Diurnal activity budgets of breeding Eurasian Oystercatchers *Haematopus ostralegus* feeding on limpets on rocky shores

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The effect of different stages of the tidal cycle, weather conditions and the presence of con- and allo-specifics on the time and activity budgets of Eurasian Oystercatchers *Haematopus ostralegus* was investigated. Data were collected at a breeding site on Lundy Island in the Bristol Channel, UK, where Oystercatchers feed on limpets *Patella* spp. on rocky shores. Sixteen behaviours were recorded for 10-minute periods throughout the day. Grooming, feeding, antagonistic behaviours and alertness emerged as the four major behavioural categories from a Principal Component Analysis that was performed on the frequency and durational data. Oystercatchers were more active during low tide than high tide. Frequency and time spent on foraging were greatest during high falling and low falling tide. Time spent on grooming and frequency were high during high slack and falling tide. Alertness was at its maximum during high slack and low slack tide. No clear trend was found in relation to antagonistic behaviours. Type of habitat occupied was also found to have a significant effect on behavioural patterns. Amount of time allocated to different behaviours and the frequency of behaviours displayed a cyclical pattern based on the tide.

INTRODUCTION

Animals must allocate their time to exploit their habitat to satisfy basic requirements for food, movements, social interaction and rest. Time activity budgets have been studied extensively as the allocation of time and energy which is important to the survival of all species. A recurring idea in ecological literature is that the life history strategies of animals are inextricably linked with allocation patterns of time and energy (King 1974). Estimation of an animal's needs through the annual cycle requires an understanding of how these factors affect the pattern of activity and how the habitats are used (Frederick & Klaas 1982). Knowledge of daily activity patterns is essential for the construction of time-energy budgets and for evaluating foraging and survival strategies of animals in seasonal environments (Risenhoover 1986).

The Eurasian Oystercatcher *Haematopus ostralegus* is a bird with a marked temporal variation in its activity budget. Studies on the feeding and breeding behaviour of this bird have shown that time-activity budgets are governed by a tidal regime (e.g. Kersten & Visser 1996a, Meire 1996); tidal cycles have the effect of limiting certain behaviours. It was found that the amount of food intake as well as the choice of main prey species varied depending on whether it was high or low tide (DeVlas *et al.* 1996). There is also some evidence showing a possible connection between social behaviours and the tidal cycle (Ens *et al.* 1996).

Social interactions such as territorial encounters in relation to the tidal cycle and habitat, however, have not been studied as extensively as feeding behaviour. Furthermore, most of the studies on feeding behaviour have been conducted on Oystercatchers feeding on bivalves especially mussels (see review by Blomert *et al.* 1996, Goss-Custard 1996). The effects of different habitats have also been studied: estuaries (e.g. DeVlas *et al.* 1996, Kersten 1996) and sandy beaches (e.g. Zwarts *et al.* 1996a) have been the most commonly studied sites. This pattern of research poses the question whether there are differences between behaviours at the various types of observation site. Indeed, a study conducted by Kersten (1996) in the Dutch Wadden Sea showed that behaviours did differ depending on the type of territory occupied; different habitats led to different behavioural time allocations. Hence the present paper which is aimed at describing the time budget of Oystercatchers and the factors that control it.

STUDY AREA

Lundy Island (51°10'N, 4°40'W), with an area of 3.5 km^2, is located in the Bristol Channel, 17 km off the north coast of Devon, England (Fig. 1). There are many habitat types along its shoreline, ranging from sheltered coves to jagged rocks that are frequently exposed to vigorous wave action and strong winds. The two study sites at which observations were made were selected for their varying exposure to wave action and distribution of rocks. The Landing Bay is east facing, bordered by an eroding slate cliff, about 30 m high, and is partly sheltered. The North Lighthouse is a steep, exposed,

