BVG Trust

J. Sci. Trans. Environ. Technov. 2007, 1(1): 29-35

Scientific Transactions in Environment and Technovation

Foraging strategies of Eurasian Oystercatchers *(Haematopus ostralegus)* on rocky shores: influence of tide, substrate and kleptoparasitism

R. Edwards, L. Rossiter and R. Nagarajan*

10.20894/STET.116.001.001.005
www.stetjournals.com

School of Psychology, University of Exeter, Washington Singer Laboratories, Perry Road, Exeter, EX4 4QG, United Kingdom

Abstract

We investigated how the foraging strategies and success of limpet-feeding Eurasian Oystercatchers (*Haematopus ostralegus*) varies with different factors: tide condition, nature of rock, position of limpet and density of potentially kleptoparasitic gulls and conspecifics. The influence of different limpet-opening techniques upon aspects of foraging time were also investigated. Observations were made of oystercatchers on Lundy Island, U.K. using focal animal sampling. A total of 362 limpet attacks were observed (223 successful). Multiple regression analyses revealed that selection of limpet length and handling time were influenced negatively by gull density. Tide was found to influence length of limpets selected and searching and carrying time. Limpet-opening technique influenced opening time only. Binary logistic regression found only limpet length was significant predictor of attack success, with success decreasing as limpet length increased. Oystercatchers appear to forage flexibly, adapting aspects of their foraging strategy in accordance with environmental factors.

Keywords: foraging technique, *Haematopus ostralegus*, kleptoparasitism, limpet, oystercatcher, substrate condition, tide

INTRODUCTION

A number of species are known to forage flexibly, by adapting their foraging strategies in relation to various internal and external factors (Krebs and Davies, 1993). Foraging behaviour involves a number of choices such as where and how to search for prey, which prey to select and what foraging technique to employ (Sih, 1993; Sutherland *et al.*, 1996). The foraging behaviour of Oystercatchers (*Haematopus* spp) has been widely studied (Goss-Custard *et al.*, 1987; Goss-Custard, 1996). Much of this research has focused on Eurasian Oystercatchers (*Haematopus ostralegus*) that predate bivalves such as mussels and cockles in estuarine habitats (e.g., Goss-Custard *et al.*, 1987; Blomert *et al.*, 1996). Such studies have identified a range of factors believed to influence foraging behaviour including tide and weather (McConkey and Bell, 2005), human disturbance (Stillman and Goss-Custard, 2002) andintra and inter-specific kleptoparasitism (Brockman and Barnard, 1979; Stillman *et al.*, 2000). Only a few studies have investigated Oystercatchers feeding on limpets (*Patella* spp*)* that forage in a marine environment along rocky shores (e.g., Feare, 1971; Coleman *et al.*, 1999).

Limpet feeding Oystercatchers have been observed to use a range of limpet-opening techniques (Feare, 1971; Hockey, 1981; Wootton, 1997). It is not clear how Oystercatchers choose which opening technique to use during foraging. This has been studied in mussel feeding Oystercatchers where individuals are often seen to specialize in one prey opening technique but are capable of using an alternative under certain conditions (Sutherland *et al.*, 1996).

Oystercatchers appear not to select the largest limpets when foraging; which suggests that their foraging decisions are influenced by factors other than maximizing energy intake (Harris, 1965; Feare, 1971). Limpet size is likely to determine the amount of effort required to dislodge a limpet from the rock, with larger limpets being more difficult to dislodge than smaller limpets, due to stronger foot muscles (e.g. Feare, 1971; Hockey and Underhill, 1984).

Hockey (1981) and Frank (1982) found that limpet-feeding Oystercatchers feed near the waters' edge where limpets are active and their shells are less adhered to the substratum. Similarly, Ghosh *et al.* (2003) found that foraging frequency and duration was highest during high-falling and low- falling tides, where limpets are exposed and more active, thus increasing their vulnerability. The position of the limpet on the rock could influence foraging behaviour and success. It could be that a bird will need less force to remove a vertical limpet where a clear strike can be made without bending its neck. Also, Santini *et al.* (2004) found that the timing of limpet activity varies between those attached to vertical and horizontal surfaces.

