

Does tide affect foraging and antagonistic behaviours in the Eurasian oystercatcher
(*Haematopus ostralegus*)?

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Introduction

Rising sea levels are predicted to dramatically impact intertidal habitats, reducing up to 70% of current area. The most severe losses are expected in areas where the coastline is prevented from moving inland by steep topography (Galbraith et al., 2002). When considering the ecological and potential conservation implications, the behaviour of intertidal species is thus an imperative topic for research (Nagarajan, Lea, & Goss-Custard, 2015).

Few studies focus on how tide influences behaviour. One species studied in this context is the Eurasian oystercatcher (*Haematopus ostralegus*), which mainly feeds on intertidal bivalves (Blomert, Ens, Goss-Custard, Hulscher, & Zwarts, 1996; Goss-Custard, 1996), although some others solely feed on limpets (Nagarajan et al., 2015). This distinction in prey type may be crucial since bivalves and limpets possess vastly differing ecological strategies, relying differently on tide (Goss-Custard, 1996). Subsequently, this may influence the effects of tide on foraging behaviour.

Research indicates that quantity of food intake and choice availability vary depending on tide (DeVlas, Bunskeke, Ens, & Hulscher, 1996). Ghosh, Spering, Wilshaw and Nagarajan (2003) further suggested that oystercatchers become increasingly dispersed as tide recedes and intertidal environment expands. This may reduce the need for intraspecific resource competition and territorial conflict. Since oystercatchers defend foraging territories (Vines, 1980), it may be interesting to assess whether tide influences the relationship between foraging and aggression. Ghosh et al. (2003) found a relationship between tide and foraging,

whereby foraging increased at lower tide and since roughness of the sea was found to predict foraging, it was argued that oystercatchers use the wet substrate to make foraging easier. Further, the wetness of the substrata may facilitate foraging (Nagarajan et al., 2015). Moreover, substrate type has also been implicated in intertidal wader foraging ability (Burger, Howe, Hahn, & Chase, 1977).

This study aimed to further explore the effect of tide on behaviours, which have been previously shown to form a significant part of oystercatchers' daily activity (Ghosh et al., 2003). As suggested by Ghosh et al. (2003), it is hypothesised that tide will affect oystercatcher foraging behaviour and competition. Additionally, if indeed oystercatchers are defending a feeding territory, it is hypothesised that there will be a relationship between foraging and aggression, which may also be influenced by tide. Specifically, it is predicted that as the tide recedes, foraging will increase due to an increase in food quantity, as a larger portion of the intertidal environment is uncovered. Furthermore, competition is predicted to increase with rising tide as food abundance decreases.

Methods

Study area

The study was conducted in Lametry Bay, Lundy Island ($51^{\circ}10'N$, $4^{\circ}40'W$), Devon, England (Figure 1), where oystercatchers only feed on limpets (Nagarajan et al., 2015). The bay is surrounded by steep topography, therefore providing a suitable location for testing the hypotheses. The bay was sectioned into three habitat types (see Figure 2). Observations were undertaken during daylight hours over six consecutive days in April 2015. Observers were located on the cliff overlooking the bay to ensure observer presence did not influence the birds' behaviour.