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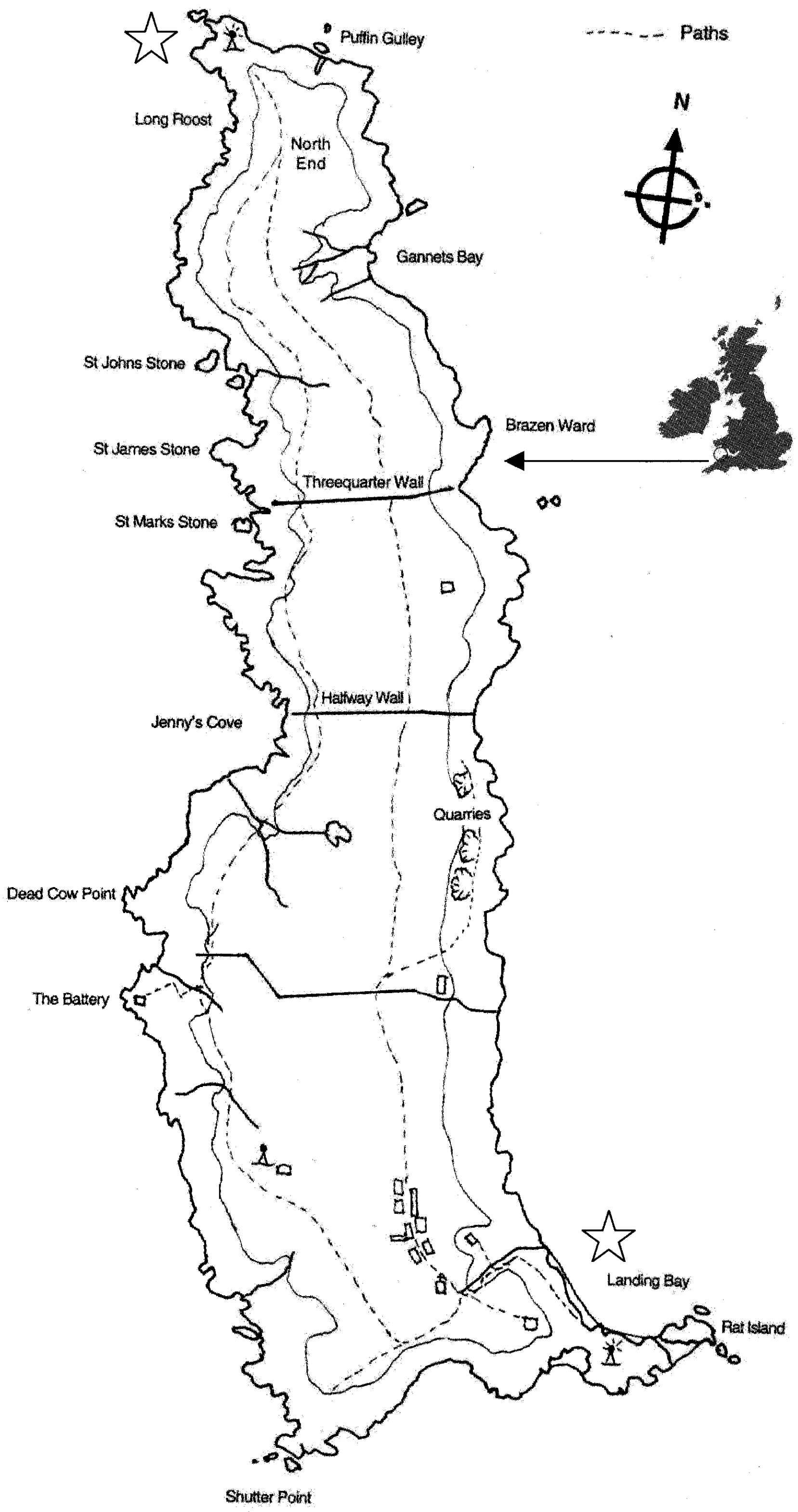

Fig. 1. Lundy Island in the Bristol Channel, SW England showing the two study sites (star symbol): the Landing Bay and the North Lighthouse.

granite cliff site on the north west side of the island. In spring, the prevailing winds are from the northwest and make the area relatively rough and exposed.

Each year, 15–20 pairs of Oystercatchers breed along Lundy's shoreline where they feed mainly on common limpets *Patella vulgata* and black-footed limpets *P. depressa*. These occur at both sites where they are exposed at low water (R. Nagarajan unpublished data). Compared with the numerous studies of Eurasian Oystercatchers feeding on blue mussels *Mytilus edulis* and common cockles *Cerastoderma edule*, there have only been a few studies of Oystercatchers feeding on limpets (e.g. Harris 1964, Feare 1971, Coleman *et al.* 1999).

