th>
<th>Spearman's rank correlation</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>r</td>
<td>p</td>
<td>r</td>
</tr>
<tr>
<td>ΔD = 0.24 + 0.59 ΔH</td>
<td>0.34</td>
<td>&lt; 0.01</td>
<td>0.35</td>
</tr>
<tr>
<td>ΔD = 0.62 + 0.11 ΔE</td>
<td>0.17</td>
<td>&gt; 0.1</td>
<td>0.22</td>
</tr>
<tr>
<td>ΔD = 0.23 + 0.62 ΔH - 0.02 ΔE</td>
<td>0.34</td>
<td>&lt; 0.05</td>
<td>-0.02</td>
</tr>
<tr>
<td>ΔD = 0.87 - 0.19 ΔC</td>
<td>-0.17</td>
<td>&gt; 0.1</td>
<td>0.04</td>
</tr>
</tbody>
</table>

5. ANTICIPATION OF LOW TIDE: IN THE AVIARY
We have done two experiments to test if captive oystercatchers can anticipate times of food availability. The experiments were carried out in the aviaries of the Netherlands Institute for Sea Research (NIOZ). Four cages, each housing a single oystercatcher, were used simultaneously. Each cage (Fig. 11) was provided with a feeding tank (60 × 30 × 30 cm) full with running sea water and reachable from one side over a sandy slope. This tank was located close to an observation hide at the non-preferred side of the cage. In the distant part, two basalt blocks...
provided roosting posts. Food was presented by placing fresh mussels at the bottom of the feeding tank at more or less random times of day. The mussels were unavailable in ca 28 cm of water, but a pump, turned on by a switching clock, emptied the tank at preset times within ca 20 minutes which gave the bird access to the food. The mussels remained in a few centimeters of sea water for ca 3 hours, when the pump was turned off and the water level automatically rose from a sea water tap. Neither the mussels nor the water level could be seen from the far end of the cage where the birds spent nearly all of their time unless when they went looking for food in the tank.

We recorded on an Esterline Angus event recorder each time a bird crossed a line half way across the slope. This was done by visual observation from the observation corridor behind the cages in a pilot series of experiments (September 28 to October 19, 1975). These observations were restricted to several hours around the time of low water. In a final

Fig. 12. Sample records of feeding attempts (per 1/2 hour) in 2 caged oystercatchers in natural daylight conditions (outdoors). Firstly, 2 day of continuous food availability are shown (March 10, 11), and from March 17 onwards, food availability was restricted to two 3-hour periods per day (hatched bars): a. at fixed clock hours, with a phase shift on March 24; and b. at clock hours shifting 0.8 h per day.
series (March 10 to 28, 1977) visits to the feeding tanks were continuously monitored using an infrared light beam across the talud. Fig. 12 illustrates the experimental protocol as well as results for 2 of the 4 birds. Two birds were exposed to a food schedule in which the "tide went out" twice a day at 6.00 h and at 18.00 h, or—after a phase shift in the schedule on March 24—at noon and midnight. Simultaneously, the other 2 oystercatchers experienced a schedule with food availability times delayed by 0.8 hours every day. In all birds, one low tide period was skipped on March 24 to judge whether food deprivation increased the frequency of visits to the tank, which it did not obviously. Empty mussel shells were strewn by the oystercatchers all through the cage, but especially in the preferred distant part of it. They revealed that feeding occurred during both the diurnal and the nocturnal "low tides". Total daily food intake was 36 gram ash free dry weight, in close correspondence with values in experiments by Hulscher (1974). On this the birds retained their body weight during the experiment (Table III).