The length of limpets selected may also be related to the density of gulls and other Oystercatchers as inter and intra-specific kleptoparisitism has been well documented for Oystercatchers (Brockman and Barnard, 1979; Stillman *et al.*, 2000). Past research has found that Oystercatchers will decrease the size of prey taken in the presence of gulls when foraging for oysters (Tuckwell and Nol, 1997).

*Corresponding author
R.Nagarajan@ex.ac.uk

The present study aimed to investigate how the foraging behaviour and success of limpet-feeding Eurasian Oystercatchers varies with different environmental factors: tide condition, wetness of rock, position of limpet on the rock and density of potentially kleptoparasitic gulls and conspecifics. Also, how limpet-opening techniques may influence foraging time and success. The key questions addressed were: (1) What are the different techniques that Oystercatchers employ to open limpets? (2) Are there differences in searching, opening, carrying and handling times between these different techniques? (3) What other factors affect searching, opening, carrying and handling times? (4) What factors affect the length of limpet selected? and (5) What factors influence whether the attack on the limpet is successful or not?

MATERIALS AND METHODS

Study area

Research took place on the island of Lundy, situated in the Bristol Channel, England (51° 10′N, 4° 40′W). The island has an area of 3.5 km^2 and consists of several shoreline habitats types both sheltered and exposed. Data were collected on different habitats *viz.*, Landing bay, Victoria beach, and Ugly beach of south east of the island (Fig. 1).

Behavioural observations

A number of Eurasian Oystercatchers were studied, that belonged to a population of around 30-40 individuals resident on Lundy Island (Nagarajan, personal observation). These birds feed primarily on common limpets *Patella vulgata* and black footed limpets *P. depressa* (Nagarajan, unpublished data).

Data were collected during daylight hours, throughout the tidal cycle, during March and April 2006. Foraging behaviour was recorded using focal animal sampling, with focal birds selected at random (Altmann, 1974). Continuous observations were made for at least five minute observation periods, using a 15-60x telescope. A minimum distance of 30 m was maintained, to minimise observer disturbance. All observations were made by two researchers, an observer, who dictated behaviour and a recorder who scribed and measured the durations of behaviours using a stopwatch. Opening techniques were described and recorded. An attack was taken to be successful when a limpet was dislodged and unsucessful if attacked but not dislodged. The duration in seconds, of searching, opening, carrying and handling for each limpet consumed was recorded. Opening time was the time from the bird's first attempt to open a limpet to the moment the limpet was detached