METHODS

Data collection

The diurnal time activity budgets of Oystercatchers were studied during April 1998. Observations were made from a distance of 30–70 m, thus keeping observer disturbance to a minimum. Other human disturbance was infrequent and did not appear to affect the birds' behaviour. During all observations, 1–8 Oystercatchers were present.

Diurnal time activity budgets were compiled by sampling focal animals, as described in Altman (1974), for 10-minute observational periods throughout the tidal cycle. Focal birds were selected at random. Observations were occasionally curtailed by the departure of the birds; but those lasting >7 minutes were used in the analysis, giving a sample size of 77 periods. The number of intra- and inter-specific kleptoparasites such as Herring Gulls *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* within a 3 m radius from each focal bird were also counted. All kleptoparasitic encounters were noted. Observations were made using a 15–60× telescope and 8×40 binoculars. All observations were made by two observers who dictated a continuous record of the behaviour of focal birds to one recorder. The recorder measured the frequency and duration of each behaviour using a stopwatch.

Behavioural descriptions

The frequency and duration of each behaviour was recorded as well as all periods of inactivity using a focal animal sampling method. Sixteen different behaviours were observed. These were assigned to the following major categories: grooming, foraging, antagonistic behaviours and alertness. These categories match the behaviour classifications made in previous studies (e.g. Ens & Goss-Custard 1986, Heg *et al.* 1993). The category definitions are:

Grooming covers preening and relaxation, which is defined as short, 1–2s periods of rest between preening episodes and may include various shaking movements.

Foraging covers searching, handling and swallowing.

Antagonistic behaviour has three components: piping, chasing and pseudosleeping. In this study, pseudosleeping is defined as a form of apparent resting where alertness is maintained. It occurs during territorial encounters (Ens *et al.* 1996).

Alertness has two components: major and minor vigilance. Major vigilance is a state of high alertness where the target is identifiable and is characterised by a sudden head or body movement. Minor vigilance does not involve any body movement, just a slight outward head movement.

Inactivity is resting and sleeping on one or two legs with the head tucked between the wings.

Conditions

Roughness of sea was measured using the Beaufort Wind Scale (Kerman 1993) and rainfall (mm) information was obtained from the Lundy Island Weather Records. The proximity and number of other Oystercatchers and sea birds close to the focal animal were also noted.

Tidal cycle

Observations were made during complete tidal cycles. During the study, tidal amplitude ranged from 2.29 m to 5.10 m. The tidal cycle was divided into six segments of approximately two hours each: high slack, high falling, low falling, low slack, low rising and high rising. The segments high slack and low slack were the two-hour periods centred on high water and low water respectively.

Data analysis

Principal Component Analysis (PCA) was used to group the behaviours. This method was used to factorise a group of 16 different behaviours and Varimax rotation was used for factor extraction. Factors with an eigenvalue >1 were extracted and the variables were ordered and grouped by the size of loadings to facilitate interpretation. The 2–3 behaviours with highest scores were considered as significant loading in each factor. A comparison of behaviours was made using PCA because it is a multivariate technique that helps to elucidate underlying factors without any *a priori* assumptions. Stepwise multiple regression was used to predict different groups of behaviours. The explanatory variables used were: time of day, habitat, roughness of sea, rainfall, presence of other Oystercatchers, presence of other birds and the six stages of the tidal cycle. For the categorised variables of tide and conspecifics, low slack tide and pairs of Oystercatchers were used as reference categories as they were the modal categories within their respective variable groups. Where significant results were obtained, indicating that further analysis was appropriate, stepwise regression analyses were then conducted to determine the most efficient way to describe the data. As inter- and intra-tidal cycles are highly correlated, each variable was analysed separately with all the other variables. Analysis using intra-tidal variation resulted in more precise models than those with inter-tidal variations and were thus used throughout the analysis.