<table>
<thead>
<tr>
<th>Bird</th>
<th>Sex</th>
<th>Body weight (g)</th>
<th>Daily food intake</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>4 March 30 March</td>
<td>Mussels (numbers)</td>
</tr>
<tr>
<td>1</td>
<td>?</td>
<td>516 466</td>
<td>35.4 ± 4.0</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>522 519</td>
<td>46.6 ± 4.6</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>483 521</td>
<td>48.4 ± 3.9</td>
</tr>
<tr>
<td>4</td>
<td>♀</td>
<td>505 512</td>
<td>46.1 ± 4.6</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>507 505</td>
<td>44.1 ± 2.2</td>
</tr>
</tbody>
</table>

The records of Fig. 12 demonstrate for both birds a slight increase in the frequency of visits to the feeding tank in anticipation of the time of low tide. The anticipation was most pronounced for the bird exposed to the shifting tide; both the nocturnal and the diurnal low tides were preceded by an increase in the number of visits to the feeding tank, although this anticipation was more obvious for the daytime tide. In the other bird feeding times seemed to be preceded by increased activity equally in the morning and evening. On the 24th, after a change in the schedule, there were peaks in feeding attempts around 6.00 h and 20.00 h, thus at the times of prior food availability. After this phase shift there was no clear return of a pattern of anticipatory activity associated with the new schedule.
The results are summarized quantitatively for both birds on each feeding schedule together in Fig. 13. In both schedules, we see that the largest average numbers of light beam interruptions in the 6 hours before low tide occurred in the last half hour. This peak in feeding attempts around the expected time of food availability was most obvious in the diurnal tide of the shifting schedule (Fig. 13b) and in the 18.00 h tide of the fixed schedule (Fig. 13a). The nocturnal and early morning feeding time were less clearly anticipated. This may be related to a negative influence of darkness on the willingness of the birds to approach the feeding tank. Comparing the time course of anticipatory activity in daytime in the two schedules, we see that the increase towards the peak started 3 hours before low tide in the shifting schedule and only 1.5 hours in the fixed schedule. Such differences are certainly in need of confirmation.

On March 29, 1977, the water pumping system broke down due to freezing. When the frost was over and the system repaired, the cages had to be used for a different purpose. A more conclusive follow-up of these pilot experiments remained in the planning stage. The data are
nevertheless helpful to suggest possible mechanisms behind the endogenous timing of foraging.

6: DISCUSSION: HYPOTHETICAL TIMING MECHANISMS

Oystercatchers fly out to tidal mudflats around the time of expected ebb tide. They do so apparently without seeing the tidal water movements and without using other signals directly associated with these. When the tide is late, the oystercatchers fly early, when the tide is early, the birds are too late. Some timing stimulus, whether internal or external, triggers their foraging flights. What can this be?

The literature is of little help. PALMER (1974) mentions only one bird in his extensive review, the Australian Reef heron which similarly would fly from an inland rookery to the sea at low tide. Its behaviour seems not to have been studied, however, and the reference was lost (PALMER, in litt.). Many studies deal with foraging by birds in the intertidal in relation to tidal cycles (e.g. Goss-Custard, 1969; Delius, 1970; Slater, 1976; Evans, 1979), but the question of timing has apparently not been raised. For analogies, we may, however, look into the vast literature on the rhythmic organization of fishes and invertebrate organisms living in the intertidal zone itself (Palmer, 1974; De Coursey, 1976; Naylor & Hartnoll, 1979; Neumann, 1981).