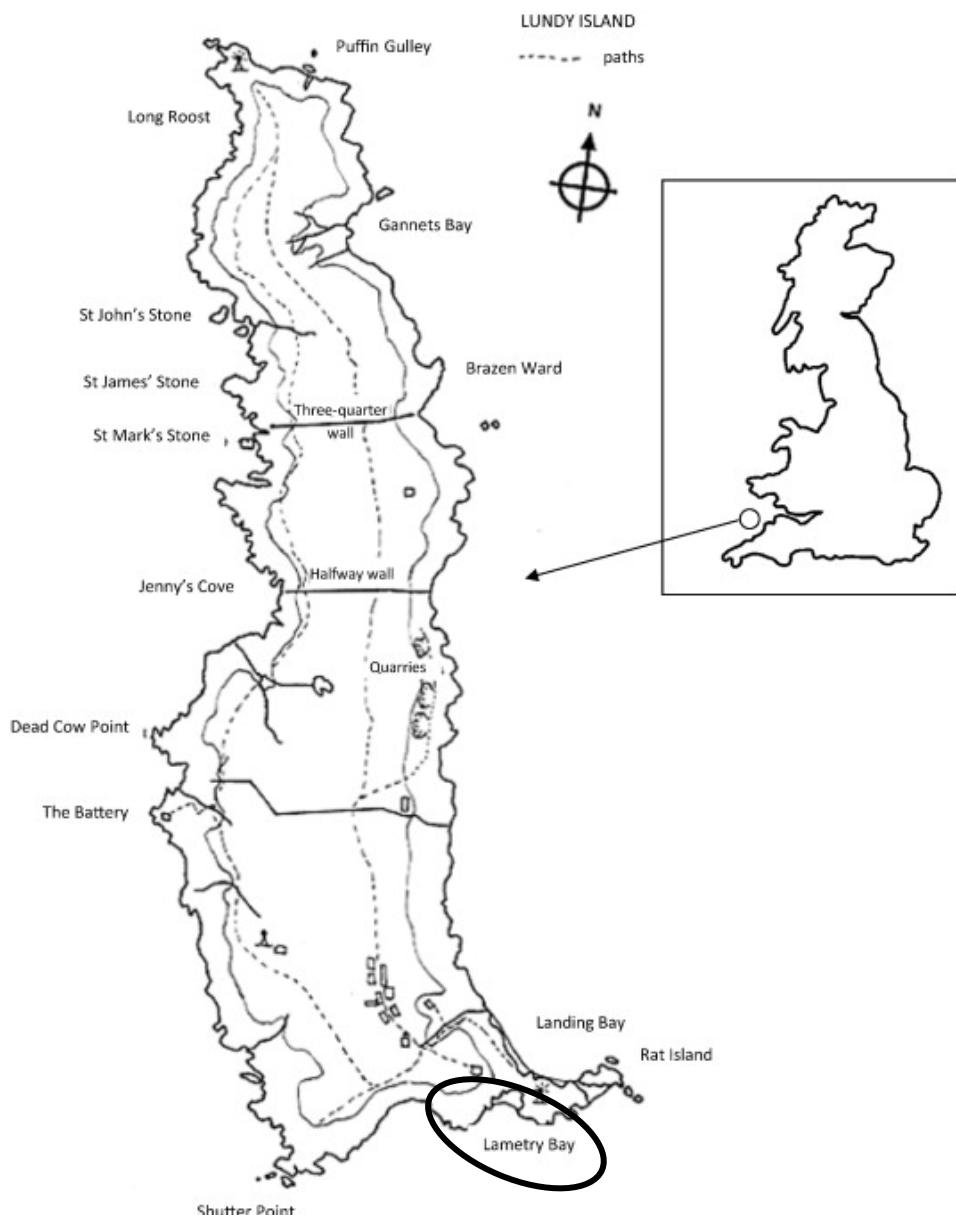


Figure 1: Map of Lundy Island located in the Bristol Channel, sourced and adopted from Nagarajan et al. (2015), highlighting the location of the study site.

Study design

Using Bushell 8x42 binoculars, oystercatchers were observed for 15-minute periods three hours before low tide through to three hours after low tide in 15-minute intervals; this was to prevent issues with pseudoreplication (Hurlbert, 1984). This resulted in 12 observation periods over a six-hour tide cycle. Tide height ranged from 0.29m-8.65m over observation days. As birds could not be individually identified, it was assumed for each observation that