RESULTS

Behavioural groups

A Principal Component Analysis with Varimax rotation confirmed, for both frequency and duration of behaviour, that the *a priori* groupings of behaviour were appropriate and that they were mutually orthogonal. Four factors corresponding to grooming, foraging, antagonistic behaviour and alertness based on the original 16 observed behaviours emerged for both the frequency and duration of behaviours (Tables 1 and 2). The four factors cumulatively explained 65.5% of the variance in the frequency data. The duration data yielded six factors – feeding, antagonistic behaviour, grooming, contact,

Table 1. Principal Component Analysis with varimax rotation on frequency of observed behaviours in Oystercatchers (n=77). Numbers in bold denote behaviours used in comprising the factors.

observed behaviours	Factor 1 grooming behaviours	Factor 2 feeding	Factor 3 antagonistic	Factor 4 alertness
major vigilance	0.179	–0.055	0.007	**0.614**
minor vigilance	–0.215	–0.102	0.167	**0.680**
balancing	–0.235	–0.525	–0.113	–0.271
preening	**0.967**	–0.003	0.006	0.098
relaxing	**0.941**	–0.004	–0.016	0.133
searching	–0.133	**0.915**	–0.030	–0.256
swallowing	–0.136	**0.912**	–0.035	–0.251
chasing	–0.081	–0.060	**0.873**	–0.070
pseudosleeping	–0.134	–0.014	**0.877**	0.169
piping	0.382	0.027	**0.665**	0.007
calling	0.151	0.009	–0.027	0.572
comfort	–0.127	–0.378	0.137	–0.293
Eigenvalue	2.558	2.134	1.950	1.215
% of variance explained	21.3	17.8	16.3	10.1
cumulative % explained	21.3	39.1	55.4	65.5

exploring and alertness – and these factors explained 84% of total variance. Factors that arose in the durational data were exploring (walking and scanning) and contacting (flying and calling). However, these were not analysed further due lack of sample size of these behaviours during the observation periods.

Time activity budgets

Time activity budgets of Oystercatchers both frequency and duration of the activities are shown in Figures 2 and 3. Both the time spent on foraging and the frequency of foraging behaviour were greatest during high falling and low falling tide. Grooming and alertness (vigilance) behaviours also showed an apparent cyclical pattern corresponding to time within the tidal cycle. Grooming duration and frequency were greatest during high slack and high falling tide, while alertness frequency and duration were highest during low rising and low slack tide. Antagonistic behaviours did not have an apparent trend.

Factors influencing the behaviour

Grooming behaviour was influenced positively by roughness of the sea and negatively by rainfall. Also, there was a difference between the habitats indicating that grooming frequency was higher in the Landing Bay than at the North Lighthouse. The models for foraging behaviour, both frequency and duration, yielded the same variables. Foraging behaviour was positively influenced by rainfall and increased in relation to roughness of the sea. It was also prevalent during high falling and low falling tide. Frequency and duration models accounted for 37.2% and 45.8% of the total variance explained

Table 2. Principal Component Analysis with varimax rotation on duration of observed behaviours in Oystercatchers (n=77). Numbers in bold denote behaviours used in comprising the factors.

observed behaviours	Factor 1 feeding behaviours	Factor 2 antagonistic	Factor 3 grooming	Factor 4 contacting	Factor 5 exploring	Factor 6 alertness
major vigilance	–0.009	0.015	–0.032	0.066	0.268	**0.848**
minor vigilance	–0.082	0.047	–0.020	0.023	–0.133	**0.889**
preening	–0.023	–0.051	**0.937**	–0.016	0.145	–0.029
relaxing	–0.062	–0.019	**0.942**	0.007	0.111	–0.022
walking	–0.001	0.251	0.220	–0.101	**0.768**	0.074
flying	–0.001	0.026	0.015	**0.943**	0.019	0.084
searching	**0.958**	–0.052	–0.116	–0.057	–0.083	–0.109
swallowing	**0.934**	–0.032	–0.087	–0.057	–0.116	–0.124
chasing	–0.034	**0.907**	–0.053	–0.004	0.047	–0.052
pseudosleeping	–0.045	**0.787**	–0.105	–0.043	0.017	0.158
piping	0.051	**0.815**	0.097	0.048	0.209	–0.034
calling	–0.016	–0.030	–0.024	**0.935**	–0.021	0.003
scanning	–0.046	0.030	0.063	0.067	**0.897**	0.023
inactivity	–0.760	–0.098	–0.237	–0.203	–0.409	–0.300
Eigenvalue	2.779	2.403	2.108	1.942	1.505	1.019
% of variance explained	19.8	17.2	15.1	13.9	10.7	7.3
cumulative % explained	19.8	37.0	52.1	65.9	76.7	84.0