Many marine organisms in the intertidal possess endogenous circatidal rhythmicity. Such a timing system allows a juvenile plaice to leave the mudflat in advance of the falling tide (Gibson, 1973), isopods to bury in the sand before they can be washed away by the surf waves (Enright, 1963) and a limpet to rush home before being exposed by the ebb to dehydration on foreign ground (Funke, 1968). They exhibit periodic changes in their behaviour which persist in constant conditions with a frequency of about once per 12½ hours. Quite frequently, there are systematic differences between alternating peaks in e.g. locomotor activity. It is then preferable to consider the rhythm as one with a basic period of about 25 hours and a bimodal distribution of activity per cycle. PALMER (1973, 1974) has emphasized this point. He introduced the term "circalunadian" for such rhythms, since the basic period approximates the lunar day rather than the solar day. This is quite often appropriate both in view of the fact that the two daily tides are commonly unequal on many shores and because organisms have developed asymmetric activity distributions adaptive to this inequality (Enright, 1972). Some researchers (e.g. Gibson, 1973) have suggested that the oscillator responsible may be basically of circadian nature. Indeed in constant conditions we can not distinguish between circadian and circalunadian rhythms. They both will exhibit spontaneous free-running
periods well within the *circa*-ranges of both 24.0 and 24.8 hours. The only sensible discriminating criterion seems to be the frequency to which they are entrained in the natural environment. This criterion would imply restrictions on the sensitivity to various zeitgebers. In contrast with circadian systems, a circalunadian oscillator should generally be insensitive towards light and darkness as a zeitgeber. It should exhibit a phase response to stimuli like pressure, turbulence, wave action, perhaps even gravity itself, or any other signal associated with the tides in order to keep synchrony. LD-sensitivity for a circalunadian rhythm would interfere with its function, just like tide-entrainment would interfere with circadian function. Few phase response curves have been described for intertidal organisms. The isopod *Excirnana chiltoni* shows phase shifts in response to mechanical wave action (*Enright*, 1976) and a similar response is known in the intertidal midge *Clunio marinus* (*Neumann*, 1981). In tidal birds no such information is available. Yet the theoretical distinction between circadian and circalunadian systems on the basis of zeitgeber sensitivity is useful for a discussion of potential mechanisms of tidal anticipation.

There are at least 5 types of mechanisms capable of generating tidal anticipation of the kind described in this paper for the oystercatcher: exogenous cues; hourglass timer, circatidal, circalunadian or circadian timers.

**Exogenous cues.**—In principle, the birds might use some geophysical factor varying throughout the day in association with the tides. This could not be related directly with the water level, but there might be variations like in gravity or atmospheric density associated with the rotation of the moon around the earth. Effects of the moon on animal behaviour are well known, although they mostly deal with direct influences of moonlight (*e.g.* *Jahoda*, 1973; *Neumann*, 1981). In daytime the phase of the moon affects for instance orientation in homing pigeons (*Larkin & Keeton*, 1978). The use of hitherto unknown factors for temporal orientation in oystercatchers can hence not be excluded.

Other knowledge of avian timing systems (*Gwinner*, 1975) does not precisely make such a hypothesis intuitively appealing. Tests should produce a demonstration of rhythms in constant conditions free-running with frequencies different from known geophysical cycles, or alternatively, positive identification of the environmental factor responsible.

**Hourglass timer.**—If there is no exogenous cue responsible, there should be some internal signal. The simplest timing systems are of the hourglass type: non-repetitive. One’s initial guess might be that the
Oystercatchers return to the mudflat when they are hungry, *i.e.* after a certain period of digestion of the stomach content collected during the previous low tide. Such a mechanism is unlikely on several grounds. Firstly, the birds do forage quite regularly also on their roost meadow inland during high tide (Fig. 5), apparently “hungry”, but not taking the trouble to fly out to sea. Secondly, in our aviary experiments, after skipping a single tide (and hence food deprivation of the birds) there was no increase in feeding attempts but this increase came as usual at the expected time of the next meal (Fig. 12). Thirdly, the day-to-day variations in the incoming tide—*i.e.* the time at which the mudflats were covered and the birds had to finish eating and fly inward—had no predictive value whatsoever for the timing of the next seaward flight (Fig. 10c).

Hourglass timers are not exactly popular among animals coping with a periodic environment. They are incidentally adequate: for an intertidal example see Pflüger (1973). However, most animals have evolved rhythmic timers or clocks which render them less dependent on occasional vagaries in the environment.