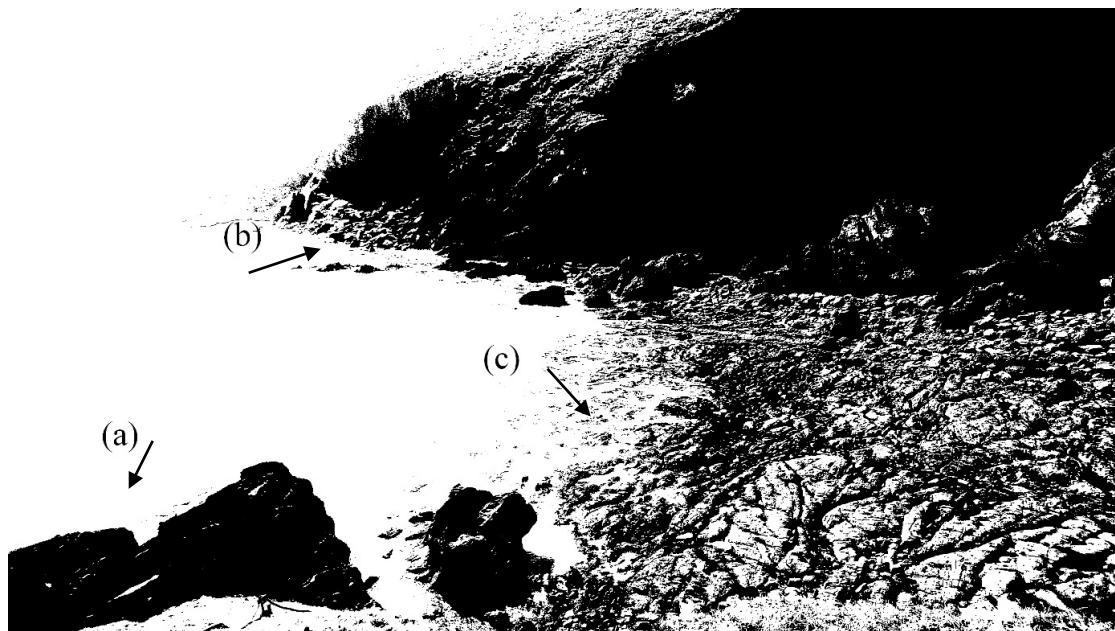


Figure 2: The study site, Lametry Bay, taken from near the south light house where observers were located. Habitat (a) represents jagged rock, which contained few seaweed and rock pool areas. Habitat (b) was characterised as cliff rock, which was mainly dry and did not contain any seaweed areas. Habitat (c) was titled beach, which was characterised by round boulders and contained many rock pools and seaweed areas.

the bird was a different individual. Focal birds were selected at random from 0-7 individuals present at any one time. Two researchers observed and dictated behaviours whilst two additional researchers noted them. When a bird was out of sight, the period was recorded and accounted for during analysis. If the focal animal left the bay or habitat, sampling stopped.

Data collection

Using focal continuous event sampling, foraging and antagonistic behaviours were recorded. Foraging behaviours included searching, swallowing and pecking, whilst antagonistic acts included piping and chasing (previously defined by Ens & Goss-Custard, 1986). The rate of foraging and antagonism was subsequently calculated by dividing the frequency of events by the total observation time for each focal.

Additional variables recorded are defined in Table 1.

Table 1: Additional measures collected during behavioural observations

Measure	Description
Tide	Tide was split into 7 states, up to: 3 hours before, 2 hours before, 1 hour before, low tide, up to: 1 hour after, 2 hours after, 3 hours after.
Habitat	Type of substrata observed upon: jagged rock, cliff rock, beach-as described in Figure 1
Habitat condition	Wet or dry substrata
Sea state	Measured using the Beaufort Sea Scale (Huler, 2004). This was included since Ghosh et al. (2003) found sea state was a significant predictor of oystercatcher foraging.
Heterospecifics near focal	Maximum number of heterospecifics within 10 body lengths of focal individual
Conspecifics near focal	Maximum number of conspecifics within 10 body lengths of focal individual
Time of day	Time of observation was split into four categories: 10am-12pm, 12pm-3pm, 3pm-5pm and 5pm-7pm

Statistical analysis

An ANCOVA tested for differences between tide and foraging rate whilst controlling for sea state. Despite attempts to transform foraging rate, data violated the normality assumption. A stepwise multiple regression determined which variables best predicted foraging. Predictors included were: tide, time of day, conspecifics and heterospecifics near focal, habitat, habitat condition and sea state. The modal categories were used as references for categorical predictors: jagged rock for habitat, 3 hours before low tide for tide and 12pm-3pm for time of day. The highlighted outlier ($\pm 3SD$) was not influential so was retained. To achieve approximate normality of residuals, foraging rate was log transformed. Independent samples t-test, with the assumption of normality through the central limit theorem, tested for

differences within the significant predictor. The effect of tide on the significant predictor could not be tested for since too many expected cases were below the threshold.

