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## Localisation of cockles (*Cardium edule* L.) by the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight

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**LOCALISATION OF COCKLES (*CARDIUM EDULE* L.) BY THE  
OYSTERCATCHER (*HAEMATOPUS OSTRALEGUS* L.) IN  
DARKNESS AND DAYLIGHT**

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1. INTRODUCTION

On intertidal flats Oystercatchers feed extensively on the bivalve mollusc *Cardium edule*: the cockle, buried just beneath the substrate surface. Feeding takes place at low tide, by day as well as by night (Drinnan 1957, Hulscher 1964 and 1974, Davidson 1967). How the buried prey is localised by Oystercatchers is an unsolved problem. This also applies to most other waders feeding on sub-terrestrial prey.

In 1966 I made observations in daylight and in darkness (with the aid of infra-red binoculars) of Oystercatchers feeding on cockles on a mudflat under experimental conditions. Results of this study relevant to the problem of localisation of buried cockles are presented in this paper.

2. STUDY AREA AND MATERIALS

The experiments were carried out on the intertidal flats of Schiermonnikoog, a Frisian island in the Dutch Waddensea. A fixed place was chosen on a cockle bed that was exposed 5½ hours (mean) per low water period. The substrate was muddy sand. The main representatives of the

infauna were: the bivalve molluscs *Cardium edule* L., *Macoma balthica* L.; the polychaete worms *Arenicola marina* L., *Nereis diversicolor* O. F. Müller, *Scoloplos armiger* O. F. Müller; the decapod crustaceans *Crangon crangon* L., *Carcinus maenas* L.. The observations were made in eight-sided cages made of cloth, surface area 21 m<sup>2</sup>, height 75 cm. A hide (1 m<sup>2</sup>) was placed outside the cage against one of the corner stakes. The cage walls and the hide were removed after each observation-day, but the stakes were left in position.

All experiments were done with a single adult Oystercatcher (code name W/R) that was caught on 29 May 1966 on Schiermonnikoog while incubating. The primaries of both wings were clipped. When not used for experiments the bird was housed in an outdoor cage and fed with cockles ad libitum. Food was always removed 7 hours before experiments started, corresponding with the average submersion period of the feeding grounds of the free living Oystercatchers.

The bird was transported in a wicker basket with lid, and placed inside the cage at the start of each experiment. The lid of the basket was pulled up with a string from the hide. The bird always jumped out of the basket immediately and lost no time in starting to feed. At the end of an experiment the bird was caught with a moth net and replaced in the basket. During day time observations were made with the naked eye, as the bird was within 1-6 meters distance. In darkness infra-red binoculars were used. All observations were done by the author, dictated notes were jotted down by one or two assistants.

The cockles used for the experiments were taken from the local population consisting of cockles of one yearclass with a fairly uniform size (shell length 25-36, mean 31.4 mm). Cockle density was manipulated by removing or adding a known number of cockles on the investigation area. Freshly added cockles buried themselves within a quarter of an hour and were found not to displace themselves in the horizontal plane. First the local density was measured outside the cage by extensive sampling, then a calculated number of cockles was removed or added according to the experiment planned. Observations started only after the investigation area had been submerged during at least one high water period. At the end of each experimental day the cockles eaten were replaced by the same number of live cockles. During the course of an experiment cockles eaten were not replaced. Experiments in daylight were performed at cockle densities 13, 40, 150 and 450 per 1 m<sup>2</sup>, in darkness at densities 40 and 150. After each series of experiments at a particular density the cockle density in the cage was verified.

### 3. DESCRIPTION OF THE FEEDING BEHAVIOUR

#### 3.1. IN DAYLIGHT

In daylight the bird generally made pecking movements when foraging. Pecks can be classed as single or multiple. A single peck consists of one quick movement of the practically closed bill into the substrate from a few millimeters up to about two centimeters. The bill is usually held at an angle of about 60-80 degrees towards the substrate, though it could also be held at quite low angles down to 15 degrees.

A multiple peck consists of a series of quick movements up and down at about the same place in the substrate with the bill held open about 1-2 mm and at a rate of 3 to 7 pecks per second, without retracting the tip entirely from the substrate. The depth could vary from a few millimeters upto the total length of the bill, on average one third of the bill length. The bill is held at an angle of 70-90 degrees towards the substrate. Single and multiple pecks are placed in front of the walking bird but may be directed to either side of the body. Distinction between both types was usually obvious. Single and multiple pecks alternated frequently at short intervals. About 80% of all pecks are single. Pace rate during pecking was about 1-3 steps per second, peck rate about 0.2-0.4 pecks per second.

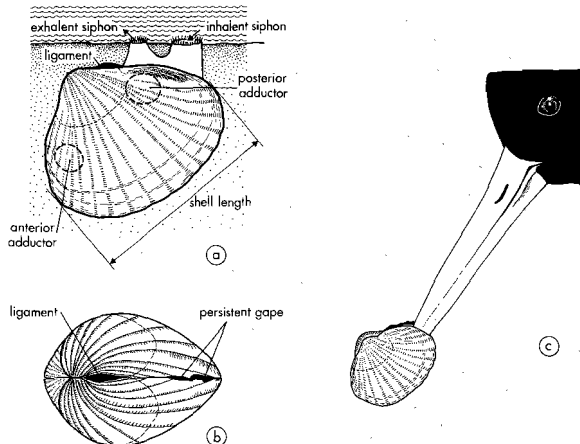


Fig. 1. Cockle buried in the substrate with siphons extended, as seen from the side (a) and from above with siphons retracted (b) showing the persistent gape, point of attack of the Oystercatcher. The cockle may seize upon the bill and is then retracted from the substrate in situ (c), revealing the point of attack of the Oystercatcher.