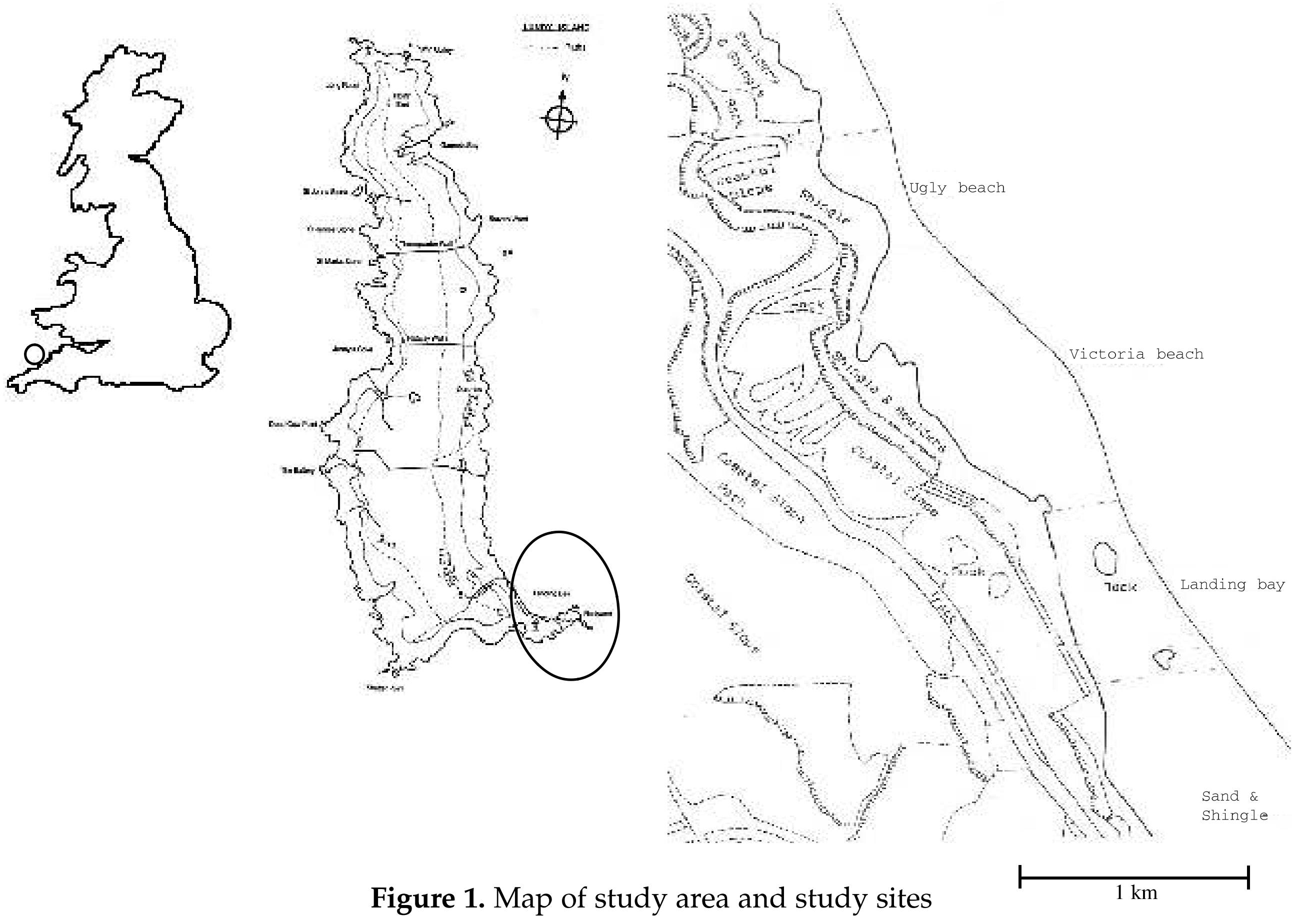

Figure 1. Map of study area and study sites

from the rock. Handling time was measured from the moment the limpet detached away from the rock to when the bird had finished consuming the limpet. If the bird carried the limpet within its consumption then it was recorded as carrying time. Searching time for the next limpet would begin as soon as handling had finished. The foraging technique used on each limpet was noted. The success/failure of an attack was also recorded. The maximum length of limpets attacked was estimated as a percentage of bill length and converted into millimeters assuming a mean bill length of 75 mm and correcting for observer bias (Goss-Custard *et al*., 1987). Density of gulls and Oystercatchers was measured by recording the number present within the beach of the focal Oystercatcher, at the beginning and end of the observation period and then by dividing the mean number of birds was then divided by the area of the beach in km^2. The nature of the rock on which a limpet was attacked was classified as, 'dry', 'wet', or 'splashed'. The limpet's position on the rock was recorded as on a 'horizontal' or 'vertical' surface. The stage of the tidal cycle was also recorded for each observation. Tide was divided into six stages: high-slack, high-falling, low-falling, low-slack, low-rising and high-rising. The stages high-slack and low-slack represent high water and low water, respectively.

