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THE EFFECT OF HUMAN DISTURBANCE ON THE FORAGING BEHAVIOUR OF THE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS* ON THE ROCKY SHORE

by

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

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The Effect of Human Disturbance on the Foraging Behaviour of the Oystercatcher *Haematopus ostralegus* on the Rocky Shore

Sarah Carless

Abstract

The aim of this thesis was to investigate the effects of human disturbance on animal foraging behaviour using oystercatchers foraging on the rocky shore as a model system. The primary focus of this thesis was the balance between vigilance and foraging, and the variation in this balance with changes in environmental factors and the application of experimentally controlled human disturbance. On the structurally complex rocky shore foraging and vigilance are generally mutually exclusive behaviours and so an individual must trade-off energy acquisition with predator avoidance. The extent of the trade-off was expected to vary spatially and temporally dependant upon an individual's needs and perceived predation risk.

The foraging behaviour and prey selection of individual oystercatchers on the rocky shore was observed from September to March when the birds were most vulnerable to starvation. A preliminary experiment conducted in the winter of 2001-2002 used experimental and observational methods in an attempt to identify which types of human recreational activities had the greatest effect upon oystercatcher behaviour. In the winter of 2002-2003 changes in oystercatcher behaviour and prey selection with environmental factors such as the weather, temperature, wind speed, season and tidal state; and additional factors such as individual age, and the distance to and species of the focal oystercatcher's nearest neighbour were investigated. Oystercatcher foraging behaviour and prey selection before, during and after human disturbance was also observed in order to examine whether any losses to energy intake as a result of human disturbance could be compensated for by feeding more intensively, changing prey selection or lowering their baseline level of vigilance so that foraging time increased.

Oystercatchers did not vary in their response to disturbance dependant upon the type of activity, but did vary spatially which could be a factor of the structural complexity of the shore. Human disturbance significantly reduced oystercatcher foraging as their vigilance increased, but oystercatchers returned to feeding at pre-disturbance levels almost immediately after the disturbance had ceased. Oystercatcher success rate on the rocky shore varied significantly with temperature and season, which may reflect an increase in feeding effort in response to the increased energetic costs of thermoregulation when colder temperatures ensue. Having another oystercatcher as a nearest neighbour significantly decreased oystercatcher success rate, although the distance separating an oystercatcher and it's nearest neighbour had no significant effect. Wind speed did not affect oystercatcher success rate but did significantly reduce peck rate, whilst an oystercatcher's age and the state of the tide (the amount of the shore that was uncovered) had no significant effect on oystercatcher behaviour. Prey selection varied with the state of the tide which could reflect prey availability. Oystercatcher energy intake over the time for which their rocky shore prey items were uncovered by the tide was just over half their estimated daily requirement, suggesting that feeding in supplementary feeding areas at high tide or at night may be an important part of the oystercatchers' foraging regime. Prey selection did not vary with disturbance, and no compensatory mechanisms were observed. It is possible that short-term disruptions to feeding double as digestive pauses or that there are potential constraints to energy intake rates such as the risk of bill damage, inexperience of foraging, interference, and prey availability.

It is suggested that implications for health are greatest when the individual is subject to human disturbance frequently and for extended periods of time, and when vigilance and foraging are mutually exclusive behaviours. Individuals naturally vary in their foraging behaviour and energy intake rate based on numerous individual, temporal and spatial factors; subsequently they will vary in the extent to which they respond to human disturbance which has implications for their risk of starvation. Where potential constraints to energy intake rates exist individuals may struggle to meet their energy requirements and be more likely to suffer a greater decline in health when prevented from feeding or forced to expend extra energy as a result of human activities.

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Chapter 1: Introduction and Literature Review

1.1. Introduction

Understanding the relationship between animals and their environment is key to determining animal behaviour and the distribution of populations (Begon *et al.* 1997). Animals will make decisions so as to enhance the probability of their survival, which means meeting their requirements for maximal fitness. Individuals within a population will vary in their requirements temporally and spatially. Time is a limited resource, and so an individual will adjust the time it apportions to various activities, that are imperative for maximal fitness, dependant upon its needs in a particular space and time (Caraco 1979a). A fundamental aspect of time-budgeting is the balance between the avoidance of predators and the acquisition of energy (Lima 1986, Lima & Dill 1990, McNamara & Houston 1990b, Lima & Bednekoff 1999b). The trade-off between vigilance and foraging has been studied extensively over the years and has implications for animals' habitat choice and fitness (see Lima 1998 for review, Duriez *et al.* 2005).

Predator detection is essential for survival. The earlier a potential predator is detected the higher the probability that an individual will successfully escape a predator attack. An individual may be able to limit the risk of being successfully preyed upon by adapting it's behaviour so as to enhance the probability of predator detection, and by occupying areas where predator attacks are rare and early predator detection is possible. When the threat of predation is increased, individuals will respond by altering their behaviour so as to ensure a successful escape. The response of animals to human disturbance is assumed analogous to the response of animals to a predation threat (Frid & Dill 2002). Recently, attention has been focussed on the effect of human disturbance on the behaviour and distribution of individuals (Gill *et al.* 1996, Hill *et al.* 1997) as human disturbance to animals is becoming increasingly frequent. Commercial activities such as the harvesting of shellfish and forestry; and an increase in the frequency and duration of recreational activities are placing increasing pressure upon animal resources (Cayford 1993). The work presented in this thesis aims to assess the impact of human recreational disturbance on the behaviour and energy intake of foraging individuals, and to identify any immediate compensatory mechanisms that may be adopted in response to a reduction in foraging time, by individuals that may already be pressured with regards to their time-budgets.

1.2. Risk Allocation Hypothesis

The risk of an individual being successfully preyed upon ultimately depends on the behavioural decisions it makes and the site it inhabits (Lima 1985). Predation risk will vary with factors such as where an individual feeds in relation to a refuge and the structural complexity of the area, when an individual feeds, whether it feeds alone or as part of a group, its pattern of scanning for predators, its time-budget, the frequency of and technique of its predator's attacks, and its prey handling technique and feeding efficiency (see Lima & Dill 1990 for review, Scannell *et al.* 2000).

The vigilance an individual demonstrates will fluctuate around a baseline level of vigilance, dependant upon the state of the individual and the predation risk (see Lima 1998 and references therein). Often vigilance and foraging are mutually exclusive behaviours which may cause hungry individuals to decrease their vigilance in order to intensify their foraging and increase their intake rate (Godin & Smith 1988, Swennen *et al.* 1989, Pravosudov & Grubb 1995, 1998), whilst those subject to a higher perceived predation risk may demonstrate elevated levels of vigilance at the cost of foraging (Lima & Bednekoff 1999b). They may shorten the intervals between their scans of the environment, increase the frequency of their scans, and/or extend the duration of their scans, when the risk of predation is increased (Lendrem 1983a, Hart & Lendrem 1984, Metcalfe 1984b, Pravosudov & Grubb 1995, 1998, Dyck & Baydack 2004, Fernádez-Juricic *et al.* 2004b, Trouilloud *et al.* 2004). The anti-predatory response of individuals has also been shown to vary with the temporal pattern of risk (Sih & McCarthy 2002). Theoretically, the greater the frequency and duration of high predation risk, the lower the level of vigilance should be when predation risk is reduced, as individuals attempt to compensate for lost foraging time (Lima & Bednekoff 1999b).

If an individual feeds upon prey items which can only be handled when in a head-down position and scanning is only possible when the individual has their head raised, then vigilance is traded-off with foraging (Metcalfe 1984b). Vigilance and foraging, however, may not always be mutually exclusive behaviours (Lima & Bednekoff 1999a, Guillemain *et al.* 2001). Some animals are able to handle prey items with their heads raised and may actually be better at detecting a predator when foraging at a greater rate (Cresswell *et al.* 2003); whilst others have the visual capacity to monitor the environment whilst simultaneously foraging with their head-down (Guillemain *et al.* 2002), providing the area in which they forage is of low structural complexity (Bednekoff & Lima 2005) and their feeding strategy accommodates vigilant-foraging (Guillemain *et al.* 2000, 2001). For example, dabbling ducks use two feeding methods, shallow feeding where vigilance and foraging behaviour can be performed simultaneously, and the riskier deep-water feeding where foraging and vigilance are mutually exclusive (Guillemain *et al.* 2000, 2001). Only when food is depleted from shallower waters do dabbling ducks feed using the riskier strategy (Guillemain *et al.* 2000).

The trade-off that occurs between foraging and vigilance is likely to vary dependant upon an individual's foraging efficiency and biotic and abiotic environmental factors. Increased energy requirements are associated with colder temperatures as extra fuel is metabolized in order to keep the individual warm (Kersten & Piersma 1987, Wiersma & Piersma 1994). Individuals, such as the young, deformed or naturally less efficient foragers that may be pressured to meet their energy requirements and be particularly vulnerable to starvation (Swennen & Duiven 1983), may be forced to spend significantly more time foraging at the cost of alternative behaviours, such as vigilance (Alonso & Alonso 1993). Alternatively they may attempt to compensate for increased energy expenditure by feeding in areas with more food but where predation risk is heightened, or by extending their foraging either by feeding at night, on supplementary grounds or simply by remaining at their daytime foraging site for longer (Bélanger & Bédard 1990, Velasquez & Hockey 1992, Urfi *et al.* 1996, Yasué *et al.* 2003, Duriez *et al.* 2005). This has implications for the risk of their being successfully preyed upon.

The structural complexity of an individual's surroundings will also affect its perceived predation risk, dependant upon the nature of predatory attacks (Frid & Dill 2002). For example, birds foraging on the ground and at risk from terrestrial predators may associate those areas without trees or shrubs for potential retreats as being more risky. Whilst birds subject to attack by aerial predators which may initiate attacks from trees, could perceive foraging in close proximity to the tree line as being a greater threat (Lima *et al.* 1987, Cresswell 1994a, Fernández-Juricic *et al.* 2001, Walther & Gosler 2001, Whitfield 2003b). Structurally complex areas may also restrict visibility making it less likely that an individual will detect a predator in time to initiate an effective escape response (Metcalfe 1984b).

Optimal escape theory predicts that animals will allow a predator to approach more closely when the costs of escaping are greater. Thus, in times when energy requirements are high, feeding opportunities are reduced, or food is limited, prey may initiate a much slower escape response (Cooper *et al.* 2003, Cooper & Peréz-Mellado 2004). It is imperative, however, that an individual initiates an escape before the predator reaches the critical distance, i.e. the distance at which prey is unable outrun the approaching predator and take refuge. Thus the distance at which prey will allow a predator to approach before fleeing (flight initiation distance) will be also be dependant upon the speed at which the predator approaches (Cooper *et al.* 2003).

The risk of predation to each individual can be lowered by foraging in groups (Caraco *et. al.* 1980, Beauchamp 2004). Many studies have shown that feeding in groups or flocking reduces an individual's predation risk through dilution, confusion and the 'many eyes' effect (Lazarus 1979, Cresswell 1994b, Lima 1995a, Roberts 1996, Whitfield 2003b). In the event of a predator attack, the greater the number of potential prey, the less likely it is that any one individual will be successfully preyed upon; furthermore as the group flees, a greater level of confusion will ensue, decreasing the chance of a successful attack. In addition, greater numbers of individuals increase the likelihood of a predator being detected at an early enough stage for an effective escape response (Pulliam 1973, Caraco 1979b, Kenward 1978). As a group, the combined level of vigilance demonstrated is very high, whilst the level of vigilance required from each individual may only be very small (Bertram 1980, Elgar 1989, Lima & Dill 1990). Group foraging, therefore, not only decreases the chance of each individual being preyed upon but also increases the time available for other behaviours, such as foraging, as individual vigilance is reduced (Lazarus 1979, Fernández-Juricic *et al.* 2004c). Theoretically, in groups where foraging and vigilance are mutually exclusive, and predator detection by one individual effectively alerts another, the benefits to group foraging could be increased further if individuals were to coordinate their vigilance, so that at no time were they unguarded nor was time wasted due to numerous individuals being vigilant at the same time (Bednekoff *et al.* 2003, Fernández-Juricic *et al.* 2004a); as yet empirical studies have failed to shown such co-ordination (Elcavage & Caraco 1983, Beauchamp 2002).

There are, however, also disadvantages to foraging in groups. The greater the number of conspecifics present, the closer the proximity in which individuals will be forced to feed, which can lead to increased competition and interference, and thus a decline in energy intake (Goss-Custard 1980, Vines 1980, Ens & Goss-Custard 1984, Dolman 1995, Cresswell 1997, Triplet *et al.* 1999). Competition for food resources lowers intake rates as the prey consumed by one individual depletes the prey available to another (Zwarts & Drent 1981, Sutherland 1996), whilst interference occurs when one individual reduces the access of another to a resource (Goss-Custard 1976, Sutherland 1983, Selman & Goss-Custard 1988). Interference includes kleptoparasitism i.e. the stealing of prey items from another (Ens & Goss-Custard 1984, Triplet *et al.* 1999), aggressive interactions over feeding patches and the avoidance of competitors to reduce such situations (Ens & Cayford 1996). Kleptoparasitism generally occurs when food availability within patches is relatively low (Brockman & Barnard 1979, Triplet *et al.* 1999) or there is variation in energy intake between individuals, causing those individuals feeding at a rate lower than the average intake rate to steal from those feeding at or above it (Bautista *et al.* 1998, Goss-Custard *et al.* 1998). Younger individuals, with less foraging experience may initiate a higher number of unsuccessful kleptoparasitic attacks but actually suffer a greater number of prey losses to other kleptoparasites, compared to adults (Goss-Custard 1980), causing them to avoid other birds (Goss-Custard *et al.* 1982a). Interference also occurs when prey availability is reduced due to the response of potential prey to the disturbance created by another individual (Selman & Goss-Custard 1988, Stillman *et al.* 2000a, Yates *et al.* 2000), and the presence of a competitor along another's optimal foraging path forces the individual to exhibit avoidance behaviour (Ens & Cayford 1996, Goss-Custard 1980).

Although individuals will vary in their intake rate both when feeding alone and in a group (Cresswell 1998), the susceptibility of an individual to interference and competition is generally a function of resource density (Dolman 1995) and individual dominance (Greig *et al.* 1983, Ens & Goss-Custard 1984, Sol *et al.* 1998, Smith *et al.* 2001). Whilst less dominant individuals may be forced to monitor and avoid competitors at the expense of foraging, dominant individuals may become significantly more successful when foraging in flocks as opposed to foraging as isolates (Baker *et al.* 1981, Alonso & Alonso 1993, Smith *et al.* 2001). An individual's dominance, feeding efficiency and competitive ability can be dependent upon the condition of its body, its age and experience of feeding, and its aggressiveness (Greig *et al.* 1983, Sol *et al.* 1998).

The monitoring of conspecifics can also be beneficial to an individual. 'Scroungers' monitor other individuals, known as 'producers', to locate food (see Giraldeau & Caraco 2000 for overview). Some studies suggest that in times of increased predation risk scrounging is an effective way of locating food whilst simultaneously increasing the chance of predator detection (Beauchamp & Giraldeau 1996, Barta & Giraldeau 2000, Beauchamp 2001, Robinette & Ha 2001), however others argue that scrounging and vigilance behaviour differ slightly and are not necessarily compatible (Barta *et al.* 2004). Furthermore, gathering information about its environment and the threat of predation by monitoring the actions of others using peripheral vision can be an effective way for an individual to be vigilant whilst simultaneously foraging (Bednekoff & Lima 2005, Fernández-Juricic *et al.* 2005). The finding that birds demonstrate a higher level of vigilance and variation in scanning pattern when restricted from viewing conspecifics

(Bednekoff & Lima 2005, Fernández-Juricic *et al.* 2005) supports this. Birds unable to view the reactions of others may be at a greater risk of failing to respond in time to a predator attack, and so must increase their own level of vigilance. The closer the proximity of individuals, the quicker they will observe the reactions of others and respond to an increased predation risk appropriately (Hilton *et al.* 1999a). Individuals have to decide, however, whether another's actions are indicative of an imminent predatory attack, or whether it is a response to some other factor, so as to limit false alarms and thus the energetic and temporal costs associated with avoidance behaviour (Lima 1995b). Furthermore, individuals must trust that conspecifics will not cheat and rely solely on the response of others, but will demonstrate their fair share of vigilance; and be aware when foraging in mixed-species groups, that the response of species will differ dependant upon their predators and associated predatory strategies, and therefore will not necessarily benefit themselves (Metcalfe 1984a).

The behaviour of individuals is further dependant upon their body mass. Declining temperatures may force individuals to work harder at increasing their energy intake in order to build nutrient reserves. Such reserves are essential for survival should feeding be restricted, the energy content of prey decrease or prey availability be reduced as a result of harsh weather conditions, or individuals be unable to meet their increasing daily energy requirements in the future months (Witter & Cuthill 1993, Mitchell *et al.* 2000, Goss-Custard *et al.* 2001, Kelly *et al.* 2002). It is important that birds have the ability to store energy when readily available in preparation for uncertain food availability (Barboza & Jorde 2001). Body mass may be increased by reducing activity and thus energy expenditure, by increasing intake rates if not already foraging at a maximal rate, and by increasing the time spent foraging and consequently extending the risk of predation (Marcum *et al.* 1998). Furthermore, individuals that are in better condition are more likely to successfully escape from a predator than those that are weaker, thus juveniles, subdominants, less efficient foragers and those with physical defects may be more susceptible to being successfully preyed upon (Bijlsma 1990). Increased body mass, however, may limit agility and the speed of escape should a predator attack (Rogers & Smith 1993, Witter & Cuthill 1993). Furthermore, metabolic rates and the energy required to flee from a potential predator, would be significantly greater if the individual had a larger body mass than it would be if the bird were lighter (Lima 1986, Witter & Cuthill 1993). The birds must balance the risk of starvation with the risk of unsuccessfully out-manoeuvring a predator (Carrascal & Polo 1999), which may explain why some individuals have been observed decreasing their energy reserves and feeding at much lower levels than would be expected in times of cold weather when predation risk was increased (McNamara *et al.* 1994, Piersma *et al.* 2003).

An animal's habitat choice for foraging will vary dependant upon the state of the individual and its dominance (McNamara & Houston 1990a, see Kacelnik *et al.* 1992 for summary). Ideally an individual will feed in the most profitable feeding areas where prey density and prey availability are high (Fretwell & Lucas 1970, Johnstone & Norris 2000, Sutherland 1996) and so encounter rate is rapid and intake rate is increased (Goss-Custard 1977), where the roost/resting place is near and the feeding area is relatively safe from predators (Bautista *et al.* 1995). For many individuals however, it is not always possible to inhabit the best quality sites, as less dominant individuals, generally the young or deformed, are pushed out through competition and interference (Goss-Custard 1977, Monaghan 1980, Goss-Custard *et al.* 1982a, b, Goss-Custard *et al.* 1984, see Kacelnik *et al.* 1992 for summary) and forced to feed in less profitable or more risky areas (Parker & Sutherland 1986, Cresswell 1994a, Cresswell & Whitfield 1994, Bautista *et al.* 1995, Whitfield 2003a). Alternatively, individuals that have trouble meeting their energy requirements may opt to forage in additional habitats or where intake rates are higher, but where the risk of predation is increased (McNamara & Houston 1987, Cresswell 1994a, Hilton *et al.* 1999b, Yasué *et al.* 2003, Duriez *et al.* 2005).

An effective balance between energy intake and predator avoidance is fundamental for the survival of individuals, particularly when predators are abundant and predator attacks are frequent. Whilst a reduction in feeding time and thus energy intake is detrimental to health over long periods of time, one failure to detect a predator could result in immediate death (Lima & Dill 1990). Thus, it is generally those individuals with high energy demands, in areas of high predation risk are most vulnerable to predation or starvation.

1.3. Human Disturbance

Outdoor recreational activities have increased greatly in popularity over the last 40 years. This has implications for those animals that inhabit sites, now visited by humans with increasing frequency. The general response of wild animals to an approaching disturber is not dissimilar to that demonstrated when approached by a potential predator, as individuals monitor and then avoid the potential threat (Roberts & Evans 1993, Fernández-Juricic & Tellería 2000, Frid & Dill 2002). The temporal and energetic costs to individuals, associated with vigilance and avoidance behaviour, can be substantial if inhabiting a frequently disturbed area. Raising the head to monitor the approach of a potential predator can mean a reduction in time available for other important behaviours such as foraging, preening and resting, for those individuals for which vigilance and other behaviours are mutually exclusive (Owens 1977, Bélanger & Bédard 1990, Burger *et al.* 1995, Burger & Gochfeld 1998). Being vigilant at the cost of foraging can mean a decline in food intake (Coleman *et al.* 2003) and thus health. In addition, the increase in energy expenditure associated with increased stress and the energetic and temporal costs of running or flying away from the disturbance factor, puts further pressure on individuals to meet their energy requirements (Bélanger & Bédard 1990, Ackerman *et al.* 2004). If the extent of disturbance is such that the site becomes uninhabitable for individuals they may leave the site either temporarily or permanently (Mitchell *et al.* 1988, Pfister *et al.* 1992, Fernández-Juricic 2000, Cornelius *et al.* 2001) dependant upon the quality of alternative sites.

Previously it was assumed that individuals which left a foraging patch later and returned to feeding earlier when disturbed, were least vulnerable to the effects of disturbance (see Smit & Visser 1993 for summary). It was believed that such individuals were habituated to disturbance; previous encounters with human activities had been non-threatening and so individuals allowed people to approach to a lesser distance over time, and thus disturbance affected them to a lesser extent (Smit & Visser 1993, Klein *et al.* 1995, Rees *et al.* 2005). In comparison, due to the temporal and energetic costs involved in monitoring and then vacating the site, those individuals that responded to disturbance by demonstrating high levels of vigilance and retreating earlier, were considered to be most vulnerable to the effects of disturbance. Recently, however, it has been suggested that it may be the individuals that remain foraging for longer in the presence of a potential threat that are most vulnerable to disturbance (Gill *et al.* 2001, Stillman & Goss-Custard 2002). For example, Beale and Monaghan (2004a) found that turnstones *Arenaria interpres* supplied with less food and thus considered to be in a worse condition were least responsive to human disturbance, scanning less frequently for predators, fleeing at a lesser distance from the disturbance factor and flying shorter distances when disturbed. Such individuals may have no appropriate alternative foraging site to go to, or be so pushed to meet their energy requirements that they are reluctant to sacrifice valuable foraging time and energy monitoring and fleeing from the disturbance factor, until absolutely necessary, thus increasing their perceived predation risk (Gill *et al.* 2001, Stillman & Goss-Custard 2002).

Certainly, there is evidence to suggest that as the cost of being vigilant to an individual increases, their anti-predator vigilance reduces (Arenz & Leger 1999). Theoretically, only if the costs of staying in a disturbed area (i.e. loss of feeding time and reduction in energy intake) outweigh the costs of relocating (i.e. energy expended when travelling, loss of feeding time, lower quality feeding area), should individuals flee permanently or temporarily from a site (Gill *et al.* 2001).

The effects of disturbance at a population level can be substantial if the best foraging sites are lost to human activities. Generally animals will congregate in the better quality feeding areas (Goss-Custard 1977), but when human activities render such resources unavailable individuals may be displaced to lower quality sites, or to undisturbed feeding areas nearby, placing extra pressure upon resources (Bell & Austin 1985, Yalden 1992, Gill *et al.* 1996, Gill & Sutherland 2000). Intake rates may decline as food is depleted and interference and competition increases, causing the health of the population to decline and making individuals more vulnerable to starvation and predation (Yalden 1992, Goss-Custard *et al.* 2001). In addition, human disturbance could have a significant effect on breeding birds which has implications for populations (Leseberg *et al.* 2000). Flushing caused by disturbance, and the increased metabolic costs incurred as a result of stress leading to a decline in body condition, could result in the desertion of nests, thus leaving eggs open to predation or cold temperatures; whilst a reduction in energy intake may prevent individuals from gaining sufficient energy to support both themselves and their young (Keller 1989, Verhulst *et al.* 2001, Bolduc & Guillemette 2003, Beale & Monaghan 2004b). Furthermore, the movement of birds in their breeding area in response to human disturbance could highlight the presence of their nests to aerial predators (Pienkowski 1984), and adults may be restricted from delivering food to their young by the presence of humans (McClung *et al.* 2004).

Animals may vary in their response to human disturbance dependant upon the species concerned (see Smit & Visser 1993 for overview, Mori *et al.* 2001, Blumtsein *et al.* 2003, Fernández-Juricic & Schroeder 2003), their scanning behaviour (Fernández-Juricic & Schroeder 2003), their body weight and size (de Boer & Longamane 1996, Fernández-Juricic *et al.* 2001, de Boer 2002, Rodgers & Schwikert 2002, Fernández-Juricic *et al.* 2004d, Blumstein *et al.* 2005), how cryptic they are against their surroundings (Gutzwiller *et al.* 1998), the size of the group in which they feed (Gutzwiller *et al.* 1998), their distance to their refuge (Ydenderg & Dill 1986), their previous experience of the disturbance (Burger & Gochfeld 1991, see Smit & Visser 1993 for overview, Klein *et al.* 1995, Mullner *et al.* 2004), their state at the time of the disturbance (e.g. hungry or satiated), and the quality of their alternative foraging sites (Gill *et al.* 2001). Larger birds may react earlier because they are conspicuous and because it takes slightly longer for birds to take flight when of a heavier mass thus increasing their perceived predation risk (de Boer & Longamane 1996, Blumstein *et al.* 2005). Alternatively a heavier mass may enable the birds to withstand a disruption to feeding for a greater amount of time (de Boer 2002). Animals will also vary in their response to human activities dependant upon the nature of the activity, the noise produced, the speed and randomness of approach, the distance to which the disturbance factor approaches, and the frequency of disturbance (Burger 1981, Stock 1993, Fitzpatrick & Bouchéz 1998, Burger 1998, Burger & Gochfeld 1998, Fernández-Juricic & Tellería 2000, Lafferty 2001, Fernández-Juricic *et al.* 2001, Burton *et al.* 2002, Fernández-Juricic *et al.* 2003, Thomas *et al.* 2003, Rees *et al.* 2005). Large groups of noisy people; the chaotic, high speed approach of dogs off of leads; the loud and high speed approach of vehicles; aerial objects such as kites and small aircraft; and an approach to a closer proximity are all likely to heighten the response of individuals (Burger 1981, Smit & Visser 1993, Burger 1998, Burger & Gochfeld 1991, Burger *et al.* 1995, Burger & Gochfeld 1998, Beale & Monaghan 2004b).

Human activities do not only impact the health of animals by reducing their foraging time and increasing their energy expenditure. A decline in animal health may also arise due to reduced food availability if humans and animals are competing for the same resources; whilst the hunting and trampling of nests by humans and off-road vehicles may cause direct injury or death (Burger 1981, Hockey 1983, Burger & Gochfeld 1990, Pienkowski 1992). Where humans are a direct threat to an individual's survival animals may respond to a greater extent when encountering humans compared to in places where humans pose no actual threat. For example, some wildfowl demonstrate increased wariness during the shooting season (see Hockin *et al.* 1992, for summary and references therein), and variation in their response suggests that they can differentiate between hunting and non-lethal human disturbance (Madsen 1998).

Previously, in Britain, recreational disturbance tended to occur in the summer months when temperatures were warmer and so energy requirements were lower, and day length was longer and so foraging opportunities were increased. Thus, any loss of foraging time due to disturbance had limited implications for animal health. More recently, however, outdoor human activities have become increasingly prevalent throughout the year, which can place additional pressure upon animals that are already struggling to meet their energy requirements during cold spells. The loss of foraging time and energy, associated with being disturbed, may leave individuals with very little energy to support themselves through the winter months. In addition, human disturbance may force individuals to vacate their foraging areas in favour of less disturbed, but possibly less profitable ones. Thus, for those individuals that are susceptible to disturbance and have high energy requirements, the successful apportioning of their limited time to various activities that are imperative for health is essential for survival.

1.4. Compensatory Mechanisms

Some animals may have the ability to compensate for a reduction in energy intake, or to reduce the costs of human disturbance. Individuals may extend their feeding period at the cost of other behaviours (Urfi *et al* 1996) by feeding in supplementary feeding grounds (Heppleston 1971, Velasquez & Hockey 1992) or by feeding at night (Goss-Custard & Verboven 1993). In addition individuals may reschedule their feeding routine, tolerate/habituate to human activities regardless of an increase in their perceived predation risk, or increase their intake rate if not already feeding at their maximal rate (Goss-Custard & Verboven 1993, Stock & Hofeditz 1997, Fitzpatrick & Bouchéz 1998). A fundamental assumption of foraging models is that an individual will make decisions so as to feed optimally and that this generally means feeding in the highest quality areas and feeding on the most profitable prey (Cayford & Goss-Custard 1990). It is important to note, however, that feeding optimally does not necessarily mean feeding at their highest rate; there may be other important factors to consider when foraging (Ens *et al.* 1996b, Norris & Johnstone 1998, Hamilton *et al.* 1999). For example, oystercatchers *Haematopus ostralegus* have demonstrated a preference for medium sized cockles that carry a reduced parasitic load, over larger more energetically valuable items that carry a greater risk of parasitism (Norris 1999). If the birds were energetically stressed they could opt for higher energy intake over a reduced risk of parasitism. Alternatively, the birds could handle prey items at a faster rate possibly increasing their risk of bill damage. Other animals may attempt to increase their energy intake by handling prey items in situ, regardless of an elevated predation risk, instead of carrying their food item to a safer place in which to feed upon it (Lima *et al.* 1985).

1.5. Introduction to the Oystercatcher

The species used throughout this study is the Eurasian Oystercatcher *Haematopus ostralegus* L. The oystercatcher is an ideal study species as it is abundant, and easy to recognise and monitor, hence its behaviour and habitat choice has been well documented (see Goss-Custard 1996 for review). Individuals may be identified and aged to some extent by observing the colour of their plumage, legs, bill and eye, thus reducing the chance of pseudo-replication during field experiments. A large population of oystercatchers inhabit the coastal areas of Britain. Some oystercatchers over-winter in Britain, migrating from their northern territory breeding grounds, many, however, are resident throughout the year, breeding either inland, on salt marshes or high rocky outcrops.

Oystercatchers are preyed upon predominantly by peregrines, *Falco peregrinus*, although they are less vulnerable to peregrine attacks than smaller waders (Whitfield 1985, Quinn 1997). In certain estuaries, such Morecombe Bay and the Burry Inlet, oystercatchers were culled to reduce the conflict between oystercatcher feeding and human cockle harvesting (Lambeck *et al.* 1996). This practice ceased totally during the 1970s, thus in Britain oystercatchers face no true predation threat from humans and so may react to a lesser extent than those located in places where the hunting of waders still takes place.

Oystercatchers are known to live to approximately 40 years of age. Although capable of breeding from three years onwards many oystercatchers defer breeding for a couple of years (Harris 1967). This delay is attributed to oystercatchers securing a good quality breeding site, a place that is safe and close to their foraging area so that energy expended when travelling between nest and feeding site is limited (Nol *et al.* 1984, Ens *et al.* 1992, Hazlitt *et al.* 2002).

Oystercatchers feed in estuaries, rocky shores, sandy shores and fields, and on a variety of prey types including bivalves, gastropods, decapods, worms and fish (Heppleston 1971, Hulscher 1982, Hulscher 1996, Hulsman *et al.* 1996, Hilgerloh 1997). Although an individual can successfully feed upon a spectrum of prey types, many tend to specialise in feeding upon one primary prey type using one specific technique (Norton-Griffiths 1967, Goss-Custard *et al.*1982a, Goss-Custard & Sutherland 1984, Sutherland & Ens 1987). An oystercatcher's prey choice and handling technique governs, to some extent, the shape of its bill tip (Hulscher 1985). Hammering hard shelled prey items with rapid blows can blunt the tip of the bill, whilst stabbing between the valves of bivalves or probing in soft sediment can thin the bill tip through abrasion and re-growth (Huslcher 1985). When an individual changes its predominant prey type its bill shape changes accordingly, this may, however, have implications for feeding efficiency (Huslcher 1985). The initial prey type and handling technique is thought to be a factor of the individual's sex and their learning from their parents; however prey choice can change with the age of a bird as they become more efficient at feeding (Goss-Custard & Durell 1983), or with prey availability (de Vlas *et al,* 1996). Female oystercatchers have slightly thinner longer bills making them more adapted to feeding on soft bodied prey whilst the slightly thicker, more robust bills of the males are better designed for hammering hard shelled prey items (Hulscher 1985, Durell *et al.* 1993).

An individual's prey choice will depend to some extent upon the habitat in which it feeds, which can be further dependant upon its dominance (Durell *et al.* 1996). Oystercatchers are known to return to both the same breeding and over-wintering sites year after year, providing that they can fend off competitors for their patch (Goss-Custard *et al.*1982a). Juveniles and other sub-dominant individuals may be displaced from their favoured feeding site in the autumn by more dominant individuals that return from their breeding sites to over-winter, through competition and interference (Goss-Custard 1980, Goss-Custard *et al.* 1982a, b, Goss-Custard & Durrell 1983). An oystercatcher's dominance, and thus susceptibility to interference, does not only influence its habitat choice but also has implications for its energy intake rate within a foraging site (Ens & Goss-Custard 1984, Sutherland & Parker 1992, Stillman *et al.* 1996, Goss-Custard *et al.* 1984, Goss-Custard & Durell 1988). A greater dominance leads to an elevated status with in the social hierarchy, individuals lower down the social hierarchy will waste time and energy avoiding those higher up, thus reducing energy intake. The dominance of an individual will increase to some extent with age (Goss-Custard *et al.* 1982b, Caldow *et al.* 1999). Although the social hierarchy of oystercatchers may be stable over the winter period, individuals can alter their rank over longer periods of time (Goss-Custard *et al.* 1982b, Caldow & Goss-Custard 1996). Individual intake rate is not only dependant upon dominance, but also foraging efficiency (Goss-Custard & Durell 1987a, 1988, Sutherland 1996, Caldow *et al.* 1999) which is particularly influential at low competitor densities (Stillman *et al.* 2000b). During the winter months in coastal areas, oystercatchers that are less successful/efficient foragers, either due to their dominance, age and thus inexperience of foraging, physical deformities or natural inability to forage successfully, may be forced to feed on supplementary grounds such as fields at high tide in order to meet their energy requirements (Heppleston 1971, Caldow *et al.* 1999). Shorebirds are extremely vulnerable to cold weather (Goede 1993, Mitchell *et al.* 2000); the areas they inhabit are often subject to harsh environmental conditions which lead to an increase in energy demand whilst simultaneously reducing prey availability. Thus, particularly cold spells can lead to high oystercatcher mortality (Swennen & Duiven 1983, Camphuysen *et al.* 1996). Individuals must consume enough energy to support their needs; thus an oystercatcher's prey choice may vary according to availability (Sutherland 1982a, Goss-Custard & Durell 1983, Zwarts *et al.* 1996a, b, Wanink & Zwarts 2001). Alternatively prey selection may vary as the energetic value and thus profitability of various prey items change throughout the season (Frank 1982).

1.6. The Oystercatcher-Rocky Shore System

The rocky shore is an ideal site to observe any trade-off between vigilance and foraging (Metcalfe 1984b), and furthermore any compensatory mechanisms demonstrated by the birds during their low-water feeding period. The structural complexity of the rocky shore restricts oystercatcher visibility, limiting the possibility of the birds feeding whilst simultaneously monitoring the environment. Also the prey items that the oystercatchers attack and consume, on the rocky shore, are easy to observe and identify. Mussels attacked by oystercatchers can be identified by the way in which they are attacked and by the fact they are located within a clump. Mussel size can be estimated by comparing the length of the mussel to the length of the oystercatcher's bill during handling using the average oystercatcher bill length of 75mm as a guide (Goss-Custard *et al.* 1987). Mussels that are stabbed *in situ* may have their size estimated when the oystercatcher's bill penetrates their shell whilst adopting the stabbing method. Oystercatchers using the stabbing method have to insert their bill to the very depths of the mussel in order to severe the adductor muscle giving an indication of mussel size relevant to bill size. Alternatively, mussels that are hammered are pulled from a clump and carried to a flat surface, and it is during this transfer that their size may be estimated against the oystercatcher's bill. Individual limpets, regardless of whether they are solitary or aggregated, are easy to observe on the rock; in the same way that mussel size is estimated limpet size may be estimated as the oystercatcher dislodges, flips over the limpet shell and cuts free the flesh. In comparison, other gastropods are generally picked up and turned over allowing for an estimation of size. Thus, any variation in prey choice as a response to human disturbance may be confidently observed during this study.