A cockle is usually localised after a single peck. The bird subsequently tries to pierce the two valves at the "persistent gape", the site of siphon extrusion (Fig. 1b) (Drinnan 1957). Most cockles are attacked by the Oystercatcher from such a position that the persistent gape is in one line between the bill and the ligament. An angle of attack 180 degrees the other way around is less frequent. The angle of attack could be determined precisely in those cases where the cockle was withdrawn from the substrate, shut tightly around the tip of the bill (Fig. 1c). Often the bird reoriented itself before pecking into a cockle. Reorientation could be minute, only a small movement of head and bill, or considerable, including the whole body. Reorientation movements presumably aim to bring the bill in a favourable position with regard to the cockle. Once the bill is pierced into the shell the cockle may be lifted from the substrate and opened after being transported some distance, or it may be opened in situ. In both cases the bird tries to sever the posterior adductor muscle (Fig. 1a) by thrusting the bill through with strong pushing movements. Success in opening a cockle strongly depends on the degree to which the bird manages to sever the posterior adductor at the first jab of the bill.

### 3.2. IN DARKNESS

Localisation of cockles in darkness is quite another story. I have called the technique applied "sewing" because the movement of the bill makes me think of the industrious up and down movements of the needle of a sewing machine.

When the bird commences it makes one or two steps forward, then it places the bill at an angle of about 70 degrees into the substrate, and continues to walk in a straight line at a rate of one to two steps per second, while the bill makes quick "sewing" movements in the substrate at a rate of about four to six per second to a depth of two centimeters at the most. The sewing procedure stops abruptly, presumably when a cockle is touched. Often reorientation movements and trials to open the cockle, as described for daylight, follow. This change in behaviour was usually quite obvious and was used as criterion that a cockle was localised. The sewing process makes characteristic straight furrows in the mud surface. Furrows up to a length of about 150 cm were made. If the bird changes direction in sewing the bill is retracted from the substrate first and subsequently re-inserted after the change of direction.

Sewing trials can be counted very easily. An interesting point is that my experimental bird now and then switched to the nocturnal sewing technique in daylight when feeding on low cocle densities (13 and 40/m<sup>2</sup>).

#### 4. FEEDING EXPERIMENTS WITH THE OYSTERCATCHER

##### 4.1. OBSERVATION METHODS

The bird was allowed to feed during an observation period amounting to 100-240 minutes. In daylight the behaviour of the bird was observed and recorded continuously, in darkness however, observations and recordings were made at irregular intervals.

The following recordings were made. Per minute: total number of sewing trials and number of steps per registered number of sewing trials; number of single and multiple pecks; number of cockles localised, eaten and not-eaten when either pecking or sewing; number of other prey consumed; time (measured with a stopwatch in seconds) spent in handling either cockles consumed (irrespective of their manner of localisation), or other prey consumed (handling a consumed prey was measured as the continuous time spell between the moment of first attack till the swallowing of the last remains of that prey); handling time of prey not eaten was not measured. Per ten minutes: time (measured with a summing stopwatch in seconds) spent in sewing and in non-feeding activities (the latter only in daylight).

##### 4.2. MEASURING LINEAR DISPLACEMENT OF THE SEWING BILL

In order to be able to analyse the sewing technique knowledge of the linear distance the tip of the bill moves through the substrate is required. This distance can be estimated by multiplying mean walking rate with mean step length, or by multiplying sewing time with the mean displacement rate of the bill. Step length can be measured by counting the number of steps,

displacement rate by counting the number of seconds, both with respect to a known distance. Both methods require a set of reference points to be passed by the bird, arranged transversely in front of the observer. A set of little sticks, 50 cm apart, in a cross or grid pattern, was tried in vain. The bird was hindered too much by the sticks and determinations in darkness with the infra-red binoculars were entirely impossible. However, I managed to collect some measurements at very early dawn with the naked eye, when the bird still exhibited the nocturnal sewing behaviour. In this case reference sticks were placed along the cage walls.

On July 15, 1966, at cockle density of  $40/m^2$ , the bird moved its bill over a distance of 2270 cm in 163 seconds, giving a displacement rate of 13.9 cm/sec. The simultaneously determined mean walking rate during sewing (over 150 seconds) was 1.69 steps/sec, resulting in a mean step length of  $13.9 : 1.69 = 8.2$  cm. In June 1967 I once again made observations on step length at early dawn at the same site as in 1966. Now four strings were strung parallel, 50 cm apart, right across the cage at the height of the bird's breast. Along two lines reference sticks, 50 cm apart, were placed. For a total of 105 steps the "sewing" bird required 855 cm, which makes a mean step length of  $855 : 105 = 8.2$  cm, identical to that obtained a year before.

## 5. LOCALISATION OF CARDIUM IN DARKNESS

### 5.1. RANDOM-SEARCHING HYPOTHESIS

Searching behaviour in darkness — the use of the sewing technique — suggests a chance encounter with cockles. In order to verify this supposition

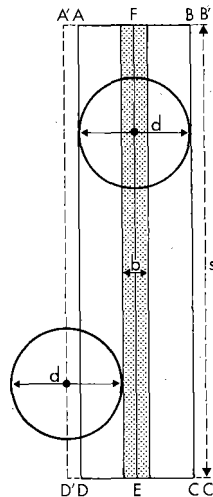


Fig. 2. Scheme for calculating the number of cockles localised during sewing. Further explanation in the text.