Statistical analyses

The data was split into successful and unsuccessful limpet attacks for analysis. Multiple regression analyses were performed on all successful attack data to produce five models with the dependent variables, searching time, opening time, carrying time, handling time and limpet length. The explanatory variables used throughout the models were, nature of rock, position of limpet, limpet-opening technique, density of gulls, and conspecifics and the three stages of the tidal cycle where feeding was observed. Limpet length was included as an explanatory variable in the four models in which it was not the target variable. For the categorized variables of tide and nature of rock, low- rising and splashed rock were used as the respective reference categories. Compliance with assumptions such as homoscedasticity, linear relationship and normality was established by standard tests (Nagarajan *et al*., 2002a). Binary logistic regression was used to investigate factors affecting the success of a limpet attack by an Oystercatcher, using both successful and unsuccessful attack data (Nagarajan *et al*., 2002b).

RESULTS

Limpet-opening techniques

Three limpet-opening techniques were observed. The techniques were

1) **Levering:** a fissure is made at the shell margin and the limpet is levered off with the bill. Levering was used to attack 80.23% of limpets.

2) **Chipping:** bird uses the tip of its bill to stab at the shell margin, usually only one or two stabs are required to dislodge the limpet.

3) Levering and Pulling: the bird levers the limpet loose from the rock with its bill and then removes it from the rock by grasping the entire limpet and pulling.

Limpet length selection

Successfully attacked limpets ranged in length from 24.3 to 50.8 mm with a mean length of 30.3 ± 0.36 mm (mean ± S. E.; $n = 201$) (Table 1). Length of limpets selected was influenced negatively by gull density. There was a significant difference between the three tide stages analysed, with low-falling tide having the longest limpets and low-rising the shortest limpets sucessfully opened (Table 2).

Factors affecting foraging behaviour

Oystercatchers were not observed to forage during any of the high water stages of the tidal cycle. The foraging behaviour and density of potentially kleptoparasitic gulls and conspecifics varied in relation to tide, substrate and foraging techniques (Table 1). Multiple regression models for, searching time, opening time, carrying time, handling time and limpet length were significant ($P<0.05$; Table 2). Searching time was significantly longer at low-falling than at low-slack and low-rising tide and was influenced positively by limpet length. Opening time was significantly shorter for chipping than the other two techniques and was also positively influenced by Oystercatcher density. Handling time was influenced negatively by gull density and was significantly longer on wet rock compared to dry and splashed rocks. Carrying time was significantly longer at low-falling tide than the other two tide stages analysed.

Limpet attack success

The percentage of successful limpet attacks was 61.6%. The mean length of unsuccessfully attacked limpets was 33.5 ± 6.12 mm ($n = 139$) which is 10.6% longer than successfully attacked limpets. Binary logistic regression with attack success as the dependent variable and all other variables as predictors, found that limpet length was the only significant predictor ($P<0.001$; Table 3). The success of a limpet attack varied with limpet length; failure increased as limpets increased in length.

DISCUSSION

Limpet-opening techniques

Three limpet-opening techniques were observed. Only levering had been previously recorded for the Lundy

Table 1: Behavioural observations of Oystercatchers (mean ± S.E.) in relation to various factors, for both successful and unsuccessful attacks on limpet. The values in parentheses are number of observations