The low numbers of oystercatchers inhabiting the rocky shore reduces the effects of flocking and interference on oystercatcher foraging behaviour, highlighting the effects of a predation threat at an individual level. If the low numbers of oystercatchers present on the rocky shore are considered indicative of a site of a lower quality, some insight may be gained into the effects of human disturbance on those individuals most vulnerable to starvation in Britain during the winter months.

1.7. Aims

The aims of this thesis were to observe the effects of human recreational disturbance on the foraging behaviour of wading birds and to investigate any compensatory mechanisms that were employed to off-set the potential loss of energy intake as a result of disturbance. In chapter 2 I describe a preliminary experiment in which experimental and observational methods were used to investigate the effects of various types of recreational disturbance on oystercatcher foraging behaviour, with a view to establishing which types of recreational disturbance are most disruptive to foraging birds. This preliminary experiment provides an approximation of the time taken for oystercatchers on the rocky shore to recover from a disturbance event, which has implications for the experimental design of Chapter 5. Chapters 3 and 4 describe the foraging behaviour of oystercatchers on the rocky shore. Although much work has been done, over the years, on the foraging behaviour of oystercatchers, the majority of this work has focussed on oystercatchers foraging in estuarine areas, thus very little is known about the behaviour of oystercatchers foraging on the rocky shores of Britain. It was necessary, therefore, to gain some knowledge of oystercatcher foraging on the rocky shore before the effects of disturbance could be fully considered. Chapter 3 also investigates the effects of environmental factors such as weather, temperature and wind speed on oystercatcher foraging behaviour, whilst Chapter 4 examines oystercatcher prey selection on the rocky shore.

In chapter 5, I observe whether oystercatchers compensate for any reduction in energy intake as a result of disturbance, by increasing their intake rate after the disturbance had ceased through changing their prey choice or increasing their foraging intensity.

Finally in chapter 6, I discuss the foraging of oystercatchers on rocky shores with a view to understanding why comparatively few individuals utilise what appears to be such a good resource. I discuss the effects of disturbance on oystercatcher foraging and the implications of the absence of compensatory behaviour. Finally I discuss what my findings mean for the conservation and management of coastal areas.

Chapter 2: Effects of Human Disturbance on Oystercatcher Foraging Behaviour

2.1. Introduction

Understanding the effects of human disturbance on wildlife has become increasingly important over recent years, as an increasing number of people participate, more frequently and for a greater proportion of the year, in outdoor recreational activities. Numerous studies have shown that animals respond to a predation threat and non-predatory human disturbance in a similar way (see Frid & Dill 2002 for summary). Foraging organisms, must make a trade-off between energy intake and predator avoidance (Gill *et al.* 1996); as awareness of an apparent predator causes time to be re-allocated to monitoring potential threats (Burger & Gochfeld 1998), thus limiting foraging time. This trade-off is particularly relevant to shorebirds because their foraging time is often restricted by tides, and in some cases, daylight. Furthermore, the areas they inhabit are often subject to severe weather and so daily energy requirements can be very high, especially during the winter (Kersten & Piersma 1987).

Previous work on the effects of human disturbance on foraging birds has tended to focus on the response of populations (e.g. Madsen 1998, Marsden 2000) or flocks (e.g. Burger 1981, Fox *et al.* 1993, Roberts & Evans 1993). Fewer studies have examined in detail the effects on individual foraging behaviour (but see Urfi *et al.* 1996, Fitzpatrick & Bouchéz 1998, Coleman *et al.* 2003). A foraging bird may react to a disturbance event in a number of ways; it may alter foraging behaviour only slightly if habituation has occurred (Davidson & Rothwell 1993, Urfi *et al.* 1996). Alternatively, the bird may monitor the disturbance by increasing vigilance as the disturbance agent approaches (Yalden & Yalden 1989, Rodgers & Smith 1997) until eventually the bird begins to exhibit avoidance behaviour (Burger & Gochfeld 1998), and may be displaced from the disturbance site (Pfister *et al.* 1992). This displacement may be permanent (Ferns *et al.* 2000) or temporary (Madsen 1998, Stillman & Goss-Custard 2002). Relocating may incur energetic costs, as energy, and time previously budgeted to foraging, are used to relocate to a site that may be much less profitable and where intake rate may be lower. However, if the costs associated with dispersion are less than the energy gained within the new patch, then the disturbance may have had no significant impact on the bird (Gill *et al.* 2001) other than to heighten its' perceived predation risk (Stillman & Goss-Custard 2002). Furthermore, had the bird remained at the disturbance site and suffered a reduction in intake rate, the costs may have been greater than if it had simply relocated (Gill *et al.* 2001).

As relocating to another area is potentially costly, workers have frequently used the dispersion response as an indicator of disturbance effects. Flight distance, the distance flown by birds when displaced from the site (Smit & Visser 1993, Beale & Monaghan 2004); the time taken after a disturbance event for the birds to return to the site and resume feeding (Madsen 1998, Stillman & Goss-Custard 2002), and the flight initiation distance (for example Kenny & Knight 1992, Boer & Longamane 1996, Fernandez-Juricic & Telleria 2000, Mori *et al.* 2001, Beale & Monaghan 2004a), have all been used to estimate the disruption of human activities to foraging birds. It was previously assumed that birds which were displaced earlier, more frequently, flew further and returned to the site later, were most sensitive to human disturbance. It has since been suggested that birds which remain at the disturbance site or return quickly to it, may have no other place to forage (Knapton *et al.* 2000, Gill *et al.* 2001) or may be pushed to meet their high energy requirements (McGowan *et al.* 2002) and have no choice but to remain foraging in a potentially unsafe area (Hilton *et al.* 1999b, Yasue *et al.* 2003), where their 'perceived predation risk' is increased (Gill *et al.* 2001, Stillman & Goss-Custard 2002).

After a disturbance event has ceased, birds may retain a heightened level of vigilance at the cost of foraging. Alternatively, they may need to compensate for lost foraging time. If the birds occupy a profitable feeding patch, where individual intake rate is restricted by a digestive bottleneck (Kersten & Visser 1996a), a small percentage of lost foraging time may be easily compensated for by increasing foraging intensity, and therefore intake rate (Swennen *et al.* 1989, Stock & Hofeditz 1997, Fitzpatrick & Bouchéz 1998). This could cause the birds to devote less time to vigilance, thus making them potentially more vulnerable to predators. Alternatively, an individual could compensate for lost feeding time by extending foraging time (Urfi *et al.* 1996); feeding nocturnally (Pienkowski 1983a, Goss-Custard & Verboven 1993), or feeding in supplementary areas such as fields, at high tide (Velasquez & Hockey 1992).

Understanding the effects of human disturbance on roosting and foraging birds has frequently been driven by the need for conservation and management of sites or species. However, many studies have focussed solely on dispersive behaviour; little information has been gathered concerning ‘sub-dispersive’ effects of disturbance (but see Fernández-Juricic *et al.* 2001, Coleman *et al.* 2003). Sub-dispersive behaviour is defined as the change in behaviour or increased vigilance which occurs prior to flight, when individuals are confronted with an approaching disturbance agent (Coleman *et al.* 2003). For the purpose of conservation and management, the effect of human disturbance on sub-dispersive behaviour is a more sensitive estimate of disturbance impact (Fernández-Juricic *et al.* 2001). Flight initiation distance may be influenced by a number of factors (Gill *et al.* 2001) and is thus imprecise in identifying those individuals most affected by disturbance. Sub-dispersive behaviour accounts for the change in behaviour as a disturbance approaches and identifies a buffer zone over which birds can adapt to disturbance before being forced to take flight (Fernández-Juricic *et al.* 2001).

Studies on behavioural responses to disturbance have often involved correlating uncontrolled human disturbance with bird behaviour (Burger & Gochfeld 1991, 1998, Fitzpatrick & Bouchéz 1998, Marsden 2000, Rees *et al.* 2005). Such an approach can lead, however, to the effects of disturbance being confounded with habituation (Underwood 1997); thus experimental studies using controlled disturbance are essential for determining causality (Cayford 1993). My research used manipulative experiments to analyse which types of human disturbance, commonly experienced by birds feeding in coastal areas, have the greatest effect on the sub-dispersive foraging behaviour of oystercatchers on the rocky shore. This preliminary experiment also provided basic information about the effects of human disturbance on oystercatcher foraging and recovery times, which has implications for the experimental design of chapter 5. The rocky shore was identified as a useful study site as the recreational use of rocky shores is generally less than that of beaches, and so 'background disturbance' was limited. Furthermore, due to the structural complexity of the rocky shore vigilance and foraging are likely to be mutually exclusive, thus highlighting any trade-off that may occur in response to disturbance. The following hypotheses were tested: compared to undisturbed birds, disturbed birds would 1) spend a greater percentage of their foraging time being vigilant (aware), 2) increase their movement (as estimated by step rate), 3) have a lower feeding rate (as estimated by peck rate), 4) spend less time handling prey items and 5) have fewer successful feeding attempts. 6) Birds were expected to retain a higher level of vigilance after the disturbance had ceased. 7) The difference between disturbed and undisturbed bird behaviour was expected to vary dependant upon the type of experimental disturbance applied, as was the flight initiation distance and the birds' recovery (the level of vigilance demonstrated by the birds after the disturbance had ceased). 8) The expected changes in foraging behaviour with the approach of a disturbance agent were expected to differ between the types of disturbance applied.

2.2. Methods

2.2.1. Study Sites

Two rocky shore sites on the South-West coast of England were used, Par Docks (50° 20' N, 04° 42' W); and Hannafore Point, Looe (50° 20' N, 04° 27' W) between September 2001 and March 2002. Observations were made during the winter season when birds were most energetically stressed and abundant at the study sites, and when the occurrence of uncontrolled human disturbance was minimal.

The study was conducted on the three days either side of spring tides, so that maximum shore was exposed and thus maximal foraging area was available to the feeding birds. Oystercatchers (*Haematopus ostralegus* L.), on rocky shores, are visual foragers; the use of midday low tides ensured that only daylight hours were used and so the foraging behaviour of the observed birds were not modified by changes in their ability to detect prey. Midday low tides also ensured that sufficient daylight hours were available for the sample days to be completed and that there was consistency across seasons. Observations began 3 hours before low tide and finished 3 hours after low tide. Previous observations had shown that oystercatchers either were not present at the study site, or did not feed, for the 2 hours over low tide, in spite of changes in prey availability (pers obs.), and so no observations were made during this period.

The majority of oystercatchers studied were non-breeding sub-adults whose diet on the rocky shore mainly consisted of limpets (*Patella* spp.), mussels (*Mytilus edulis*), whelks (*Nucella lapilus*), winkles (*Littorina* spp.) and topshells (Gibbula spp. *Osilinus lineatus*). The oystercatchers tended to forage relatively close to each other (approx. 10m between individuals).

At both the study sites observations of individual oystercatchers were made from a cliff-top position using a 20-60× telescope. This allowed detailed observations of oystercatcher foraging behaviour and a clear view of the entire study area, whilst limiting the possibility of the observer's presence affecting the birds. The observer and her position at the study sites, remained constant throughout the experiment.

2.2.2. Observations

Before an observation, a description of the focal bird, its position (bearing and distance from observer) using a magnetic compass and range finding binoculars (Leica, Portugal), and the time at which the observation began, was recorded. Each observation used a different focal bird. To minimise pseudo-replication, an attempt was made to identify individuals using indicators such as the colour of the bill, legs, eye and plumage. However, it was difficult to identify individuals that had recently flown into the area and so these birds were considered to be independent (Coleman *et al.* 1999).

A focal bird was observed for a 300s period and components of its foraging behaviour recorded in real time using a cassette tape recorder. The behaviours recorded included the number and direction of steps taken; the number of pecks and successful feeding attempts, and the proportion of their observed feeding time that the bird spent being aware, searching and handling. A peck was defined as one single strike of a prey item. A successful feeding attempt was easily identified as the birds raised their heads and moved their necks in a swallowing motion. Awareness/vigilance was defined as when the bird had its head raised (length of bill horizontal to the shore or at an angle from the shore of >50 deg) when either stationary or moving. Searching refers to the bird being in a head down orientation (length of bill vertical to the shore or at an angle from the shore of <50 deg) when either stationary or moving, and handling was defined as when an individual was continuously either handling or attacking a prey item at a rapid rate, regardless of whether it was a successful feeding attempt. The time and position of any incidental disturbance was also noted.

Seven oystercatchers were observed per day, three before low tide and four after low tide. The birds observed were divided into four groups. 'Control birds' were those studied on days with no applied disturbance. 'Pre-disturbance birds' were those studied on days when disturbance was applied, but were observed before low water, i.e. before the disturbance was introduced (LW -3 to -1hr). 'Disturbed birds' were those studied on days with applied disturbance and were observed specifically for their reactions during the disturbance event (LW +1hr), and 'Post-disturbance birds' were those studied on days with applied disturbance, but were observed after the disturbance had ceased (LW +1 to +3hr). Thus, a total of 91 birds were observed at each study site. Preliminary observations showed that birds returned almost immediately to the study site if displaced by a disturbance factor, indicating that post-disturbance behaviour could be reliably observed. As the oystercatchers foraged relatively close together they were all disturbed when the disturbance factor was applied allowing a comparison to be made between the behaviour of a target bird (disturbed) and those associatively disturbed (post-disturbance birds).

2.2.3. Disturbance Treatments

One of four controlled experimental disturbance events were applied to foraging oystercatchers per study day: a) a person walking, b) a person walking with a non-barking dog, c) a person walking with a barking dog, and d) a group of people walking. At each study site, one control day and three replicate days of each of the four disturbance factors were conducted. Disturbance factors were randomly assigned to sample days in order to increase interspersion and thus limit confounding. Measures were taken to ensure that disturbance was standardised to the highest degree possible; all disturbers approached foraging birds at approximately the same speed (average pace was 0.9 m s^{-1}), efforts were made to keep the colour of the disturbers' clothing constant, and a group consisted of three people walking side by side. An artificial dog was used for the dog treatments as a real dog would have been too variable in its behaviour. Modelled on an adult golden retriever, the dog was constructed by moulding chicken wire into shape, then covering this in fake brown fur. We attached handle for the walker to hold and to use to steer the model dog (Figure 1). The artificial dog was used in conjunction with recorded barking played on a cassette recorder at full volume (98 dB at a distance of approx. 0.5m from speaker) and carried by the walker to simulate a barking dog. The effect of real dog disturbance on foraging birds may be broken down into several components, the visual disturbance, noise, speed of approach and unpredictability of movement; the model dog allowed for the control of the speed of approach and predictability of movement whilst pinpointing the effects of having a) a dog present and b) a noisy dog present.

Fig. 1. Model Dog.

The ratio of time spent searching to time spent with head-up was used as an indicator of foraging activity, and thus sensitivity to disturbance (Burger & Gochfeld 1998, Fenández-Juricic & Tellería 2000, Coleman *et al.* 2003). It was assumed that the amount of time devoted to searching and thus feeding would decline as more time was devoted to monitoring a disturbance (referred to as awareness throughout this study). The flight initiation distance, the distance from the disturbance factor at which the bird takes flight, was also used to measure the response of birds to disturbance (Burger & Gochfeld 1991, Madsen 1998).

A disturbance treatment was applied at the beginning of the second half of the study day (1 hour after low water). The start position of the disturber (distance and bearing from the observer) was recorded; the disturber then began to directly approach the focal bird, as the observer began recording behaviour. The focal bird was observed until it took flight, at which point the disturber remained stationary, and his position was recorded. A disturbance factor was applied once per day to one focal bird; the birds were then observed for the remainder of the study period.

A calibration exercise to establish the speed of approach of the disturber was conducted using a 30-metre tape along the top of the shore; this enabled me to pinpoint the position of the disturber at different points relative to the observed bird's behaviour. The position of the focal bird before it took flight could be calculated by using the estimated stride length of an oystercatcher in conjunction with the number and direction of steps the focal bird took. Oystercatcher stride length has previously been estimated at 0.12m ± 0.03 when searching and 0.18m ± 0.05 when attacking a conspecific (Stillman *et al.* 2002), so a value of 0.15m was considered to be appropriate estimate of stride length when moving away from a disturbance factor.

2.2.4. Analysis

The data collected was later transcribed into a computer using 'The Observer' 4.0 behavioural software (1998, Noldus Technology, Waginengen). The percentage of time birds spent being aware and handling; the peck rate, step rate and the number of successes were calculated from the data. The percentage data were arc-sine transformed prior to analysis and before Analysis of Variance, homogeneity of variance was tested by Cochran's test (Underwood 1997). Most of the results were analysed using GLM, and ANOVA procedures in Minitab (Minitab Inc 2000) and GMAV (EICC, University of Sydney), respectively. SNK tests provided more detailed information about the relationships found (Underwood 1997). An odds ratio (Sokal & Rohlf, 1995) was used to compare the probability of a success when the birds are undisturbed as opposed to disturbed (Coleman *et al.* 2003).

Using data from only the disturbance days, ANOVAs were used to determine whether birds differed in the extent to which their foraging activity was reduced with the various disturbances applied, and whether any difference found was extended to birds observed after the disturbance event had ceased (i.e. post-disturbance birds). To assess the effects of disturbance type on the foraging behaviour of birds observed post-disturbance, a representation of undisturbed foraging behaviour was required for comparison. It was expected that there would be some daily variation in the birds' response, due to changes in weather or temperature and so control days would not accurately reflect undisturbed behaviour relevant to that day. Using pre-disturbance foraging behaviour as a representation of undisturbed foraging behaviour limits the effects of daily variation and seemed a much better comparison, providing that on days with no disturbance, foraging behaviour did not differ between tides. If analysis of the control data revealed that on control days foraging behaviour did not differ between tides it would be logical to expect that if post-disturbance birds were unaffected by the previous disturbance event their foraging behaviour would be similar to that of pre-disturbance birds.

The effect of disturbance in general on oystercatcher foraging behaviour was analysed using unbalanced ANOVAs where degrees of freedom were interpolated using GLM procedures in Minitab. The data from the two study sites were analysed separately because the creation of this 5-factor mixed model would not allow formal comparisons in Minitab. Post-disturbed and disturbed bird behaviour was analysed. If on the control day birds observed prior to low-tide were found to behave similarly to those observed post low-tide, and further to this on disturbance days post-disturbance birds were found to behaviour similarly to pre-disturbance birds then analysis of post-disturbance and disturbance bird behaviour would represent how 'disturbed bird' foraging behaviour differed from undisturbed foraging behaviour, highlighting the effect of human disturbance on feeding oystercatchers.

The peck rate (pecks s^{-1}), step rate (steps s^{-1}) and the percentage of time birds spent being aware and handling were calculated for every 10m that the disturbance factor moved closer to the birds. To limit the effects of non-independence regression lines were drawn for the response of each individual bird to an approaching disturbance factor, and the slope and intercept of each regression line was used in the analysis. The data were analysed, using tests for homogeneity of variance and ANOVA in GMAV, to see whether the relationship between the distance separating the disturbance factor and the focal bird, and the bird's foraging behaviour, was different with each type of disturbance applied. The start position for the approaching disturber was constant at each site, however the initial distance to the focal bird was dependant upon the birds' position, and would affect any linear relationships found between distance to the bird and behaviour (Blumstein 2003), thus limiting the pinpointing of a reliable alert distance or buffer zone.

Lastly the data for the distance between the disturbance and the focal bird before it took flight for each treatment was analysed using an ANOVA. It was predicted *a priori* that birds would allow a person walking and a person walking a silent dog to approach more closely than a group of people and a noisy dog.

2.3. Results

The level of incidental disturbance that occurred during the course of this study was very low. An average 2.9, and 0.87, disturbance agents/hr were present on the upper shore during the observation period, whilst an average 0.23, and 0.06, disturbance agents/hr directly approached the birds, at Looe and Par respectively. Disturbances generally took the form of lone walkers, group walkers and dog-walkers. These data suggests that both study sites were relatively undisturbed.

2.3.1. Control Data

Control birds did not to differ significantly in the percentage of time they spent being aware (ANOVA $F_{(1,8)} = 3.88$, NS); handling (ANOVA $F_{(1,8)} = 0.71$, NS); their peck rates (ANOVA $F_{(1,8)} = 1.77$, NS) or step rates (ANOVA $F_{(1,8)} = 0.59$, NS) before and after low tide at either site (N=12). This indicates that on disturbance days post-disturbance birds would be expected to behave similarly to pre-disturbance birds if the disturbance had no effect. Control birds differed between sites in their time spent being aware (ANOVA $F_{(1,8)} = 6.14$, $P<0.05$), but not in their handling (ANOVA $F_{(1,8)} = 1.5$, NS), peck (ANOVA $F_{(1,8)} = 0.04$, NS) or step rate (ANOVA $F_{(1,8)} = 1.02$, NS).

2.3.2. Longevity of Effects of Disturbance Event

Birds observed after the disturbance event (post-disturbance birds, observed after low tide) did not differ from undisturbed birds (pre-disturbance birds, observed before low tide), in their behaviour (Table 1, all tests NS). They did not increase their awareness/vigilance in response to the recent threat, nor did they decrease their awareness. Neither the percentage of time the birds spent handling, their peck rate nor step rate changed from pre-disturbance levels. Daily variation, possibly due to variation in weather, did occur

		Time Spent Aware (%)		Time Spent Handling (%)		Peck rate (Pecks S^{-1})		Step rate (Steps S^{-1})	
Source	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Site Si	1	890.7759	6.36*	1298.2785	8.22**	0.0003	0.02 NS	0.7602	1.44 NS
Day Da (Si)	22	140.03	2.23**	157.9418	1.61 NS	0.0139	3.33***	0.5269	3.3***
Tide Ti	1	94.6927	2.15 NS	13.7818	0.11 NS	0.0002	0.03 NS	1.0828	3.38 NS
Si X Ti	1	44.126	0.62 NS	337.0851	2.71 NS	0.0063	1.22 NS	0.7749	2.42 NS
Ti X Da (Si)	1	71.3174	1.14 NS	124.6	1.27 NS	0.0051	1.23 NS	0.3201	2.01 NS
Residual	96	62.7331		98.0839		0.0042		0.1596	
Total	143								

Table 1. Analyses of variance on the behaviour of oystercatchers before and after a disturbance event had occurred (NS – Non-significant $P>0.05$; $*P<0.05$; $**P<0.01$ and $***P<0.001$). Percentage of time birds spent being aware and handling were arc-sine transformed prior to analysis. Pre-disturbance birds are those observed before low tide and before the disturbance event takes place. Those observed after low tide were either subjected to the applied disturbance or potentially associatively disturbed. Thus tide represents whether the birds were disturbed. All data were tested by Cochran's homogeneity of variance test prior to analysis (Aware: C=0.3097**; Handling: C=0.1539 NS; Peck Rate: C=0.3572** and Step Rate: C=0.0942 NS). Any heterogeneity of variance found was assumed to have limited effect due to large sample sizes and could be ignored (Underwood, 1997).

however, within each site for three of the foraging parameters: the percentage of time spent aware, the peck rate and the step rate (Table 1); this supports the case for using pre-disturbance birds instead of control birds as examples of undisturbed behaviour. Furthermore as pre- and post-disturbance behaviour were found not to differ, post-disturbance behaviour may also be considered representative of undisturbed oystercatcher foraging behaviour.

2.3.3. Effect of a Disturbance Event on Foraging Birds

Although the disturbance agent approached only one foraging bird it was apparent that all birds on the shore, at the time, reacted in a similar way, and so the disturbed focal bird can be considered a reliable representative of the entire group.

At Looe, post-disturbed birds were found to differ significantly from disturbed birds in their peck rate, and the percentage of time they spent handling and being aware (Table 2). Birds subjected to a disturbance event were aware for an average of 68% of their feeding time; a much higher level of vigilance than demonstrated by post-disturbance birds that spent only an average 28% of their foraging time being aware (Figure 2 a). As expected, the mean percentage of time spent handling was significantly lower when birds were being disturbed (8%), compared to an average 22% as demonstrated by post-disturbed birds (Figure 2 b). Mean peck rate declined from 0.17 pecks s^{-1} for post-disturbed birds to 0.07 pecks s^{-1} for 'disturbed birds' (Figure 2 c). No significant change in step rate was observed as a result of disturbance (Figure 2 d).

At Par, post-disturbed birds were found to differ significantly from disturbed birds in the percentage of time they spent handling and being aware (Table 2). Disturbed birds spent an average 52% of their observed foraging time being aware compared to the 22%

demonstrated by post-disturbed birds (Figure 2 a). Disturbed birds also spent 18% less time handling than post-disturbed birds (Figure 2 b). Undisturbed oystercatchers, in Par, did not differ significantly from disturbed oystercatchers in their peck or step rate (Table 2). The response of the observed birds to disturbance was similar at both sites, with the exception that the oystercatchers in Looe showed a slight but non-significant reduction in peck rate as a result of disturbance (Figure 2 c).

The chance of having a successful feeding attempt when undisturbed (i.e. post-disturbed birds) was 0.0480 compared to 0.0288 for disturbed birds (Figure 3). Thus oystercatchers not being subjected to disturbance (i.e. post-disturbed birds) were 67% more likely to have a successful feed than disturbed birds (Odds ratio $\omega = 1.6662$), however these results were not significantly different from a null ratio of 1 (Fishers exact test, $P>0.05$).

2.3.4. Effect of Disturbance Type

There was no effect of disturbance type on the percentage of time spent being aware, handling, the peck rate or step rate of disturbed birds at either of the sites (all tests non-significant, Table 2). However, the percentage of foraging time that the disturbed birds were aware for in Looe was found to be significantly different from in Par (ANOVA $F_{(1,16)} = 8.52$, $P<0.05$); on average, birds in Looe were aware for 11% more of their foraging time (Figure 2 a). No treatment-disturbance interaction was found for the percentage of time that the birds spent handling, being aware, their peck or step rate at either site (Table 2).

		Time Spent Aware (%)		Time Spent Handling (%)		Peck rate (Pecks S^{-1})		Step rate (Steps S^{-1})	
Looe Source	df	Adj MS	*F*	Adj MS	*F*	Adj MS	*F*	Adj MS	*F*
Treatment Tr	3	29.08	0.31 NS	108.58	0.72 NS	0.000917	0.09 NS	0.6255	0.73 NS
Day Da (Tr)	8	94.37	1.01 NS	150.24	1.18 NS	0.010417	7.12 **	0.8544	3.44 NS
Disturbance Di	1	5530.24	59.22 ***	2071.25	16.26 **	0.085183	58.25 ***	0.0247	0.10 NS
Tr X Di	3	133.37	1.43 NS	312.42	2.45 NS	0.000472	0.32 NS	1.1179	4.49 NS
Di X Da (Tr)	8	93.38	1.59 NS	127.38	1.46 NS	0.001462	0.39 NS	0.2487	1.46 NS
Error	24	58.61		87.52		0.003773		0.1707	
Total	47								
Par	df	Adj MS	*F*	Adj MS	*F*	Adj MS	*F*	Adj MS	*F*
Treatment Tr	3	20.17	0.5 NS	82.75	0.7 NS	0.001671	0.18 NS	0.224	0.3 NS
Day Da (Tr)	8	40.39	0.8 NS	117.45	0.63 NS	0.009246	2.32 NS	0.7591	2.50 NS
Disturbance Di	1	2957.94	58.74 ***	1675.35	8.93 *	0.014105	3.54 NS	0.0138	0.05 NS
Tr X Di	3	23.87	0.47 NS	129.21	0.69 NS	0.003161	0.79 NS	0.0878	0.29 NS
Di X Da (Tr)	8	50.35	0.87 NS	187.52	2.11 NS	0.003979	1.31 NS	0.3037	1.33 NS
Error	24	57.8		88.67		0.003039		0.2292	
Total	47								

Table 2. Unbalanced GLM analyses on the difference in the foraging behaviour of oystercatchers during and after a disturbance event at two sites (NS – Non-significant $P>0.05$; $^*P<0.05$; $^{**}P<0.01$ and $^{***}P<0.001$). The percentage of time spent being aware and handling were arc-sin transformed prior to analysis Treatment refers to the type of disturbance applied. Disturbance refers to whether the bird was disturbed or not. Undisturbed birds are those observed after disturbance event had ceased (post-disturbance) whilst disturbed birds are those observed as the disturbance is applied.

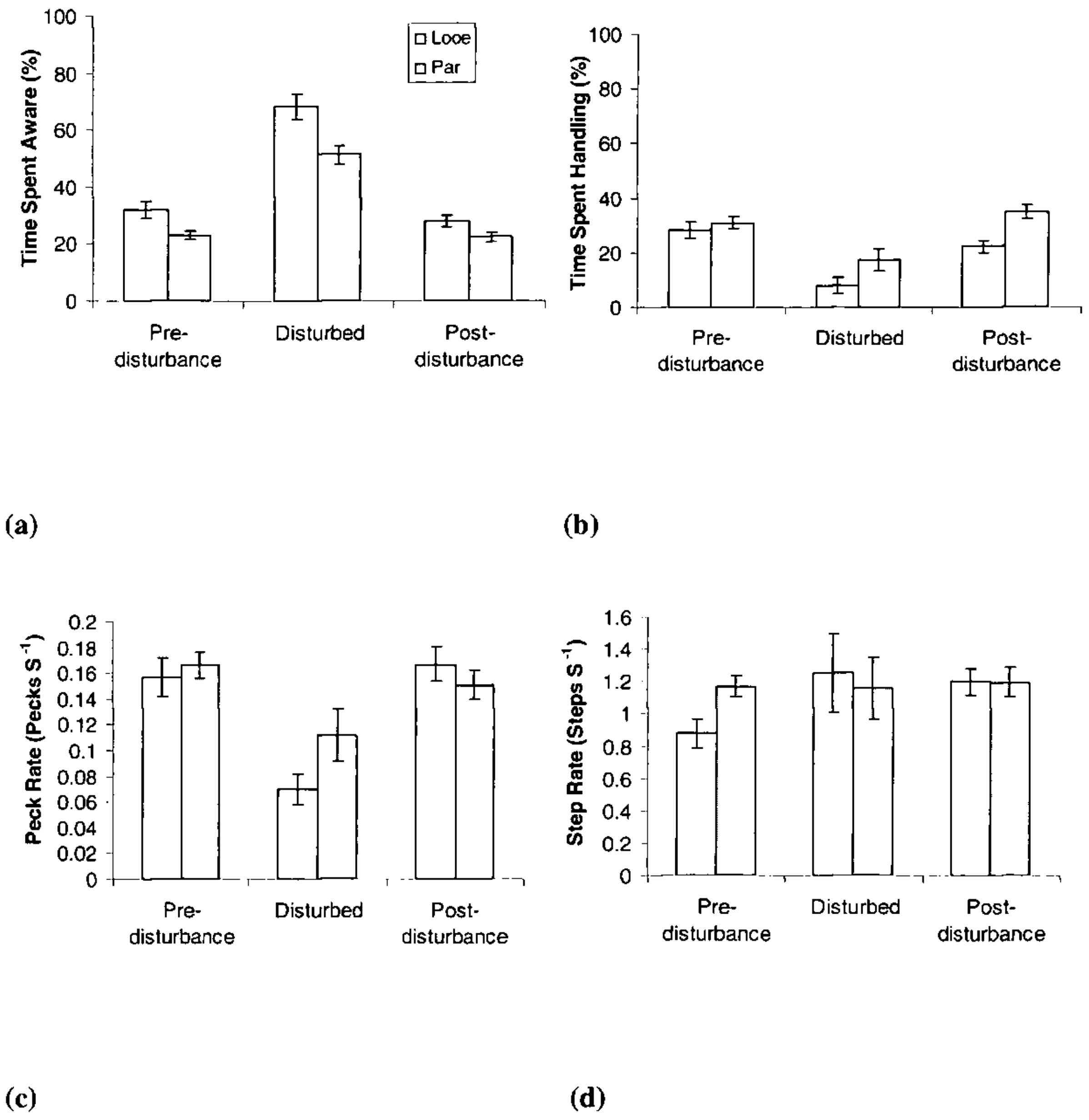


Fig. 2. The mean percentage of time oystercatchers spent being a) aware and b) handling, and their mean c) peck and d) step rate prior to the experimental disturbance event, during the disturbance and post-disturbance, at Looe and Par. Data from all disturbance types combined. A total of 84 birds were observed at each site for an approximate 300 seconds period - 36 pre-disturbance (LT -3 to-1hr); 12 disturbed (LT +1hr) and 36 post-disturbance (LT +1 to +3hrs) birds. Untransformed results are shown (mean ± SE).

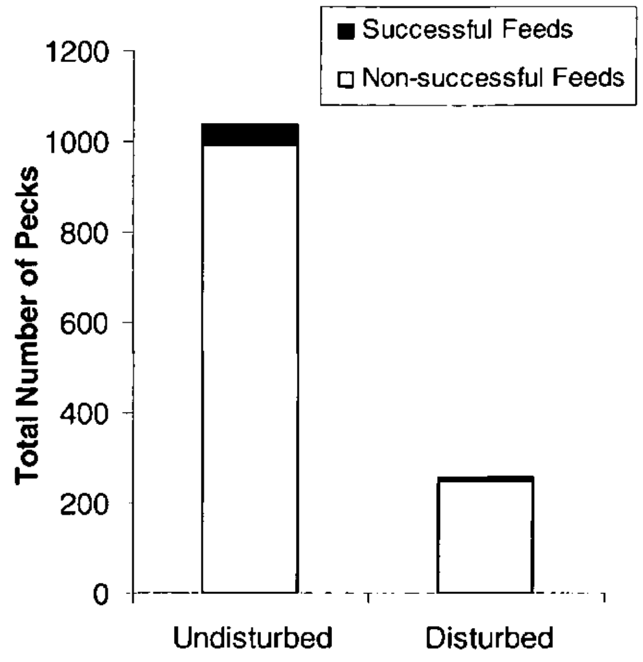


Fig. 3. Effect of disturbance on the foraging success of oystercatchers. As previous analyses had shown no difference between pre- and post-disturbance behaviour, post-disturbance birds represent undisturbed behaviour in this analysis. 24 post-disturbance (undisturbed) and 24 disturbed oystercatchers were observed. Data from both study sites combined.

2.3.5. Effect of Disturbance Type, and Distance Between the bird and Disturbance Factor on the Foraging Behaviour of Disturbed Birds

The rate of change in the percentage of time individual birds spent being aware as disturbance factors approached, did not vary significantly dependant upon the type of disturbance applied or on the study site (Table 3). As predicted awareness increased as the disturbance factor reached a closer proximity to the birds (Figure 4 a). This general and overall relationship was not, however, explained well by linear regression (overall regression line: $y = -0.2435x + 82.865$, $R^2 = 0.1854$). The rate of change in the percentage of time an oystercatcher spent handling as a disturbance factor approached to a closer proximity, did vary significantly dependant upon both the type of disturbance applied ($F_{(3,16)} = 5.32$, $P<0.01$) and the site ($F_{(1,16)} = 6.57$, $P<0.05$); a disturbance type-site interaction, however, was not apparent (Table 3). Individuals generally decreased the percentage of time they spent handling prey items as the disturbance factor got closer to them (Figure 4 b), although this overall decline was not explained well by linear regression (Overall regression line: $y = 0.0674x + 6.518$, $R^2 = 0.0282$). The rate of decline in handling time was significantly greater in Par compared to Looe (Figure 4 e, $P<0.05$). The rate of decline in handling time was also significantly greater when the birds were subjected to a person walking, compared to a person walking with a barking dog ($P<0.01$) and a group walking ($P<0.05$) (Figure 4 f). The rate of change in an individual's peck rate and step rate as a disturbance factor approached was not different for each disturbance type, nor was it different at each site (Table 3). In general, peck rate decreased as the disturbance factors approached the foraging birds (Figure 4 c), whilst step rate increased (Figure 4 d), however neither of these general and overall relationships were explained well by linear regression (Overall regression line: $y = 0.0004x + 0.0371$, $R^2 = 0.0454$ and $y = -0.0037x + 1.4161$, $R^2 = 0.0314$, respectively). A significant site-disturbance type interaction was found for oystercatcher step rate ($F_{(3,16)} = 3.59$, $P<0.05$), with oystercatchers at Looe responding to a person with a barking dog by taking fewer steps whilst those in Par responded to the same disturbance type by taking more steps ($P<0.05$, Figure 4 g).