one has to know the surface area of the buried cockles in the horizontal plane (Fig. 1b). I photographed cockles of different size partially inserted in the buried position from above and measured their surface areas with a planimeter. The surface area was found to be 0.42 times the shell length squared (Fig. 1a). In the following calculations for the hypothesis of random searching I substituted for the matter of ease the more or less elliptical surface area of a cockle by a circular one of the same size, having a diameter of 0.37 times the shell length. Theoretically one can now calculate the number of cockles encountered per known distance of sewing. Assume that all cockles are of equal size, and the bill penetrates the substrate at least to such a depth that no cockle in its path can escape detection. If the bill sews  $s$  cm (Fig. 2) through the substrate, then all cockles with their centres inside the rectangle A B C D will be localised, but a cockle with its centre just beyond this rectangle will be missed. The area of the rectangle is determined by the distance ( $s$ ) and the diameter of the cockles ( $d$ ). However, the width of the bill at the tip must not be neglected in the calculations, measuring 1-2 mm in Oystercatchers. According to Heppleston (1970) a concentration of touch corpuscles (of the Herbst type) occurs on the lateral sides of the bill over a distance till 15 mm from the tip. Therefore one can reasonably presume that cockles can be localised by the bill beyond the tip. If the width of the bill is  $b$  cm, then (Fig. 2) all cockles with centres within A'B'C'D' will be localised if the bill sews over  $s$  cm. This corresponds with an area of  $s \times (d + b)$  cm<sup>2</sup>. If the cockle density ( $D$ ) is known, the number ( $N$ ) of cockles that must be localised can be calculated as  $N = s \times (d + b) \times D \times 10^{-4}$  (1);  $s$ ,  $d$  and  $b$  in cm,  $D$  in cockles/m<sup>2</sup>. Although the width of the bill ( $b$ ) as measured in my bird was 0.1 cm, the furrows on the mud surface averaged 0.5 cm (see 5.2.1). In my calculations I have employed both values, to give a range rather than a discrete number, as the expectation.

## 5.2. TESTING THE RANDOM-SEARCHING HYPOTHESIS IMITATING THE SEWING BIRD

### 5.2.1. On the cockle beds

I experimented with an Oystercatcher bill on the cockle beds with densities of 40 and 150 cockles/m<sup>2</sup>. The head was attached to a pin with a string of 70 cm length. I pricked the pin arbitrarily into the substrate, then I stuck the tip of the bill into the substrate next to the pin about two cm deep, and subsequently moved the bill through the mud away from the pin, imitating the sewing technique as well as possible, till the string was stretched. I jotted down the number of cockles that was touched and marked their exact places with thin sticks. The presence of the cockles was verified by digging them up afterwards. This procedure was repeated many times. At density 40 a distance of 4060 cm was covered, at density 150 4340 cm. The groove the bill made through the substrate was about 5 mm wide. By

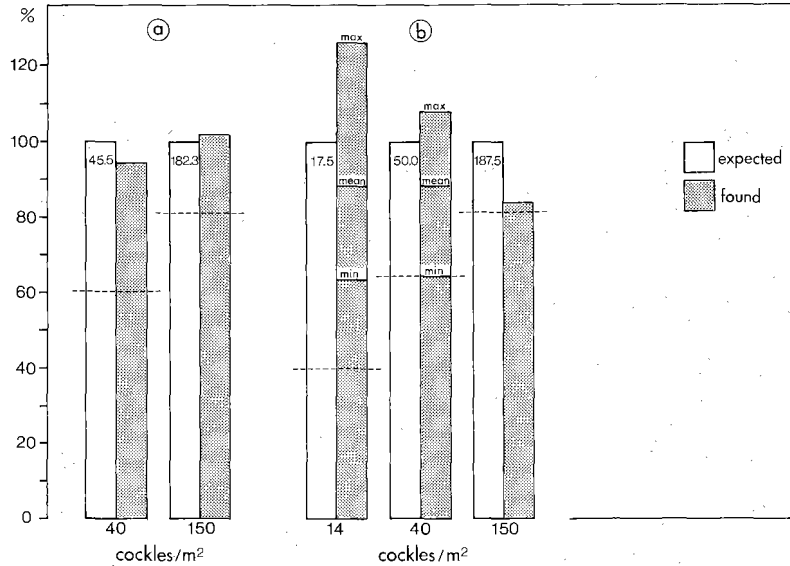


Fig. 3. Number of cockles found as percentage of the expected number when imitating the sewing technique over a known distance; bill width taken as 5 mm.

(a): With an Oystercatcher bill on the cockle beds, (b) on paper. At densities 14 and 40 minimum, maximum and mean number of cockles found is indicated for 8 experiments; for density 150 the outcome of one experiment is given. Figures under the top of the bars indicate the mean expected number of cockles; broken lines the lower limit of the 99% confidence intervals of the expected mean.

substituting in formula (1) for bill width ( $b$ ) = 0.5, the number of cockles that can be expected to be touched can be compared with the number found (Fig. 3a). There was a striking agreement between both groups.

### 5.2.2. On paper

A total of 150 "circular" cockles (assigned a number from 1-150) were randomly distributed over a piece of paper of one square meter (cockle density 150/m<sup>2</sup>), with the restriction that cockles did not overlap. The diameter of the cockles was 2.3 cm conforming to the diameter of the modal cockle of the population the Oystercatcher was feeding upon. In imitating the sewing technique a pencil was placed on the paper at a randomly chosen site and a straight line was drawn across the rest of the field in a direction randomly chosen from one of the sixteen directions of the compass. The number of cockles touched within the area up to 2.5 mm to either side of the pencil line was counted, representing the path covered by a bill with a width at the tip of 5 mm. The identity of the cockles touched was noted. This procedure was repeated many times. In total a distance of 4463 cm was covered across the "cockle field". Subsequently fields with densities of 14



and 40 cockles per square meter were simulated. In eight series I grouped together 14 and 40 cockles respectively of the original 150 numbered cockles and checked from my notes how many cockles in these groupings had been hit. Results for these density classes were thus obtained from the original "pencil predator" in the 150/m<sup>2</sup> series.

Because the cockles were randomly distributed the numbers of cockles that can be expected to be touched over a known distance covered by the pencil, follows a Poisson distribution from which the standard deviation equals the square root of the mean (s.d. =  $\sqrt{m}$ ), and the 99% confidence interval of the mean is found by  $2.58 \sqrt{m}$ . The mean can be calculated by

Table 1. Summary of the observations on feeding behaviour of the caged Oystercatcher at different prey densities and under different light conditions.