Due to the limited occurrence and large spread of the data, antagonism was binary coded (no antagonism vs. antagonistic event occurred) for each observation. A Pearson's chi squared tested for associations between tide and antagonism. Due to low expected counts for the observations three hours after low tide, data was excluded from this test. A binary logistic regression determined the effect of additional potential predictors on antagonism. The same predictors as the stepwise regression were used, with the exception of sea state, which was excluded due to linearity of the logit violations despite transformations. Heterospecifics data was log transformed to remove the influential case.

Due to violations of assumptions, a Spearman's rank-order correlation determined the relationship between foraging and antagonistic rates.

Results

Foraging

Foraging rate did not differ significantly between tide stages, when controlling for sea state ($F(6, 126) = 0.63, p = .709$) and without the covariate ($F(6, 127) = 0.56, p = .763$). Habitat was the only significant predictor of foraging rate (Table 2). Habitat predicted 21% of the variation in foraging rate ($R^2_{adj} = .210$).

Foraging rate differed significantly between all three habitats (Figure 3), with the highest foraging rate occurring on the beach (jagged versus beach, $t(102) = -5.92, p < .001$, jagged versus cliff, $t(103) = -2.33, p = .022$; beach versus cliff, $t(57) = 2.94, p = .005$). Although it could not be tested for significance, tide may influence habitat use (as suggested

by Figure 4). There was a significant but weak correlation between foraging and antagonism rates ($r_s(134) = -.273, p = .001$).

Table 2: Predictors used in a stepwise multiple and logistic regression for foraging rate and antagonism respectively. For foraging, values show the only significant predictor and the significance of the model. For predictors of antagonistic events, statistics show the Wald statistic and significance within the full model. * = $p < .05$, ** = $p < .01$

Predictor	Foraging	Antagonism
Time of day	-	* $\chi^2(3) = 8.65, p = .034$
Tide	-	* $\chi^2(6) = 15.57, p = .016$
Habitat	* $F(1, 130) = 5.78, p = .018$	** $\chi^2(2) = 13.25, p = .001$
Habitat condition	-	$\chi^2(1) = 0.56, p = .454$
Conspecifics near focal	-	$\chi^2(1) = 2.16, p = .142$
Heterospecifics near focal	-	* $\chi^2(1) = 5.49, p = .019$
Sea state	-	-