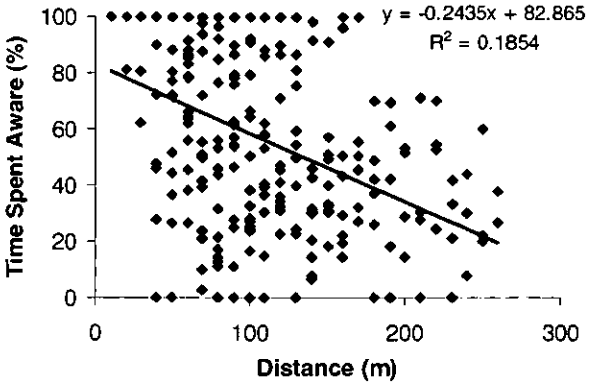
2.3.6. Effect of Disturbance Type on the Flight Initiation Distance

No significant difference was found for the flight initiation distance between sites (ANOVA $F_{(1,16)} = 0.32$ NS), between treatments (ANOVA $F_{(3,3)} = 6.64$ NS) or between treatments within sites (ANOVA $F_{(3,16)} = 0.1$ NS). The average flight initiation distance for foraging oystercatchers was 39m (S.E. = 5.3). Disturbance type did not alter the distance focal birds allowed disturbance factors to approach before taking flight (Figure 5).

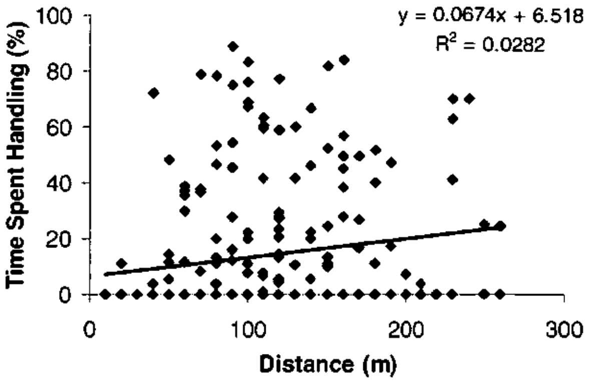
Slope		**Time Spent Aware (%)**		**Time Spent Handling (%)**		**Peck Rate (Pecks S^{-1})**		**Step Rate (Steps S^{-1})**	
Source	df	MS	F	MS	F	MS	F	MS	F
Site	1	0.632	1.46 NS	0.1926	6.57*	0	1.14 NS	0.0003	0.47 NS
Disturbance	3	0.2506	0.58 NS	0.1558	5.32**	0	0.01 NS	0.0007	1.17 NS
Site X Disturbance	3	0.1697	0.39 NS	0.0855	2.92 NS	0	0.86 NS	0.0011	2.02 NS
Residual	16	0.4322		0.0293		0		0.0006	
Total	23								

Intercept		**Time Spent Aware (%)**		**Time Spent Handling (%)**		**Peck Rate (Pecks S^{-1})**		**Step Rate (Steps S^{-1})**	
Source	df	MS	F	MS	F	MS	F	MS	F
Site	1	521.2303	0.27 NS	321.3656	1.12 NS	0.0014	0.11 NS	0.3862	0.12 NS
Disturbance	3	1284.469	0.66 NS	554.2512	1.94 NS	0.0011	0.08 NS	2.9949	0.96 NS
Site X Disturbance	3	780.8983	0.4 NS	222.5503	0.78 NS	0.0365	2.77 NS	11.1388	3.59*
Residual	16	1954.997		285.804		0.0132		3.1064	
Total	23								

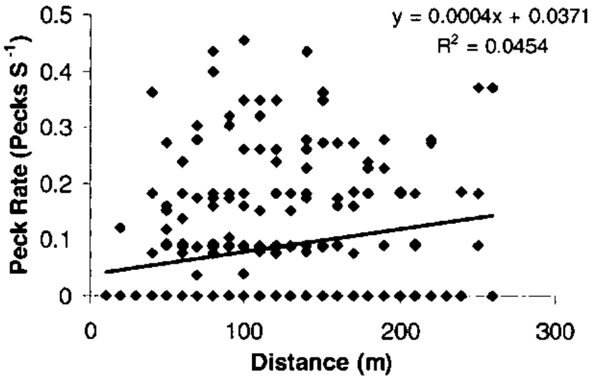
Table 3. Analyses of variance on the effects of disturbance type and site on the rate of change in oystercatcher behaviour as the disturbance factors approached focal birds (NS – Non-significant $P>0.05$, $*P<0.05$, $**P<0.01$ and $***P<0.001$) . Disturbances were a person walking (PW), a person walking with a non-barking dog (PWND), a person with a barking dog (PWBD) and a group walking (GW). Sites were Par and Looe. Prior to analyses data were tested using Cochran's homogeneity of variance test. Data used were the slopes and intercepts of individual regression lines describing the relationships between the distance separating the bird and disturbance factors and components of oystercatcher behaviour. A total of 24 birds were observed, 12 at each site.


y = -0.2435x + 82.865
R² = 0.1854
Time Spent Aware (%)
0
20
40
60
80
100
0
100
200
300
Distance (m)

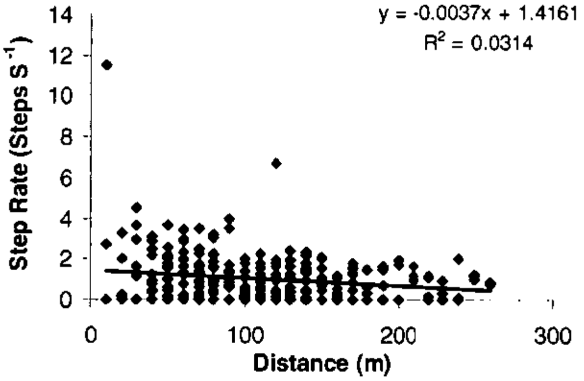
(a)


y = 0.0674x + 6.518
R² = 0.0282
Time Spent Handling (%)
0
20
40
60
80
100
0
100
200
300
Distance (m)

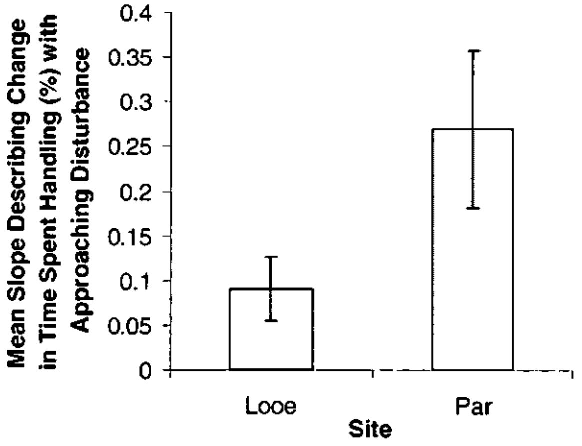
(b)


y = 0.0004x + 0.0371
R² = 0.0454
Peck Rate (Pecks S -1)
0
0.1
0.2
0.3
0.4
0.5
0
100
200
300
Distance (m)

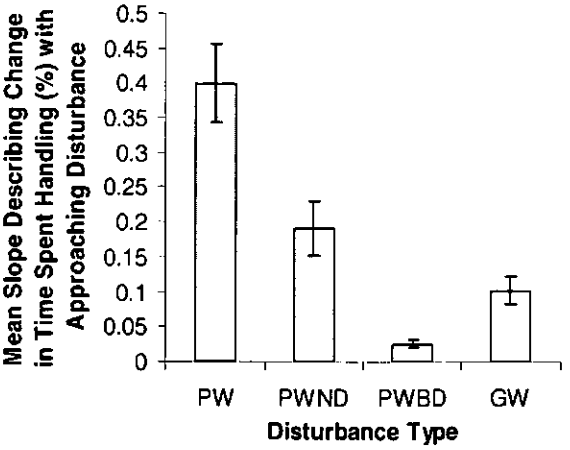
(c)


y = -0.0037x + 1.4161
R² = 0.0314
Step Rate (Steps S -1)
0
2
4
6
8
10
12
14
0
100
200
300
Distance (m)

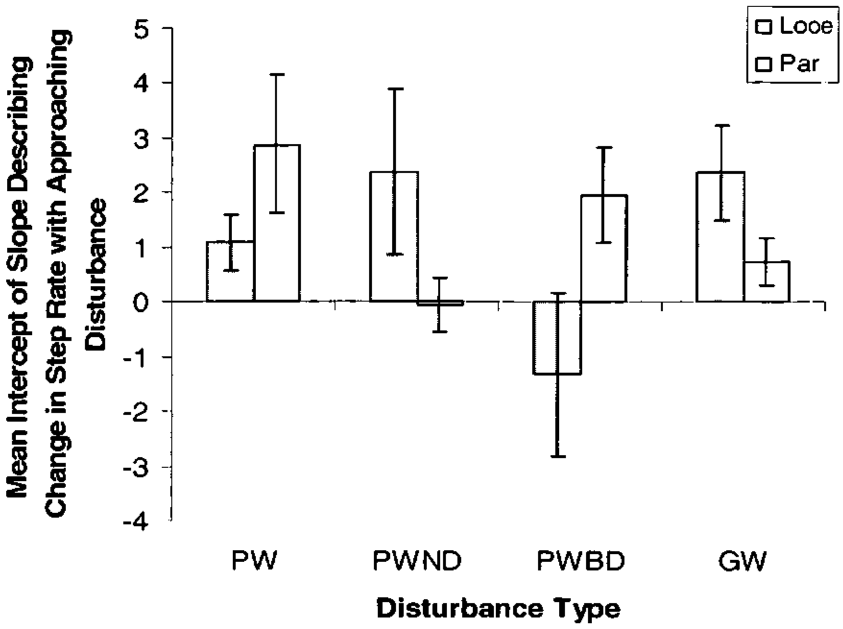
(d)


Mean Slope Describing Change in Time Spent Handling (%) with Approaching Disturbance
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
Looe
Par
Site

(e)


Mean Slope Describing Change in Time Spent Handling (%) with Approaching Disturbance
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
PW
PWND
PWBD
GW
Disturbance Type

(f)



(g)

Fig. 4. Trendlines for the percentage of time that disturbed oystercatchers spent being aware (a) and handling (b), and their peck (c) and step rate (d) as the disturbance agent drew closer. 24 birds were observed. Raw data are presented. Measurements were calculated at 10m intervals for each individual bird and individual regressions performed, however overall trendlines are presented here to show general trends. ANOVAs were performed using the slopes and intercepts of each individual regression, to test whether disturbance type or site had an effect on the rate of change in an oystercatcher's behaviour (see Table 4.3). Mean (±SE) rates of change in the percentage of time oystercatchers spent handling, as the disturbance agent approached at different sites (e) and under different disturbances, are presented. Disturbances were a person walking (PW), a person walking a non-barking dog (PWND), a person walking a barking dog (PWBD), and a group walking (GW). Mean (±SE) intercepts of regression lines for oystercatchers step rates observed in response to each type of disturbance at each site are presented (g) (See Table 4.3 for analyses). 3 birds were observed responding to each disturbance type at each site, a total of 24 birds were observed.

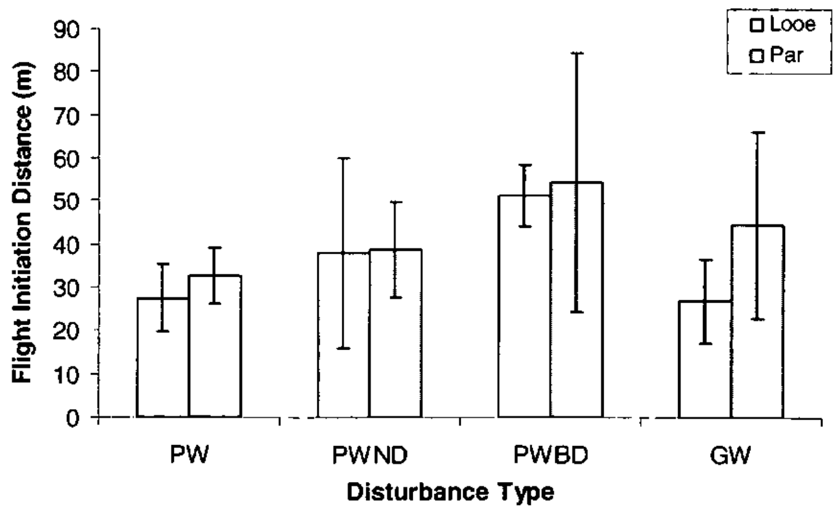


Fig. 5. The mean distance between focal birds and disturbance factors, as the birds took flight. Untransformed results shown (mean ± SE), at Looe and Par. A total of 24 birds were observed, 12 at each site.

2.4. Discussion

2.4.1. Effect of a Disturbance Event

Oystercatchers foraging on the rocky shore responded to experimentally applied human disturbance by increasing the time they spent being vigilant at the cost of time spent foraging, before eventually taking flight. Thus, vigilance and overall foraging activity (searching or head down, handling and pecking) were traded-off against each other (Fernandez-Juricic & Telleria 2000). If peck rate is considered in isolation, however, a trade-off with vigilance was not apparent in Par, suggesting that foraging and vigilance may not always be mutually exclusive (Lendrem 1984, Lima & Bednekoff 1999a, Guillemain *et al.* 2001). It is suggested that whether a trade-off occurs may be dependant upon the structural complexity of the foraging area. Birds feeding on relatively flat areas are unrestricted in their view of approaching potential threats and so may have the capacity to be vigilant whilst in the head-down/feeding position (Lima & Bednekoff 1999a, Guillemain *et al.* 2001, Whittingham *et al.* 2004), however when visually restricted, the birds are forced to raise their heads to visually detect threats (Metcalfe 1984b), thus reducing feeding. Of the two sites used in this study, Looe was much more structurally complex, i.e. the scale of the complexity was such that it could impede the capability of the bird to detect an oncoming threat (pers. obs.). As expected, the control birds observed feeding in Looe spent a higher percentage of their time with their head up and a lower percentage of their time handling, than the birds in Par. Furthermore, when disturbed, the birds in Looe suffered a reduction in peck rate whilst those in Par were able to retain their pre-disturbance peck rate whilst simultaneously increasing vigilance (Coleman *et al.* 2003). In the study by Coleman *et al.* (2003) oystercatchers, foraging on soft sediments interspersed pecking with vigilance but still suffered a decline in successful feeding attempts, suggesting a trade-off between vigilance and energy intake. At Looe energy intake was limited as the disturbed birds had less feeding attempts; the birds at both sites were not, however, any less likely than undisturbed birds to be successful in their feeding attempts. In contrast, in a study by Fitzpatrick and Bouchéz (1998), birds on a less structurally complex shore than the one used in this study, increased vigilance and actually foraged more successfully with moderate disturbance. However, this could be due to the fact that the experiment was conducted in the benign conditions of summer when the birds may not have been feeding at their highest intensity, allowing time for both an increase in vigilance and foraging intensity.

2.4.2. Longevity of Effects of Disturbance Event

The effects of human disturbance on oystercatcher foraging behaviour were considerable, but only very short-term as birds returned to feeding at pre-disturbance levels shortly after the disturbance event had ceased (within 5 to 10 minutes of disturbance). By remaining in an area that has been recently disturbed, the birds increase their perceived predation risk, however, post-disturbance birds did not retain an elevated level of vigilance as a precaution after the recent threat, nor did they decrease their awareness in order to forage more intensively and thus compensate for lost foraging time (Swennen *et al.* 1989). It is possible that the birds had no choice but to return to 'normal' feeding behaviour, if they were pushed to meet their high energy requirements, and unable to increase their foraging intensity due to an increased probability of bill damage (Hulscher 1996) or because they were already feeding at a maximal rate (Meire 1996). Certainly, undisturbed oystercatchers had very few successful feeds in relation to the number of foraging attempts (Coleman *et al.* 2003), suggesting that it is important that the birds forage for as long as possible in order meet their energy requirements. In addition, they may have been unable to extend their foraging period due to the restrictions of tide, and as visual feeders, the restrictions of light. The extent to which the vigilance and peck rates of post-disturbance birds returned to pre-disturbance levels varied between days and could also be dependant on factors such as temperature and weather. Colder temperatures require increased energy intake (Goede 1983, Kersten & Piersma 1987), and so a quicker recovery time might be expected (Stillman & Goss-Custard 2002). Furthermore, numerous studies have shown that when temperatures are lower, birds are willing to feed in areas, that although may be more profitable, are of a higher predation risk (e.g. Cresswell 1994a, Duriez *et al.*, 2005). It is possible that the oystercatchers observed during this study were not finding conditions difficult, as indicated by their lack of feeding over low tide, and so did not need to compensate for lost foraging time. Furthermore, a single disturbance may not have interrupted feeding long enough to stimulate compensatory behaviour (Urfi *et al.* 1996), and the period for which the birds were vigilant may have simply doubled as a digestive pause. Although the effects of a single disturbance event appear to be only very short-term, if human disturbance was continuous, the birds may be forced to compensate for lost foraging time which could involve limiting vigilance regardless of the threat (Lima & Bednekoff 1999b); alternatively they may be forced to leave the feeding area temporarily or permanently, which could have serious implications for the health of individuals if they have no alternative foraging area or are forced to feed on areas of lower quality, especially during the winter months.

A major assumption upon which the analysis of the disturbance data is based is that the oystercatchers observed on the control day were feeding 'normally', i.e. in a way similar to that demonstrated on the majority of other days. As the birds on the control day fed similarly pre- and post- low tide, it was considered appropriate to assume that on disturbance days pre- and post- disturbance birds would behave correspondingly if there was no extended effect of disturbance. Furthermore, as pre- and post- disturbance birds were so alike in their behaviour it was further assumed that comparing disturbed birds to post-disturbance birds was the equivalent to comparing disturbed birds to undisturbed birds.

As only one control day was recorded at each site however, it is impossible to know whether the behaviour witnessed on that day is representative of behaviour on most other days, which has possible implications for the results gained. For example, if the control day results are not representative of 'normal' behaviour and oystercatchers usually forage more intensely before low tide, then the assumptions above would not allow us to detect an increase in post-disturbance foraging behaviour that may occur in response to lost foraging time. In addition, if post-disturbance birds did actually increase the intensity of their foraging then the effect of disturbance on disturbed birds compared to undisturbed birds would be over-estimated. Thus, as a result of the assumptions made, the extent of the effects of disturbance on disturbed and post-disturbed birds may not be fully understood. It is important to note, however that there is no reason to believe that oystercatchers observed on the control day were not behaving normally; no predatory attack or considerable disturbance event took place on that day. Also, the control days from both the study sites used in this experiment showed the same trend, that the behaviour of pre-and post-disturbance birds were not significantly different; whilst the results from the experiments conducted at Trebetherick (Chapter 3 and 4) showed that foraging behaviour did not vary significantly with the state of the tide.

2.4.3. Effect of Disturbance Type on Disturbed Birds

Disturbed birds reacted similarly to a disturbance event regardless of its nature, which suggests that all disturbance factors carry the same perceived risk. This contradicts previous studies where birds responded differently dependant upon the type of disturbance applied (Burger 1981, Burger & Gochfeld 1998, Thomas *et al.* 2003, Rees *et al.* 2005). However, these studies have generally been correlative, and the results open to bias, either due to the duration (Hill et al. 1997) or cumulative effects of, or habituation to, the disturbance (Cayford 1993). Furthermore, we must consider that the model dog used during this study lacked some element of 'dogginess', i.e. the varying speed of approach and change in direction that unrestrained domestic dogs demonstrate. It may be these elements of dog behaviour that cause birds to react in a greater way than they would if subject to a less variable type of disturbance (Davidson & Rothwell 1993, Kirby *et al.* 1993). In studies by Burger (1981) and Fitzpatrick and Bouchéz (1998) birds reacted to a greater extent when approached at a rapid rate by a potential predator; however oystercatchers failed to significantly increase their vigilance with the presence of free-running dogs (Fitzpatrick & Bouchéz 1998). In addition, the noise created during the barking dog treatment and by the group of people walking, may not have been loud enough to initiate a greater response. It is possible that a higher level of response occurs only as a result of very extreme types of disturbance or disturbance created by 'natural', avian, predatory events. Whilst many animals react to human disturbance and an 'actual' predation threat in a similar way, it is possible that birds such as those observed during this study which are predominantly preyed upon by aerial predators, perceive human disturbance to be less of a predation threat.

2.4.4. Effect of Distance between Disturbance and Birds on Foraging Behaviour

Disturbed birds increased their vigilance, as a result of their increased perceived predation risk, as the disturbance factors approached. Neither the total percentage of time that disturbed birds spent being vigilant nor the rate at which vigilance increased as the disturbance factors approached the focal birds, differed dependant upon the type of disturbance applied. Thus it appears that, at least with regards to the types of disturbance applied here, all disturbances are perceived to carry the same risk.

Oystercatchers decreased their time spent handling and peck rate as the disturbance factors approached. The rate of decline in the percentage of time an individual spent handling was greater in Par than in Looe, which may be a factor of the initial distance separating the disturber and bird (Blumstein 2003). The rocky shore of Par, at approximately 26677 m^2, has a significantly smaller area than Looe, at an estimated 305410 m^2 thus the distance from which the disturbance factor begins to approach the focal bird, will be much closer at Par than at Looe. This is likely to influence the rate of change in behaviour, especially regarding aspects of behaviour that require an individual to remain with it's head down, and its visibility reduced, for longer periods of time. This could be the reason that the rate of change in handling differs between sites but not the rate of change in peck rate. Certainly, there is some evidence to suggest that starting distance has an effect on the flight initiation distance of birds (Blumstein 2003). The rate of change in the percentage of time oystercatchers spent handling also varied with the type of disturbance applied, a person walking was associated with a more rapid drop in handling than a person walking with a barking dog or a group walking. Again this may be due to handling and vigilance being mutually exclusive on the rocky shore; the noise created by a barking dog and a group of people may be used by the birds, to evaluate the distance to the disturbance when in a head down position, thus reducing their predation risk and allowing them to forage for longer as the disturbances approach. Alternatively, the larger the group approaching, the easier it may be for the birds to monitor their approach visually. The response of oystercatchers, with regards to their movement, as disturbance factors approached was variable within and between sites dependant upon the type of disturbance applied. These results show that individual response to disturbance varies, and that birds from different sites may react differently possibly due to factors such as structural complexity of the site, food availability and dispersion, individual vulnerability, age, previous experience of disturbance, environmental factors, and availability of an alternative feeding site.

2.4.5. Flight Initiation Distance

Oystercatchers foraging on the rocky shore did not vary in the distance they allowed different disturbance factors to approach, before taking flight (Thomas *et al.* 2003). The mean flight initiation distance for oystercatchers foraging on the rocky shore was 39 metres; this is similar to the flight initiation distance found for oystercatchers at three sites along the Exe estuary; they flew at 48, 41 and 26 metres dependant upon the level of disturbance they were regularly subjected to (Urfi *et al.* 1996). Urfi *et al.* (1996) found that birds flew at a greater distance when occupying relatively undisturbed areas but allowed disturbance factors to approach to a much shorter distance when occupying areas frequently subject to disturbance, which suggested that habituation had occurred. Of course an alternative interpretation of the results of Urfi *et al.* (1996) may be that the frequently disturbed birds were unable to afford the temporal and energetic costs of frequent relocation and so tolerated a much closer approach by humans. In comparison, oystercatchers in the Dutch Wadden Sea area took flight at a much greater, 85 metre, distance from the disturbance (Van der Meer 1985 loc cit Smit & Visser 1993). This flight initiation distance is thought to reflect the fact that oystercatchers resting in the area are at risk from hunting and therefore consider humans to be much more of a threat. Certainly in a study by Madsen (1998) hunting from mobile punts was found to elicit the greatest response in wildfowl compared to other human waterborne activities.

Over recent years many studies have recommended that efforts be made to restrict the types of human disturbance considered to be the ‘most disruptive’ to feeding, roosting or breeding birds, in areas that the birds inhabit, at times when they are most vulnerable (for example Madsen 1998, Thomas *et al.* 2003). During this study the birds were found to respond similarly regardless of the disturbance type, which could have important consequences for the conservation and management of coastal areas that are used as feeding sites by wading birds. If all disturbance is equally disruptive to the birds limiting certain human activities would appear to be ineffectual management strategy, whilst limiting human activities in general in feeding areas would be implausible. The response of foraging birds to disturbance is variable (see Smit & Visser 1993 for summary) and is likely to be affected by factors such as the weather; temperature; season; quality and size of the feeding site; presence and quality of an alternative feeding site (Gill *et al.* 2001); sensitivity of the species (Burger 1981, Klein *et al.* 1995, Boer & Longamane 1996, Burger & Gochfeld 1998, Blumstein *et al.* 2005); age of birds; foraging efficiency of birds; the condition of the birds (Beale & Monaghan 2004); presence of conspecifics; and previous experience of disturbance (Smit & Visser 1993). It is very difficult therefore to apply effective conservation measures to a site without first having a previous knowledge of the sensitivity of the species concerned and possible consequences of the disturbances, that are to be prevented. However, ultimately it is clear that intermittent, occasional disturbance is unlikely to pose a serious threat to foraging oystercatchers.

Chapter 3: Foraging Behaviour of Oystercatchers on the Rocky Shore in Relation to Environmental Parameters

3.1. Introduction

Optimising time allocations between fundamental tasks has been selected for in many organisms. At a very basic level and on a day to day basis, individuals must balance the need to forage with avoiding predators (McNamara & Houston 1990b; Lima & Dill 1990). Additional considerations may include defending territories, travelling, socializing, resting, tending to young, nest building, preening, retaining water or heat, and building up energy/food stores for hibernation/winter feeding (Stephens & Krebs 1986). The amount of time apportioned to each activity will vary between individuals dependent upon their physiological state, and are temporally and spatially co-dependant upon environmental factors (e.g. Caraco 1979a; Caraco *et al.* 1980; Gauthier-Clerc *et al.* 2000; Pravosudov & Grubb 1995, 1998, Houston 1993).

3.1.1. Individual variation

Non-breeding oystercatchers, *Haematopus ostralegus*, must trade-off the need to forage in order to meet their energy requirements, be vigilant against potential predators, roost, socially interact to gain dominance and potentially move up the social hierarchy, and preen in order to maintain healthy feathers; all of which are imperative for fitness. Individual oystercatchers may differ in their time allocation to each activity dependant upon their age, physiological state, foraging efficiency, prey handling efficiency, and dominance. Younger birds, less experienced at foraging than older birds (Ens & Cayford 1996), may take significantly longer to meet their energy requirements (Caldow *et al.* 1999). They may be forced to attempt to steal prey items from older individuals in order to gain sufficient energy (Goss-Custard *et al.* 1998), have prey items stolen from them by more dominant individuals (Ens & Cayford 1996), or be unable to meet their energy requirements over the winter, thus increasing the probability of starvation (Kersten & Brenninkmeijer 1995, Swennen & Duiven 1983, Heppleston 1971). In addition, individuals harbouring physical defects, often in the form of a damaged bill, maybe hindered from efficient foraging (Swennen & Duiven 1983), whilst others may be simply less successful at feeding.

Oystercatchers have a social hierarchy where more dominant individuals that are better at fighting and feeding, and thus in better condition, inhabit the best feeding (Goss-Custard *et al.* 1982a, b), roosting (Swennen 1984) and breeding sites, i.e. sites where food is abundant and available, where it is safe and where the feeding and roosting/nesting sites are in close proximity to each other. Sub-dominant individuals unable to fight to retain or gain such territories are displaced (Leopold *et al.* 1989), and may be forced to spend significantly longer travelling between suitable sites that are further a field, thus limiting their foraging time or requiring them to extend it at the cost of other important behaviours. Forfeiting vigilance could heighten the risk of a successful predator attack upon an individual, whilst reducing the time spent preening, roosting or interacting may have implications for long-term fitness. The tending of feathers is important for water and wind resistance and thus reduces energy expenditure, as does roosting which is essential for wading birds in the winter. Social interactions are necessary to elevate an individual's status within the social hierarchy and to establish a place within the sites of the highest quality (Ens & Goss-Custard 1984). Nevertheless, ultimately, vigilance should always be a high priority as it can take only one failure to detect a predator to result in instant death, whilst starvation is gradual, and so any reduction in energy intake has the potential to be compensated for at future date (Lima & Bednekoff 1999a).

3.1.2. Temporal variation

Wading birds may also vary in their behaviour with the weather, tide, temperature, season, disturbance, predation risk, and migration. Over winter, temperatures drop causing energy expenditure to rise due to the increased costs of thermoregulation (Wiersma & Piersma 1994, Kelly *et a*l. 2002), forcing oystercatchers to feed for longer (Urfi *et al.* 1996) or more intensively (Swennen *et al* 1989) in order to meet their energy requirements. Furthermore, some studies have shown that cold temperatures can reduce prey availability (Goss-Custard 1969, Zwarts *et al.* 1996a), subsequently heightening the risk of starvation (Dare & Mercer 1973). The storing of energy reserves and reduction in energy expenditure through limiting activity, prior to severe weather, increases an individuals' chance of survival by prolonging the time it can go without food if prey availability is reduced. In addition, it allows for the increased energy expenditure associated with fleeing to alternative foraging sites should prey availability be totally restricted (Kelly & Weathers 2002). Increased foraging activity at the cost of vigilance and increased body mass which may hinder locomotion (Lima 1986, Witter & Cuthill 1993) however, could leave the birds open to a greater predation risk. Kelly *et al.* (2002) found that dunlin (*Calidris alpina*) regulated their energy consumption and thus their body mass in response to environmental cues. Increased rainfall appeared to be a cue to increase body mass, possibly in anticipation of oncoming winter storms (Kelly *et al.* 2002). This suggests that body mass is generally limited when conditions are improved, so as to limit the costs of a heavier body mass (Kelly *et al.* 2002).

Increased energy consumption may not only be associated with the winter season. Foraging activity may increase pre- and post-migration as the birds attempt to accumulate or replenish energy reserves (Kersten & Piersma 1987, Velasquez & Hockey 1992). Foraging activity may also increase during the breeding season with the additional temporal and energetic costs associated with making numerous trips between foraging and breeding grounds, and the need to acquire a sufficient amount of food to support both themselves and their young (Ens *et al.* 1992). In contrast, warmer temperatures reduce energy expenditure requiring a lower amount of energy intake (Goede 1993, Zwarts *et al.* 1996d). The summer months, however, bring an increase in human activities on the shore, requiring the birds to display a heightened level of vigilance, possibly at the expense of foraging. Furthermore, human disturbance can lead to temporary or permanent habitat loss as the birds are displaced from their foraging site (Pfister *et al.* 1992, Stillman & Goss-Custard 2002).

There is also some evidence to suggest that oystercatchers vary in their foraging behaviour with tidal state. Goss-Custard *et al.* (1984) demonstrated that oystercatchers increased their foraging intensity as the tide came in ending the time available for foraging. Similarly, Swennen *et al.* (1989) found that captive oystercatchers increased their intake rate when tidal manipulations limited the available foraging time, although Meire (1996) found no such compensatory mechanism. Thus, it appears that increasing the rate at which they can successfully feed may be possible for oystercatchers not already feeding at their maximum capacity; but for those less efficient or successful at foraging, increasing foraging intensity is not an option, and effective time-budgeting is imperative. Furthermore, additional sites, such as fields, used at high tide (Heppleston 1971, Goss-Custard & Durell 1983, Quinn & Kirby 1993), may be extremely important in aiding wader survival when energy requirements are unlikely to be met in a single low-water feeding period.

Environmental factors such as the tidal cycle, tidal height (which is also influenced by the direction and strength of the wind) (Feare 1966) and weather conditions (Pienkowski 1981, 1983) also affect prey behaviour and determine the amount of food available to the birds (Rippe & Dierschke 1997). Rain could benefit oystercatcher foraging by prolonging prey availability. For example, limpets on rocky shores clamp down when uncovered by the tide in order to preserve water, whilst some organisms in soft sediments burrow deeper, making them difficult to reach, as the top layer of sediment begins to dry out (Evans 1976); rain may delay desiccation and thus the need for the prey to react as rapidly, hence prolonging prey availability. Alternatively, rain may cause organisms adapted to saline conditions to bury down to further depths, clamp their valves together or clamp down upon the rock to avoid osmotic shocks as a result of freshwater flow. It is also suggested that high wind speeds will reduce foraging efficiency by consistently pummelling the birds (Pienkowski 1981), and significantly increase energy consumption through wind chill. Certainly in studies by Dugan *et al.* (1981), Davidson (1981) and Zwarts *et al.* (1996d) the body mass of waders decreased with increasing wind speed. Additionally, rain or strong winds may make it difficult for waders to see potential predators (Hilton *et al.* 1999b, McGowan *et al.* 2002), whilst the sun may encourage human activities on the shore, forcing the birds to exhibit elevated vigilance or avoidance behaviour at the cost of foraging.

3.1.3. Spatial variation

Bird density changes with the quality of a feeding site, and *vice-versa*. As predicted by the ideal free distribution model (Fretwell & Lucas 1970), areas with plenty of food, where intake rate is greatest, will attract more birds than less profitable patches (Krebs 1978), assuming that other factors such as predation risk are equal (see Kacelnik *et al* 1992 and Sutherland 1996 for overview). As bird density increases, however, so does competition for resources, and interference (Goss-Custard *et al.* 1981, Sutherland & Koene 1982, Ens & Goss-Custard 1984, Goss-Custard & Durell 1987a). Competitors deplete the resources available to an individual (Zwarts & Drent 1981, Sutherland 1996), whilst interference to an individual includes: a) the stealing of prey items by dominant birds (Ens & Goss-Custard 1984, Triplet *et al* 1999), b) the depression of prey items as conspecifics disturb them and render them inaccessible (Selman & Goss-Custard 1988, Stillman *et al.* 2000a, Coleman *et* *al.* 2004) and c) the need to avoid more dominant conspecifics situated along the individual's search path (Ens & Cayford 1996, Goss-Custard 1980). As the carrying capacity of a site is reached some birds, usually sub-dominants, will be forced to feed elsewhere, usually less preferred areas (Goss-Custard 1977, Goss-Custard *et al.* 1982a), as they are out-competed for food and thus the territory, forming the basis of the ideal despotic distribution (Fretwell 1969). Although high bird densities encourage an awareness of conspecifics, such vigilance may be offset by the benefits to group foraging. The advantages to group foraging (Lazarus 1979) include the 'dilution' effect, which limits the chance of an individual being the target in an attack; the 'confusion' effect, where more birds means more confusion, should an attack occur (Cresswell 1994b); and the 'many eyes' effect, which increases predator detection whilst limiting the vigilance required from each individual, thus allowing more time to be devoted to feeding (Pulliam 1973, Roberts 1996, Whitfield 2003b, see Krause & Ruxton 2002 for review). Thus the time-budgeting of oystercatchers is expected to vary with the number of birds present in the area.

Various sites may have differing levels of risk associated with them dependant upon the oystercatchers' previous experience of the area, and the structural complexity of the shore, which is likely to affect the birds' time-budgeting. Although feeding and vigilance have previously been assumed to be mutually exclusive behaviours (Bertram 1980, Hart & Lendrem 1984, Lima & Dill 1990), more recently it has been suggested that individuals have the ability to have their head down feeding whilst simultaneously keeping an eye on the surrounding area, if the visibility is good (Arenz & Leger 1997, Lima & Bednekoff 1999a, Lendrem 1984, Metcalfe 1984b, Cresswell 1994b, Bednekoff & Lima 2005). If however, birds feed in areas that are structurally complex, vigilance can only be effective if the birds raise their heads at the subsequent cost of feeding (Metcalfe 1984b). It is expected, therefore, that oystercatchers foraging on a structurally complex rocky shore, will be more pressured with regards to their time-budgeting than those feeding on estuarine flats. In addition, assuming that oystercatchers foraging on the rocky shore search visually (as opposed to estuarine foragers that feed through touch as well as visual cues), their feeding time could be further restricted by light, especially during the winter months when daylight is limited. Of course it is possible that the birds can feed by moonlight, and certainly the African Black oystercatcher, *Haematopus moquini*, forages nocturnally on the rocky shore (Hockey & Underhill 1984), but feeding in this way may be risky with regards to bill damage. European oystercatchers (*Haematopus ostralegus*) may use a secondary foraging site, possibly fields, where nocturnal foraging is possible, in order to meet their energy requirements (Heppleston 1971a).

The level of disturbance the oystercatchers encounter at a site will also affect their behaviour. In places where human disturbance is frequent, vigilance is likely to be high, but possibly less high than expected due to habituation (Burger & Gochfeld 1991). This is an important adaptation, so that birds, already pressured with regards to time-budgets, do not suffer a severe reduction in foraging time, and thus habitat loss, as a result of the increasing human disturbance in coastal areas.

3.1.4. Oystercatcher Foraging on the Rocky Shore

Over the last 30 years much work has been conducted on the foraging behaviour of wading birds. Many of these studies have focused on the behaviour of populations of the European oystercatcher foraging in estuarine environments, predominantly because in Europe estuaries support the majority of the oystercatcher population (see Goss-Custard 1996 for review). Less is known, therefore, about the foraging behaviour of the European oystercatcher in alternative habitats, such as the rocky shore (see Feare 1971, Coleman *et al.* 1999 for exception). However, with a rise in the oystercatcher population in Britain coupled with prominent human commercial activities such as cockle harvesting, increased pressure is being exerted upon estuarine resources (Norris *et al.* 1998, Goss-Custard *et al.* 2004). Thus, for oystercatchers, it may be that alternative foraging sites become of increased importance in future years.