Cockles per m <sup>2</sup>	Light conditions	Total observation (minutes)	Number of							
			sewing trials	steps during sewing	pecks					
1	2	3	4	5	6					
13	daylight	550	1142	5132	1819					
40	darkness	292	2182	13063	84					
40	daylight	310	435	—	3458					
150	darkness	317	1862	6603	118					
150	daylight	480	—	—	4259					
450	daylight	480	—	—	5824					
		Searching time (seconds)		Handling time (seconds)		Non-feeding time (seconds)				
		sewing	%	pecking	cockles eaten		other prey eaten			
		7	8	9	10		11			
13	daylight	3001	25.6	8704	872	92	20326			
40	darkness	6372	—	—	1601	339	—			
40	daylight	805	7.5	9957	1657	49	6132			
150	darkness	3475	—	—	2482	90	—			
150	daylight	—	—	12603	2831	238	13128			
450	daylight	—	—	12693	3598	438	12071			
		No. of cockles localised								
		sewing				pecking				No. of other prey eaten
		eaten	%	not eaten	%	eaten	%	not eaten	%	
		13	14	15	16	17	18	19	20	
13	daylight	6	4.3	134	95.7	18	27.3	48	72.7	30
40	darkness	34	5.5	590	94.5	3	—	1	—	5
40	daylight	2	2.3	84	97.7	46	20.2	182	79.8	7
150	darkness	69	12.1	500	87.9	4	—	—	—	4
150	daylight	—	—	—	—	96	30.9	215	69.1	24
450	daylight	—	—	—	—	116	48.5	123	51.5	18

formula (1), where  $s = 4463$ ;  $d = 2.3$ ;  $b = 0.5$  and  $D = 14, 40$  or  $150$ . From figure 3b it can be seen that for densities 14 and 40 the mean and the total range in the number of localised cockles found with eight trials falls within the 99% confidence interval of the expected mean number. The same pertains for the one trial at density 150.

### 5.3. RESULTS OF THE OYSTERCATCHER WHILE SEWING

Table 1 summarizes all data (pooled per density) of the feeding behaviour of the Oystercatcher in darkness and in daylight. The results of sewing and pecking are included in one table because in daylight at low cockle densities both techniques occurred together.

The number of cockles that can be expected to be localised by the bird is calculated in two ways: based on the number of steps in combination with mean step length and based on total sewing time in combination with mean displacement rate of the bill. For mean step length 8.2 cm is taken, for mean displacement rate 13.9 cm/sec, assuming no differences in these parameters while sewing at different cockle densities or under different light conditions (see above). The expected numbers of cockles are calculated with formula (1), using for bill width (b) a range of 0.1 to 0.5 cm, corresponding

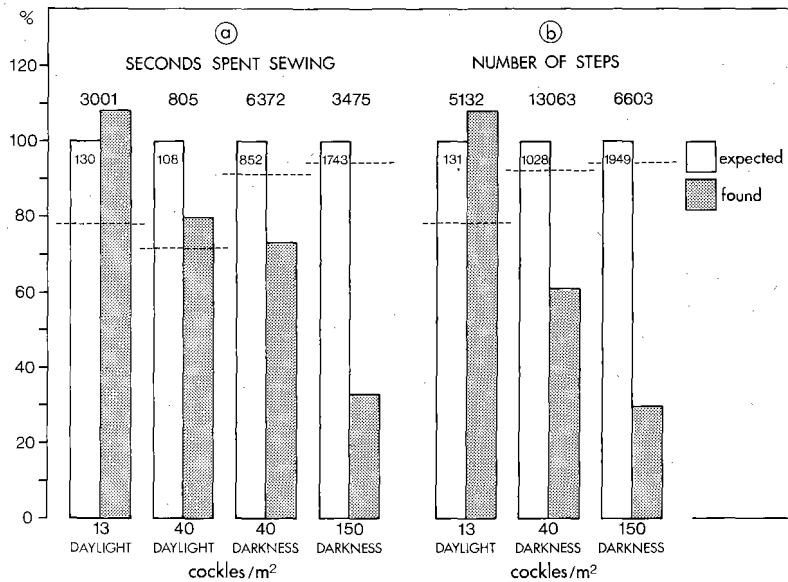


Fig. 4. Number of cockles found by the Oystercatcher as percentage of the expected number when sewing on the cockle beds (bill width taken as 1 mm).

(a): Based on total sewing time and displacement rate of the bill.

(b): Based on total number of steps and mean step length.

Figures under the top of the bars indicate the mean expected number of cockles; broken lines the lower limit of the 99% confidence interval of the expected mean. See also Table 1.

respectively with the actual width at the tip and the breadth of the groove in the substrate when I was imitating the sewing technique with an Oystercatcher bill. The lower limit of the 99% confidence interval of the mean is calculated for a bill width of 0.1, the upper limit for a bill width of 0.5 cm. The results are depicted in figure 4a and b.

It was found that at density 13 the number of cockles localised accorded well with the expectation. At density 40 in daylight the number of cockles localised was within the 99% confidence interval of the mean, but in darkness the number localised was somewhat too low and at density 150 in darkness the numbers localised were much too low.

In addition to the experiments described I tried to predict cockle density by observing a sewing Oystercatcher. This was the case in June 1967 when I made observations in darkness with W/R on the same cockle beds at a place of unknown density. During a period of 611 seconds spent sewing, 92 cockles were localised while the mean walking rate was 2.32 steps/sec. Accepting a mean step length of 8.2 cm the distance covered by the bill was  $611 \times 2.32 \times 8.2 = 11624$  cm. The mean shell length determined from cockles beyond the experimental field was 31.8 mm, corresponding with a diameter of 2.33 cm in our model. In assuming the width of the bill 0.1 cm, the cockle density (D) can be calculated with formula (1)

$$D = \frac{92 \times 10^4}{11624 \times (2.33 + 0.1)} = 32.6$$

If we start in the calculations from a displacement rate of the bill of 13.9 cm/sec, the distance covered by the bill was  $611 \times 13.9 = 8493$  cm and the corresponding cockle density  $44.6/m^2$ . After the experiment the cockle density in the cage as determined by sampling turned out to be  $33.3/m^2$ .