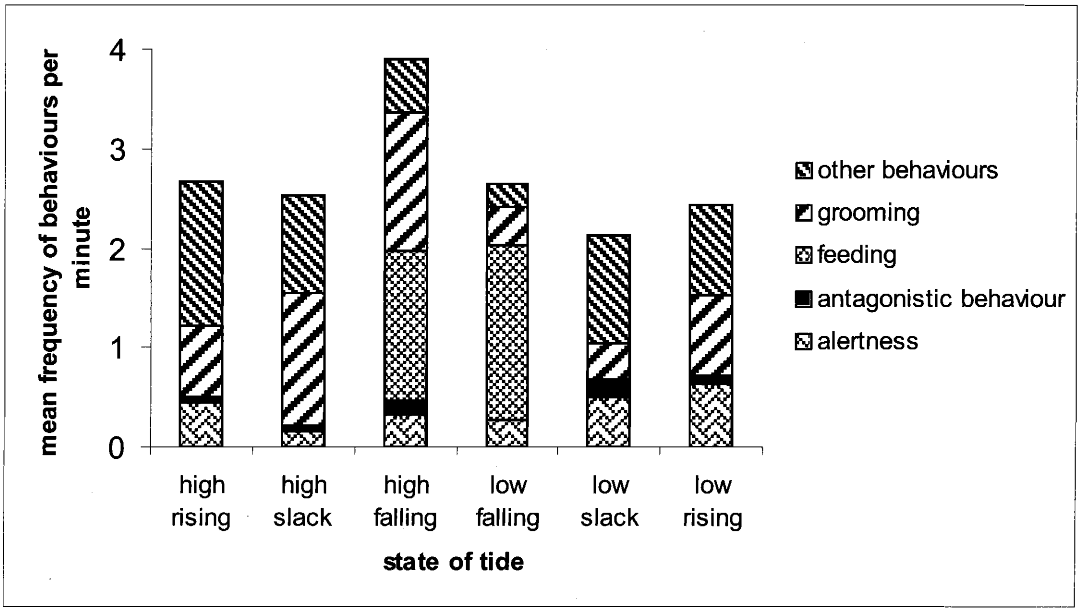

Fig. 2. Mean frequency of alertness, antagonistic behaviour, feeding, grooming, and other behaviours occurring over the six segments of each tidal cycle.

respectively. Models of antagonistic behaviour showed that both frequency and duration decreased across the day as well as during the low rising and low falling tide. The time spent on antagonistic behaviours increased depending on the roughness of the sea whereas frequency of antagonistic behaviour decreased. The alertness frequency model explained 22.5% of the total variance. Frequency of alertness differed significantly between the two study sites: Oystercatchers were more alert in the Landing Bay than at the North Lighthouse. In the presence of other Oystercatchers, alertness decreased. Alertness frequency decreased during high slack and low falling tide but increased during low rising tide (Table 3).

DISCUSSION

The Principal Component Analysis yielded factors that fit into the behavioural categories derived from earlier studies confirming the appropriateness of these categories. For most behaviours, both frequency and duration varied significantly with the tidal cycle as shown by the regression analysis. Some behaviours were also influenced by weather conditions.