3.1.5. Aims of Study

This is a baseline study on shorebirds that inhabit the rocky shore, the number and the species of birds that frequent it, and the behaviour of the oystercatchers that forage there. I also aimed to observe the effects of oystercatcher age, the weather, season, temperature, wind speed, and distance to and species of nearest neighbour, on components of oystercatcher behaviour. The general hypotheses were that oystercatchers would spend a greater proportion of their observed time on the shore actually foraging (searching for and handling prey items) a) as temperatures fell during the winter in response to increased energy expenditure, b) in cloudy weather, c) when at a greater distance from their nearest neighbour due to reduced interference, d) in lower wind speeds when foraging is expected to be easier, and e) when the oystercatchers were of a younger age due to their inexperience, and thus their expected inefficiency, of feeding. I also investigated whether oystercatchers respond immediately to changes in environmental factors, or whether their response is delayed. For example, oystercatchers may increase their foraging time, if the on the previous day temperature was reduced. Increased energy requirements may be compensated for the day after the drop in temperature, if they had failed to meet their energy requirements at the time.

3.2. Methods

3.2.1. Study Site

Experiments were conducted on the 25, 924m^2 area of rocky shore, exposed at low tide, between Daymar Bay, Trebetherick and Polzeath, along the north coast of Cornwall, UK (50° 33' N, 04° 55' W). Observations were made between autumn and spring (September 2002 – March 2003) when birds were assumed to be most energetically stressed and abundant at the study site and when the occurrence of uncontrolled human disturbance was minimal.

3.2.2. General Methodology

The study was conducted on the two days before and after each spring tide, so that maximum shore was exposed and thus the potential maximal foraging area was available to the feeding birds. Oystercatchers on rocky shores are visual foragers; the use of midday low tides ensured that only daylight hours were used, and so the foraging behaviour of the observed birds was less likely to be modified by changes in their ability to detect prey. Midday low tides also ensured that sufficient daylight hours were available for the sample days to be completed and that there was consistency across seasons. Observations began 3 hours before low tide and finished 3 hours after low tide. Previous observations had shown that it was difficult to observe exactly what the birds were doing for the two hours over low tide. This was due to the fact that the distance between the focal bird and the observer was at its greatest as the birds followed the tide out, visibility was often reduced due to the weather, and because there was greater structural complexity of the shore at the lower levels, and so no data were collected during this period.

The majority of oystercatchers studied were non-breeding sub-adults. Potential oystercatcher prey items present on the rocky shore were limpets (*Patella* spp.), mussels

(*Mytilus edulis* L.), whelks (*Nucella lapillus* L.), winkles (*Littorina* spp.) and topshells (*Gibbula* spp., *Osilinus lineatus* da Costa.) (Hulscher 1996).

Observations of individual oystercatchers were made from four cliff-top positions, on the coastal path, using a 20-60× telescope. This allowed detailed observations of oystercatcher foraging behaviour and a clear view of the entire study area, whilst limiting the possibility of the observer's presence affecting the birds. The observer changed position only when either all the birds in the area had been sampled or all the birds in the observed patches had left the local area.

Before an observation, a description of the focal bird, its position (bearing and distance from observer) using a magnetic compass and range finding binoculars (Leica, Portugal), and the time at which the observation began, was recorded. Each observation used a different focal bird. To minimise pseudo-replication, an attempt was made to identify individuals using indicators such as the colour of the bill, legs, eye and plumage, and the size of the oystercatcher's 'dog collar'. The 'dog collar' is the band of white feathers visible just below the oystercatcher's head. It was difficult, however, to identify individuals that had recently flown into the area and so these birds were considered to be independent (Coleman *et al.* 1999). Descriptions were further used to estimate the age of the focal birds. Younger birds tended to have legs and a bill which were very pale coloured, a brownish eye, and dark brown feathers with limited amount of white apparent. In comparison, adult birds had legs, a bill and an eye that were bright red, and feathers that were black and white. Thus the age of a focal oystercatcher was estimated dependant upon intensity of colour of its bill, eye, legs and plumage.

3.2.3. Bird Behaviour

A focal bird was observed for a 300s period and components of its foraging behaviour verbally recorded in real time using a cassette tape recorder. The behaviours recorded included the number of steps taken, the number of pecks and successful feeds, and the number of interactions with other individuals, and the proportion of the observed time that each bird spent with their head down searching or feeding, walking, preening, involved in an interaction, and being alert. A peck was defined as one single strike of a prey item, a step defined as one oystercatcher stride. A successful feeding attempt was easily identified as the birds raised their heads and moved their necks in a swallowing motion. An interaction included fighting, kleptoparasitism, chasing/ retreating, regardless of the species involved or whether the focal oystercatcher initiated or was subjected to the interaction. Foraging refers to the bird being in a head down orientation (length of bill vertical to the shore or at an angle from the shore of <50 deg) when either stationary or moving, thus including time spent searching for, carrying and handling (defined as when an individual was continuously either handling or pecking at a prey item at a rapid rate, regardless of success), prey items. Walking refers to the bird being in a head up orientation (length of bill horizontal to the shore or at an angle from the shore of >50 deg) when moving, whilst alert refers to the same elevation of the head but whilst the bird was stationary. Finally preening included the tending of feathers and bathing.

3.2.4. Tidal Effects on Foraging

Six oystercatchers were observed per day, three before (ebb) and three after low tide (flood). The birds observed were divided into six groups within the twelve sample days. '*Group 1*' were those observed at the beginning of the observation period when the tide was high (Low Water –3hrs to –2hrs), '*Group 2*' were observed as the tide ebbed (approximately LW –2hrs), and '*Group 3*' were those observed at almost low tide (LW –

1hr to –2hrs). '*Group 4*' were observed at the beginning of the second half of the study day, as the tide began to flood (LW +1hr to +2hrs), '*Group 5*' were observed mid-flood (approximately LW +2hrs) and '*Group 6*' as the shore had almost completely covered the rocks (LW +2hrs to +3hrs). It is important to note that although high tide does not occur until LW +6hrs, the rocks upon which oystercatcher food were present were completely submerged approximately 3.5hrs after low tide. The top shore consisted of sand, upon which oystercatchers were never observed feeding, and rock that was devoid of food and remained uncovered even at high tide.

3.2.5. Environmental Factors

Environmental parameters were recorded at the beginning and the end of each two hour sampling period. An anemometer measured wind speed (ms^{-1}) and temperature (°C, approximating wind chill), whilst the weather was scored as sunny, cloudy or rainy. Information on the approximate temperature and wind speed at the study site, on the day prior to the sample day was gathered from meteorological office records for RAF St Mawgan, Newquay (approximately 20km north of study site). Further information was gathered on the number and species of all birds present in the entire study area at the beginning and end of each 300s sample period. In addition, prior to each sample, the species of and distance to the nearest neighbour of the focal bird was recorded.

3.2.6. Analysis

The bird behaviour recorded during fieldwork was transcribed into a computer using the 'Observer' 4.0 behavioural software (Noldus Technology, Waginengen, 1998). The percentage of time birds spent foraging, being alert, preening, being involved in interactions and walking; peck, success and step rates and the number of interactions and preening bouts, were then calculated from the data. The occurrence of an interaction/ preening bout was so infrequent that further analysis on these data was considered meaningless. All of the percentage data of the remaining behavioural parameters were arc-sine transformed prior to analysis. Regression analysis was used to show the relationship between the behavioural data and a) the temperature and wind speed at the time of each observation, b) the average temperature and wind speed for the whole study day, and c) the average temperature and wind speed for the day prior to the study day. General Linear Models (GLMs), for unbalanced data sets, were used to analyse the effects of a) the weather at the time of each observation, b) the average weather on the day prior to the study day, c) the season, and d) the age of the focal bird, on the birds' behaviour. In addition, ANCOVA procedures were used to analyse the effects of the species of and the distance to the focal birds' nearest neighbour on the focal birds' behaviour; whilst balanced, one-way ANOVAs were used to analyse the effects of tidal state on oystercatcher behaviour. Levene's test for equality of error variances was completed prior to analyses (Sokal & Rohlf 1995). Step, peck and success rates were log-transformed (LN + 1) where appropriate to stabilise variances. Any failure to pass Levene's test after transformation could not be corrected and so the untransformed data were used. Failure to pass Levene's test was irrelevant if no significant relationship was found between the environmental and behavioural parameters. Where a significant relationship was found, however, heterogeneity of variance may have increased the chance of a type II error occurrence (Underwood, 1997) and so the results must be interpreted with caution. Most of the results were analysed using procedures in SPSS (SPSS Inc, Chicago,1989-2000), except for the analyses on tidal state that were completed using Cochran's test for heterogeneity of variance and ANOVA procedures in GMAV (EICC, University of Sydney). The results were Bonferroni corrected where appropriate (Sokal & Rohlf 1995).

3.3. Results

3.3.1. Bird Density and Foraging Behaviour on the Rocky Shore

Oystercatchers, gulls (*Larus argentatus, Larus marinus*), turnstones (*Arenaria interpres*), curlews (*Numenius arquata*), little egrets (*Egretta garzetta*), crows (*Corvus corone corone*), knot (*Calidrus canutus*), grey plovers (*Pluvialis squatarola*), cormorants (*Phalacrocorax carbo*) and shag (*Phalacrocorax aristotelis*) all occupied the rocky shore at various times throughout the study (Figure 6). Densities of approximately 10.4 total birds ha^{-1} (SE ± 0.52) and 4.0 oystercatchers ha^{-1} (SE ± 0.23) were calculated using the area of the study site and the number of birds observed per sweep over all seasons (Figure 6). The highest mean density of oystercatchers apparent on the rocky shore occurred in autumn (4.7 birds ha^{-1}, SE ± 0.46), whilst oystercatcher density was similar in winter and spring, at 3.3 oystercatchers ha^{-1} (SE ± 0.23) and 3.6 oystercatchers ha^{-1} (SE ± 0.23), respectively. The number of gulls observed on the rocky shore also varied with season with an increasing number occupying the shore through autumn, winter and spring (Figure 6).

Many of the birds observed on the rocky shore appeared not to use the site as a primary foraging ground; shags, cormorants and crows predominantly rested at the site, whilst curlews, egrets, plovers and knots appeared to pick at prey items between bouts of preening and roosting. Gulls and turnstones randomly pecked at potential prey items, scavenged the flesh from the shells of prey items previously fed upon by oystercatchers, and sometimes stole oystercatcher prey whilst the oystercatcher was in the process of handling it, although this was infrequent (see infrequent behaviour section for interaction rate).

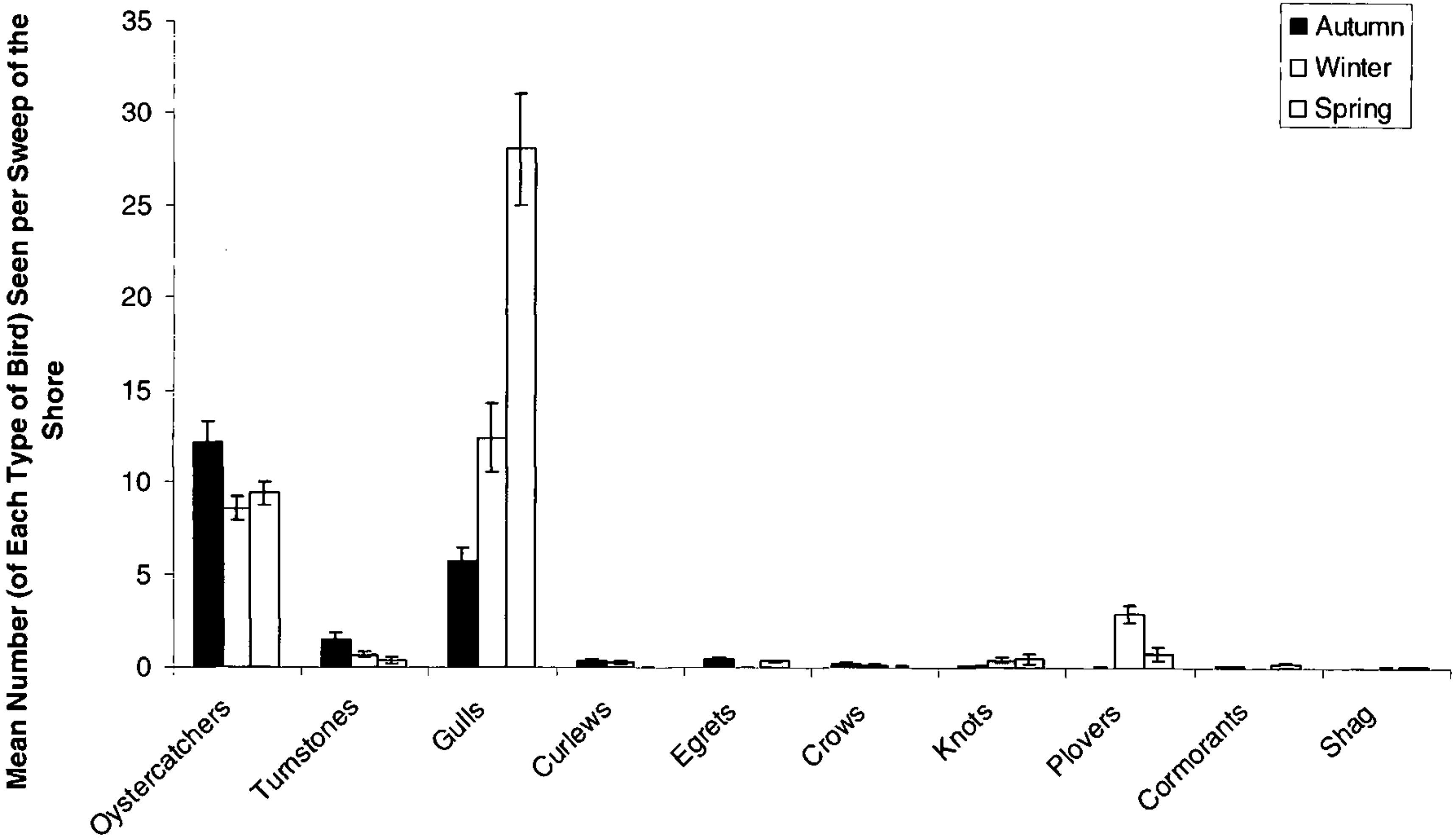


Fig. 6. The mean number (±SE) of oystercatchers, turnstones, gulls, curlews, egrets, crows, knots, plovers, cormorants, and shags observed on the rocky shore per sweep. Counts made during sweeps of the shore taken at approximately 10 minute intervals, in autumn (October-November), winter (December-January) and spring (February-March).

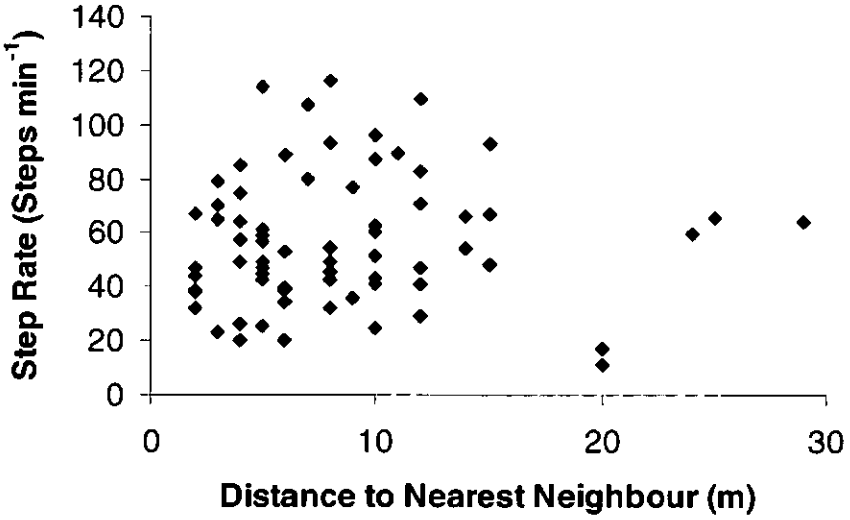
3.3.2. Infrequent Behaviour Demonstrated by Oystercatchers on the Rocky Shore

Oystercatchers spent none of the 300s observation period roosting. Oystercatchers also only interacted with other individuals on average 0.125 times (SE ± 0.052) per 300s observation period, and had an average 1.333 preening bouts (SE ± 0.333). When infrequent interactions did occur they only lasted an average 5.085 seconds (SE ± 3.036), the equivalent to 1.695% (SE ± 1.012%) of the time they were observed for. Similarly, preening bouts only lasted an average 3.063 seconds (SE ± 0.81) or 1.021 % (SE ± 0.270%) of the time the oystercatchers were observed. Thus, it appears that the oystercatchers observed during this study spent the vast majority (approximately 97%) of their time on the rocky shore feeding.

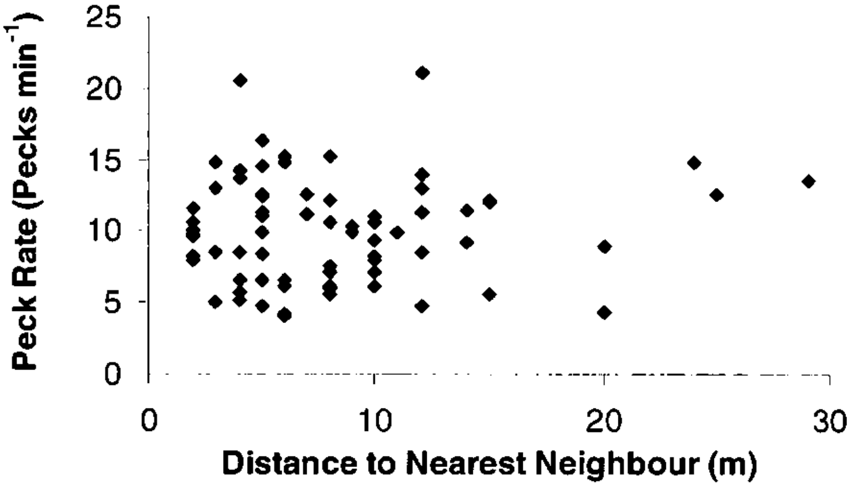
3.3.3. Effect of Neighbours on Oystercatcher Foraging Behaviour

Oystercatcher step rate and peck rate, did not change significantly with the distance to, nor species of, the focal bird's nearest neighbour (Figures 7 a & b, Table 4), neither did the percentage of time focal oystercatchers spent walking, foraging, and being alert (Figures 7 c-e, Table 4). Success rate was also not found to vary with the distance between the focal bird and its nearest neighbour (Figure 8 a) but did vary dependant on the species of the nearest neighbour (Figure 8 b, Table 4). A significantly lower success rate was associated with having a gull, turnstone or oystercatcher as a nearest neighbour compared to the 'other' species (Figure 8 b). The success rate data, however, did not pass Levene's test for equality of error variances, even after transformation ($F_{(3,68)} = 5.566$, $P<0.01$). As the residual is large, however, the effects of heterogeneity of variance are very small and can be discounted (a large residual is defined as that being >29 according to Underwood 1997, or >10 according to Sokal & Rohlf 1995).

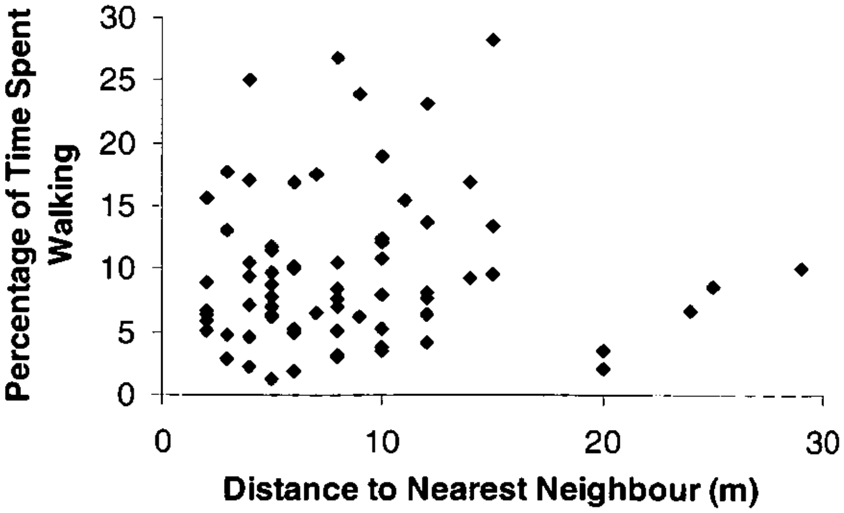
(a)


Step Rate (Steps min^{-1})
140
120
100
80
60
40
20
0
0
10
20
30
Distance to Nearest Neighbour (m)

(b)


Peck Rate (Pecks min^{-1})
25
20
15
10
5
0
0
10
20
30
Distance to Nearest Neighbour (m)

(c)


Percentage of Time Spent Walking
30
25
20
15
10
5
0
0
10
20
30
Distance to Nearest Neighbour (m)

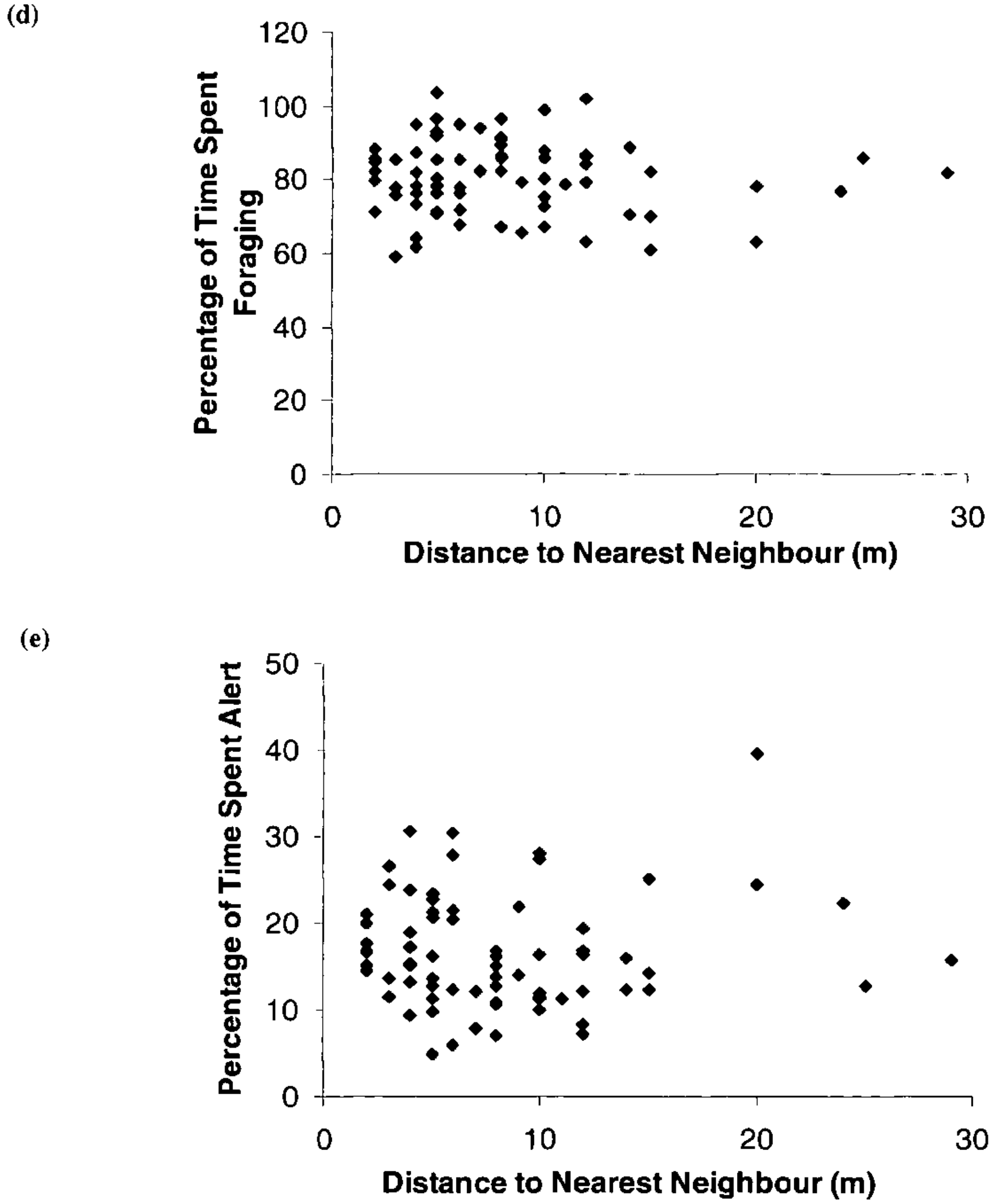
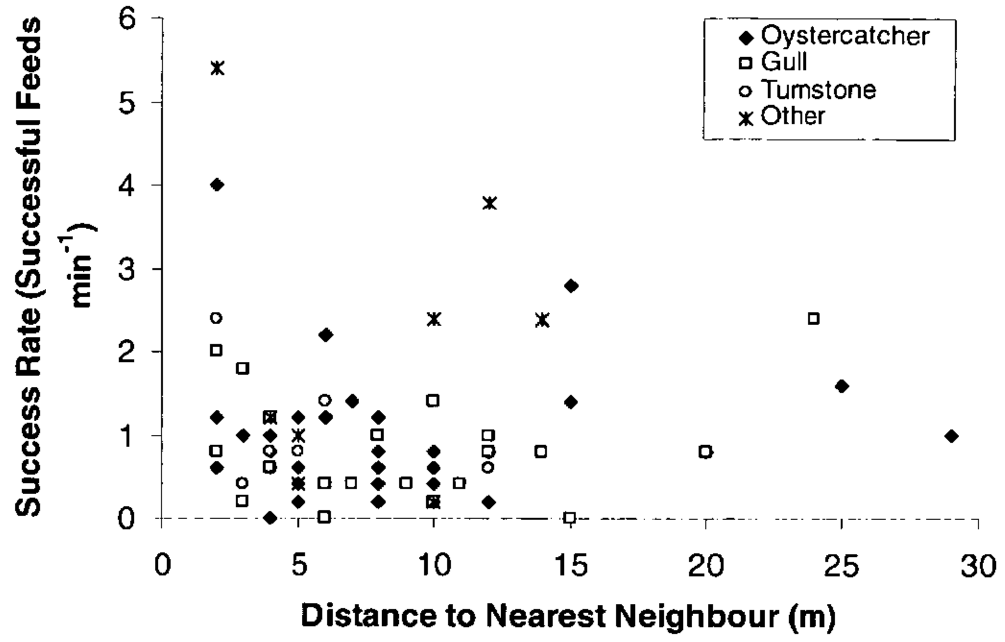


Fig. 7. The relationship between the distance to a focal bird's nearest neighbour (m), and the focal bird's a) step rate (steps min^{-1}), b) peck rate (pecks min^{-1}), c) percentage of time spent walking, d) percentage of time spent foraging and e) percentage of time spent alert. These components of oystercatcher behaviour on the rocky shore were unaffected by both the distance separating a focal bird and it's nearest neighbour and the species of the nearest neighbour. A total of 72 birds were observed, each for a 300 second period.

(a)



(b)

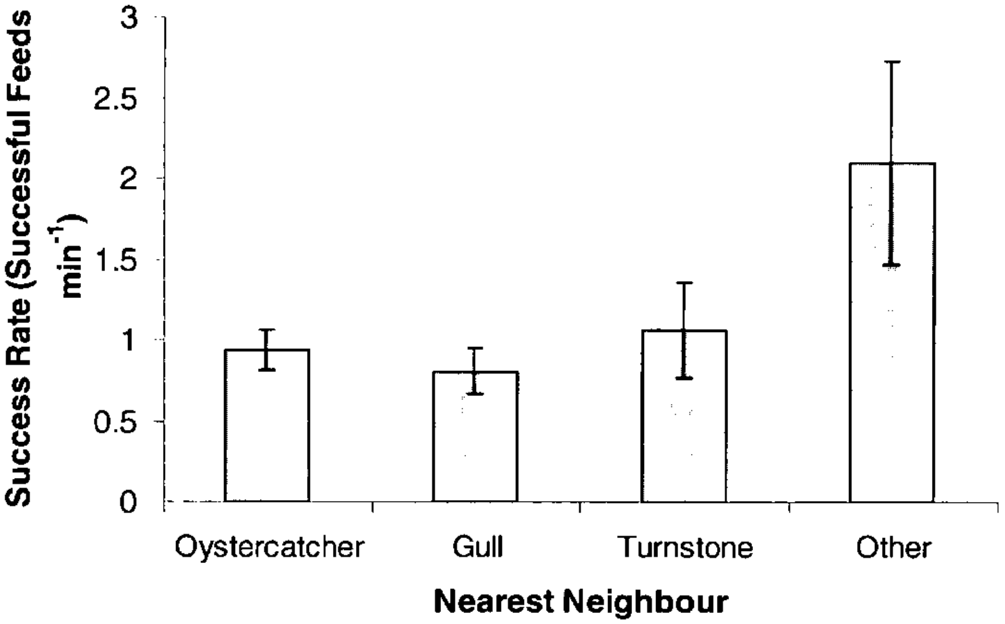


Fig. 8. a) The relationship between the distance to (m), and species of, a focal bird's nearest neighbour, and the focal birds success rate (successful feeds min^{-1}). The distance separating a focal bird and its nearest neighbour had no significant effect, but the species of the nearest neighbour did. For clarity see b), the mean success rate of a focal oystercatcher when it's nearest neighbour is a gull, turnstone, another oystercatcher or another type of species. Species other than oystercatchers, gulls and turnstones were pooled together to form 'other' due to the low number of observations citing them as the nearest neighbour. A total of 72 birds were observed for a 300 second period, 37 nearest neighbours were oystercatchers, 21 were gulls, 6 were turnstones and 8 were 'other' species. Untransformed results are shown (±SE).

Behaviour	Species of Nearest Neighbour	Trendline		ANOVA		Heterogeneity of Slopes		Heterogeneity of Intercepts	
		Equation	R^2	df	*F*	df	*F*	df	*F*
Step Rate	Overall	No Valid Equation	0.003	1,70	0.242 NS	3,64	1.493 NS	3,67	0.724 NS
Peck Rate	Overall	No Valid Equation	0.008	1,70	0.590 NS	3,64	0.995 NS	3,67	1.816 NS
Success Rate	Oystercatcher	No Valid Equation	0.003	1,35	0.094 NS	3,64	0.267 NS	3,64	4.308**
	Gull	No Valid Equation	0.023	1,19	0.447 NS				
	Turnstone	No Valid Equation	0.167	1,4	0.799 NS				
	Other	No Valid Equation	0.002	1,6	0.012 NS				
% of Time Walking	Overall	No Valid Equation	0.002	1,70	0.119 NS	3,64	0.786 NS	3,67	2.112 NS
% of Time Foraging	Overall	No Valid Equation	0.005	1,70	0.371 NS	3,64	0.809 NS	3,67	2.418 NS
% of Time Alert	Overall	No Valid Equation	0.002	1,70	0.135 NS	3,64	1.014 NS	3,67	0.847 NS

Table 4. Analyses of covariance on the effects of the species of, and distance to, a focal bird's nearest neighbour, on components of the focal bird's behaviour (NS – Non-significant $P>0.05$, $^{*}P<0.05$, $^{**}P<0.01$ and $^{***}P<0.001$). The species of nearest neighbour were oystercatchers, gulls, turnstones and 'other'. Data were tested using Levene's homogeneity of variance test. Proportion data were arc-sine transformed prior to analysis; rates were log-transformed (LN +1) where appropriate. In all cases of homogeneity of variance after transformation, raw data was used following recommendations by Underwood (1997) and Sokal & Rohlf (1995). Data was tested for homogeneity of slopes and intercepts. The distance separating the focal birds from their nearest neighbours was analysed as a covariate during analyses. A total of 72 birds were observed. Overall regression lines are given where homogeneity of slopes tests were passed.

3.3.4. Effect of Wind Speed on Oystercatcher Behaviour

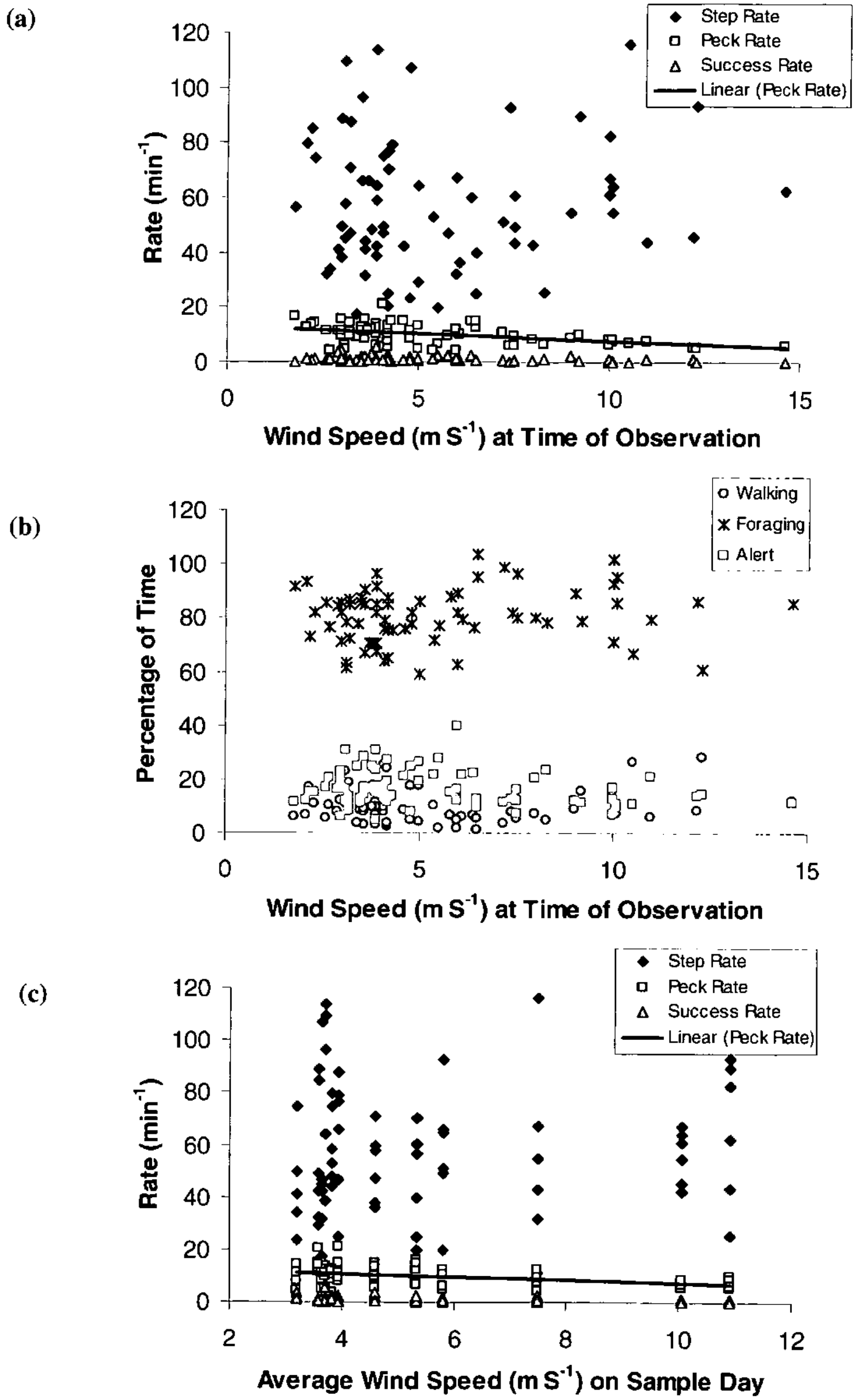
Oystercatcher behaviour on the rocky shore was not generally affected by wind speed (Table 5). Oystercatcher step rate and success rate, and the percentage of time oystercatchers spent walking, foraging and being alert were unaffected by the wind speed at the time of the observation and the average wind speed for the whole study day (Figures 9 a-d, Table 5). Only oystercatcher peck rate varied with the wind speed, both at the time of the observation and with the average wind speed for the day (Figure 9 a & c, Table 5). As wind speed increased oystercatcher peck rate very slightly decreased (Figure 9 a & c). However, only a small percentage of the peck rate data are explained by wind speed on the observation day (Table 5). The average wind speed on the day prior to the observation day had no effect on any aspect of the oystercatchers' behaviour on the rocky shore (Figure 9 e & f, Table 5).