The observations on the known density field of 13 and predicted density field of 33 seem to justify the conclusion that the localisation system used by the bird conforms to the sewing hypothesis; that is randomly moving the bill through the substrate till a cockle shell is touched by chance.

It is reasonable to suppose that the localisation system applied during sewing is identical at all densities. Why, then did the bird seem to find too few cockles at densities 40 (in darkness) and 150? The moment of localisation of a cockle at sewing is revealed to the observer as the abrupt ceasing of the sewing movement of the bill, followed by attacking movements. However, I soon got the impression that the mean time spent in trying to open a localised cockle decreased with increasing cockle density. This was especially evident at density 150. Perhaps the bird actually did localise all the cockles he theoretically ought to have encountered, but he made the decision of opening or not opening a cockle instantaneously after localisation, so that the observer was prevented from distinguishing between the fraction of the moment of localisation and continued sewing. This view is supported by

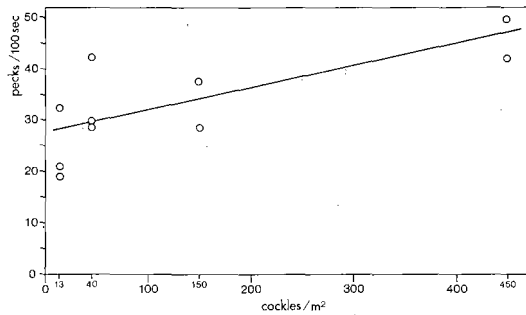


Fig. 5. Peck rate in relation to cockle density. Line of least square regression is shown.

comparing the percentages of cockles definitely observed to be localised, with those that were successfully opened and consumed (Table 1, column 14). The results reflected in this ratio strongly suggest that with increasing cockle density the Oystercatcher became more selective in the sense that he selected cockles with a greater probability of opening them successfully.

#### 6. LOCALISATION OF CARDIUM IN DAYLIGHT

In daylight a foraging Oystercatcher exhibits pecking behaviour. In darkness, when the possibility for visual localisation is excluded or at least reduced the peck level is very low (Table 1, column 6). The most plausible explanation may be that pecking is elicited by visual stimuli. The frequently occurring reorientation movements of the bird preceding precise pecking into a cockle support this supposition. In addition there is strong experimental evidence that the Oystercatcher can localise *Macoma* visually by means of marks on the surface (Hulscher, in prep.).

The visual stimuli involved may be present at the substrate surface, but their nature is not known. Even upon careful scrutiny I usually did not find any superficial signs giving away the presence of a buried cockle (see also Davidson 1967). Sometimes however, one or both holes made by the siphons can be seen, or a small elevation of the substrate over a cockle, a mound

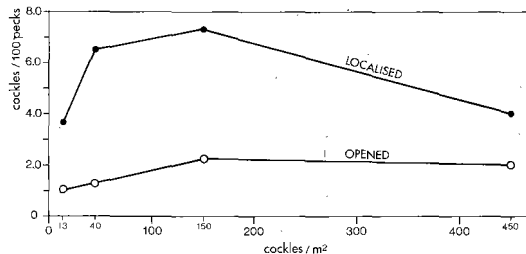


Fig. 6. Relation between cockle density and the number of localised and successfully opened cockles/100 pecks.

resulting when the cockle violently closes its valves. Occasionally these marks informed me as to the orientation of the cockle in the substrate and I was able to thrust a knife (or an Oystercatcher bill) swiftly into the shell via the persistent gape. In particular the holes of the siphons were useful in orienting the thrust because they differ in size, the smaller being that of the exhalent siphon situated nearest to the ligament (Fig. 1a). Fairly often cockles were seen to spout a jet of water into the air, particularly shortly after exposure. However, I have never seen my captive Oystercatcher react to spouting cockles.

A variety of marks of other prey occur on the surface, especially holes of different sizes, as the large funnel entrance of the *Arenicola* burrow, the *Nereis* burrow, the siphon holes of *Macoma*, and also little holes that are probably not of animal origin. Most of these marks were so small in size that it was impossible to see if pecking was directed to them.

Pecks may be successful or unsuccessful. A successful peck is defined as a peck followed by the actual opening of a cockle. Pecks are unsuccessful when not followed by recognisable attacking movements of the bill (for whatever reason), or followed by recognisable attacking movements that do not lead to the successful opening of the cockle. "Cockles localised" include the latter together with the cockles opened successfully.

Mean peck rate (number of pecks/100 seconds of pecking) and cockle density were positively correlated (Fig. 5, data pooled per day per density;  $r = 0.74$ ;  $P < 0.02$ ). The yield of pecking, either the number of cockles localised or the number successfully opened per 100 pecks, increased up to density 150, beyond that density the former decreased, whereas the latter remained constant (Fig. 6, all data pooled per density). This means that the proportion of localised cockles that was opened successfully increased with cockle density. At density 450 nearly one on every two pecks was successful (cf. Table 1, column 18). The bird became increasingly selective in pecking, apparently reacting progressively to stimuli giving a higher chance to success.

Table 2. Food intake of the caged Oystercatcher in daytime and in darkness under comparable conditions.

	daylight (1360 min)	darkness (1380 min)	Chi-square P
Cardium	185	203	>0.50
Macoma	112	7	<0.01
Carcinus	2	11	<0.01
small prey	38	12	—
flesh (grams total dry weight) <sup>1)</sup>	77.5	77.8	>0.95

<sup>1)</sup> small prey excluded

## 7. FOOD INTAKE

### 7.1 OVERALL FOOD INTAKE IN DAYLIGHT AND DARKNESS

The shells of *Cardium* and *Macoma* and the carapaces of *Carcinus* emptied by the bird were collected and measured after each experiment by day as well as by night. Food intake was calculated by means of curves relating the dry weight of the flesh (ash included) to the shell (carapace) length. This method of calculating food intake does not take into account small prey that is swallowed entirely, mainly small shrimps and worms. This category is underestimated in darkness when observations did not always cover the total time span of the experiment. The total number of consumed small prey was very small, however, so that their contribution to the total food intake may be neglected without making serious mistakes. Table 2 summarizes the food intake of W/R during 1360 minutes in daylight and 1380 minutes in darkness, under comparable conditions.