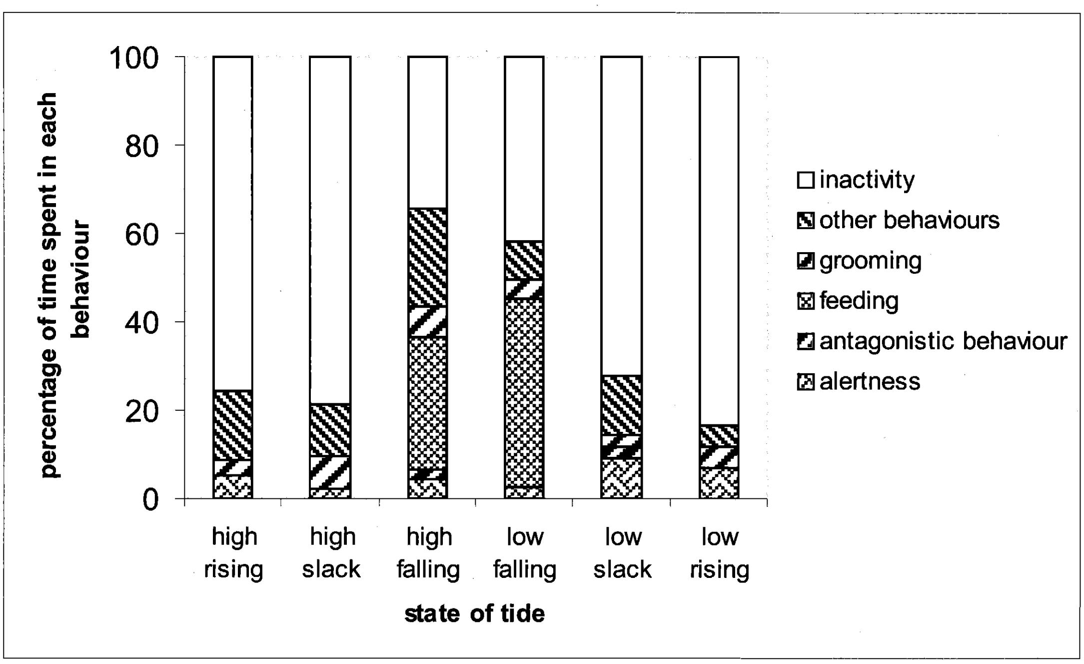

Fig. 3. Percentage of time spent in alertness, antagonistic behaviour, feeding, grooming, other behaviours and inactivity occurring over the six segments of each tidal cycle.

Table 3. Results of stepwise multiple regression analyses. Values are unstandardised co-efficients with standard errors in parentheses

Independent variables	grooming frequency	feeding frequency	feeding duration	antagonistic duration	antagonistic frequency	alertness frequency
time of day	–	–	–	–0.035**	–0.124**	–
	(0.008)	(0.031)	–			
habitat	2.132**	–	–	–	–	0.268**
	(0.749)	–	–	–	–	(0.085)
other birds	–	–	–	–	–	–
	–	–	–	–	–	–
solitary	–	–	–	–	–	–
	–	–	–	–	–	–
other	–	–	–	0.017	–	–0.290**
oystercatchers	–	–	–	(0.009)	–	(0.102)
rainfall	–0.120**	0.085*	0.015*	–	–	–
	(0.039)	(0.035)	(0.006)	–	–	–
roughness	0.635*	0.471**	0.081**	0.005	–0.019	–
of sea	(0.283)	(0.135)	(0.024)	(0.003)	(0.010)	–
high rising	–	–	–	–	–	–
	–	–	–	–	–	–
high slack	–	–	–	–	–	–0.374**
	–	–	–	–	–	(0.111)
high falling	–	1.036*	0.219**	–	–	–
	–	(0.467)	(0.082)	–	–	–
low rising	–	–	–	–0.027*	–0.099*	0.186
	–	–	–	(0.010)	(0.042)	(0.122)
low falling	–	1.444**	0.347**	–0.031**	–0.134*	–0.267*
	–	(0.393)	(0.069)	(0.010)	(0.041)	(0.112)
R^2adj	11.9%	37.2%	45.8%	18.6%	10.6%	22.5%
F	11.29**	12.24**	17.06**	5.33**	5.51**	6.52**

* denotes $p < 0.05$, ** denotes $p < 0.01$.

Grooming

Grooming frequency was predicted by habitat, rainfall and roughness of sea. However, there was no significant model for the duration of grooming, suggesting that this behaviour may be triggered in a ballistic manner, for example by spray from waves.