Variable		Limpet length (mm)		Searching time (s)		Opening time (s)		Handling time (s)	Carrying time (s)	Gull density (number/km^2)	Oystercatcher density (number/km^2)
		Successful attack	Unsuccessful attack	Successful attack	Unsuccessful attack	Successful attack	Unsuccessful attack	Successful attack	Successful attack	Successful attack	Successful attack
Stage of tide	Low-falling	33.0 ±1.65 (16)	33.9 ±1.60 (9)	35.1 ±8.54 (14)	38.1 ±7.45 (14)	4.1 ±0.68 (16)	3.7 ±0.61 (15)	5.7±0.90 (16)	14.4 ±7.49 (5)	1.6 ±0.11 (16)	0.0 ±0.00 (16)
	Low-slack	31.1 ±0.46 (103)	34.6 ±0.85 (45)	24.8 ±3.75 (110)	42.6 ±5.99 (78)	8.2 ±1.14 (118)	7.0 ±0.87 (78)	8.6 ±0.77 (115)	3.5 ±0.34 (54)	2.6 ±0.12 (118)	0.8 ±0.09 (118)
	Low-rising	28.3 ±0.38 (76)	31.9 ±1.33 (28)	17.1 ±2.82 (74)	15.3 ±2.49 (38)	5.1 ±0.68 (82)	6.7 ±1.01 (40)	6.7 ±0.47 (82)	2.6 ±0.38 (31)	1.5 ±0.08 (82)	1.5 ±0.14 (82)
Nature of rock	Dry	28.7 ±0.48 (75)	33.1 ±1.20 (29)	17.8 ±2.44 (73)	22.3 ±3.40 (42)	5.8 ±1.26 (77)	5.9 ±0.75 (44)	6.6 ±0.63 (77)	5.1 ±1.43 (29)	2.2 ±0.16 (77)	1.1 ±0.12 (77)
	Wet	30.6 ±0.40 (111)	34.1 ±0.91 (45)	24.1 ±3.63 (118)	33.7 ±4.05 (79)	7.4 ±0.85 (130)	7.0 ±0.91 (79)	8.4 ±0.66 (127)	3.1 ±0.37 (57)	2.1 ±0.10 (130)	1.0 ±0.12 (130)
	Splashed	36.1 ±2.70 (9)	32.6 ±1.98 (8)	48.4±15.44 (7)	93.2 ±36.31 (9)	3.4 ±0.67 (9)	5.1 ±1.21 (10)	6.7 ±1.96 (9)	4.0 ±1.47 (4)	1.5 ±0.28 (9)	0.1 ±0.10 (9)
Position of limpet	Horizontal	29.3 ±0.33 (139)	33.9 ±0.94 (53)	19.1 ±2.13 (135)	33.8 ±5.01 (87)	6.1 ±0.68 (150)	6.7 ±0.81 (90)	7.2 ±0.43 (148)	3.0 ±0.27 (63)	2.2 ±0.10 (150)	1.0 ±0.09 (150)
	Vertical	32.2 ±0.77 (56)	33.0 ±0.88 (29)	30.2 ±6.05 (63)	35.0 ±6.04 (43)	8.1 ±1.62 (66)	6.2 ±0.80 (43)	8.9 ±1.16 (65)	5.6 ±1.59 (27)	1.9 ±0.13 (66)	1.0 ±0.16 (66)
Foraging technique	Levering	31.0 ±0.42 (136)	33.9 ±0.69 (78)	26.5 ±3.26 (141)	35.3 ±4.08 (123)	7.8 ±0.89 (154)	6.6 ±0.63 (126)	7.9 ±0.59 (152)	4.1 ±0.69 (66)	2.0 ±0.09 (154)	0.9 ±0.10 (154)
	Chipping	26.9 ±0.34 (41)	27.6 ±0.00 (3)	12.1 ±2.55 (36)	8.0 ±3.06 (3)	2.1 ±0.15 (41)	6.3 ±3.84 (3)	6.3 ±0.80 (41)	2.3 ±0.50 (16)	2.4 ±0.23 (41)	1.4 ±0.18 (41)
	Levering and Pulling	31.0 ±1.11 (18)	26.0 ±1.66 (2)	14.6 ±3.28 (21)	19.8 ±8.21 (4)	7.8 ±2.03 (21)	5.0 ±0.91 (4)	8.7 ±1.19 (20)	4.0 ±0.98 (8)	2.1 ±0.26 (21)	1.1 ±0.19 (21)