There was no difference in the number of cockles eaten in darkness and in daylight, but more *Macoma* and less *Carcinus* were consumed in daylight. This may mean that *Macoma* is mainly localised by sight and *Carcinus* by touch. The *Macoma* consumed, shell length 8-22, mean 15.6 mm, were buried at a mean depth of 5 to 6 cm, probably too deep to allow localisation by sewing. The small *Carcinus*, carapace breadth 18-35, mean 28.4 mm, buried themselves to a depth of a few millimeters, enabling the bird to find them by sewing. The bird gave no sign of seeing them in daytime.

The total food intake, based on the dry weight of the flesh of the registered prey was the same in darkness as in daylight (Table 2), with an overall intake rate of 3.40 grams per hour (feeding and non-feeding periods included). The cockle beds the caged bird was feeding upon, were exposed 5½ hours per tide. If the bird exploits both exposure periods per daily cycle to the full extent its food intake would be  $11 \times 3.40 = 37.4$  grams per 24 hours (ash included). The mean food intake of three captive Oystercatchers in summer was 35.3 grams per 24 hours of cockle and mussel flesh (ash-free dry weight), or 40.6 grams ash included, virtually identical to the daily ration estimated for the caged bird on the tidal flats (Hulscher 1974). The captive birds always had an excess of food at their disposal and they did not have to search for it. I therefore suspect that the observed overall intake rate of W/R under the experimental conditions in the field was somewhat too low to balance expenditure.

### 7.2. INTAKE RATE DURING SEWING AND PECKING CONTRASTED

The intake rate, defined as the number of cockles eaten per 100 seconds of searching, either sewing or pecking, is compared in figure 7. Using one technique at a time, either sewing in darkness or pecking in daylight, at the same cockle density (40 or 150) the intake rate of sewing was higher. This

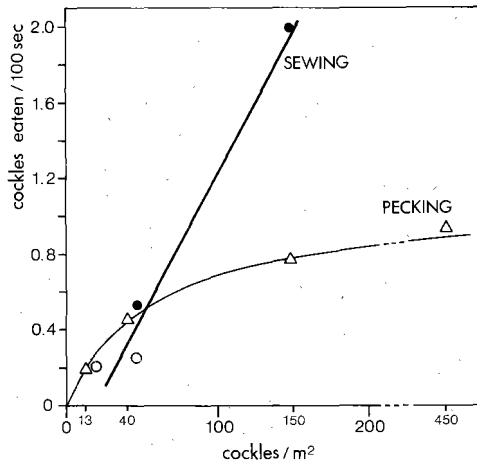


Fig. 7. Number of cockles successfully opened and consumed per 100 sec of sewing or pecking in relation to cockle density.  
 Open symbols: daylight observations  
 Filled symbols: observations during darkness.

must mean, because the overall food intake in darkness and in daylight was the same, that in darkness more time was spent in non-feeding activities. Unfortunately no data on time allotment in darkness were collected. When sewing and pecking were both used (in daylight at densities 13 and 40) the intake rate of sewing and pecking was the same at the lower density (13) but intake rate of pecking was 1.8 times higher at the higher density (40). The percentage of searching time spent in pecking was higher at density 40 than at density 13. The observations at density 40 in daylight suggest that probably

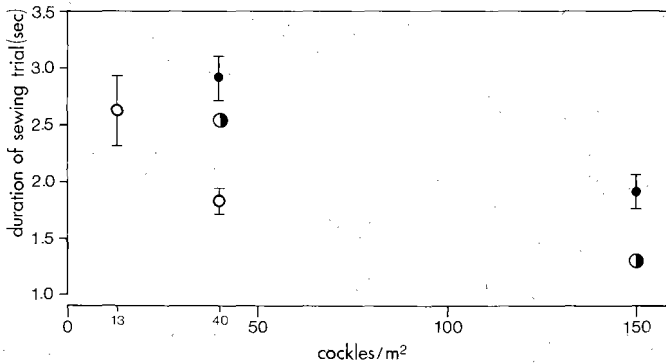


Fig. 8. Mean duration of a sewing trial in relation to cockle density under different light conditions.  
 Vertical bars indicate the 99% confidence intervals of the series means (see text).  
 Open circles: daylight observations. Filled circles: observations during darkness. Half-filled circles: observation in the transition period from daylight to darkness.

more energy is expended in finding a cockle, that can be opened successfully, when sewing than when pecking.

Pecking and sewing may interact. Apparently sewing appears in daylight at low cockle densities when pecking cannot be performed adequately, owing to a scarcity of visual stimuli. Also the lower intake rate of sewing at density 40 in daylight as compared to that in darkness (Fig. 7) points to interaction (although the difference is not statistically significant). At densities 13 and 40 in daylight, pecking and sewing alternated swiftly in a constant ratio during searching. Apparently the sewing bird is continuously distracted by visual stimuli, resulting in a lower success than when it is not distracted, as is the case in darkness. Support for this statement may be the shorter duration of a sewing trial when light intensity increases (Fig. 8). To illustrate this I split up the observation period per day in consecutive subperiods (series) in such a way that each series included a sewing time of at least 200 seconds. This gave for density 13 7 series, for density 40 in daylight and in darkness 3 and 13 series respectively, for density 150 in darkness 8 series. Of the series at densities 40 and 150 in darkness one series was performed in the transition period from daylight to darkness.