Circatidal timer.—A true circatidal rhythm has a period of *ca* 12.5 hours, and hence should not exhibit systematic differences between tidal cycles per day. Such asymmetries were clearly present in our oystercatchers in the aviary (Fig. 13b). The anticipation patterns have no correspondence between consecutive tides but correlate in intervals of two tides (Fig. 125). A circatidal timing system, where anticipation of food availability would be dependent on the previous low tide is therefore unlikely. A crucial test would involve exclusion of the interference of the natural light-dark cycle, and attempt to demonstrate in constant conditions effects of food availability on anticipatory behaviour in *ca* 12.5 hours intervals.

Circalunadian timer.—A 24.8 hour periodicity is certainly present in both the field and the aviary data, and it is possible that this is the product of an endogenous pacemaker running with that frequency. In view of the distinction with circadian timers made above, a test of the circalunadian hypothesis should demonstrate phase insensitivity of the system to light-dark stimuli, and identify the stimuli associated with the moon cycle which keep it from drifting away.

Circadian timer. Clearly the rhythmic behaviour of the oystercatchers discussed has a period deviating from 24 hours. Yet it is not excluded that a circadian timing mechanism, synchronized to 24 h by the light dark cycle is responsible. We have seen by a shift in the food restriction
time (Fig. 12a) indications that increased activity occurs in the clock hours of food availability on the previous day. One day later the effect has gone. If a circadian timer running at 24 hours would each day induce activity at the time of meals on the previous day, but reveal nothing about meal times 2 or more days ago, a shifting anticipatory pattern would be predicted, almost exactly as observed in Fig. 12b.

There is precedence for such induction of patterns in circadian behavioural systems due to both feeding schedules (e.g. Bolles & Moot, 1973; and in birds Stein, 1951) and single experiences (Holloway & Wansley, 1973). This is not restricted to locomotor activity but may affect highly specific behaviours and decisions (Beling, 1928; Daan, 1981 for review), as well as physiological detail such as intestinal enzyme activity which increases in association with “expected” food (Stevenson et al., 1975; Suda & Saito, 1979). Demonstration of such a system as the basis for timing of oystercatcher foraging flights would require phase shifts in the anticipatory behaviour induced by light treatments. The hypothesis that a circadian timing system may also be used for anticipation of a tidal food source obviously requires further investigation. It’s demonstration would extend the range of functional exploitation of circadian rhythms to the tidal environment as a specific case of predictability of events on the basis of yesterday’s information.

7. SUMMARY

The tidal movements of flocks of oystercatchers foraging on mudflats at low tide and roosting inland behind a dike at high tide were studied and the effects of day-to-day variations in the time of mudflat exposure by ebb analysed.

High mean water levels and short low tides led to reduced intake during low water due to increased bird densities in addition to temporal constraints (Fig. 4). Increased feeding around the roost apparently compensated for some of the reduced intake (Figs 6 and 7) although accurate intake measurements could be made for foraging on the tidal flats only. It is argued that optimal timing of foraging flights to coincide with exposure of the mussel banks would contribute to exploitation of this tidal food source.

The median departure time from the roosts relative to the time of mudflat exposure was early on days when the tide went out late and late when the tide was early (Figs 8 and 9). Daily variations in departure time were predicted by the daily variations in tabulated high water times, but not by variations in mudflat exposure or coverage (Fig. 10). The conclusion is drawn that the birds employ a timing mechanism not directly associated with the tidal water movements.
In some pilot experiments in caged oystercatchers, feeding schedules elicited feeding attempts in anticipation of expected food. The anticipatory patterns were different for fixed and tidally shifting daily food schedules, and moreover differed between the two feeding times per day (Figs 12 and 13).

Five possible mechanisms for tidal anticipation are discussed, making use either of unknown exogenous cues, or of—likewise unknown—endogenous timers of hourglass type or rhythmic with circatidal, circalunadian or circadian period. Experimental tests for these possibilities are outlined.

8. References