Table 2: Results of stepwise multiple regression analyses for successfully opened limpets. Values are unstandardised coefficients with standard errors in parentheses. Dash indicates that the variable did not have significant influence. The stage of the tide, nature of rock, position of limpet and foraging techniques are used as dummy variables in the regression model. Variables, namely, low-rising splashed rock, and levering and pulling and levering are used as reference variables

Independent variables	Limpet length	Searching time	Opening time	Handling time	Carrying time
Stage of tide					
Low-falling	0.063**	0.361*	-0.113	-0.120	0.486**
	(0.015)	(0.173)	(0.114)	(0.100)	(0.158)
Low-slack	0.070**	0.061	-0.004	0.071	0.199*
	(0.011)	(0.099)	(0.063)	(0.077)	(0.080)
Nature of rock					
Wet rock	-0.027	-0.204	0.179	0.258*	0.077
	(0.016)	(0.210)	(0.123)	(0.104)	(0.156)
Dry rock	-0.020	-0.114	0.160	0.157	0.261
	(0.018)	(0.227)	(0.133)	(0.115)	(0.166)
Position of limpet	0.008	0.025	-0.058	0.026	0.070
	(0.007)	(0.088)	(0.055)	(0.048)	(0.075)
Foraging technique					
Levering	0.005	-0.006	0.076	-0.087	-0.013
	(0.011)	(0.129)	(0.082)	(0.073)	(0.113)
Chipping	-0.013	-0.087	-0.412**	-0.063	-0.135
	0.013	(0.154)	(0.096)	(0.085)	(0.136)
Gull density	-0.062**	-	-	-0.063*	-
	0.013	-	-	(0.027)	-
Oystercatcher density	-	-	0.174**	-	-
	-	-	(0.063)	-	-
Length of limpet selected	-	0.027**	-	0.024**	-
	-	(0.010)	-	(0.006)	-
R^2_{adj}	48.7%	7.1%	24.4%	26.4%	26.4%
F	17.75**	2.36*	7.32**	7.24**	4.54**

* denotes P<0.05, ** denotes P <0.01.

Table 3: Binary logistic regression equation to investigate the factors that affect limpet foraging success by Oystercatchers. Dependent variable is nature of attack and is coded as 1= successful and 2 = unsuccessful. The habitat is entered as dummy variable and the Landing bay is used as reference variable.

Variable	Coefficients	*P*
Constant	-5.867 ± 1.125	P<0.001
Limpet length	0.118 ± 0.026	P<0.001
Ugly beach	1.222 ± 0.596	P<0.05
Victoria beach	1.458 ± 0.545	P<0.01
log-likelihood = -159.5; G =26.70; df = 3; P<0.001		

Island Oystercatcher population (Nagarajan, unpublished data). Two new techniques, 'chipping' and 'levering combined with pulling' were observed, adding to knowledge of limpet predation by Oystercatchers. Opening time was significantly shorter for chipping than the other two techniques. Length of limpets selected was found to significantly vary according to technique, with the smallest limpets targeted when the chipping method was employed. This could explain the short opening time for chiping since the smallest limpets were the easiest to dislodge from the rock. Furthermore, the chipping method was mainly observed when the weather was sunny and windy and the Oystercatchers were feeding on dry rocks suggesting that certain conditions have to be met before the chipping method is profitable enough to be employed. Durell *et al.* (1993) found that two different techniques of mussel-opening, stabbing and hammering, were both profitable but under different conditions.

Mussel-feeding Oystercatchers often show a strong specialization for one opening technique (Sutherland *et al.*, 1996); however, limpet feeding Oystercatchers on Lundy have previously been observed using two methods simultaneously (Nagarajan unpublished data).

Limpet length selection

The study's findings support those of Harris (1965) and Feare (1971) that Oystercatchers appear not to select the largest limpets when foraging, instead Oystercatchers mostly selected limpets within the size class 26 – 35 mm. This may be due to the difficulty of dislodging large limpets from the rock (Feare, 1971; Hockey and Underhill, 1984). Length of limpets selected was found to vary with tide and gull density.