### 7.3. HANDLING TIME OF CONSUMED COCKLES

When feeding at a certain cockle density (40 or 150) the mean handling time of successfully opened and consumed cockles, found by either sewing or pecking, was longer in darkness than in daylight (Fig. 9). At density 150 the variance of the handling time was greater in darkness than in daylight ( $P < 0.01$  F-test), at density 40 there was no difference ( $P < 0.95$  F-test). These facts suggest that it is more difficult to attack and open a cockle successfully in darkness than in daylight. In this respect the results of 25 July are

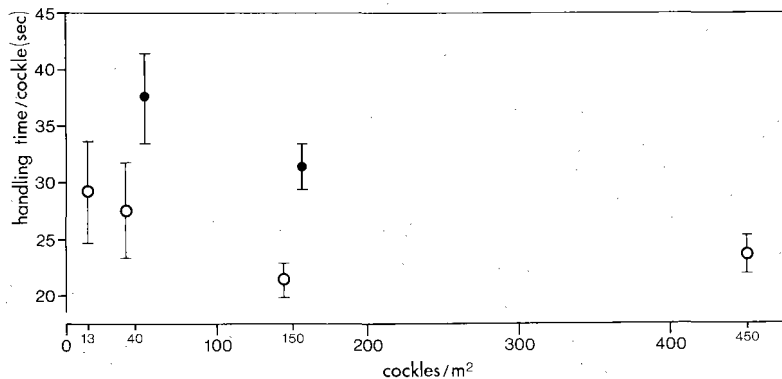


Fig. 9. Mean handling time of consumed cockles in relation to cockle density. Vertical bars indicate 95% confidence intervals of the mean of the daily totals. Open circles: daylight observations. Filled circles: observations during darkness.



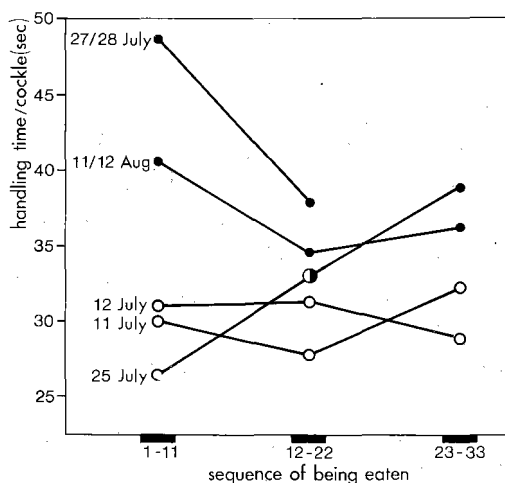


Fig. 10. Mean handling time of the first, second and third group of eleven cockles consumed at density 150 cockles/m<sup>2</sup>. Daylight/darkness code as in Figure 8.

instructive, when observations started in daylight and ended in darkness (Fig. 10). In this figure the mean handling times are presented for the first, second and third group of eleven cockles consumed on several different occasions at density 150. With decreasing light intensity the handling time increased, whereas a similar obvious trend was not apparent for the other days.

Handling time involves two different acts: opening the cockle and removing the flesh from the shell. The parameters were not measured separately, but the time span spent on opening the cockle was quite variable, depending upon the extent to which the posterior adductor muscle was severed at the first jab. Placing a successful jab largely depends on the right information concerning the orientation of the cockle. Removing the flesh was performed in a much more constant time. Other factors probably influencing handling time such as motivational state (hunger), reward rate (flesh consumed per time), etc. cannot be ruled out.

#### 8. DISCUSSION

Perceiving the exact orientation of a cockle in the substrate is an important matter for the Oystercatcher. Attack must be precise, for as we have seen, the bird was only successful in opening cockles if he managed to sever the posterior adductor muscle sufficiently at the first jab of the bill. It frequently happened that, if the bill had not penetrated far enough into the shell, the bird subsequently walked around for minutes trying to shake off the cockle that was tightly pinched around the bill tip. This also happened with W/R when feeding on mussels (*Mytilus edulis* L.) under experimental conditions. In one case a mussel was removed by me after more than 90 minutes. Apparently feeding on large bivalves is not without risk for

Oystercatchers and may sometimes even lead to their death. This may be concluded from short notes in the literature mentioning Oystercatchers found dead with large bivalves (mostly mussels) closed around their bills.

During sewing, localisation of a cockle is assumed to be achieved by touching the shell with the bill. Information on the orientation of the cockle in the substrate is picked up by touch. At this moment the bird has to determine whether the shell is oriented in a way amenable to attack, or whether attack is only possible after reorientation. The latter situation gives a lower chance of success because in the meantime the cockle closes its valves more tightly.

The ratio between the number of cockles opened successfully and those observed as being localised is higher for pecking than for sewing, when feeding at the same cockle density (Table 1, column 18 and 14). This suggests the bird was more selective in pecking than in sewing, probably because he had better information about the orientation of the cockles in the substrate when pecking than when sewing. Firstly, the chance of gathering the right information on the orientation per localised cockle is higher for pecking in connection with the different nature of localisation: in sewing a cockle is actually touched, this reduces the chance on success during the subsequent attack; in pecking a cockle is not necessarily touched but seen firstly, before it is attacked. Secondly, the number of cockles encountered per time searching may have been higher during pecking (Fig. 11). The number of

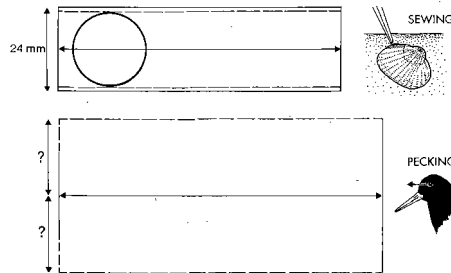


Fig. 11. Area effectively searched per time unit during sewing and pecking.

cockles encountered per time sewing is determined by mean walking rate and diameter of cockles and bill width. In pecking the number of cockles noticed per time is determined by walking rate, the proportion of the cockles with a noticeable surface mark, and the distance to either side of the bird within which it can adequately react visually to cockle surface marks. Walking rate does not differ very much during sewing or pecking, but at density 40 in daylight it was slightly ( $P < 0.01$  Chi-square) higher (mean 2.33 steps/sec, measured over 3042 steps) than in darkness (mean 2.02 steps/sec, measured over 12684 steps). However, the proportion of cockles with surface marks and the reaction distance of the bird are not known. If the number of

encountered cockles per time searching is indeed substantially higher when pecking, then the bird probably can concentrate to a higher degree on cockles with the best clues on orientation during pecking than when sewing. This hypothesis is supported by the shorter handling time of cockles consumed in daylight than in darkness, when feeding on the same cockle density (Fig. 9).