3.3.5. Effect of Temperature on Oystercatcher Behaviour

The temperature at the time of the observation, the average temperature on the observation day and the average temperature on the day prior to the observation day appeared to have no significant effect upon oystercatcher step rate or peck rate, or the percentage of time oystercatchers spent walking, foraging or being alert (Table 6). Success rate, however, varied significantly with all three factors (Table 6). Oystercatchers became very slightly less successful as temperatures increased (Figure 10 a, c & e), however only a small percentage of the success rate data are explained by temperature (Table 6).

	Behaviour	Trendline Equation	R^2	ANOVA df	*F*	Significance after Bonferroni Correction
Wind Speed at Time of Observation						
	Step Rate	No Valid Equation	0.008	1,70	0.537 NS	
	Peck Rate	y = -0.5055x +12.826	0.155	1,70	12.815***	**
	Success Rate	No Valid Equation	0.053	1,70	3.897 NS	
	% of Time Walking	No Valid Equation	0.004	1,70	0.315 NS	
	% of Time Foraging	No Valid Equation	0.016	1,70	1.174 NS	
	% of Time Alert	No Valid Equation	0.034	1,70	2.470 NS	
Average Wind Speed						
	Step Rate	No Valid Equation	0.004	1,70	0.290 NS	
	Peck Rate	y = -0.539x +13.014	0.139	1,70	11.263**	*
	Success Rate	No Valid Equation	0.053	1,70	3.903 NS	
	% of Time Walking	No Valid Equation	0	1,70	0.025 NS	
	% of Time Foraging	No Valid Equation	0.019	1,70	1.358 NS	
	% of Time Alert	No Valid Equation	0.024	1,70	1.705 NS	
Average Wind Speed on Previous Day						
	Step Rate	No Valid Equation	0	1,70	0.058 NS	
	Peck Rate	No Valid Equation	0.002	1,70	0.149 NS	
	Success Rate	No Valid Equation	0.049	1,70	3.581 NS	
	% of Time Walking	No Valid Equation	0.001	1,70	0.037 NS	
	% of Time Foraging	No Valid Equation	0	1,70	0.001 NS	
	% of Time Alert	No Valid Equation	0.007	1,70	0.493 NS	

Table 5. Regression analyses on the effects of wind speed (m S^{-1}) on components of the focal oystercatchers' behaviour (NS – Non-significant $P>0.05$, $*P<0.05$, $**P<0.01$ and $***P<0.001$). The effects of the wind speed at the time of the observation, the average wind speed on the study day, and the average wind speed on the day prior to the study day were all tested. Proportion data were arc-sine transformed prior to analysis; rates were log-transformed (LN +1) where appropriate. Regression line equations are shown where significant relationships were found following the Bonferroni correction (Sokal & Rohlf 1995). A total of 72 birds were observed.


(a)
Step Rate
Peck Rate
Success Rate
Linear (Peck Rate)
Rate (min^{-1})
0
20
40
60
80
100
120
0
5
10
15
Wind Speed (m S^{-1}) at Time of Observation
(b)
Walking
Foraging
Alert
Percentage of Time
0
20
40
60
80
100
120
0
5
10
15
Wind Speed (m S^{-1}) at Time of Observation
(c)
Step Rate
Peck Rate
Success Rate
Linear (Peck Rate)
Rate (min^{-1})
0
20
40
60
80
100
120
2
4
6
8
10
12
Average Wind Speed (m S^{-1}) on Sample Day

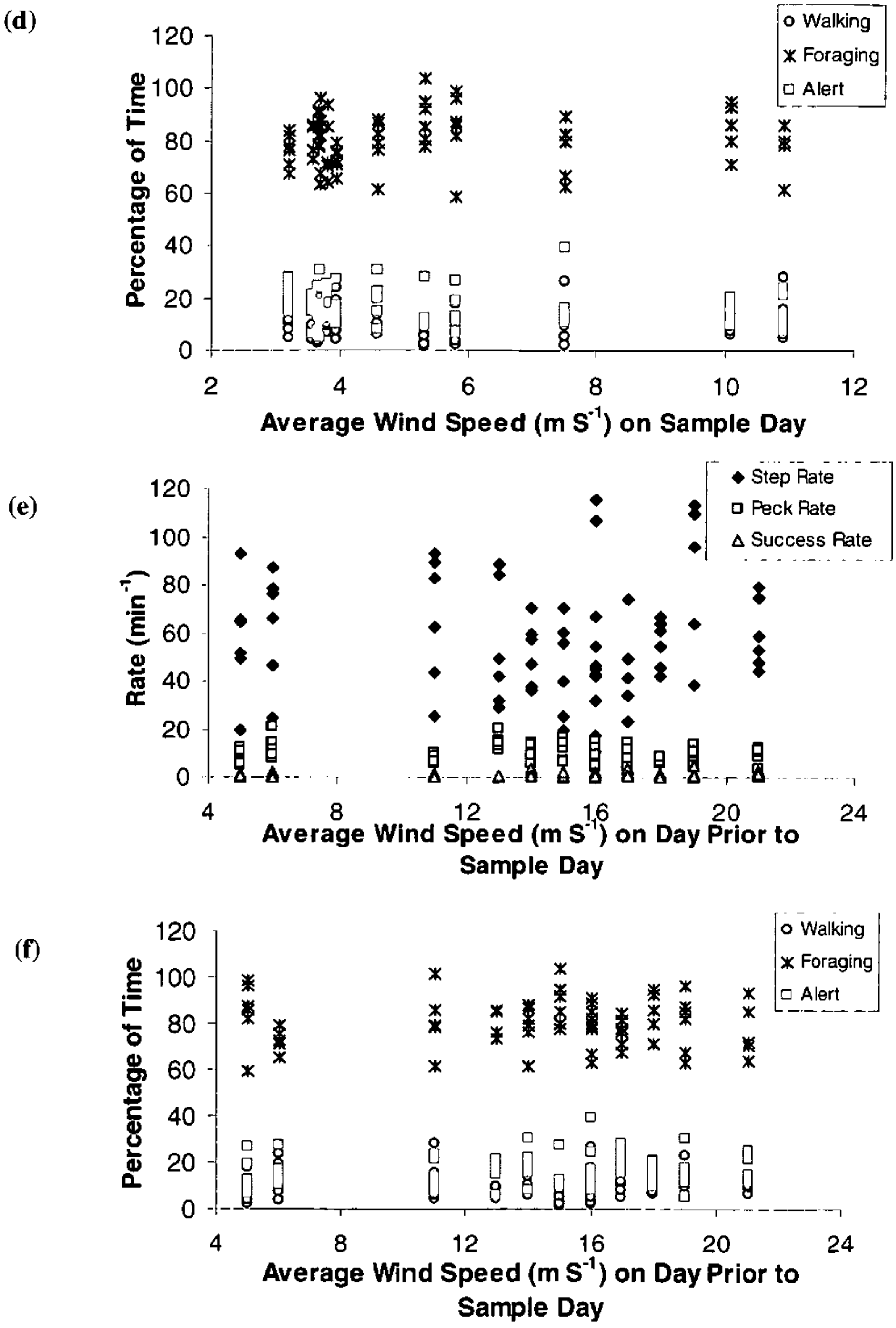
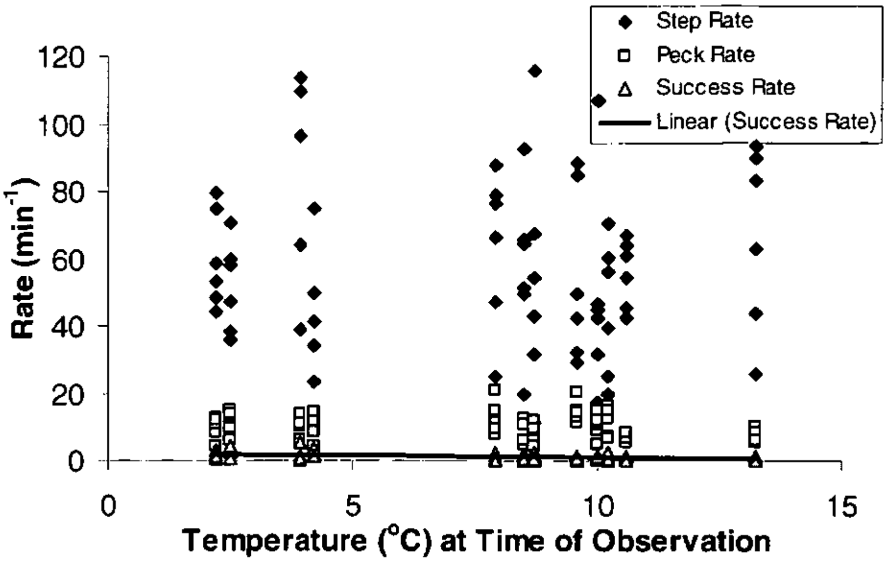


Fig. 9. The relationship between the wind speed (m s^{-1}) at the time of the observation and a) oystercatcher step rate, peck rate and success rate and b) the percentage of time oystercatchers spent walking, foraging and being alert. The relationship between the average wind speed over a study day and the oystercatchers', c) step rate, peck rate and success rate and d) percentage of time spent walking, foraging and alert. The relationship between the prior day's average wind speed and e) oystercatcher step rate, peck rate and success rate and f) the percentage of time oystercatchers spent walking, foraging and being alert. A total of 72 birds were observed for a 300 second period. Untransformed results are shown.

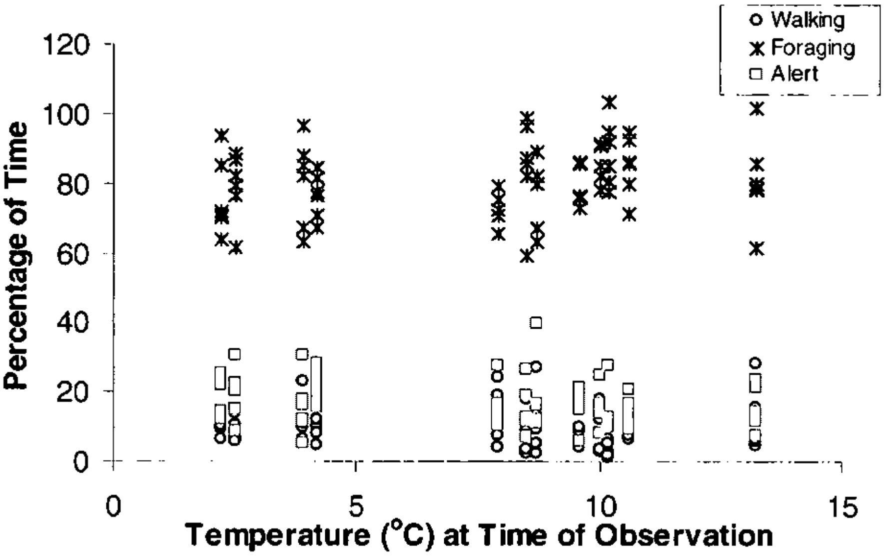
		Trendline		ANOVA		
	Behaviour	Equation	R^2	df	F	Significance after Bonferroni Correction
Temperature at Time of Observation						
	Step Rate	No Valid Equation	0.001	1,70	0.047 NS	
	Peck Rate	No Valid Equation	0.004	1,70	0.247 NS	
	Success Rate	y = -0.002x +0.032	0.183	1,70	15.683***	**
	% of Time Walking	No Valid Equation	0.007	1,70	0.464 NS	
	% of Time Foraging	No Valid Equation	0.052	1,70	3.816 NS	
	% of Time Alert	y = -0.347x +26.196	0.0058	1,70	4.304*	NS
Average Temperature						
	Step Rate	No Valid Equation	0	1,70	0.005 NS	
	Peck Rate	No Valid Equation	0	1,70	0.014 NS	
	Success Rate	y = -0.114x +2.220	0.153	1,70	12.600***	**
	% of Time Walking	No Valid Equation	0.001	1,70	0.086 NS	
	% of Time Foraging	No Valid Equation	0.019	1,70	1.345 NS	
	% of Time Alert	y = -0.351x +27.183	0.054	1,70	3.998*	NS
Average Temperature on Previous Day						
	Step Rate	No Valid Equation	0.003	1,70	0.186 NS	
	Peck Rate	No Valid Equation	0.001	1,70	0.073 NS	
	Success Rate	y = -0.119x +2.262	0.149	1,70	12.228***	**
	% of Time Walking	No Valid Equation	0	1,70	0 NS	
	% of Time Foraging	No Valid Equation	0.012	1,70	0.858 NS	
	% of Time Alert	No Valid Equation	0.029	1,70	2.113 NS	

Table 6. Regression analyses on the effects of temperature (°C) on components of the focal oystercatchers' behaviour (NS – Non-significant $P>0.05$, *$P<0.05$, **$P<0.01$ and ***$P<0.001$). The effects of the temperature at the time of the observation, the average temperature on the study day, and the average temperature on the day prior to the study day were all tested. Proportion data were arc-sine transformed prior to analysis; rates were log-transformed (LN +1) where appropriate. Regression line equations are shown where significant relationships were found following the Bonferroni correction (Sokal & Rohlf 1995). A total of 72 birds were observed.

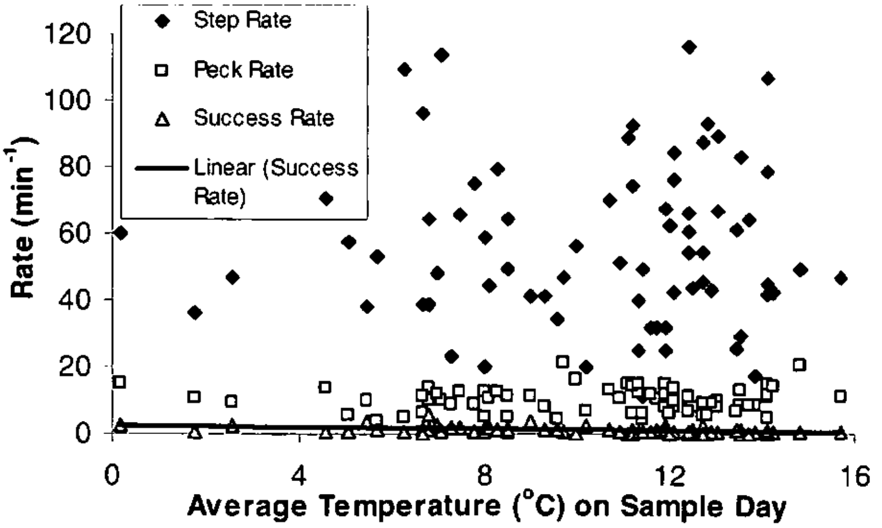
(a)


Step Rate
Peck Rate
Success Rate
Linear (Success Rate)
120
100
80
60
40
20
0
Rate (min^{-1})
0
5
10
15
Temperature (°C) at Time of Observation

(b)


Walking
Foraging
Alert
120
100
80
60
40
20
0
Percentage of Time
0
5
10
15
Temperature (°C) at Time of Observation

(c)


Step Rate
Peck Rate
Success Rate
Linear (Success Rate)
120
100
80
60
40
20
0
Rate (min^{-1})
0
4
8
12
16
Average Temperature (°C) on Sample Day

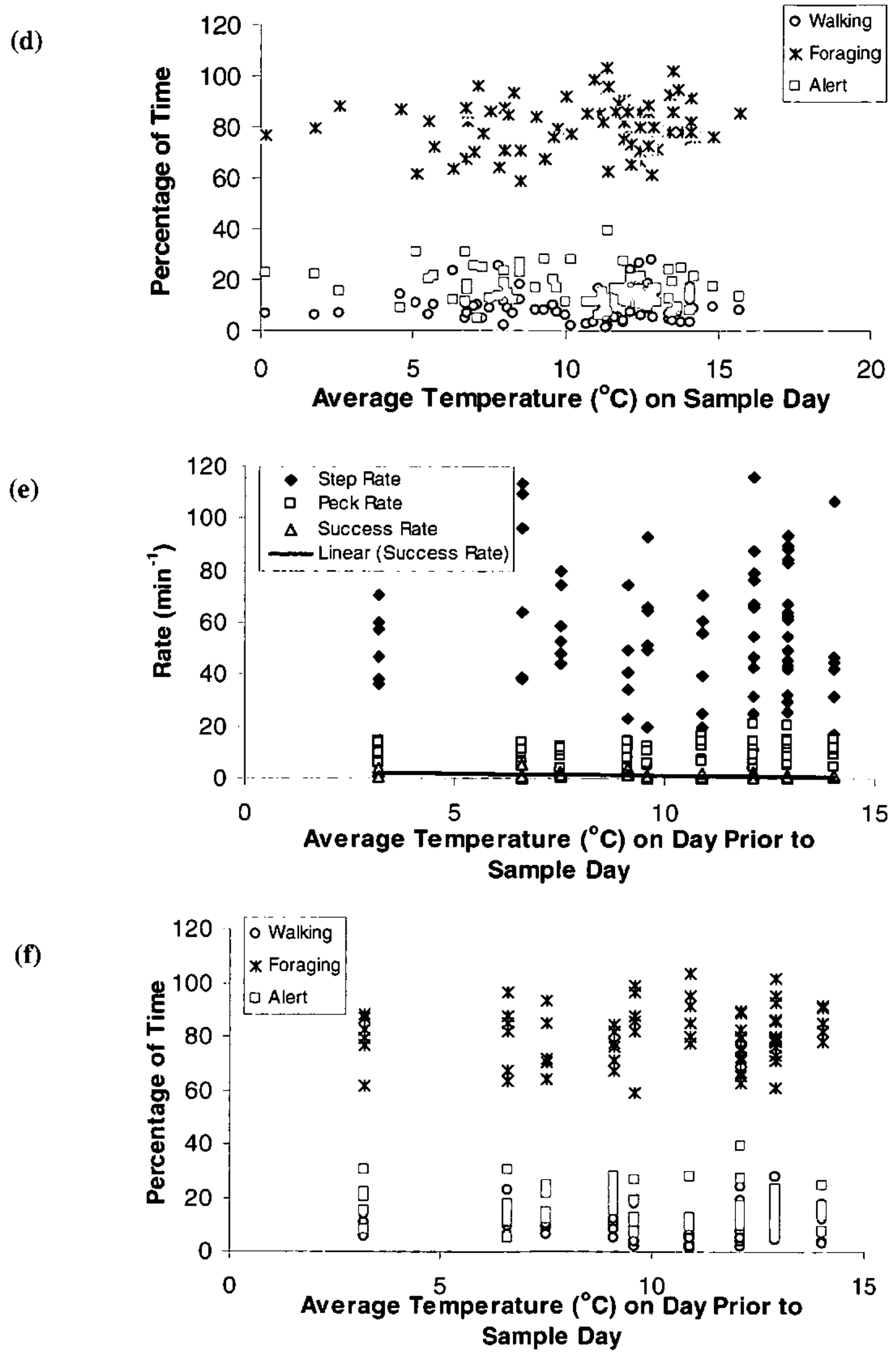


Fig. 10. The relationship between the temperature (°C) at the time of the observation and a) oystercatcher step rate, peck rate and success rate and b) the percentage of time oystercatchers spent walking, foraging and being alert. The relationship between the average temperature over a study day and the oystercatchers', c) step rate, peck rate and success rate and d) percentage of time spent walking, foraging and alert. The relationship between the prior day's average temperature and e) oystercatcher step rate, peck rate and success rate and f) the percentage of time oystercatchers spent walking, foraging and being alert. A total of 72 birds were observed for a 300 second period. Untransformed results are shown.

3.3.6. Effect of Season on Oystercatcher Behaviour

Oystercatchers varied significantly in their success rate (GLM ANOVA $F_{(2,69)} = 7.899$, $P<0.01$) with season (Figure 11 a). Oystercatcher success rate was significantly higher in winter (Mean = 1.61 successes min^{-1}, SE ± 0.263), compared to autumn (Mean = 0.70 successes min^{-1}, SE ± 0.089) and spring (Mean = 0.84 successes min^{-1}, SE ± 0.159) (Figure 11 a). Although the success rate data did not pass Levene's test for equality of error variances after transformation ($F_{(2,69)} = 3.389$, $P<0.05$), the large residual limits the effects of heterogeneity of variance and so it can to some extent be ignored (Sokal & Rohlf 1995, Underwood 1997). Oystercatcher step rate (GLM ANOVA $F_{(2,69)} = 0.147$, NS), peck rate (GLM ANOVA $F_{(2,69)} = 4.247$, NS), and the percentage of time oystercatchers spent walking (GLM ANOVA $F_{(2,69)} = 1.878$, NS), foraging (GLM ANOVA $F_{(2,69)} = 4.817$, NS) and being alert (GLM ANOVA $F_{(2,69)} = 2.497$, NS) did not vary significantly with season (Figure 11 a & b).

3.3.7. Effects of Weather on Oystercatcher Foraging Behaviour

Oystercatcher behaviour did not vary with the weather at the time of the observation (Figure 12 a & b, Table 7). Step rate, peck rate, success rate, the percentage of time oystercatchers spent walking, foraging and being alert also did not change significantly with the weather on day prior to the observation day (Figure 12 c & d, Table 7).

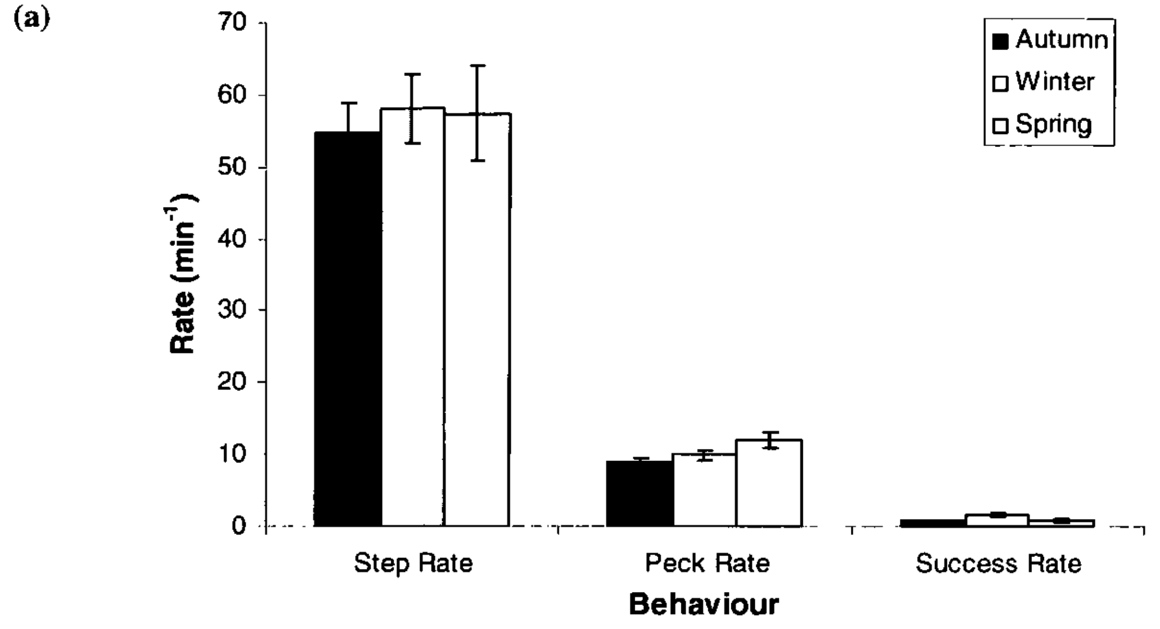


Fig. 11. The effect of season on the foraging behaviour of oystercatchers. The mean oystercatcher a) step rate, peck rate and success rate, and b) percentage of time spent walking, foraging and alert are shown for autumn, winter and spring feeding. A total of 72 birds were observed for a 300 second period, 30 birds were observed in the autumn, 24 in the winter and 18 in the spring. Untransformed results are shown (±SE).

	Weather at Time of Observation				**Average Weather on Previous Day**			
Behaviour	df	Adj MS	*F*	Significance after Bonferroni Correction	df	Adj MS	*F*	Significance after Bonferroni Correction
Step Rate	2,69	0.006	0.035 NS		2,69	0.096	0.587 NS	
Peck Rate	2,69	0.16	4.783*	NS	2,69	0.006	1.674 NS	
Success Rate	2,69	0	1.197 NS		2,69	0	0.749 NS	
% of Time Walking	2,69	0.912	0.028 NS		2,69	49.93	1.611 NS	
% of Time Foraging	2,69	3.636	0.165 NS		2,69	63.798	3.144*	NS
% of Time Alert	2,69	3.566	0.142 NS		2,69	29.471	1.211 NS	

Table 7. Unbalanced GLM analyses on the effects of weather on the behaviour of oystercatchers (NS – Non-significant $P>0.05$, $*P<0.05$, $**P<0.01$ and $***P<0.001$). Weather types were sunny, cloudy and rainy. Data was tested using Levene's homogeneity of variance test. Proportion data were arc-sine transformed prior to analysis; rates were log-transformed (LN +1) where appropriate. In all cases of homogeneity of variance after transformation, raw data was used following recommendations by Underwood (1997) and Sokal & Rohlf (1995). Results were corrected for using the Bonferroni method (Sokal & Rohlf 1995). A total of 72 birds were observed.

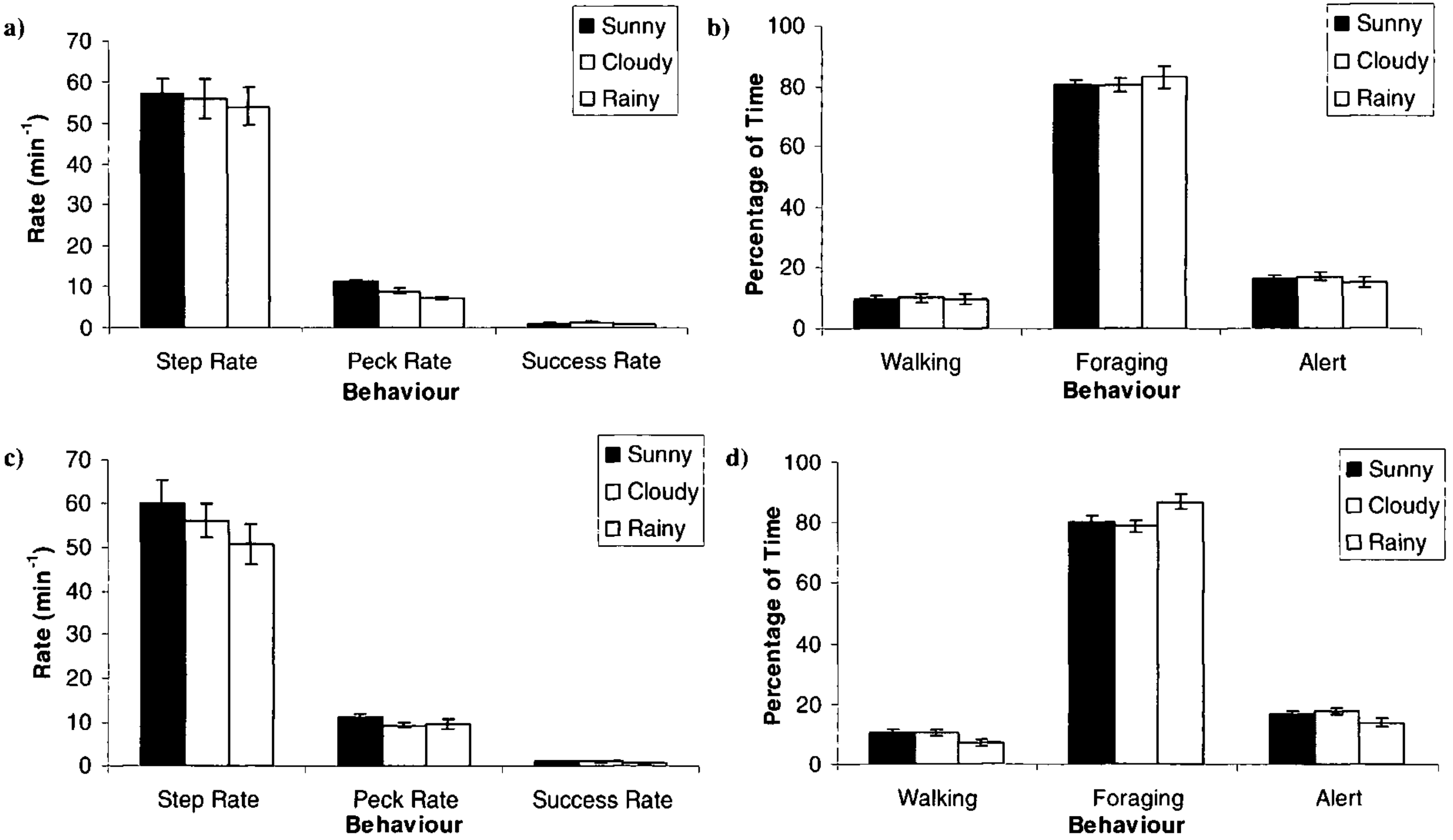
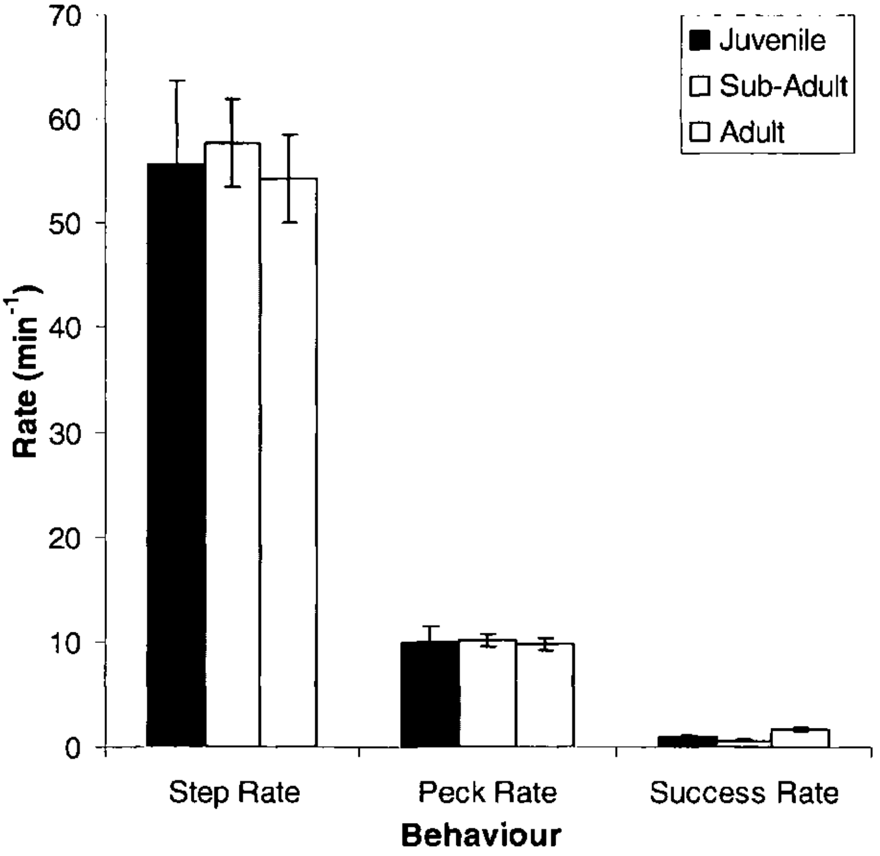


Fig. 12. i) The effect of the weather at the time of the observation on the foraging behaviour of oystercatchers. The mean oystercatcher a) step rate, peck rate and success rate, and b) percentage of time spent walking, foraging and alert are shown for sunny, cloudy and rainy weather feeding. A total of 72 birds were observed for a 300 second period, 39 birds were observed feeding in sunny weather, 28 feeding in cloudy weather and 5 feeding in rainy weather. Untransformed results are shown (±SE). ii) The effect of the prior day's average weather on the foraging behaviour of oystercatchers. The mean oystercatcher c) step rate, peck rate and success rate, and d) percentage of time spent walking, foraging and alert are shown for oystercatcher foraging when the prior day's weather was sunny, cloudy and rainy. A total of 72 birds were observed for a 300 second period, 24 birds were observed feeding when the previous day it had been predominantly sunny, 36 when previously it had been cloudy and 12 when it had been rainy. Untransformed results are shown (±SE).

3.3.8. Effects of Oystercatcher Age

Step rate (GLM ANOVA $F_{(2,69)} = 0.156$, NS), peck rate (GLM ANOVA $F_{(2,69)} = 0.060$, NS), and the percentage of time oystercatchers spent walking (GLM ANOVA $F_{(2,69)} = 0.505$, NS), foraging (GLM ANOVA $F_{(2,69)} = 0.703$, NS) and being alert (GLM ANOVA $F_{(2,69)} = 1.148$, NS) did not vary significantly with the age of the oystercatcher (Figure 13 a & b). Success rate, however, did vary with an oystercatcher's age (GLM ANOVA $F_{(2,69)} = 11.972$, $P<0.001$); adults were significantly more successful at foraging (Mean = 1.69, SE ± 0.249, successful feeds min^{-1}), than sub-adult or juvenile individuals which had a mean 0.66 (SE ± 0.074) and 0.93 (SE ± 0.271) successes min^{-1}, respectively (Figure 13 a). Again, these results did not pass Levene's test for equality of error variances after transformation ($F_{(2,69)} = 10.107$, $P<0.001$), but as the sample size is large the effects of homogeneity of variance is minimal (Sokal & Rohlf 1995, Underwood 1997).

(a)



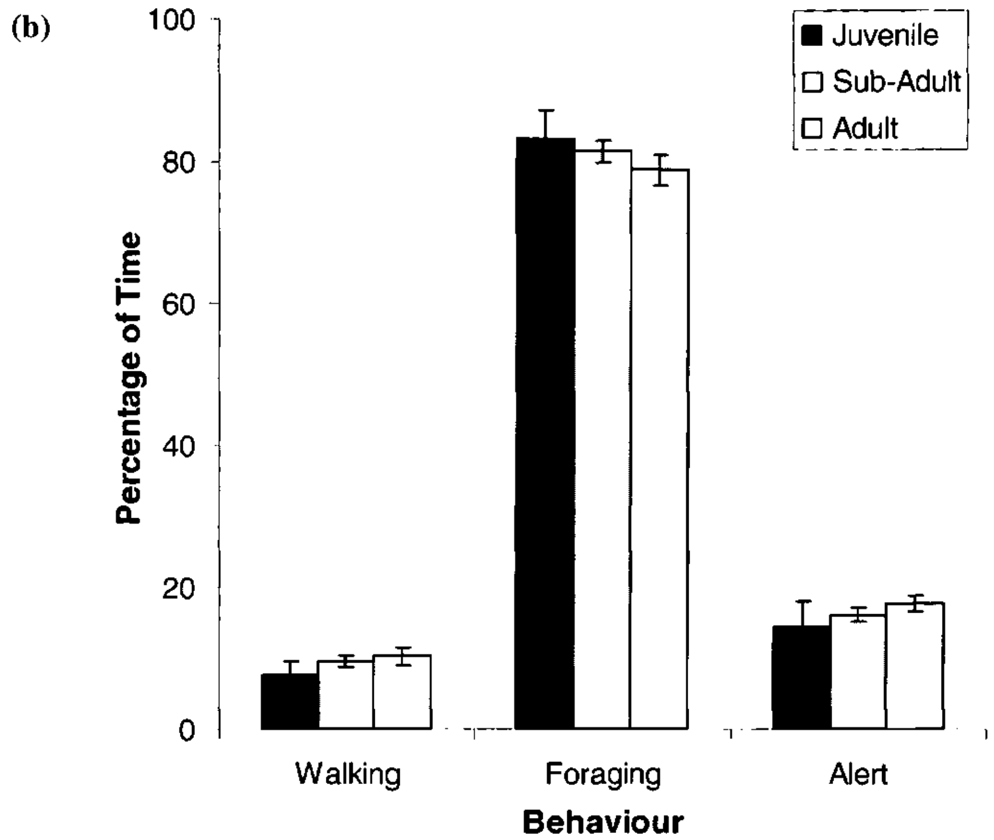
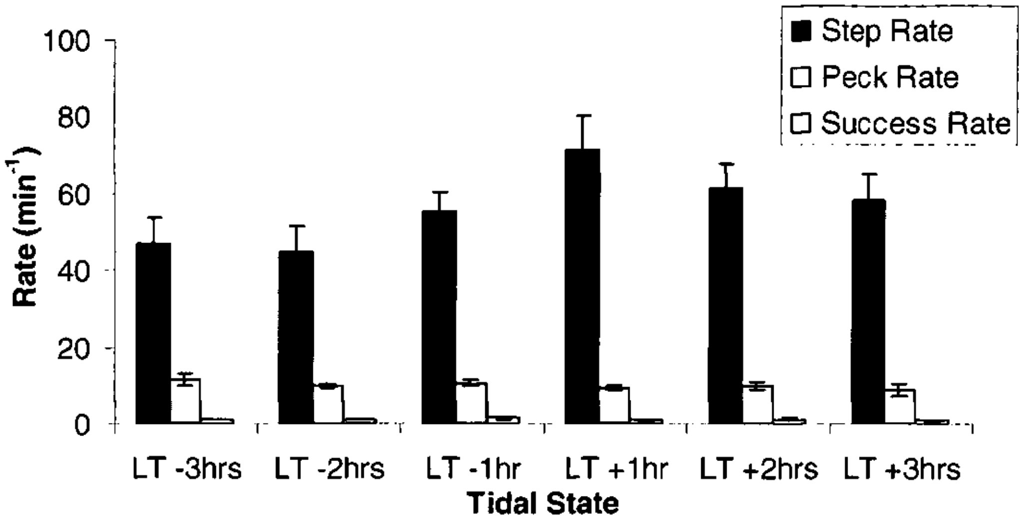


Fig. 13. The effect of the oystercatchers' estimated age on their foraging behaviour. The mean oystercatcher a) step rate, peck rate and success rate, and b) percentage of time spent walking, foraging and alert are shown for juvenile, sub-adult and adult birds. A total of 72 birds were observed for a 300 second period, 6 birds were estimated to be juvenile, 41 sub-adult and 25 adult. Untransformed results are shown (±SE).