Foraging

Both frequency and duration measures of foraging showed that it increased with greater rainfall and roughness of sea, and during high falling and low falling tide. These results are similar to the findings of previous studies of Oystercatchers feeding on other prey types (Kersten & Visser 1996a, Meire 1996). As might be expected, foraging is greatest during falling tides as prey is exposed and still active thus making it more vulnerable than in other phases of the tidal cycle. Time spent searching for prey also increased in high rainfall and roughness of sea. This could be due to weather conditions having an adverse affect on the accessibility of the limpets, so that longer periods of searching behaviour are required to yield the same benefits; or it could be that the repeated re-exposure of limpets under rough conditions made foraging more profitable so that the birds devoted more time to it. Rainfall causes worms to bury deeper in the sand in the Waddensea, making them less or even completely inaccessible to the predators (Dankers *et al.* 1981). Possibly this is why, during heavy rain on the island of Schiermonnikoog in the Netherlands, Oystercatchers were observed to stop foraging altogether (D. Heg personal communication). In contrast, exactly the opposite results were observed in the current study. On Lundy during rough weather, the Oystercatchers took larger limpets from wet rocks, and ran among the rocks as soon as waves splashed on them in order to prey on larger limpets (R. Nagarajan personal observation). Hockey (1981) and Frank (1982) reported that other oystercatcher species feed near the water's edge where the limpets are active and their shells do not adhere tightly to the substratum. Therefore, the rain could make the limpets more vulnerable to Oystercatchers by wetting the rocks.

Antagonistic behaviours

The duration of antagonistic behaviour was significantly related to time of day, the presence of other Oystercatchers, roughness of sea, low rising and low falling tide. The increase in the presence of other Oystercatchers is to be expected, as the focal animals were engaged in protecting their territory from other birds. The frequency of territorial behaviours also increased with a higher roughness of sea. This might be due to the rough sea disturbing Oystercatchers from their roosting and low-level foraging sites, and causing them to congregate. In this way they may make intrusions into one another's territories, leading to antagonistic encounters. On the island of Schiermonnikoog during extreme high tides and stormy weather, breeding Oystercatchers are sometimes disturbed by the sea from their roosting sites. This can cause neighbouring pairs or individuals to roost closer together, increasing the frequency of aggressive encounters. It can also mean that some Oystercatchers are ousted from their feeding territories altogether, making intrusions into other (neighbouring) territories more likely to occur (D. Heg, personal communication). The effect of the time of day on antagonistic behaviour was a decrease in the afternoon; antagonistic behaviours also decreased during low rising and low falling tide, probably because the birds were more dispersed.

Alertness

Alertness decreased during high slack and low falling tide but increased during low rising tide. It might be expected that vigilance behaviour will increase during the high slack period, when other behaviours, such as feeding, would not be as frequent due to the inaccessibility of prey. However, this was not the case.

Previous studies have shown that the behaviour of Oystercatchers is affected by the presence of gulls leading to a loss of foraging time (Harris & Wanless 1997). However, our results do not show that the presence of other species had any significant impact on alertness. Similarly, the presence of other Oystercatchers resulted in a decrease in the amount of vigilance behaviour.

Vigilance behaviour differed between our two study sites in that alertness occurred more often at the Landing Bay than at the Lighthouse. This might be due to more human activities near the Landing Bay. We also noted synchronised vigilance behaviour by pairs. This is consistent with similar observations by of Ens *et al.*(1996).

CONCLUSIONS

The largest variations in behaviour were the increase in foraging during high falling and low falling tide and overall, the level of activity was greatest during high falling tide. This result is what would be expected on *a priori* grounds, and is consistent with results for Oystercatchers foraging on other prey types. However, in several cases variations in the less dominant behaviours were not as predicted. One of the most striking features of this study is the considerable proportion of time spent inactive: an overall average of 85% of time per 10-minute observation period. Can the Oystercatcher's allocation of so much time to inactivity be regarded as efficient? However, inactivity could also be considered as "surplus time" that may be reallocated to the most profitable of other activities (Kersten 1996). Moreover, the physiological need for rest for the proper and efficient functioning of the metabolic system also needs to be considered. This compensation of energy expenditure indicates that the time spent inactive, for example digestion after feeding, is not an inefficient allocation of time but rather an activity that must be engaged in for the overall fitness of the bird, since Oystercatchers can ingest food at a much greater rate than it can be digested (Kersten & Visser 1996b, Zwarts *et al.* 1996b). Despite the restriction of observations to daytime hours and the moderate number of observations made, the present study does show clear trends in the time allocation of behaviours.

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