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#### 10. SUMMARY

This article describes feeding behaviour of an Oystercatcher with clipped wings by day and by night on cockles buried just beneath the substrate surface. In daylight the bird generally makes pecking movements, probably directed visually at cockle surface marks. In darkness the bird places the bill at an angle of about 70 degrees 1-2 cm into the substrate and walks in this posture in a straight line while the bill makes quick "sewing" movements (little ups and downs) without retracting the bill from the mud. When the bill touches a cockle sewing stops abruptly and the Oystercatcher tries to pierce its bill as quickly as possible between the two valves at the "persistent gape".

In daytime at low densities (13 and 40 cockles/m<sup>2</sup>) both the pecking and sewing technique are applied. The sewing technique suggested a chance encounter with cockles by the foraging bird (random-searching hypothesis). This was tested experimentally by observing the foraging bird on cockle beds at different densities. The number of cockles found was compared with the number calculated that could be found when random searching. Calculations are possible if the distance the bill tip travels through the mud is known, as well as the density and size of the cockles (Fig. 2). The distance the bill tip traveled through the substrate during sewing was calculated in two ways: by counting the number of steps taken (steplength 8.2 cm) and by determining the total time spent in sewing (displacement rate of the bill tip 13.9/sec).

In daylight, the number of cockles localised at densities 13 and 40/m<sup>2</sup> using the sewing technique were in agreement with the random-searching hypothesis. At night at a density of 40 cockles/m<sup>2</sup> just too few cockles were found, at a density of 150 cockles/m<sup>2</sup> quite a lot too few were found according to the random-searching hypothesis (Fig. 4).

It is suggested the bird actually did localise all cockles it theoretically ought to have encountered, but it made the decision of opening or not opening a cockle instantaneously after localisation, so that the observer was prevented from distinguishing between the fraction of the moment of localisation and continued sewing.

Overall food intake in daylight and in darkness under comparable conditions is identical: 3.40 grams flesh (total-dry-weight) per hour (Table 2). Procentually more cockles localised with pecking were opened successfully than with sewing (Table 1). It is assumed that in daylight the bird is better informed on the orientation of cockles in the substrate via surface marks than in darkness. The bird thus has a greater chance of thrusting its bill precisely between the two valves of the cockle while attacking, in order to sever the adductor muscles. This fits in with the fact that in daytime less time is spent in opening and eating a cockle than in darkness (Fig. 9).

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## 12. SAMENVATTING

In dit artikel wordt beschreven hoe een gekortwiekte Scholekster overdag en 's nachts ingegraven kokkels vindt. Overdag gebeurt dit d.m.v. pikken, die waarschijnlijk gericht zijn op oppervlaktesporen van de kokkel. 's Nachts is het gedrag anders. De vogel steekt dan zijn snavel 1-2 cm schuin in het substraat en al lopende maakt hij vlugge op- en neergaande bewegingen met de snavel, zonder deze helemaal uit het substraat te trekken. Op deze manier worden ondiepe voren in het substraat geploegd, vandaar dat dit gedrag „ploegen” is genoemd. Als de snavel hierbij op een kokkel stuit probeert de vogel deze daarna te openen door zijn snavel zo snel mogelijk tussen de beide kleppen te wringen. Bij lage dichtheden (13 en 40 kokkels/m<sup>2</sup>) wordt overdag naast pikken ook geploegd.

De vraag wordt gesteld of kokkels bij het ploegen door toeval worden gevonden of niet. Dit wordt nagegaan d.m.v. waarnemingen bij verschillende kokkeldichtheden, waarbij het door de vogel gevonden aantal kokkels wordt vergeleken met het aantal dat door toeval kan worden gevonden, en dat kan worden berekend als bekend zijn de afgelegde weg van de snaveltop door het substraat, de dichtheid en de afmetingen van de kokkels (Fig. 2). De afgelegde weg van de snaveltop werd op twee manieren berekend: door het aantal gemaakte stappen tijdens het ploegen te tellen (paslengte 8,2 cm) en door de totale tijdsduur van het ploegen te bepalen (verplaatsingssnelheid van de snavel 13,9 cm/sec.). Gevonden werd dat overdag bij dichtheden van 13 en 40 kokkels/m<sup>2</sup> het aantal gevonden kokkels binnen de door het toeval bepaalde grenzen lag. 's Nachts werden bij een dichtheid van 40 kokkels/m<sup>2</sup> iets te weinig, bij 150 kokkels/m<sup>2</sup> veel te weinig kokkels gevonden dan volgens toeval (Fig. 4). Verondersteld wordt nu dat alle kokkels die de snavel bij het ploegen toevallig tegenkomt wel degelijk worden gelokaliseerd, maar dat de tijd die besteed wordt om te onderzoeken of een kokkel met succes is te openen bij hogere kokkeldichtheden zo kort wordt, dat de waarnemer niet meer aan het gedrag van de vogel kan zien dat er een kokkel was gevonden.

De voedselopname 's nachts en overdag onder vergelijkbare omstandigheden is gelijk: 3,40 gram vlees (totaal drooggewicht) per uur (Tabel 2). Het percentage van het aantal gelokaliseerde kokkels dat met succes wordt geopend, was groter bij pikken dan bij ploegen (Tabel 1). Aangenomen wordt dat overdag bij pikken de vogel met behulp van oppervlaktesporen beter op de hoogte is van de oriëntatie van de kokkel in het substraat dan 's nachts bij het ploegen, waardoor de snavel bij het pikken trefzekerder tussen de kleppen van de kokkel kan worden geplaatst, wat belangrijk is bij het beschadigen van de sluitspieren. In overeenstemming hiermee is de kortere tijd die overdag nodig is om een kokkel te openen en op te eten (Fig. 9).