3.3.9. Effects of Tide

The state of the tide (i.e. the amount of the shore that was uncovered) had no significant effect on any of the oystercatchers' behaviour (balanced ANOVA, Step rate $F_{(5,66)} = 2.06$, NS; peck rate $F_{(5,66)} = 0.78$, NS; success rate $F_{(5,66)} = 0.57$, NS; percentage of time spent walking $F_{(5,66)} = 1.22$, NS; percentage of time spent foraging $F_{(5,66)} = 0.36$, NS; and percentage of time spent alert $F_{(5,66)} = 1.84$, NS) (Figures 14 a & b).

(a)



(b)

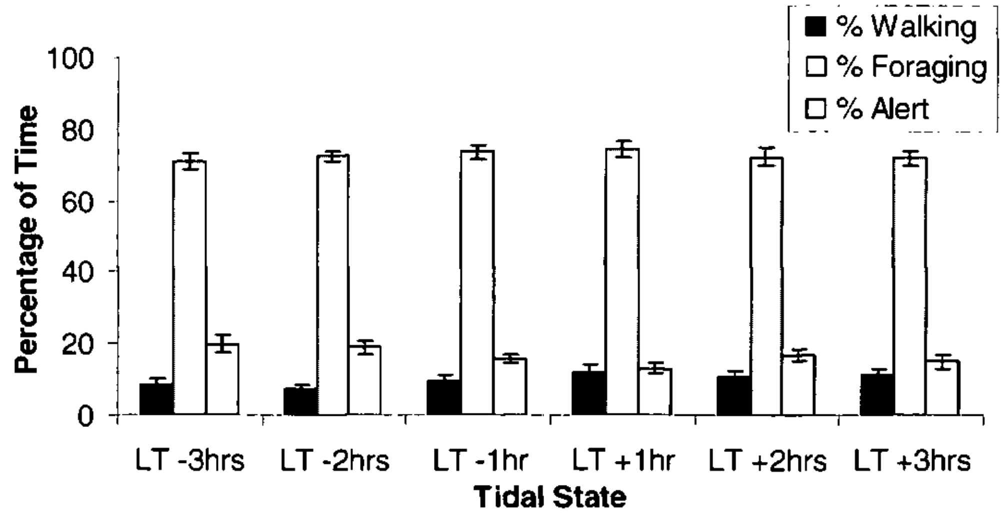


Fig. 14. The effect of the state of the tide, which represents the amount of shore uncovered, on the foraging behaviour of oystercatchers. The mean oystercatcher a) step rate, peck rate, and success rate, and b) the percentage of time spent walking, percentage of time spent foraging, and percentage of time spent alert are shown for Low Tide -3hrs, LT -2hrs, LT -1hr, LT+1hr, LT+2hrs, and LT+3hrs. A total of 72 birds were observed for a 300 second period, equal numbers observed for each tidal state. LT-3 and LT +3hrs represent very little shore uncovered, and LT -1 and LT+1hrs represent almost the maximum area of shore is uncovered. Untransformed results are shown (±SE).

3.4. Discussion

3.4.1. Bird Density on the Rocky Shore and the Effects on Foraging Behaviour

The density of birds inhabiting the rocky shore was very low (less than 11 birds ha^{-1}) in comparison the numbers that have been reported in some estuarine environments (a range of 10 - 1500 birds ha^{-1}) (Goss-Custard & Durell 1988). Furthermore, of the birds present, only oystercatchers were observed intensely foraging on the rocky shore. Gulls have been found to feed upon limpets when on the rocky shore, however gulls did not compete directly with oystercatchers for food as they appeared to take significantly smaller prey items than those selected for by oystercatchers (Harris 1965). The gulls observed throughout this study, however, did not appear to forage regularly upon rocky shore organisms. The gulls were observed on occasion attempting to steal prey items from oystercatchers, although this was very infrequent, as demonstrated by the low rate of interaction recorded between focal oystercatchers and other birds.

Although oystercatchers were found occupying the rocky shore in slightly higher densities in the autumn, their numbers remained consistently low over the wintering period, at an average 4 birds ha^{-1}. The low number of oystercatchers recorded could partly be due to the fact that some individuals were hidden between rocks and in gullies when counts were taken. There is no doubt however, that oystercatcher density on the rocky shore over the winter period is much lower than that observed on the Exe estuary (Goss-Custard *et al.* 1982a). Calculated from data presented by Goss-Custard *et al.* (1982b) oystercatcher densities, between September and February, were an average 22.2, 19.8 and 8.8 oystercatchers ha^{-1} in the best, intermediate and worst feeding sites on the Exe estuary respectively. It may be because so few oystercatchers inhabit the rocky shore that interactions between the birds were so infrequent. A low density of birds limits the possibility of interference (Stillman *et al.* 1996, Holmgren 1995, Moody & Houston, 1995) as a result of avoidance, and increases dispersion which limits the occurrence of an individual blocking another's search path. In addition, a low density of competitors for oystercatcher food resources limits interference through prey depletion, prey depression and klepto-parasitism whilst simultaneously reducing the need for individuals to fight over patches of food.

Species likely to compete with a focal oystercatcher for food resources on the rocky shore are gulls, turnstones and other oystercatchers. It is not surprising, therefore, that oystercatcher success rate was found to be significantly lower when the nearest neighbour was one of these species as opposed to other types of bird. It is surprisingly that the percentage of time an individual spent being alert and foraging did not also vary with the species of its nearest neighbour. It is possible that there are two types of vigilance, 'overt', when an individual's head is raised, and 'peripheral', when the head is down (Bednekoff & Lima 2005). An oystercatcher's foraging efficiency may therefore be compromised by increased peripheral vigilance in response to competitors, without the oystercatcher demonstrating overt alertness. The structural complexity of the rocky shore, however, would be expected to render the use of peripheral vigilance ineffective (Metcalfe 1984b). Alternatively, it may simply be that as 'other' species were so infrequently the focal birds' nearest neighbours the results have been seriously influenced by heterogeneity of variance, resulting in the demonstration of a relationship between an individual's success rate and the species of its' nearest neighbour, that does not truly exist. Certainly the data did not pass Levene's homogeneity of variance test, however as the experimental design of this study is quite large ANOVA is robust against the effects of heterogeneity of variance (Sokal & Rohlf 1995, Underwood 1997).

Oystercatcher behaviour was not affected by the distance separating an individual and its nearest neighbour. This is likely to be due to the fact that in an area where bird density is low, such as the rocky shore, the birds can choose the proximity in which to feed to each other and can easily move away if this is having a negative effect upon their foraging. In fact, many of the birds observed during this study fed much closer to each other than the space available dictated (the birds were observed foraging at an average 8.25m from their nearest neighbour when a maximum distance of 961.67m was possible, based on the average 10.4 birds ha^{-1} observed per sweep of the shore). This may be, to some extent, a factor of prey distribution. Alternatively, it could be because the birds were unthreatened by the proximity of a competitor; this would make sense as interactions between individuals were so infrequent. Furthermore, foraging in relatively close proximity to others may be an anti-predatory response by oystercatchers occupying an area that is structurally complex, and thus where vigilance and foraging cannot be combined, but are mutually exclusive (Metcalfe 1984b). If this is correct, it would be expected that birds in closer proximity to their nearest neighbour would be less alert, allowing more time to be available for foraging, compared to individuals further apart (Fernandez-Juricic *et al.* 2004a); however this was not the case. The birds may simply be relying on the vigilance of others to enhance their predator detection, in what could be perceived as a 'higher risk area' due to reduced visibility, instead of substituting their own basic level of vigilance with other behaviours. By foraging closer together individuals may glean more information from each other than if situated further apart (Fernandez-Juricic & Kacelnik 2004). Alternatively, it may simply be that the benefits of foraging closer together are offset by the need to monitor competitors, and thus a distance effect is not found.

3.4.2 General Foraging Behaviour on the Rocky Shore

Oystercatchers spent the majority of their time on the rocky shore foraging; very little of their observed time was spent preening or involved in social interaction, and none of their time was spent roosting. Thus it appears that the rocky shore is visited by oystercatchers as a foraging site only, with little of their time spent there involved in other behaviours. The mean success rate of oystercatchers foraging on the rocky shore (at slightly less than 1 successful feed $\min^{-1}$) appears to be similar to the success rates observed whilst oystercatchers fed on the Exe estuary; a mean 1.1 successful feeds $\min^{-1}$ (Goss-Custard & Durell 1988) and 0.7 successful feeds $\min^{-1}$ (Goss-Custard 1977). It is interesting therefore that, what appears to be a foraging site with plenty of food, remains a relatively untapped resource. Of course, success rate is not an accurate indicator of intake rate, as different prey species and sizes vary in their energetic value; consequently oystercatchers frequenting estuarine foraging areas may be ingesting significantly more energy than oystercatchers on the rocky shore, if the prey items taken are more energetically valuable. In addition, the fact that the average success rate, observed on the rocky shore where bird density was low and foraging was unlimited by interference, is similar to that on the Exe estuary, where bird density was high and so interference occurs, indicates that rocky shore feeders may be restricted in their energy intake in some way. The rocky shore, essentially a two-dimensional feeding arena, may have a much lower prey density, or lower prey availability, than the estuary, where prey is distributed three-dimensionally. Furthermore, rocky shore foraging may be risky due to an increased threat of bill damage or a higher risk of predation, as a result of the structural complexity of the shore and a lower number of conspecifics, respectively. The rocky shore could be an 'overspill' site where less dominant individuals, pushed out of higher quality or safer areas, congregate to forage.

3.4.3. Effects of Tidal State on Foraging Behaviour

Previous studies on the foraging behaviour of oystercatchers have demonstrated a change in foraging intensity with the tidal cycle, primarily the increase in foraging intensity as the tide covers the shore marking an end to the oystercatchers foraging period at that site (Goss-Custard *et al.* 1984). Such an increase in foraging intensity is thought to be an attempt by oystercatchers to gain as much energy as possible before the food present is rendered unavailable by the tide. No such increase in foraging intensity was found for oystercatchers foraging on the rocky shore; they did not a) increase their step rate in order to cover more ground and thus encounter a greater number of potential prey items, b) decrease the percentage of time they spent travelling in order to increase foraging time, c) increase their peck rate in an effort to establish if more prey items were worth attacking, or d) increase their success rate by becoming more efficient. Furthermore, the expected extension of time spent foraging at the cost of being alert (Metcalfe & Furness 1984) did not occur. This lack of response to the tidal state may be because the birds were already feeding at their optimal rate, were unwilling to forfeit vigilance in case of a predatory attack, or had a supplementary foraging ground to use at high tide and thus had no need to increase their foraging intensity.

3.4.4. Effects of Age on Foraging Behaviour

The age of an individual was found to have no effect on the way in which it behaved on the rocky shore, but did affect its success rate. As expected, adult oystercatchers were far more likely to have a successful feed than juveniles and sub-adults (Goss-Custard *et al.* 1996a), although the low numbers of juvenile birds (N = 6), compared to sub-adult (N = 41) and adult (N = 25) birds, observed on the rocky shore mean that these results must be interpreted with some caution. Nevertheless, it makes logical sense that younger birds, less experienced at foraging (Ens & Cayford 1996) will be less efficient foragers (Caldow *et al.*

1999). It is surprising however, that the age of a bird did not affect its foraging behaviour in other ways; it may have been expected that less efficient individuals would extend their foraging time at the expense of time spent being alert (Metcalfe & Furness 1984) in order to compensate for reduced energy intake, or alternatively, attempt to intensify their foraging by attacking more prey items, had they the capacity to do so. Ultimately, assuming that the energy requirements of all the birds observed during this study are similar (as non-breeding population this is likely to be the case), younger birds, that have a lower energy intake than older birds, may be much in worse condition. If unable to compensate for low energy intake they may die from starvation in times of food shortage or increased energy expenditure (Kersten & Brenninkmeijer 1995, Swennen & Duiven 1983, Heppleston 1971a). Alternatively, compensating for low energy intake by extending their foraging period at additional sites, either at high tide (Goss-Custard & Durell 1983, Davidson & Evans 1986) or at night, may require them to feed in riskier conditions (Duriez *et al.* 2005, Yasué *et al* 2003) and in addition, restrict the time they have available for other behaviours important for oystercatcher health, such as preening, roosting and social interaction.

3.4.5. Effect of Weather on Foraging Behaviour

The foraging behaviour of oystercatchers was not found to vary with the weather at the time of the observation or the weather on the previous day. Oystercatchers did not increase their vigilance at the cost of foraging in rainy weather, due to reduced visibility and thus the heightened risk of failing to detect predator before it reached the critical distance. The results may be to some extent be dependant upon the fact that in heavy rain, when visibility was bad, the observer was unable to monitor the behaviour of oystercatchers, and so any effect of heavy rain was not observed. It was expected that weather would also have some effect upon prey availability (Pienkowski 1981). When uncovered by the tide, mussels keep their valves closed and limpets clamp down upon the rock in order to conserve their water content. Sunny weather may increase water loss through evaporation causing limpets and mussels to clamp down, or together, more rapidly and tightly in order to conserve water when uncovered by the tide, thus decreasing their availability to oystercatchers. In comparison, cloudy or rainy weather may allow limpets and mussels to respond more slowly after exposure. Oystercatchers observed during this study did not vary in their success rate with weather, suggesting that prey availability did not change with weather conditions. These results could reflect the fact that oystercatchers tended to feed on the areas either recently uncovered by the tide or still slightly covered by water, thus prey items had not been uncovered long enough for their availability to be influenced by the rate of evaporation, as dictated by the weather. In addition, the rock pools and damp crevices of the rocky shore, may encourage prey availability regardless of the weather; and limpets may clamp down and mussels close their valves in response to rain in order to reduce osmotic shock. Ultimately it may be a combination of environmental factors such as weather, wind speed and temperature that affect prey availability and thus oystercatcher behaviour.

3.4.6. Effect of Wind Speed on Foraging Behaviour

As the wind speed at the time of an observation, and the average wind speed over the whole day, increased, oystercatcher peck rate decreased very slightly. Strong winds may cause imbalance, making it difficult for oystercatchers to peck accurately prey items (Pienkowski 1981). It is interesting however, that success rate remains unaffected, especially as this suggests that with fewer pecks but just as many successes, the birds actually improve their efficiency with increasing wind speed. So while the mechanics of foraging are hindered, foraging efficiency is not. It could be that high winds deter birds from using exploratory pecks to identify vulnerable prey items, due to an increased risk of bill damage. It may be that birds are less selective about their prey when feeding in strong winds, and attack prey items that are smaller or easier to handle; prey items for which exploratory pecks are not required. Strong winds may also deter oystercatchers from using single forceful blows to dislodge or open prey items, encouraging them instead to attack items with a series of rapid, but less powerful, blows referred to in this study as handling. On a hard substratum, such as a rocky shore, foraging on hard-shelled prey items may be dangerous and requires a high level of precision. The incorrect handling of mussels could lead to their valves clamping down upon the end of an oystercatcher's bill, whilst over zealous handling of limpets may cause the end of an oystercatchers bill to snap off, both of which limit oystercatcher foraging and could lead to starvation (Hulscher 1985, 1996, Swennen & Duiven 1983). The addition of strong winds on the exposed shore is likely to make precise blows that much more difficult and heighten the risk of bill damage, requiring increased concentration and accuracy. Thus it is not foraging *per se* that is affected by wind speed, but may simply be the way in which the birds forage. This contrasts with work on wading bird foraging in an estuarine area, where increased wind speeds caused a more rapid drying of the substratum, reducing prey availability and thus wader success rate (Pienkowski 1981).

3.4.7. Effect of Season on Foraging Behaviour

Oystercatcher behaviour generally did not vary between seasons. Only oystercatcher success rate significantly differed between seasons as oystercatchers had double the number of successful feeds in the winter compared to in the autumn or spring. This is not surprising as the oystercatchers' energy requirements are increased due to the thermoregulatory costs associated with colder temperatures (Wiersma & Piersma 1994). It is surprising, however, that oystercatcher peck rate and the percentage of time spent foraging did not also increase, suggesting that oystercatchers became more efficient at foraging during the winter months. This appears to contradict the fundamental assumptions of rate-maximising models that state that individuals should always feed at their maximal rate in the bid for maximal fitness (Stephens & Krebs 1986). This suggests that oystercatchers are choosing to feed at a lesser rate, possibly due to the restrictions of a digestive bottleneck, or in order to reduce the risk of bill damage or being successfully preyed upon by limiting energy stores. There is some evidence that captive oystercatchers have the ability to increase their intake rate when their feeding time is restricted (Swennen *et al.* 1989), although other studies on free-living oystercatchers have found no such response (Meire 1996, Urfi *et al.* 1996). Success rate does not, however, necessarily reflect energy intake rate. Oystercatchers may become less selective about their prey over the winter in an attempt to gain as much energy as possible. Oystercatchers may choose prey items that are more frequently encountered which are likely to be smaller, and of a lower energetic value, but easier to ingest. For example, the flesh of may gastropods can simply be plucked from their shells (Feare 1971), whereas mussels and limpets are more complicated to handle and require some degree of precision (Hulscher 1996). Furthermore, the forces exerted upon an oystercatcher's bill when prising a limpet off of a rock, or hammering or prising open the valves of a mussel, can on occasion cause bill damage; and an undamaged bill is essential for oystercatcher survival over the winter (Swennen & Duiven 1983). Alternatively, colder temperatures may reduce prey availability as observed in estuarine environments (Goss-Custard 1969; Pienkowski 1981, Zwarts *et al.* 1996c) although as yet there is no data to support this theory on rocky shores. If, in the winter, oystercatcher success rate increases, but energy intake remains similar to that in autumn and spring as a result of prey choice, then an increase in energy requirements in the winter would suggest that the birds are suffering an energy deficit. This would not be the case, however, if oystercatcher intake was of a high enough level, that energy requirements are met or can at least be covered by fat stored, when previously energy intake surpassed energy expenditure. Alternatively, if the birds are unable to meet their energy requirements over low tide they may be forced to feed in alternative sites, such as fields, at high tide (Heppleston 1971a, Goss-Custard & Durell 1983, Quinn & Kirby 1993).

3.4.8. Effect of Temperature on Foraging Behaviour

An oystercatcher's success rate varied with the temperature at the time of an observation, the average temperature of the day, and the average temperature of the prior day. Success rate decreased as temperature increased. This is can be explained in the same way as the season data as the coldest temperatures occur during the winter. The birds, using more energy keeping warm in colder temperatures, require a greater energy intake in order to survive (Wiersma & Piersma 1994). As success rate increased but peck rate and foraging time did not, it must be assumed that the birds simply become better at successfully foraging in colder conditions or that they become less selective in their prey choice. Alternatively, the increase in success rate could be a factor of reduced prey availability, causing birds to take smaller or easier to handle prey items. Surprisingly, oystercatchers did not trade-off energy intake against vigilance as their energy requirements increased, suggesting that either their energy requirements were met during the time they did spend foraging, although this is unlikely as oystercatcher food intake is limited by a digestive bottleneck (Kersten & Visser 1996a), or that they were unwilling to increase their predation risk, regardless of the risk of starvation. It may be that oystercatchers on the rocky shore have a baseline level of vigilance which is never compromised, but which increases only in response to an overt increase in predation risk.

Whilst the foraging behaviour of the oystercatcher has been extensively studied over the last 40 years, the majority of the work published has focussed on populations on estuaries (see Goss-Custard 1996 for review). Of the limited number of studies conducted on the rocky shore (e.g. Hartwick 1976, Frank 1982, Hockey & Underhill 1984), only a few observed the behaviour of the European Oystercatcher (Feare 1971, Feare & Summers 1985, Coleman *et al.* 1999). Although Britain's estuaries are reported to support the majority of Britain's over-wintering oystercatcher population (an estimated 227,000 birds in January 1994/1995-1998/1999), a significant 68,080 oystercatchers were found to over-winter in non-estuarine coastal areas (Rehfisch *et al.* 2003), thus high-lighting the importance of alternative oystercatcher foraging sites.

Oystercatcher success rate on the rocky shore varied to some extent with temperature, the species of the individual's nearest neighbour, season, and the age of the individual. It is important therefore that when predicting the effects of changes in habitat on the health of the oystercatcher population, such environmental and individual-based parameters are considered.

Chapter 4: Prey Selection of Oystercatchers Foraging on the Rocky Shore

4.1. Introduction

A fundamental assumption of many rate-maximising and state-dependant models of foraging behaviour is that organisms will forage at their maximum efficiency (Stephens & Krebs 1986, Houston 1993). Foraging with maximal efficiency renders more time available for alternative behaviours, imperative for optimal health (see Chapter 3 for summary on time -budgets); and enhances fat reserves which are important should further feeding be restricted or energy expenditure increase. Foraging optimally has implications for where individuals feed (see Sutherland 1996 for review) and what they feed upon (Wanink & Zwarts 1996a, Pienkowsi 1981, Thompson & Barnard 1984); and it is prey selection that is the focus of this study.

The functional response describes the relationship between food abundance and intake rate (Begon *et al.* 1997). Assuming all competitors to be equal, the intake rate of an individual should rise with increasing prey density, until constrained by either the handling time required to process prey items (Holling 1959), the individual reaching satiation, prey depletion or a reduction in prey availability (Sutherland 1996). Higher prey densities facilitate a reduction in search time as prey items are encountered more frequently. Foragers would therefore be expected to congregate where prey density is highest (Fretwell & Lucas 1970). When individuals are unequal in their competitive ability intake rate may, however, be limited by interference and competition (Goss-Custard 1980, Milinski & Parker 1991, Giraldeau & Caraco 2000), causing the redistribution of less competitive foragers away from the best quality sites (Goss-Custard *et al.* 1982b, 1984, Fretwell 1969, see Sutherland 1996 for overview).

It is important to note, however, that high prey density does not necessarily reflect high prey availability (Silva *et al.* 1999, Gawlik 2002, Coleman *et al.* 2004). Some prey behaviour in soft sediments, for example, can result in periods of time when prey items are buried at depths too deep for their predators to reach (Pienkowski 1983b). Furthermore individuals do not eat everything that they encounter, instead they generally select the prey species and sizes that are most profitable, i.e. those prey items from which there is the most net energy gain per unit time spent handling (Sutherland 1982b, Goss-Custard *et al.* 1996b, Meire & Ervynck 1986, Cayford & Goss-Custard 1990). For foraging oystercatchers, feeding on bivalves, this may mean rejecting very small prey items which offer very little energy return for the time required for handling (Sutherland & Ens 1987, Norris & Johnstone 1998), and selecting much larger prey items instead. Of course, the birds could, and have on occasion, been observed swallowing small bivalves and gastropods whole, instead of removing the flesh before consumption (S.Carless *pers. obs.*), thus limiting pre-consumption handling times and possibly increasing prey profitability. Such occurrences are rare, however, and may be curbed by the fact that oystercatcher foraging is often limited by a "digestive bottleneck" (Kersten & Visser 1996a); any shell swallowed is likely to increase post-consumption handling costs and will take up valuable space in the gut. Alternatively, larger prey items that are richer in energy may be avoided, in order to reduce 'wasted' handling time (the time spent attacking items from which successful feeds never occur), to avoid the parasite load that is often associated with larger items, or to reduce the risk of bill damage (Norris & Johnstone 1998). Oystercatchers use three techniques for handling bivalves, dorsal or ventral hammering (see Hulscher 1996 for summary), or stabbing (Norton-Griffiths 1967). Stabbing involves inserting the bill rapidly between the valves of a bivalve when they are gaping or loosely closed in an attempt to sever the adductor muscle holding the valves together and cut out the flesh (Norton-Griffiths 1967). Whilst hammering involves a series of blows to either the ventral or dorsal side of the bivalve in order to create a hole into which the bill is inserted, and the posterior and anterior muscles are cut, before the flesh is removed and consumed (Norton-Griffiths 1967). Vigorous hammering can result in parts of the oystercatcher's bill snapping off, whilst stabbing birds, if unsuccessful in their severing of the adductor muscle, can get their bill stuck between the valves if they clamp down as a reaction to the bivalve being attacked (Hulscher 1988 *loc cit* Hulscher 1996). Any damage to an oystercatchers bill could seriously hamper foraging, causing a decline in health and ultimately death (Swennen & Duiven 1983). Thus, it is reduced profitability, as a result of wasted handling time, and an increased risk of bill damage that is thought to explain why oystercatchers have been observed ignoring large mussels (Sutherland & Ens 1987) and actively selecting only thin-shelled prey items (Ens & Alting 1996, Durell & Goss-Custard 1984, Meire & Ervynck 1986, Cayford & Goss-Custard 1990). In addition, oystercatchers foraging in estuarine environments have also demonstrated selectivity with regards to parasite load (Hulscher 1982) and water content (Nagarajan *et al.* 2002). Oystercatchers foraging in the Exe estuary demonstrated a preference for mussels containing less water (Nagarajan *et al.* 2002), which was suggested to be due to restricted space in the gut. Whilst, oystercatchers feeding on cockles in the Burry Inlet fed upon intermediate sized prey, which was suggested to be a trade-off between selecting larger items that would increase energy intake, and smaller items that limited parasite ingestion (Norris 1999).

The prey species that an individual oystercatcher selects is thought to be initially down to the structure of its bill (Hulscher & Ens 1992), and the need to avoid bill damage. Oystercatchers with longer and thinner bills, often females, tend to feed on soft bodied prey such as worms or use the stabbing technique for opening bivalves, whilst oystercatchers, usually male, with thicker, stouter, and more robust bills tend to use a hammering technique for prey items such as limpets and mussels (Swennen *et al.* 1983, Hulscher 1985, Durell *et* *al.* 1993). Although individuals are known for being specialized in feeding on certain prey species in a specific way (Norton-Griffiths 1967, Goss-Custard *et al.* 1982a, Hulscher 1985, Ens *et al.* 1996b, Sutherland *et al.* 1996), prey choice can change with the tidal cycle (de Vlas *et al.* 1996, Ens *et al.* 1996c) and season (Zwarts *et al.* 1996b, Goss-Custard & Durell 1983, Ens *et al.* 1996c, Bunskoeke *et al.* 1996, Cayford & Goss-Custard 1990), dependant upon prey availability (Zwarts *et al.* 1996a, Wanink & Zwarts 2001) and profitability. As prey choice changes so may the handling technique the oystercatchers employ (Goss-Custard & Sutherland 1984).

In the longer term, it seems logical that oystercatchers would choose to feed on prey species that provide the most energy, especially as bill shape can adapt over time and to a certain extent, through abrasion and re-growth, so as to accommodate a particular prey choice and handling technique (Swennen *et al.* 1983, Hulscher 1985, Hulscher & Ens 1992). Oystercatcher prey choice may, however, be governed by much more than just bill shape and structure; oystercatchers may vary in their natural foraging ability and efficiency (Caldow *et al.* 1999), with some lacking the skills to successfully feed upon more energetically valuable prey items that are difficult to handle; others may be out-competed for the favoured prey species, or of a lower social status and so forced to feed in areas where the favoured prey species are less abundant. Juveniles, inexperienced in handling prey and yet to establish a social status, are especially vulnerable to such factors (Heppleston 1971a, Goss-Custard & Durell 1983, Caldow *et al.* 1999). So, for foraging wading birds, the proportion of any prey species or size that can be exploited is not only dependant upon their profitability but also their availability.

Availability is a function of prey abundance, how easy an item is to detect (Bosman *et al.* 1989), how accessible it is and how easy it is to ingest (Bosman *et al.* 1989), and can often be altered by prey behaviour (Pienkowski 1983b, Zwarts & Wanink 1993, Sih 1993, Bunskoeke *et al.* 1996, Coleman *et al.* 2004). For shorebirds prey availability is dependant upon the tide. As the tide retreats, the potential prey of the oystercatcher is uncovered, those sessile species with the greatest tolerance to desiccation, higher temperatures, oxygen shortage and reduced feeding time, being uncovered first (Levington 1995). As the potential prey items are exposed they will bury deeper into the substrate, clamp down upon the rock, tightly close their valves or become less mobile in an attempt to conserve their water content or avoid a predatory attack, dependant upon the habitat and the species concerned (Levington 1995). Thus, oystercatchers can be seen feeding on the water's edge where prey items still immersed in a shallow amount of water are possible to reach and are also vulnerable to attack (Feare & Summers 1985). No effect of tide on oystercatcher success rate was observed in chapter 2, however, this may be a factor of changing prey choice in response to varying prey availability. Alternatively, it may be the damp crevices and rock pools of the rocky shore extend the time for which certain prey items are available to oystercatchers. The success with which various types of prey item are exploited, by oystercatchers specifically, is further dependant upon factors such as intrinsic foraging efficiency/ability, age (Goss-Custard & Durell 1983, 1987a, Caldow *et al.* 1999), the status within the social hierarchy and thus susceptibility to competition and interference (Ens & Cayford 1996 for summary), sex (Dare 1977, Swennen *et al.* 1983, Durell *et al.* 1993, Hulsman *et al.* 1996), and physiological state (Houston 1993) of each individual bird.

Although much work has been conducted on the prey selection and foraging behaviour of *Haematopus ostralegus* in estuarine environments (e.g. Hulscher 1982, Cayford & Goss-Custard 1990, Goss-Custard *et al.* 1993, Ens *et al.* 1996a, b, Norris & Johnstone 1998), little is known about their prey choice on the rocky shore (see Feare 1971, Coleman *et al.* 1999, 2004 for exception); although more information is available on the rocky shore feeding habits of other species of oystercatcher world-wide (e.g. Leg 1954, Hartwick 1976, Levings *et al.* 1986, Hockey & Underhill 1984). The rocky shore appears to support high densities of potential oystercatcher prey species (Mussels *Mytilus edulis*, Limpets *Patella* spp., Dogwhelks *Nucella lapillus*, Winkles *Littorina* spp. and Topshells *Gibbula* spp., *Osilinus lineata*), and yet very few oystercatchers appear to forage there (see Chapter 3.). Certainly, the interference and competition associated with good feeding sites and high oystercatcher densities (Ens & Goss-Custard 1984, Goss-Custard 1980), is not apparent (see Chapter 3.). Prey density or availability may be significantly lower, on the rocky shore compared to estuaries. Alternatively the prey items present may be a lot smaller or have less energy content due to environmental conditions. If this is the case the rocky shore may be considered a poorer feeding area, where those oystercatchers of a lesser competitive ability or lower down the social hierarchy, either due to age, health or dominance, are forced to feed (Goss-Custard *et al.* 1982b, 1984).

The aims of this chapter were to establish the energy content of the oystercatcher's primary rocky shore prey species, and to estimate the energy present on the rocky shore feeding ground, throughout the winter. Oystercatcher foraging behaviour and prey selection on the rocky shore, was investigated in conjunction with prey density and availability. The hypotheses tested were that oystercatchers a) would increase their energy intake rate as the tide flooded in signaling an end to their foraging period (in chapter 3 success rate was considered and not the energy ingested with the flow of the tide), b) would not forage on prey species and sizes according to their abundance on the shore, but c) forage on prey sizes and species that were worth more energetically and easier to handle. It was also hypothesised that oystercatchers d) would vary their prey choice as the tide ebbed and flooded due to changing prey availability.

4.2. Methods

See the Study Site and General Methodology described in Chapter 3.

4.2.1. Energy content of site

An aerial photograph of the site, taken on a low spring tide, was used as a template to construct a map using the 'analySIS' 5.0 imaging package (2004, Soft Imaging System GmbH, Münster). Areas higher up on the shore, devoid of available prey, were marked on the map. The remaining area was divided into 12 patches of varying size dependant upon obvious physical features that allowed the patches to be distinguished during the observation period (Figure 15). The approximate area of each patch was established using the 'analySIS' software. Areas were: patch 1: 1936m^2, patch 2: 256m^2, patch 3: 352m^2, patch 4: 3636m^2, patch 5: 2704m^2, patch 6: 1356m^2, patch 7: 820m^2, patch 8: 732m^2, patch 9: 1308m^2, patch 10: 3308m^2, patch 11: 4816m^2 and patch 12: 4700m^2 (Figure 15).

Randomly placed 0.25m^2 quadrats were used to determine the distribution and density of possible oystercatcher prey items in the area where food was present, on a low spring tide for maximum shore exposure. Sampling of the shore took place over two consecutive days, repeated on three occasions; at the beginning of the field season in October; mid-season in January; and at the end of the sampling period in April. The number of quadrats sampled within each patch was dependent upon its size relative to the biggest patch, which had ten quadrats sampled within it. Where a clump of mussels was present inside the 0.25m^2 quadrat, a smaller 0.01m^2 quadrat was placed over the clump. A digital photograph was then taken of the 0. 25m^2 quadrat from directly above, so that the image filled the frame. The sub-sample of mussels (mussels inside the 0.01m^2 quadrat) and any other potential oystercatcher prey items (limpets, whelks, topshells, winkles etc) present within the 0. 25m² quadrat, were collected and frozen on the same day, until they were processed.

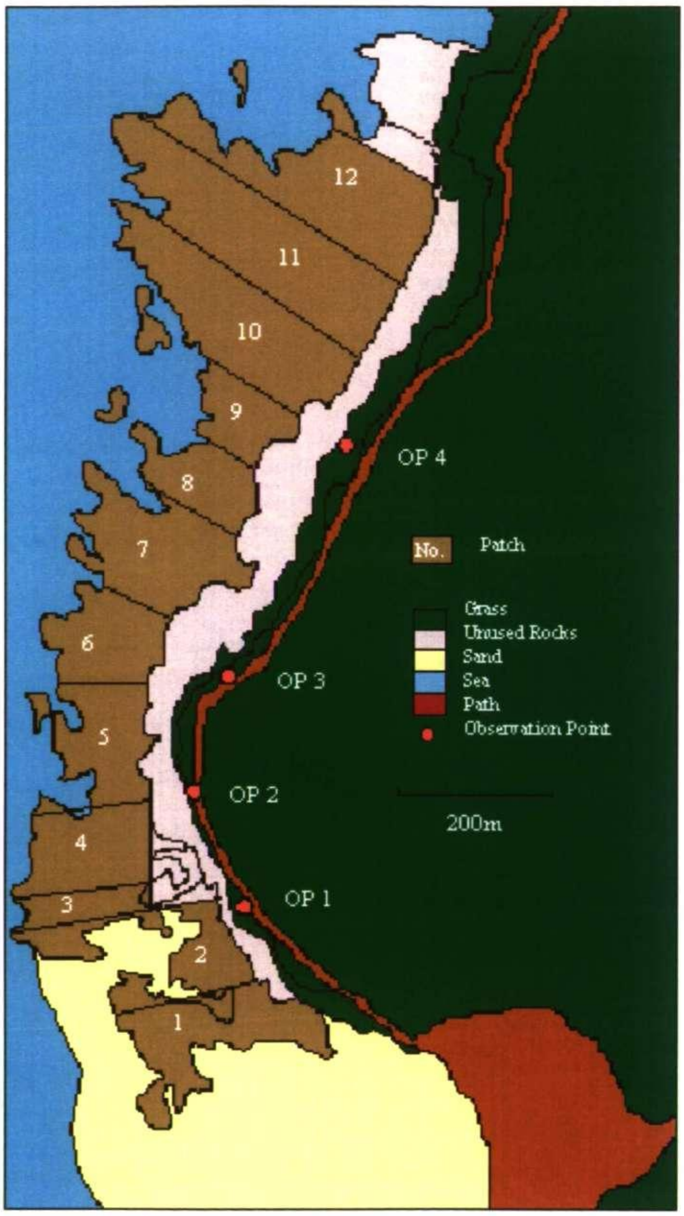


Fig 15. Rocky shore of Trebetherick divided into 12 patches of various size dependant upon physical features that were easy to define whilst on site.