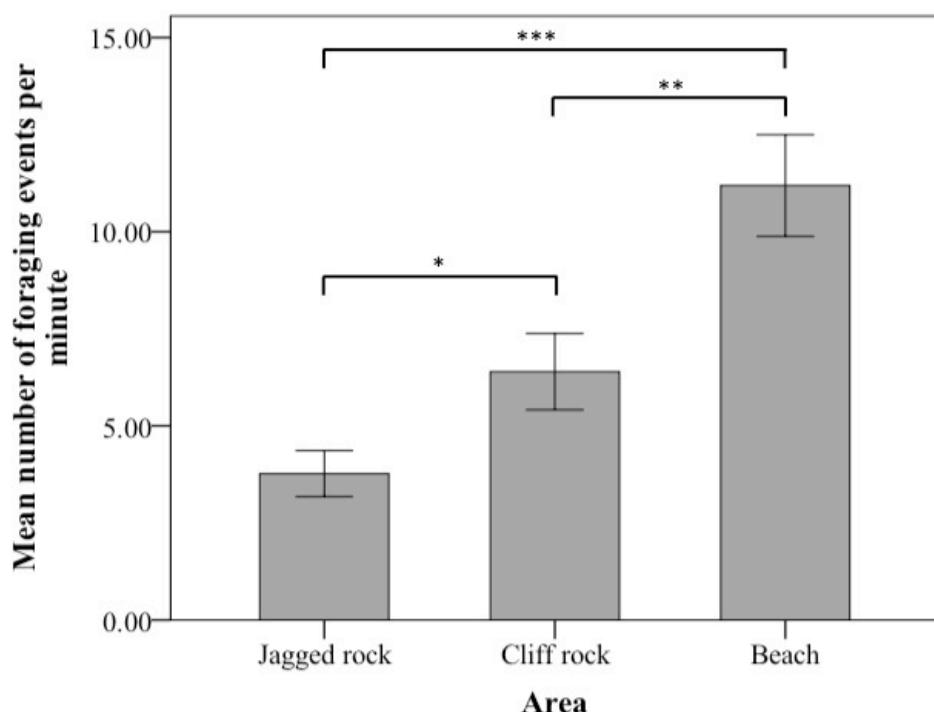


Figure 3: Foraging rate observed in different habitats of Lametry Bay, Lundy Island (Mean \pm SE) * = $p < .05$, ** = $p < .01$ *** = $p < .001$

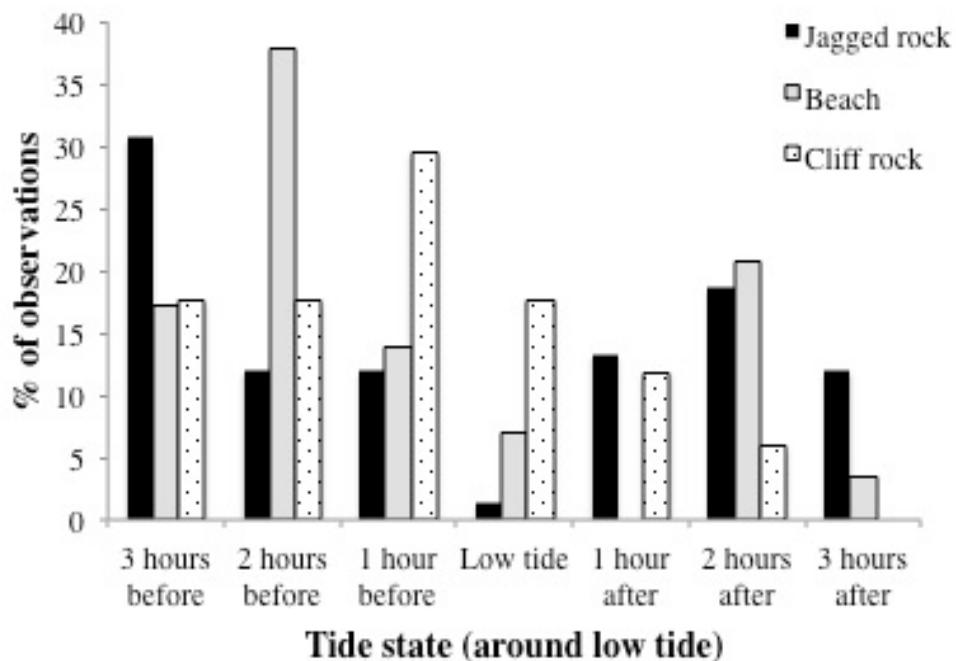


Figure 4: Changes in location of focal birds in relation to tide. Jagged rock= black, Beach= grey, Cliff rock = patterned.

Competition

Tide was significantly associated with the frequency of antagonistic events (Figure 5) with $\chi^2(5, N = 124) = 14.76, p = .011$. The highest percentage of observations containing an antagonistic act occurred one and three hours after low tide.

A binary logistic regression significantly compared ($\chi^2(14, N = 134) = 56.59, p < .001$) antagonism to the stated predictors, accounting for 49% of the variance in antagonistic interactions (Nagelkerke's $R^2 = .489$). In addition to tide (Figure 5), the number of heterospecifics near focal, time of day and habitat, significantly predicted antagonism (Table 2). The frequency of antagonism significantly increased between 12pm-3pm ($B = 1.80, p = .043, SE = 0.89$) and between 5pm-7pm ($B = 4.44, p = .012, SE = 1.76$) compared to 10am-12pm. Although, antagonism also increased for 3pm-5pm suggesting a positive relationship, this result was non significant ($B = 1.98, p = .124, SE = 1.29$). Compared to jagged rock, antagonistic events decreased on both the beach ($B = -1.86, p = .014, SE = 0.76$) and cliff

rock ($B = -3.31, p = .001, SE = 1.14$). There was a positive relationship between the number of heterospecifics near the focal and whether an antagonistic event occurred ($B = 0.22, p = .019, SE = 0.10$).