No feeding was observed during the high-tide stages. This supports previous research that limpet feeding is most common at low compared to high-tide stages (Ghosh *et al*., 2003). Oystercatchers consumed longer limpets at low-falling tide. This could be because at this stage of the tidal cycle, limpets are becoming exposed and have been recently submerged, thus, are more active and therefore more vulnerable (Ghosh *et al*., 2003). Also, limpets at low-falling tide may not yet have returned to their 'home scar' where they are most safe from attack (Coleman and Hawkins, 2000). The shortest limpets were consumed at low-rising tide. It could be that at low-falling tide fewer limpets are exposed as the water level rises and those that are accessible have been exposed for longer periods of time, thus, again limpets will be less active and less vulnerable, making large prey more difficult to remove from the rocks. Indeed, past research suggests that targeting larger limpets on dry rock could be unprofitable since the opening and handling times would be high (e.g. Frank, 1982; Ward, 1991). However, this study found that rock wetness did not significantly predict prey size.

Length of limpets selected was influenced negatively by gull density. This finding supports research indicating that for Oystercatchers, the risk of losing prey to kleptoparasitic gulls increases with prey size (Tuckwell and Nol, 1997).

Factors affecting foraging behaviour

Searching time was significantly longer at low-falling than at the other two tide stages analysed. As mentioned above, limpets are likely to be most vulnerable at low-falling tide, as they may not yet have reached their 'home scar'(Coleman and Hawkins, 2000). Therefore, the increased searching time could reflect a higher degree of selectivity; Oystercatchers may be more concerned with prey size in order to exploit the opportunity to predate larger limpets whilst they are most vulnerable. Indeed, searching time was found to increase with prey size.

Carrying time was longer at low-falling tide than the other two tide stages. This could be because during low-falling tide Oystercatchers feed closer to the water's edge, as limpets become exposed. Therefore, an Oystercatcher may need to carry its prey away from waves, before handling, to avoid being pushed from a rock or losing the prey.

Handling time was influenced negatively by gull density, which appears logical, as increased handling time could increase the opportunity for prey to be stolen (Tuckwell and Nol, 1997). Handling time was significantly longer on wet rock compared to dry or splashed rocks. It could be that limpets are less tightly adhered to their shells when they are wet than when they are dry, just as they are less tightly adhered to the substrate. Therefore limpets on splashed rocks (i.e., the wettest) would be easiest to remove from their shell and consume and so have the shortest handling time and those on dry rocks, should have the longest. The reason that limpets fed from dry rocks did not have the longest handling time may be due to the fact that no 'large' (40-50 mm) limpets were consumed on dry rock in this study, as handling time increases with limpet length.

Limpet attack success

Coleman *et al*., (1999) observed a large number of unsuccessful limpet attacks on the Dorset coast U.K. and believed that this low success rate was due to the fact that large limpets (36-38 mm) were most frequently attacked. This study too found limpet length to be a significant predictor of attack success, with the success rate decreasing as limpet length increased. This finding was not surprising as larger limpets have stronger muscles to fasten themselves to a rock making them more difficult to remove.

CONCLUSION

Three limpet-opening techniques were observed; 'levering', 'chipping' and 'levering and pulling'. Chipping had the shortest opening time and this could have implications for a birds' choice of technique. A number of factors affected foraging behaviour. Gull density influenced handling time negatively. Tide was found to influence searching time and carrying time. The length of limpet selected was influenced by tide. Limpet length significantly predicted attack success, with larger limpets being less successfully attacked. Oystercatchers appear to forage flexibly, adapting aspects of their foraging strategy in accordance with environmental factors.

ACKNOWLEDGEMENTS

We thank Professor Stephen E.G. Lea for suggestions and comments on the research, two anonymous referees for their valuable comments and suggestions and Dave Taylor and Peter Goodes for their help in arranging the logistics and equipment necessary for the research. RN gratefully acknowledges the Leverhulme Trust, UK for financial support through the Early Career Award.

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