The still frozen prey items collected from each quadrat, were counted and their shell length measured using their longest dimension; this was the length of the ventral surface from the anterior to the posterior end in mussels; the base of the aperture to the apex of the shell for snails; and the posterior to anterior margin in limpets, these were then grouped into species and then size classes of 10mm. The percentage cover of mussels in the 0. 25m^2 quadrat was estimated from the photos by placing a grid on top of the pictures, and the amount of each size class collected from the 0.01m^2 quadrat extrapolated to give the approximate number of each size class of mussel in the larger quadrat. As the mussel matrix on this rocky shore was generally limited to one layer (S.Carless *Pers. Obs.*), it was assumed prey density was approximately equal to the number of mussels visible to the birds.

4.2.2. Energy Content of Prey Items

The ash-free-dry-mass (AFDM (mg)) of a proportion of the gastropods and mussels collected, from the whole range of sizes present on the shore, were determined and length-biomass curves produced for each collection period (early autumn, mid-winter and early spring). The collected items were placed on individual crucibles if of a length >11mm, prey items measuring ≤10mm were put in a single crucible in groups of ten; the samples were dried at 60°C until constant weight. The samples were weighed and ashed in a muffle furnace at 550°C until there was no more weight loss; the samples were left to cool in the furnace and then reweighed. The weight of the ashed sample was subtracted from the weight of the dried sample to provide the AFDM for each item. The small items, in groups of ten, simply had their total AFDM divided by ten. The data on the AFDM of mussels, limpets and snails of varying sizes were $\log_{10}$ transformed and then analysed using regression analysis. The length-biomass curves produced from the data were used in conjunction with the prey density data to calculate the approximate mean energy content (AFDM/m^2) both per patch and for the overall site. This information could then be compared to the observed bird behaviour to establish whether their intake rate was related to the estimated energy content of the patch they were feeding in.

4.2.3. Bird Behaviour

A focal bird was observed for a 300s period and components of its foraging behaviour recorded in real time using a cassette tape recorder. The behaviours recorded included the number of pecks and successful feeding attempts, and the proportion of their observed feeding time that the birds spent handling. A peck was defined as one single strike of a prey item. A successful feeding attempt was easily identified as the birds raised their heads and moved their necks in a swallowing motion. Handling was defined as when an individual was continuously either handling or attacking a prey item regardless of success. The size and species of prey items handled or successfully fed upon were also recorded. Prey size was estimated by comparing the length of the prey item to the bill length of the oystercatcher handling it (Goss-Custard, *et al.*1987). Oystercatcher bill length ranges from 65mm to 85mm (Goss-Custard *et al.*, 1987) and so a mean 75mm was the assumed length for all oystercatcher bills. The time and position of any incidental disturbance was also noted.

Tidal Effects on Prey Choice (see the Tidal Effects on Foraging in Chapter 3)

4.2.4. Calibration exercise

A calibration exercise to establish the accuracy with which prey size was estimated was conducted using a stuffed oystercatcher (Goss-Custard *et al.* 1987). Varying sizes of mussel, limpet, winkle, topshell and whelk shells were held up against the bill (measuring 75mm) of the stuffed oystercatcher for five seconds at a time. The shells were attached to a piece of wire, thus limiting the possibility of the assistant's hand being used as a parameter against which to measure shell length. The observer estimated the species and size of the prey items relative to the bird's bill, from a range of distances (40m intervals up to 400m) to the bird and with the prey orientated either along the bill (0°) or at a right angle to it

(90°). The estimates were subsequently compared to the true length of the shells, and the observer's error calculated.

4.2.5. Analysis

The relationship between the $\log_{10}$ length and $\log_{10}$ AFDM of limpets, mussels and other gastropods (referred to as snails throughout this study) were analysed using regression analyses in SPSS (SPSS Inc 1989-2000, Chicago). The accuracy with which prey size was estimated when orientated at 0° and 90° was tested using the deviations from the true size in ANCOVA and regression analyses in SPSS. Prior to ANCOVA, homogeneity of variance was tested using Levene's test.

The mean AFDM present on the rocky shore, in the designated patches and in the overall site and across seasons, was estimated using the length-biomass curves previously calculated, in conjunction with the prey density estimated from the shore samples, and the area of each patch, calculated using the 'analySIS' imaging package with aerial photos of the site.

The bird behaviour recorded during fieldwork was transcribed into a computer using 'The Observer' 4.0 behavioural software (1998, Noldus Technology, Waginengen). The percentage of time birds spent handling, their foraging and handling efficiency, and intake rate were calculated from the data collected (i.e. the number of pecks and successes, the time spent handling, the size and species of the items fed upon by the birds and the AFDM (mg) associated with those prey items). The percentage data were arc-sine transformed prior to analysis; and before ANOVA, homogeneity of variance was tested by Cochran's test (Underwood 1997).

Other statistical tests were following procedures in Sokal and Rohlf (1995). The proportion of mussels, limpets, other gastropods and other prey items, eaten by the birds in autumn, winter and spring, in comparison to their abundance on the shore were analysed using G-tests adjusted by the Williams correction (Sokal & Rohlf 1995). A Kolmogorov-Smirnov two-sample test for large samples was used to compare the frequency of successful feeds on different prey sizes in relation to the frequency at which each prey size was found on the shore. *R x C* test of independence using G-test adjusted by the Williams correction was performed to find out whether the number of successful feeds oystercatchers had on limpets and mussels was dependant upon their size (Sokal & Rohlf 1995).

The number of successful feeds on different species and sizes of prey items, at various states of the tide were analysed using ANOVA procedures in GMAV (EICC, University of Sydney). The groups included in the analyses were limpets, mussels and other gastropods; the size classes were binned into groups of <7.5mm, <15mm, <22.5mm and ≥22.5mm in order to limit heterogeneity of variance. Prior to analysis data were log-transformed, Ln (X+1), and homogeneity of variance tested using Cochran's test (Underwood, 1997). In cases of heterogeneity of variance persisting after transformation, raw data were used (Underwood 1997, Sokal & Rohlf 1995). As the number of samples in this experiment is large, ANOVA is robust against departures from homogeneity of variance (Underwood 1997, Sokal & Rohlf 1995). SNK tests were used for *post-hoc* separation of levels within significant factors.

Odds ratios (Sokal & Rohlf 1995) were used to compare the probability of a successful feed when feeding on mussels compared to limpets, at varying tidal states. The Mantel-Haenszel procedure was adopted as a test of homogeneity of odds ratios for replicated 2x2 tables (Sokal & Rohlf 1995). Where homogeneity of odds ratios was not found G-tests were used for comparison (Sokal & Rohlf 1995). Odds ratios were also used to describe the chance of having a successful feed compared to a non-successful feed when foraging on prey size classes of <7.5mm, <15mm, <22.5mm and ≥22.5mm; the size data was analysed using a *R x C* test of independence using G-tests (Sokal & Rohlf 1995).

The handling times required to successfully feed upon mussels and limpets of various sizes were analysed using ANCOVA procedures in SPSS. A lack of data points due to so few other gastropods being fed upon by oystercatchers during this study meant that other gastropods were not included in this analysis. The data were analysed using tests of homogeneity of slopes and intercepts to see whether the relationship between the size of a prey item and the handling time required to ensure a successful feed was different for mussels and limpets. Where heterogeneity of variance was found after transformation, ANCOVA was not conducted; the data was interpreted using scatter plots and regression analyses.

The effect that the energy content per m^2 of the area in which the bird was located had on the bird's intake rate in autumn, winter and spring was analysed using regression and ANCOVA procedures in SPSS.

4.3. Results

4.3.1. Energy Content of Primary Prey Items

The prey types predominantly consumed by oystercatchers on the rocky shore were mussels (*Mytilus edulis)*, limpets (*Patella* spp.), and other gastropods referred to as snails in this study (*Nucella lapillus*, *Littorina* spp , *Gibbula* spp., and *Monodonta lineata*) (Figure 20). The energetic value of various sizes of mussel, limpet and snail appeared to be similar in autumn, winter and spring (Figure 16). Surprisingly, snails had a greater ash-free dry-mass (AFDM) than limpets and mussels in all seasons, although snails did not reach the sizes that limpets and mussels did (Table 8). Limpets were of a greater energetic value than mussels, the difference being greater at longer prey lengths in autumn and winter but not in the spring (Figure 16, Table 8).

		Trendline		ANOVA	
Season	Prey Type	Equation	R^2	df	*F*
Autumn	Mussels	y =3.015x -2.486	0.958	1,50	1136.0***
	Limpets	y =3.721x -3.255	0.921	1,59	688.2***
	Snails	y =2.337x -0.933	0.712	1,32	79.1***
Winter	Mussels	y =2.844x -2.298	0.967	1,68	1965.6***
	Limpets	y =3.370x -2.886	0.933	1,67	938.3***
	Snails	y =2.953x -1.934	0.777	1,29	101.2***
Spring	Mussels	y =3.029x -2.616	0.975	1,73	2862.2***
	Limpets	y =3.063x -2.501	0.951	1,69	1327.3***
	Snails	y =2.896x -1.680	0.957	1,42	943.4***

Table 8. Regression analyses on the AFDM (mg) of mussels, limpets and snails of varying size, collected in a) autumn, b) winter and c) spring. Data were $\log_{10}$ transformed prior to analyses (NS – Non-significant $P>0.05$, $^*P<0.05$, $^{**}P<0.01$ and $^{***}P<0.001$).

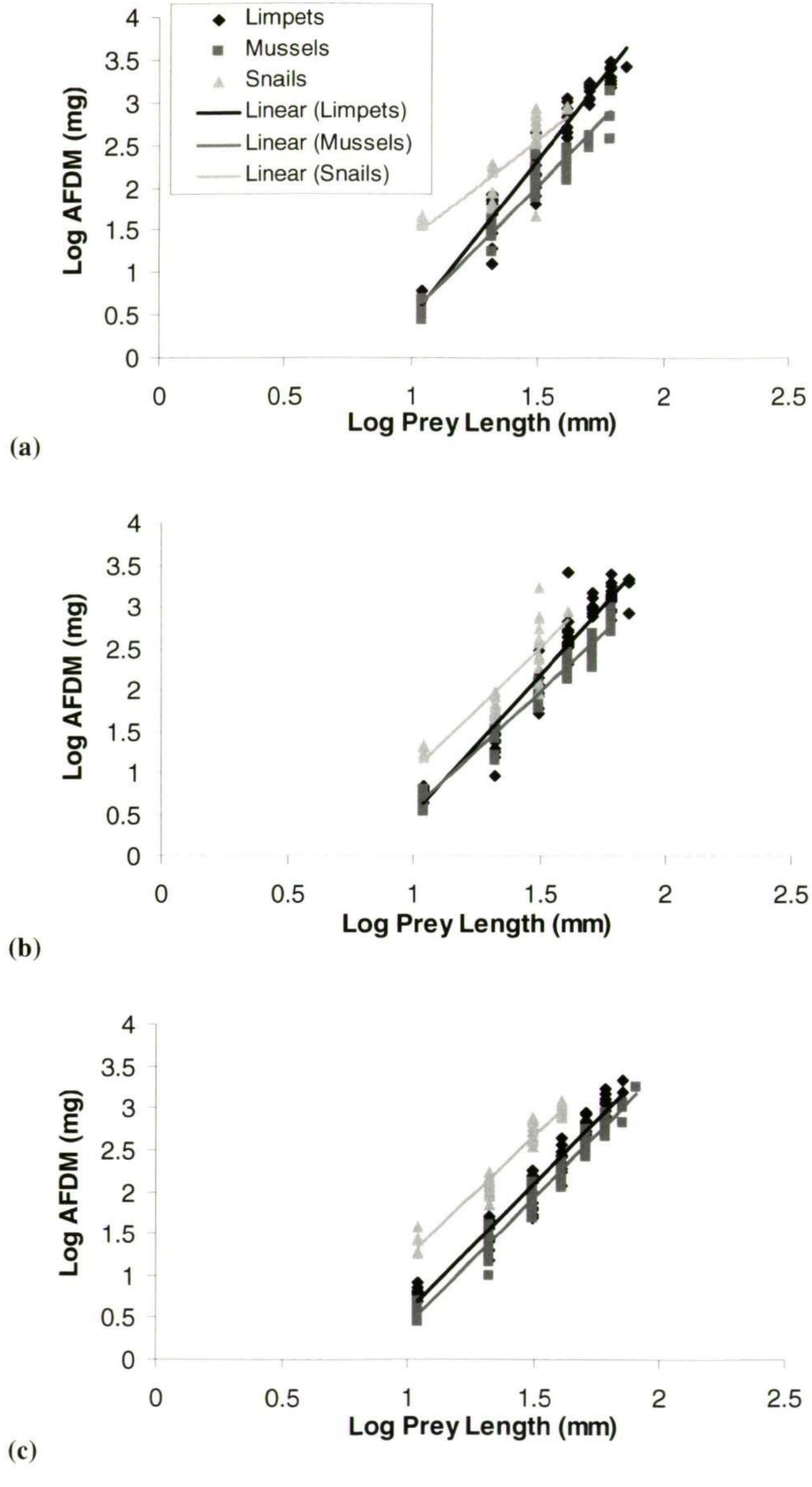


Fig. 16. The relationship between the $\log_{10}$ length and $\log_{10}$ AFDM of limpets, mussels and snails collected at Trebetherick in a) autumn, b) winter and c) spring.

4.3.2. Bird Behaviour

The percentage of time oystercatchers spent handling prey items ($F_{(5,66)} = 0.87$ NS), their handling efficiency ($F_{(5,66)} = 0.70$ NS), their foraging efficiency ($F_{(5,66)} = 0.21$ NS) and their intake rate ($F_{(5,66)} = 0.41$ NS) did not vary with tidal state (Figure 17 a-d).

4.3.3. Energy content of site

Overall the AFDM (mg)/m^2 over the whole shore increased through autumn and winter and peaked during the spring (Figure 18 a); the AFDM (mg)/m^2 in each patch varied with season (Figure 18 b, c & d), with the variability between patches increasing over autumn, winter and spring.

4.3.4. Calibration exercise

The observer showed no consistent bias in her estimation of prey species and prey size at various distances from the bird (Figure 19), however there was a significant difference in the accuracy with which prey size was estimated dependant on the orientation of the prey in the model birds' bill (Heterogeneity of slopes: $F_{(9,80)} = 1.313$ NS, heterogeneity of intercepts: $F_{(1,89)} = 8.450$ $P<0.01$). The observer underestimated the actual prey size by an average 2.2mm when the prey was orientated 0 degrees but only underestimated by an average 0.1mm when orientated at 90 degrees from the bill. Furthermore, prey species were identified with 100% accuracy. Thus, overall, the observer appeared to be reasonably accurate in her estimations (Figure 19) and could be confident in using estimated prey size to calculate intake rate.

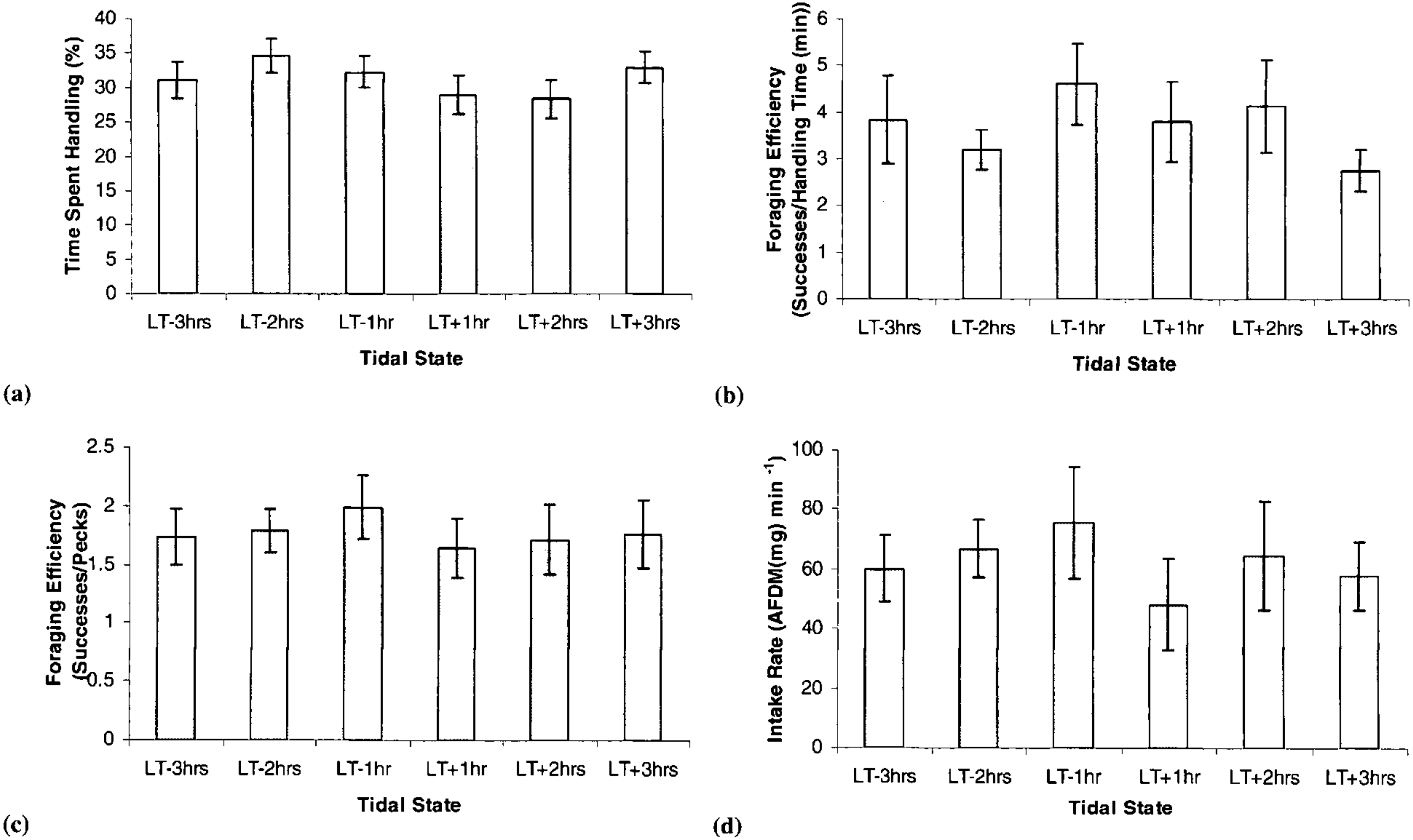


Fig. 17. The mean percentage of time oystercatchers spent handling prey items (a), their mean handling (b) and foraging efficiency (c), and their mean intake rate (d) at Low Tide -3hrs, LT-2hrs, LT-1hr, LT+1hr, LT+2hrs, and LT+3hrs. A total of 72 birds were observed for a 300 second period. Untransformed results are shown (mean ± SE).

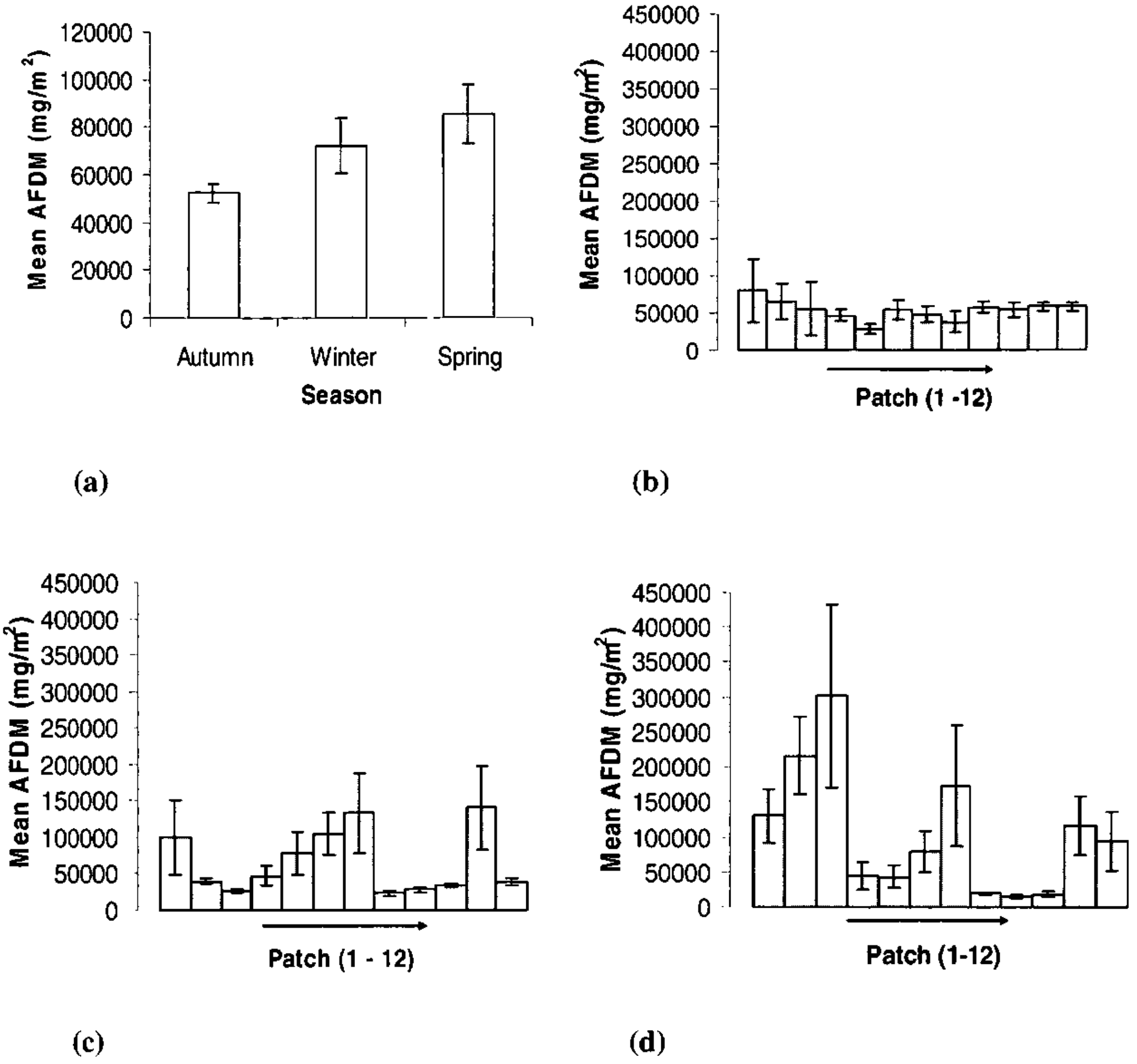


Fig. 18. The energy available on the rocky shore of Trebetherick. a) The mean (± SE AFDM/m^2 present on the whole rocky shore of Trebetherick during autumn, winter an spring. The mean (± SE) AFDM/m^2 present in each of the 12 patches, during b) autumn c) winter and d) spring.

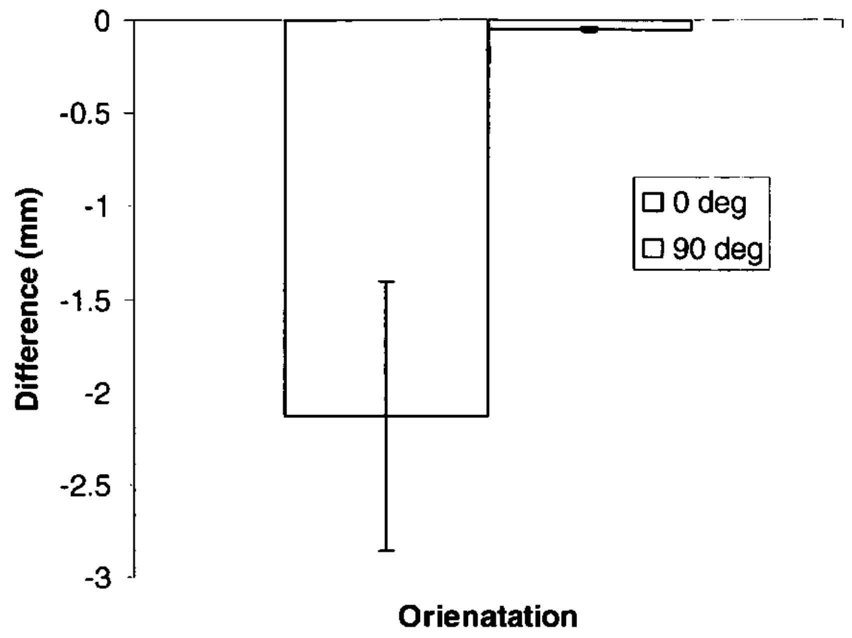


Fig. 19. The difference between the estimated prey size and actual prey size (estimated – actual) of limpets, mussels and snails (all data together) with orientation of the prey item in the birds bill. Mean values (± SE) shown for 0 degree orientation (prey length runs along the bill) and 90 degree orientation (prey length runs at right angle to the bill). 100 estimates conducted, 50 at each orientation.

4.3.5. Oystercatcher prey choice

The number of successful feeds that oystercatchers had on limpets, mussels, snails and other prey types (other prey types were grouped together) was significantly different from the expected based upon the abundance of each prey type on the rocky shore in autumn (G_{adj} = 99.300, d.f. 3, P<0.001, Figure 20 a), winter (G_{adj} = 863.149, d.f. 3, P<0.001, Figure 20 b) and spring (G_{adj} = 109.905, d.f. 3, P<0.001, Figure 20 c). In all seasons, the birds successfully fed on more limpets, and fewer mussels than would be expected from their abundance on the shore. The number of snails and other prey items consumed in relative to their abundance varied within and between seasons. ‘Other’ prey types, that the oystercatchers were observed occasionally consuming, included worms, fish and crabs. The distribution of the number of successful feeds that oystercatchers had on prey items of various sizes, was significantly different from the distribution of the abundance of the various prey sizes in the autumn (Kolmogorov-Smirnov test $D = 0.354$, $P<0.001$, $n_1 = 543$, $n_2 = 100$; Figure 21 a), winter ($D = 0.664$, $P<0.001$, $n_1 = 1961$, $n_2 = 188$; Figure 21 b) and spring ($D = 0.672$, $P<0.001$, $n_1 = 2307$, $n_2 = 75$; Figure 21 c). In general, oystercatchers took significantly fewer very small prey items compared to their abundance on the rocky shore; the majority of the prey items taken were between 11mm and 30mm in length; with oystercatchers feeding predominantly upon prey items less than 30mm in length in the autumn, items between 11mm and 30mm in length in the winter, and items 21-30mm in length in the spring.

4.3.6. Tidal State and Prey Selection

The number of successful feeds that the oystercatchers had on mussels, limpets and snails was found to differ (Table 9 a) dependant on the state of the tide (Figure 22 a). SNK tests showed that oystercatchers feeding on the rocky shore fed predominantly on mussels ($P<0.01$) as the tide began to ebb at the beginning of the observation period; as the tide retreated mussels and limpets were taken equally over snails ($P>0.01$), until just before low tide when the birds fed mostly on limpets ($P<0.01$) over mussels and snails; this transition from feeding predominantly on mussels to limpets was mirrored almost exactly as the tide advanced (Figure 22 a). Birds fed more on limpets than on mussels and snails ($P<0.05$) up until just before the shore was completely covered, when they switched to feeding on mussels over limpets and snails ($P<0.01$). Snails were generally the least favoured prey type (Figure 22 a).

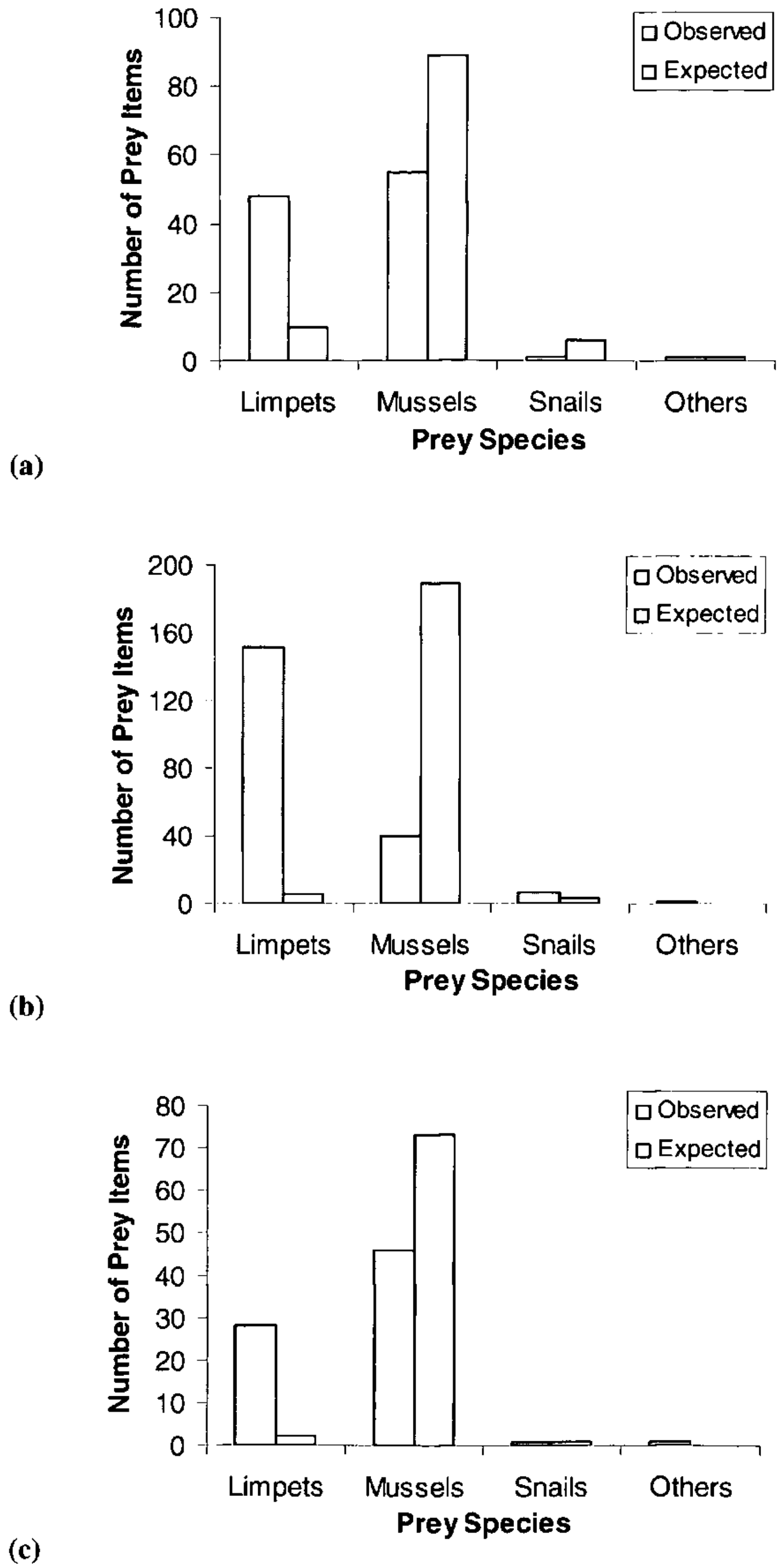


Fig. 20. The mean number of limpets, mussels, snails and other prey items successfully fed upon by oystercatchers (observed) in relation to the number that was expected based on the abundance of each prey type on the shore, in a) autumn, b) winter and c) spring.

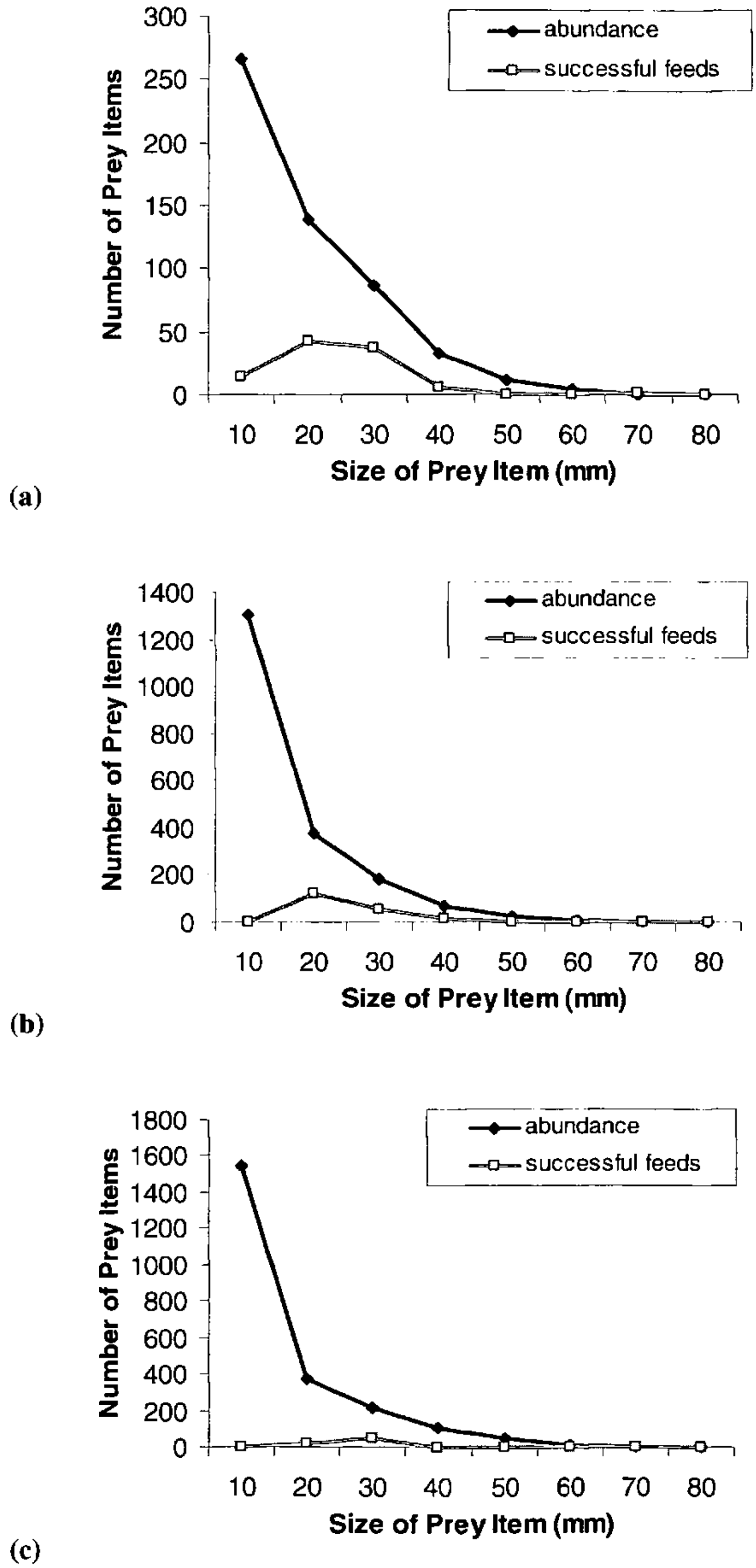


Fig. 21. The frequency distribution of the mean number of each prey size found per m^2 on the shore and the frequency distribution of the mean number of successful feeds the birds had on each prey size, in a) autumn, b) winter and c) spring.