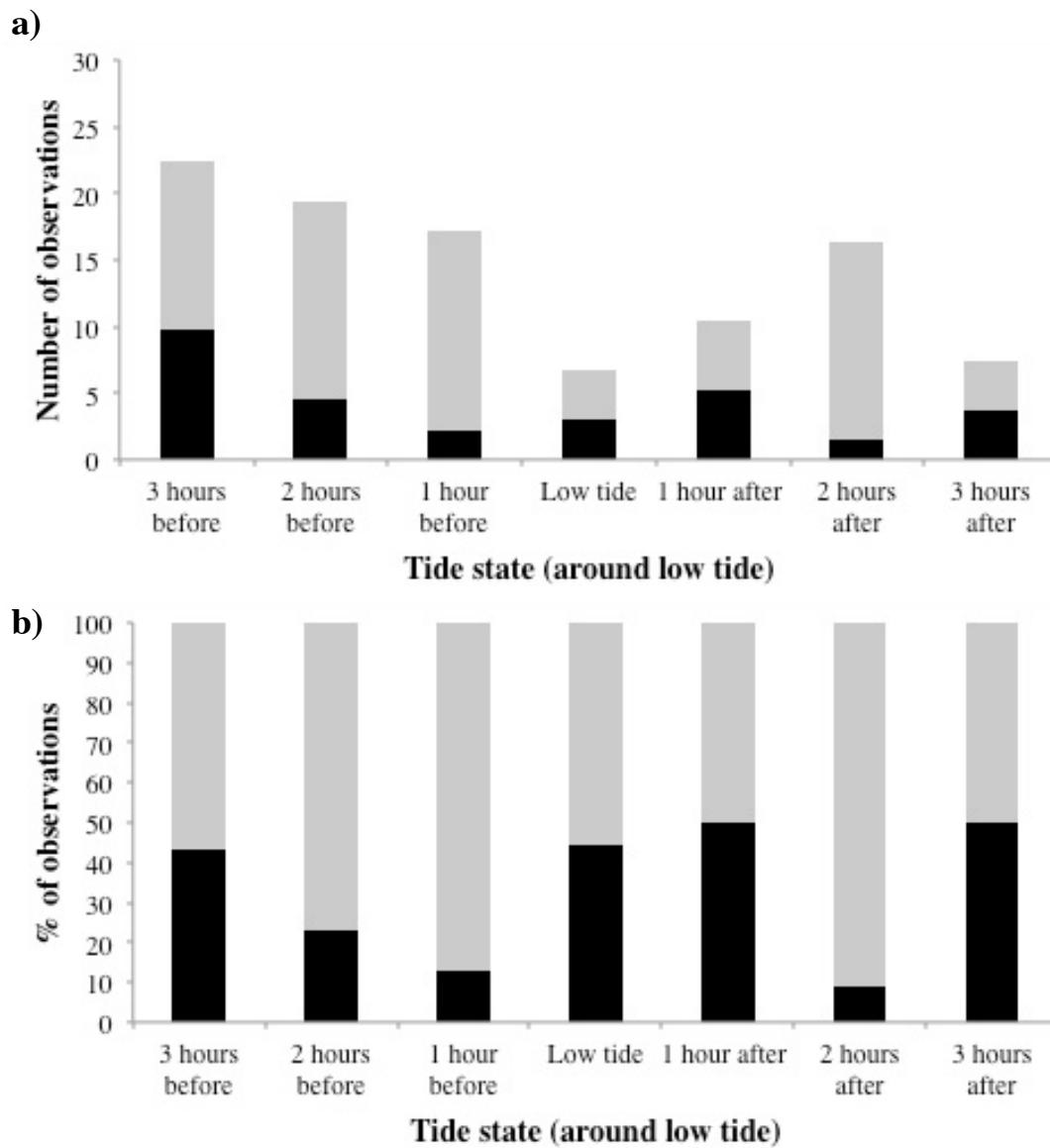


Figure 5: Total number (a) and proportion (b) of observations where antagonistic behaviours occurred (black bars) and where antagonistic behaviours did not occur (grey bars) across seven different tide states.

Discussion

The results found that tide does not affect oystercatcher foraging behaviour and habitat condition. This does not support the hypothesis and is not consistent with previous research that suggests foraging is greatest during falling tides (Ghosh et al., 2003). This instead may be explained by Vermeij (1972), who found that limpets are abundant from the low to high intertidal zone, and as this study investigated foraging around low tide, abundance may not have been a limiting factor.

Habitat was a significant predictor of foraging; limpets rely on the tide for foraging and to prevent desiccation (Hartnoll & Wright, 1977), thus oystercatchers may preferentially forage on the beach because the limpets may be more abundant, of better quality or may be easier to detach. Furthermore, jagged rock and cliff rock were elevated above the water level and never fully submerged (personal observation), thus limpets in these habitats may have been larger, as Davies (1969) found that the rate of water loss during desiccation varies inversely with body size; the larger and more desiccated limpets are harder to dislodge (Feare, 1971).

Antagonistic acts were significantly affected by tide, supporting the hypothesis, however antagonistic events occurred more often after low tide, which contrasts Ghosh et al.'s (2003) findings that antagonistic behaviours decreased during low rising and low falling tide. Overall, the results are consistent with Ghosh et al.'s (2003) conclusion: no clear trend exists between antagonistic behaviours and tide, thus further investigation is needed.

Although the results do not indicate what the aggression was in relation to, there are many reasons to suggest it was not related to food competition. This is consistent with previous research suggesting aggressive encounters may occur for additional reasons other than prey (Vines, 1980; Goss-Custard, Durell, & Ens, 1982). Firstly, foraging and

competition were weakly negatively related; since tide does not affect foraging, possibly because of the abundance of limpets, this suggests that the aggressive acts were not related to the protection of a foraging territory. Secondly, the number of heterospecifics nearby predicted aggressive acts, however gulls do not compete directly with oystercatchers for limpets (Harris, 1965).

Additionally, time of day was a significant predictor of antagonism, with aggressive acts increasing with time. Since antagonistic acts were probably not related to food competition, it might be suggested that the time of day is related to competition for space. Some studies found that oystercatchers are diurnal (Ghosh et al., 2003; Drinnan, 1958; Heppleston, 1971). Therefore, they may be becoming more aggressive later in the day as they forage less and carry out other behaviours such as resting. This is consistent with the negative correlation between foraging and antagonistic acts. Furthermore, habitat predicted antagonistic events, with the highest number of aggressive acts occurring on jagged rock. This habitat may be favourable for non-foraging behaviours as it is not as affected by the tide, thus reducing the risk of dislodgement. Conversely, other studies suggest that oystercatchers forage at night (Drinnan, 1957; Sanders, Spinks & Magarian, 2013), thus future research should investigate whether time of day affects foraging and antagonism, and whether aggression is related to competition for food or space.

A limitation of this study is that pseudosleeping was not included, thus not all antagonistic behaviours that were observed may have been recorded. One of the traits of pseudosleeping is that the oystercatcher's eyes are open, which was difficult to correctly define from the distance the observations were conducted at. However, Makkink (1942) found that pseudosleeping is frequently followed by an attack, therefore this may not have had a large impact on the results.

In conclusion, this study does not further our understanding of oystercatcher foraging behaviour in relation to tide, however rising sea levels may impact foraging on the beach. As the coastline is prevented from moving inland by the cliff walls of Lundy, oystercatchers may not be able to forage for limpets at Lametry bay in the future. Furthermore, oystercatchers were observed to engage in more antagonistic events when the tide rose, which may be reflected in rising sea levels as the intertidal habitat reduces in size, leading to more competition for food and space.

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