Source	df	MS	F
Tidal State (TS)	5	0.1023	0.2 NS
Species (Spp)	2	14.1708	28.15***
TS x Spp	10	2.0748	4.12***
Residual	198	0.5034	
Total	215		

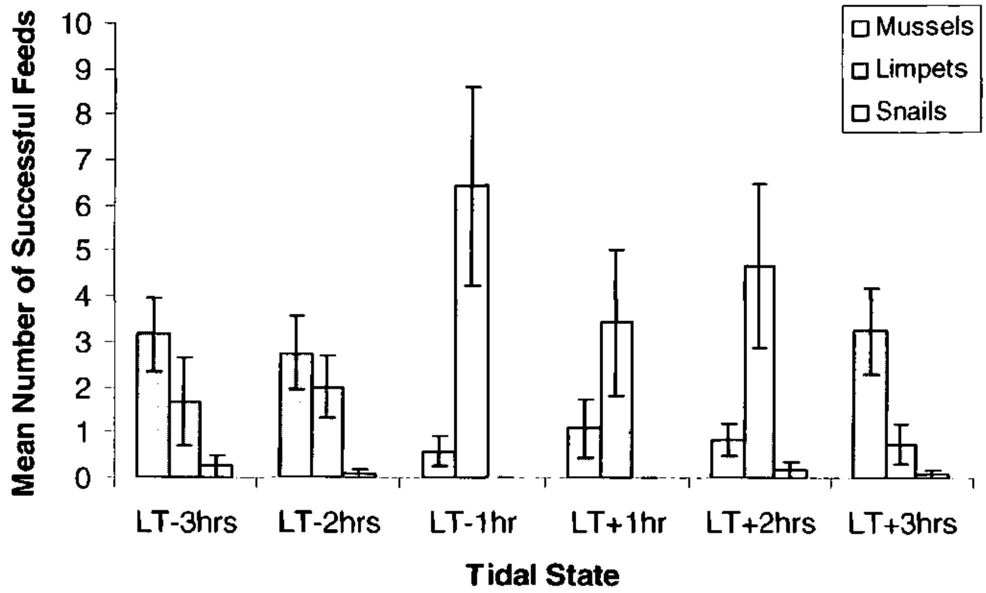
a)

Source	df	MS	F
Tidal State (TS)	5	3.4389	0.54 NS
Size (Si)	3	97.1759	15.40***
TS x Si	15	11.537	1.83*
Residual	264	6.3112	
Total	287		

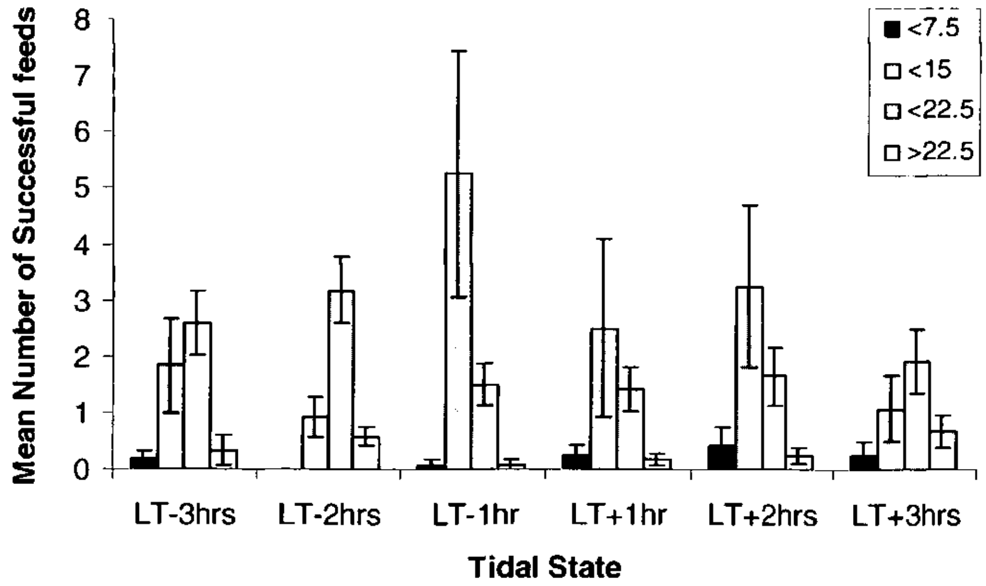
b)

Table 9. Analyses of variance on the number of successful feeds on different a) prey species (Spp) and b) sizes (Si), at various states of the tide (Ti) (NS – Non-significant $P>0.05$, $*P<0.05$, $**P<0.01$ and $***P<0.001$). Species were limpets, mussel and snails; sizes were binned into groups of <7.5mm, <15mm, <22.5mm and >22.5mm in length, to reduce heterogeneity of variance by minimising the effects of empty cells. Tidal States were Low Tide-3hrs, LT-2hrs, LT-1hr, LT+1hr, LT+2hrs and LT+3hrs. All data were tested by Cochran's homogeneity of variance test prior to analysis; if heterogeneity of variance existed the data was log transformed (Ln (x+1)) (Species: C=0.1507, NS; Size: C=0.3819, $P<0.01$). Heterogeneity of variance found after transformation was assumed to have limited effect due to large sample sizes, and could be discounted; the untransformed data were subsequently used for analysis (Underwood 1997).

The number of successful feeds that oystercatchers had on prey items <7.5mm, <15mm, <22.5mm and >22.5mm in length, also differed (Table 9 b) with the state of the tide (Figure 22 b). SNK tests showed that oystercatchers fed on all the prey sizes similarly as the tide began to ebb at the beginning of the observation period; as the tide retreated prey items 15-22.5mm in length were taken more than prey items <7.5mm, <15mm and >22.5mm in size ($P < 0.05$) until just before low tide, when prey items between 7.5mm and 15mm were most prominently fed upon ($P<0.01$) over the other sizes (Figure 22 b). As the tide began to advance the birds fed on all prey sizes similarly, whilst at mid flood although they generally fed on all prey sizes to a similar extent more 7.5-15mm sized prey items were taken than <7.5mm ($P < 0.05$) or >22.5mm ($P < 0.05$) sized prey items. All prey sizes were fed upon equally as the tide was almost completely flooded (all NS) (Figure 22 b). Thus oystercatchers on the rocky shore changed their prey selection as the tide went out and came in.



(a)



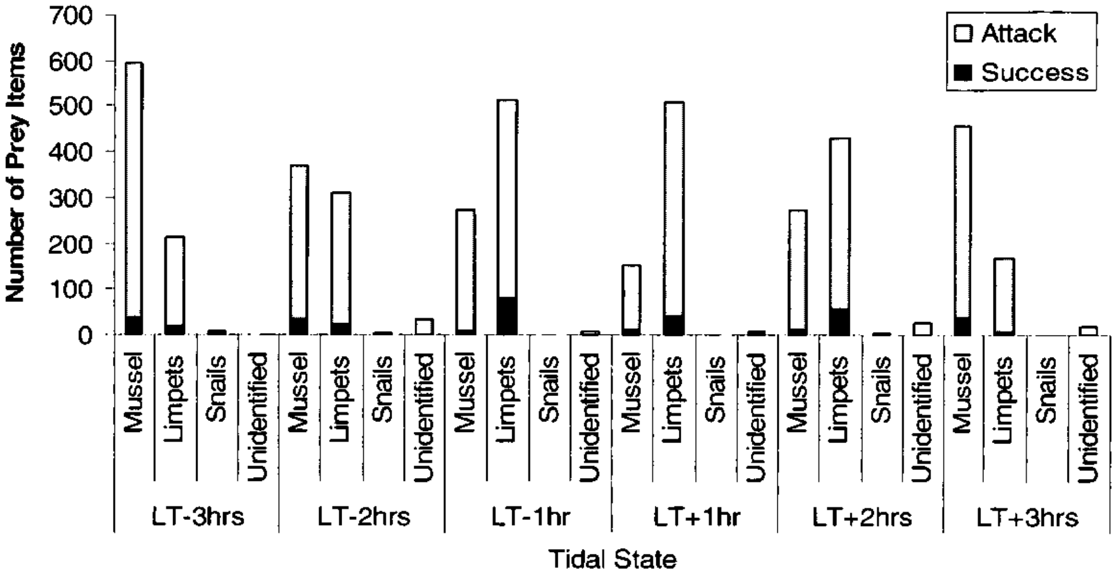
(b)

Figure 22. The mean number of successful feeds on mussels, limpets and snails (a) and the mean number of successful feeds on prey items <7.5mm, <15mm, <22.5mm, and ≥22.5mm in length (b), at Low Tide-3hrs, LT-2hrs, LT-1hr, LT+1hr, LT+2hrs, LT+3hrs. A total of 72 birds were observed for a 300 second period. Untransformed results are shown (mean ± SE).

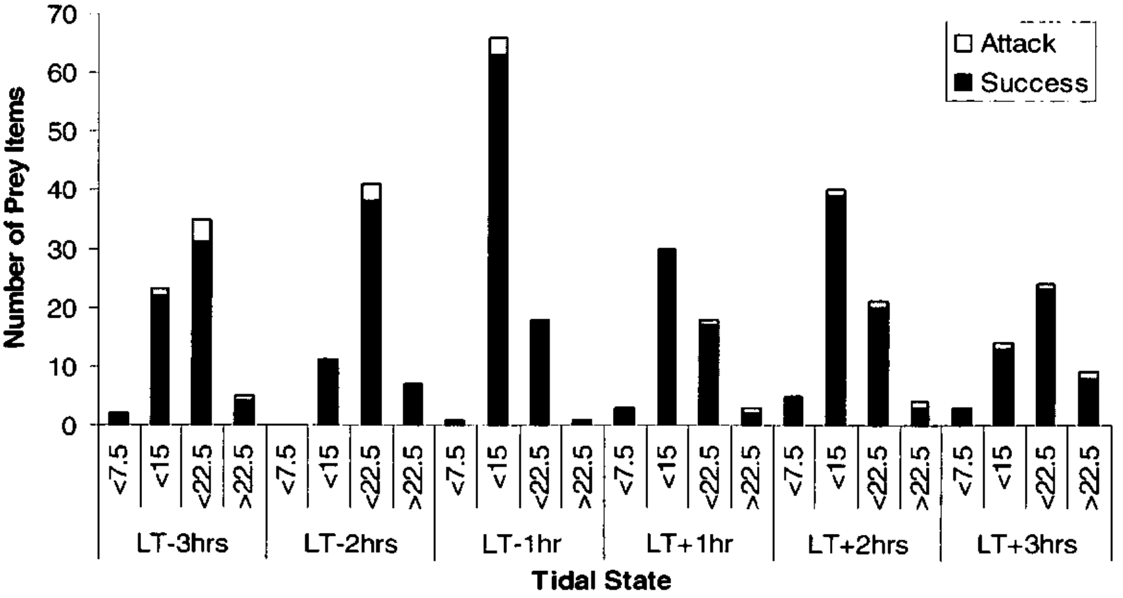
Oystercatchers were more likely to have a successful feeding attempt when foraging on limpets instead of mussels as the tide began to ebb at the beginning of the study period (LT-3hrs, odds ratio ω of 1.524) and just before the shore was completely uncovered at low tide (LT-1hr, odds ratio ω of 6.767), but very slightly more likely to have a successful feed when feeding on mussels, mid ebb (LT-2hrs, odds ratio ω of 1.164) (Figure 23 a). However, only the LT-1hr result was significantly different from the null ratio of 1 (Table 10 a). As the tide flooded oystercatchers were more likely to have a successful feeding attempt when feeding on limpets compared to mussels (Figure 23 a; Table 10 a), however only the LT+1hr result, where birds were 92% more likely to have a successful feed if foraging on limpets instead of mussels, was significantly different from the null ratio of 1 (Table 10 a). Ultimately it seems that oystercatchers are much more likely to have a successful feed when foraging on limpets as opposed to mussels. Oystercatchers did not differ significantly in their chance of having a successful feed compared to a non-successful feed when foraging on different prey sizes (Figure 23 b; Table 10 b).

4.3.7. Prey Selection, Handling Time and Successful Feeds

Data for the time that oystercatchers took to handle and successfully feed upon limpets and mussels of various sizes was found to have significant heterogeneity of variance, and so was $\log_{10}$ transformed prior to analysis. The amount of handling time oystercatchers required to ensure a successful feed was significantly different for mussels and limpets (Homogeneity of slopes: $F_{(1,346)} = 0.552$, NS; Homogeneity of intercepts: $F_{(1,347)} = 68.862$, $P<0.001$). Oystercatchers took significantly longer to handle mussels than limpets (Figure 24). The time taken to handle both species of prey items increased significantly with prey size (Figure 24). If the regression analyses for handling time are compared to those of AFDM it is apparent that limpets are more profitable prey items than mussels, with respect to the handling time required to successfully feed upon a prey item, and the energy content of the item (Figure 16 and Figure 24). Mussels took longer to handle, and had a slightly lower energy content, than limpets in autumn, winter and spring (Figure 16 and Figure 24); both the energy content and the time required to handle the prey, increased more rapidly for limpets, than for mussels, with increasing prey size (Figure 16 and Figure 24).



(a)



(b)

Fig. 23. The foraging success of oystercatchers feeding on various species (a) and sizes (b) of prey item, at Low Tide-3hrs, LT-2hrs, LT-1hr, LT+1hr, LT+2hrs, LT+3hrs. A total of 72 birds were observed for a 300 second period. The number of attacks and successful feeds are shown. For the species data attacks included handled and pecked prey items, each handled item was recorded as being attacked only once. For the size data, attacks refer to items handled by the oystercatcher only, each handled item was recorded as being attacked only once.

Tidal State	Species of Prey	Odds Ratio (ω)	G-Test (Gadj)
LT-3hrs	Mussel	0.656	2.022 NS
	Limpet	1.524	
LT-2hrs	Mussel	1.164	0.294 NS
	Limpet	0.859	
LT-1hr	Mussel	0.148	35.506***
	Limpet	6.767	
LT+1hr	Mussel	0.52	5.885*
	Limpet	1.923	
LT+2hrs	Mussel	0.434	2.677 NS
	Limpet	2.306	
LT+3hrs	Mussel	0.605	2.232 NS
	Limpet	1.653	

(a)

Tidal State	Length of Prey	Odds of having Success/Non-success	G-Test (Gadj)
LT-3hrs	<7.5mm	3	-0.023 NS
	<15mm	11.5	
	<22.5mm	6.4	
	>22.5mm	2.5	
LT-2hrs	<7.5mm	1	-2.259 NS
	<15mm	12	
	<22.5mm	9.75	
	>22.5mm	8	
LT-1hr	<7.5mm	2	-2.212 NS
	<15mm	16	
	<22.5mm	19	
	>22.5mm	2	
LT+1hr	<7.5mm	4	-2.815 NS
	<15mm	31	
	<22.5mm	19	
	>22.5mm	1.5	
LT+2hrs	<7.5mm	6	-0.848 NS
	<15mm	20	
	<22.5mm	10.5	
	>22.5mm	2	
LT+3hrs	<7.5mm	4	-0.729 NS
	<15mm	7	
	<22.5mm	12	
	>22.5mm	4.5	

(b)

Table 10. a) The odds of having a successful feeding attempt when feeding on mussels compared to limpets at various states of the tide. The odds ratios were tested for independence using G-tests, with the Williams correction (NS – Non-significant $P>0.05$; *$P<0.05$; **$P<0.01$ and ***$P<0.001$). b) The odds of having a successful feeding attempt compared to a non-successful feeding attempt when feeding on various sized prey items at various states of the tide. Size data was analysed with *RxC* tables for tests of independence using G-tests.

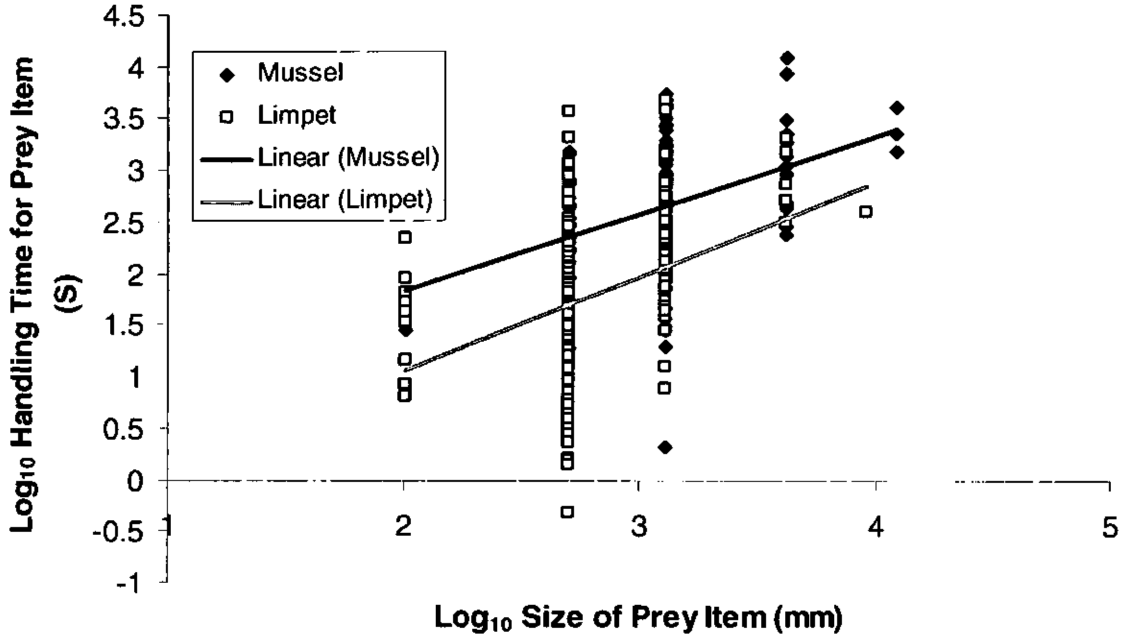


Fig. 24. The relationship between the $\log_{10}$ length of a prey item and the $\log_{10}$ handling time (seconds) required to successfully feed upon it. Data for mussels and limpets are shown. Snails were not included in the analysis due to the fact that they could be swallow whole or were simply plucked, and thus often were not handled, providing very few data points. **Mussels** $y = 0.749x + 0.331$, $R^2 = 0.136$, $F_{(1,135)} = 21.24$, $P < 0.001$; **limpets** $y = 0.916x - 0.776$, $R^2 = 0.155$, $F_{(1,211)} = 38.57$, $P < 0.001$.

The number of successful feeds oystercatchers had on mussels and limpets differed significantly with their size ($G_{adj} = 113.340$, df = 3, $P < 0.001$). Oystercatchers had a greater number of successful feeds when foraging on limpets smaller than 15mm in length than mussels of the equivalent size (Figure 20). However oystercatchers had a greater number of successful feeds when foraging on mussels larger than 15mm in length compared to limpets of the equivalent size (Figure 25).

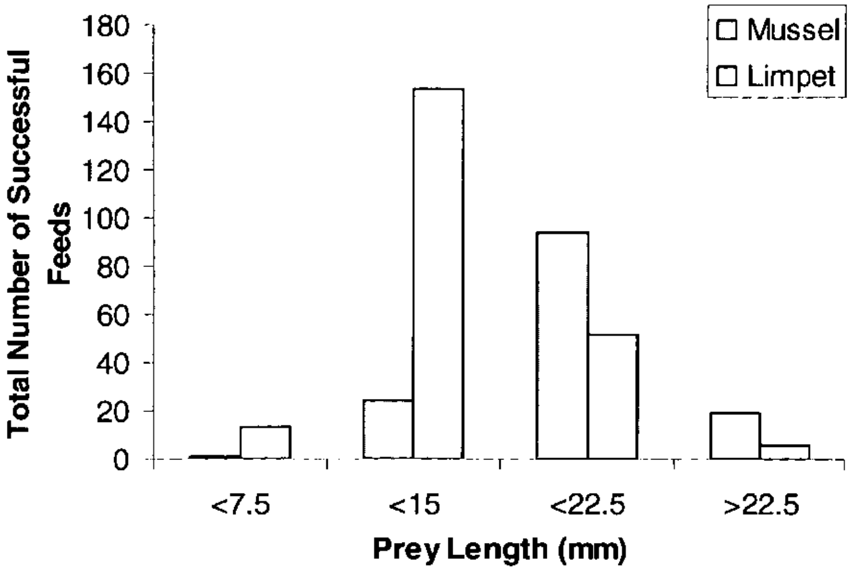


Fig. 25.. The frequency of successful feeds upon mussels and limpets, <7.5mm, <15mm, <22.5mm and >22.5mm in length.

4.3.8. Intake Rate and Patch Quality

The relationship between the intake rate of oystercatchers and the energy content of the areas they fed in, differed between seasons (Homogeneity of Slopes: $F_{(2,66)} = 6.283$, $P < 0.01$). Data for the intake rate of oystercatchers feeding in areas with varying energy content was found to have significant heterogeneity of variance, and so was transformed prior to analysis. LN (X+1) transformation was used to remove the effect of zero values. No relationship was found between oystercatcher intake rate and AFDM/m^2 during the spring ($R^2 = 0.002$, $F_{(1,16)} = 0.037$, NS), but significant relationships were found in the autumn ($y = 3.100x - 30.768$, $R^2 = 0.188$, $F_{(1,28)} = 6.481$, $P<0.05$) and winter ($y = -0.780x + 12.562$, $R^2 = 0.298$, $F_{(1,22)} = 9.357$, $P< 0.01$) (Figure 26). In the autumn the birds had a higher energy intake rate when feeding in an area with a high energy content, but interestingly, in the winter the opposite was true (Figure 26).

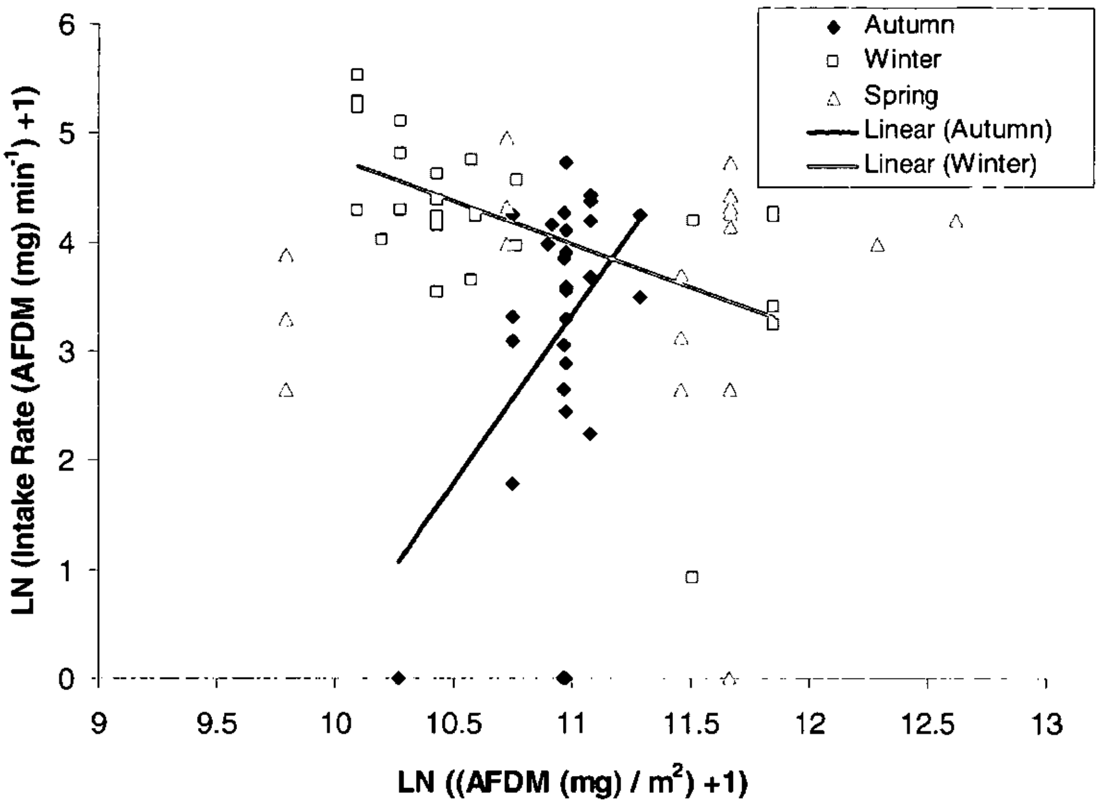


Fig. 26. The relationship between the mean AFDM (mg)/m^2 of the area the oystercatchers were feeding in and their intake rate (AFDM (mg)/ min^{-1}). The relationship between the intake rate of birds and the energy content of the area they were feeding in differed with season (Homogeneity of slopes: $F_{(2,66)} = 6.283$, $P<0.01$); a significant relationship was found in autumn ($y = 3.100x - 30.768$, $R^2 = 0.188$, $F_{(1,28)} = 6.481$, $P<0.05$) and winter ($y = -0.780x + 12.562$, $R^2 = 0.298$, $F_{(1,22)} = 9.357$, $P<0.01$) but not in spring ($R^2 = 0.002$, $F_{(1,16)} = 0.037$, NS).

The mean intake rate of oystercatchers foraging on the rocky shore was 57.91mg AFDM per minute (SE = 0.965). Assuming that oystercatchers foraged at this rate for the 6 hours that their rocky shore feeding ground was uncovered, their overall energy intake for the foraging period would be approximately 20.8g AFDM. The maximum oystercatcher intake rate observed was 113.82mg AFDM per minute, if the birds fed at this rate for the duration of their 6 hour foraging period then their overall energy intake would be 40.97g AFDM.

4.4. Discussion

4.4.1. Bird Behaviour and Tidal State

Oystercatchers did not vary in the time they spent handling, their foraging and handling efficiency, or their intake rate with the state of the tide. These results, support those described in chapter 3 (Figure 14 a & b) and show that oystercatchers did not appear to demonstrate any change in their foraging behaviour as the tide ebbed and flooded. They did not decrease the time they spent vigilant in order to devote a greater proportion of their time to feeding, nor increase their attack rate/foraging intensity, or success rate by becoming more efficient at handling or foraging, as the tide signalled an end to their foraging period. These results contradict those of Swennen *et al.* (1989). Most importantly oystercatchers did not vary in their intake rate, which could indicate one of two things, i) that the birds were unable to increase their intake rate as the tide came in, as they were already feeding at their maximum capacity based on either their internal (Kersten & Visser 1996a) or external processing of food items (Wanink & Zwarts 1996e, Meire 1996). Or ii) that they had no need to increase their intake rate as they either had another foraging site that they could use at high tide (Heppleston 1971a), could forage on the rocky shore at night (as demonstrated by the African black oystercatcher although less successfully compared to daylight foraging (Hockey & Underhill 1983)) or had already met their energy requirements. It is unlikely, however, that the birds would have met their energy requirements over the observed period. If the average energy intake per 5 minutes of an oystercatcher, observed feeding on the rocky shore throughout the tidal cycle, is extrapolated up to the six hours over which the shore was exposed, the oystercatcher's overall energy intake over the foraging period was only approximately 21g AFDM. This is almost 60 % of the minimal 36g of AFDM estimated to be required by free-living oystercatchers under thermo-neutral conditions, and just over 40% of the estimated 50g of

AFDM required when temperatures drop to 0°C (Kersten & Piersma 1987, Zwarts *et al.* 1996d). This suggests that the birds must either feed elsewhere at high tide (Velasquez & Hockey 1992, Heppleston 1971a) or at night (Goss-Custard & Verboven 1993, Hockey & Underhill 1983) to meet their energy requirements. It was assumed that if the birds could increase their intake rate during the low tide period that they would, as foraging at night on the rocky shore may increase the chance of bill damage, thus requiring the birds to forage with care and causing foraging time to be extended at the expense of other behaviours. Similarly, foraging in a supplementary area such as a field, either during the day or at night may increase the bird's predation risk, requiring it to demonstrate elevated vigilance at the cost of foraging. Terrestrial feeding increases the risk of attack by predatory mammals such as foxes and by raptors, by increasing the individual's proximity to cover (Whitfield 2003b, Cresswell 1994a), whilst feeding at night may inhibit predator detection. Furthermore the supplementary ground is likely to be a less profitable feeding area; in all cases the birds may have to work harder to retain a limited amount of energy. Goss-Custard and Durell (1987) found that free-living oystercatchers fed at half the rate at night-time compared to during the day; whilst work on captive and free-living oystercatchers have shown intake rate to be variable, but night-time intake rates not to differ significantly from day-time intake rates (Kersten & Visser 1996b, Hulscher 1974, Davidson 1967). Alternatively it could simply be that by extrapolating a five-minute observation to 6 hours the already large amount of error associated with intake rate becomes much bigger causing an underestimation of overall energy intake to occur. Furthermore the energy requirements of free-living oystercatchers foraging on the south-west coast of Britain during the winter months may be significantly less than those required by oystercatchers foraging in the more northern parts of Europe. Unfortunately, to date, only the energy requirements of over-wintering oystercatchers in northern Europe have been documented (Goede 1993, Kersten & Piersma 1987, Swennen *et al.* 1989).

4.4.2. Oystercatcher Prey Choice with Prey Abundance

Oystercatchers appeared not to feed on prey species according to their abundance on the rocky shore with changing season. The birds appeared to actively select for limpets, as they fed upon them much more frequently than would be expected based on their abundance over the whole shore, whilst the opposite was true for mussels; such results could reflect the profitability associated with each prey type (Figure 16 a-c and Figure 24). Limpets were found to be relatively quick and easy to handle; generally dislodged from the substrate with one forceful blow, they were flipped over and their flesh cut away from the shell and consumed (Feare 1971; Hulscher 1996 and references therein). In comparison, mussels required much more time, care and attention, either a continuous battering to the side of the shell in order to create a small hole into which the bird inserted it's bill or a precise and rapid stab through the small gap between the valves in order to sever the posterior adductor muscle, before the flesh was cut out and consumed (Hulscher 1996 and references therein). In addition, the energy content of a limpet was slightly greater than that of a mussel, and remained so across all prey sizes (Figure 16 a-c). Furthermore, oystercatchers were, in general, also much more likely to have a successful feeding attempt when attacking limpets (attacks referring to the number of pecks and the number of handling bouts associated with a prey item). This is probably a factor of the handling method associated with limpets; limpets may become available with one peck or two pecks if dislodged, mussels on the other hand may be subjected to a number of heavy blows if being hammered, attacks which will not necessarily result in a successful feed. Thus mussels incur a greater amount of wasted foraging time, reducing profitability. It may be that handling a mussel also carries a higher risk of bill damage; vigorous hammering of mussel shell could cause parts of the mandible to snap off, thus restricting feeding, whilst a failure to sever the adductor muscle when stabbing could result in the mussel clamping down upon the bill and can cause death through starvation (Hulscher 1988 *loc. cit.* Hulscher 1996).

Mussel abundance does not necessarily reflect potential oystercatcher food if many of the mussels fall out side the size range eaten by oystercatchers. Furthermore, the number of mussels fitting the oystercatcher's criteria may have been significantly reduced if the birds were selecting only thin-shelled mussels, which are usually more profitable (Durell & Goss-Custard 1984, Meire & Ervynck 1986, Sutherland & Ens 1987, Cayford & Goss-Custard 1990), have a lesser parasitic load and little water content (Norris 1999, Nagarajan *et al.* 2002).

Interestingly other gastropods were found to be the most energy rich prey items, for the prey sizes taken by oystercatchers throughout this study, and were the easiest to handle with smaller items being swallowed whole (*Gibbula* spp., *Littorina* spp, and *Monodonta lineata*), whilst larger items had their flesh simply pulled from their shell through their aperture (*Nucella lapillus*) (Feare 1971). However, other gastropods were only taken approximately in proportion to their abundance on the shore. This may be because they are often hidden under seaweed or in the crevices of rocks, and are difficult to reach (*Pers. Obs.*), or because oystercatchers foraging on *Nucella lapillus* do not consume all the flesh, only the head, foot and operculum, which reduces the energy they provide (Feare 1971). Alternatively it could be that although the external handling time required for snails is very small, the internal processing of snails, swallowed whole, is a lot longer; snail shell would take up space in the gut, and as oystercatchers are known to be restricted by a digestive bottleneck whilst feeding (Kersten & Visser 1996a), this loss of valuable space could be a disadvantage. Thus it may be oystercatchers are semi-opportunistic, and do not actively search for other gastropods but are willing to feed upon them if encountered whilst searching or foraging; which may be similar to the way in which they feed on 'other' prey items, such as crabs, worms and fish.

Oystercatchers appeared not to feed on different sized prey items relative to their abundance on the shore. They ignored many of the very small prey items, feeding instead primarily upon prey items between 11mm and 30mm in length in autumn and winter, and 21-30mm in spring. Prey items that were very small were abundant but were not as profitable, whilst very large prey items were worth more energetically but were very low in abundance. Larger prey items would possibly be more difficult to open or dislodge from the rocks and so the chance of bill damage is likely to increase significantly with prey size (Zwarts *et al.* 1996d). In comparison, medium sized prey items were abundant, were reasonably easy and potentially safer to handle, and provided a moderate amount of energy. In this study oystercatchers were found to feed to a greater extent upon mussels that were a larger size and limpets that were smaller. Based on the energy content of mussels and limpets, oystercatchers could be ingesting approximately the same amount of energy when taking larger mussels and smaller limpets. Interestingly, the prey sizes predominantly taken by oystercatchers throughout this study were within the size range of the limpets selected by European oysterctachers (Feare 1971, Coleman *et al.* 1999), African black oystercatchers *Haematopus moquini* (Hockey & Underhill 1984), and black oystercatchers *Haematopus bachmani* (Hartwick 1976) observed on rocky shores; but at the lower end (almost equal to the size below which items were rejected) of the size range of mussels taken in estuarine habitats (Zwarts & Drent 1981, see Zwarts *et al* 1996v for summary). This was, to some extent, explained by the abundance of each size class; as there were so few larger prey items present on the rocky shore, the size range taken was reduced. However it could also be an indicator of stress, i.e. the birds being less selective, simply taking the prey they encounter when pushed for energy, or as a precaution against bill damage, the chance of which occurring may be heightened when foraging on the rocky shore.

There are, however, possible restrictions to the conclusions that can be reliably drawn from the prey abundance/ prey choice data. It has long been established that the predominantly sessile species that inhabit the sloping rocky shore are not dispersed uniformly but are instead distributed along a gradient from upper to lower shore dependant upon their tolerance to desiccation and their competitive ability (Stephenson & Stephenson 1949, Connell 1961, Norton 1985). The abundance of various prey species available to a focal bird will therefore vary dependant upon the bird's position on the shore, which is further dependant upon the state of the tide at the time (see section 4.4.3.). The random and haphazard approach used to sample the shore during this study only provides information about the abundance of prey over the whole shore and is only representative of availability when the tide is completely out. As there were no data collected to analyse the availability of various prey species and sizes at different states of the tide it is uncertain whether, at times, oystercatchers actually are selecting the most abundant prey species/ sizes in their specific feeding area. It could be argued, however, that on a rocky shore that has a higher structural complexity, such as the shore used during this study, prey distribution may more homogeneous. Deep gullies and large rock pools can provide some organisms, less tolerant of desiccation and thus associated with the lower shore, with suitable habitats higher up the shore. Similarly, organisms that are usually found at higher shore levels, where there is less competition as organisms are exposed for longer periods of time, may occupy the lower regions of the shore if situated upon large rocks. Thus, it may be that on structurally complex shores, where large rocks, deep gullies and rock pools dominate, the distribution of various oystercatcher prey species is more homogeneous than on gently sloping shores. If oystercatcher prey species were distributed more uniformly along the shore of Trebetherick it may be expected that wherever oystercatchers were situated there would be approximately the same proportion of each prey species available to them. Sampling the abundance of various prey species over the whole shore should then yield results similar in proportion to those gained if stratified sampling had been used.

Due to the sampling method employed the prey abundance/ prey choice data must be considered with caution. However, whilst the state of the tide may change the availability of limpets and other gastropods, it seems unlikely that at any point mussels would have been unavailable to the oystercatchers, as mussels appeared to dominate the shore. Ultimately mussel abundance was much higher than limpet abundance and yet oystercatchers fed more frequently upon limpets than mussels, suggesting that oystercatchers are being selective.

4.4.3. Effects of Tide on Oystercatcher Prey Choice

Prey selection changed as the tide ebbed and flooded, which is likely to be a factor of availability on the rocky shore (de Vlas *et al.* 1996). Oystercatchers foraging on the rocky shore often fed near to the tide line where prey items became more accessible; mussels gaped underwater in the shallows or were closed only loosely having just been uncovered, and limpets were only loosely clamped down upon the damp rock. Oystercatchers fed on mussels at the beginning of the observation period probably because they were the first available prey type to be uncovered as the tide ebbed. Patches 1 to 3, which were mussel dominated, were both the first to be uncovered and occupied by the birds (Figure 15, *Pers. Obs.*). As the tide retreated, limpets and mussels were fed upon to a similar extent, probably due to increased availability, or abundance, of limpets, although transects of the shore were not taken and so there are no data to support this hypothesis. Just before low tide, limpets were fed upon to the greatest extent, which is unsurprising as there was both a higher chance of having a successful feed when foraging upon limpets and they were more profitable, compared to mussels. As the tide flooded, an almost exact mirror trend was found for prey selection. Oystercatchers fed on all prey sizes to a similar extent as the tide ebbed, at mid-ebb items between 15mm and 22.5mm in length were taken over other prey sizes, whilst just before low tide the majority of prey items fed upon were between 7.5 and 15mm in length; this may be a factor the prey species taken. The oystercatchers may simply be opportunistic when foraging on mussels on the upper shore taking those items that are gaping and are thus easier to feed on. Limpets were predominantly fed upon just before low tide and the species of limpet that is found at the lower tidal levels, *Patella depressa*, is often a lot smaller than the species that dominates the higher shore, *P. vulgata*, and so this could account for some of the drop in the prey size taken. As the tide came in, oystercatchers took all prey items to a similar extent, although more 7.5-15mm items were taken compared to larger (>22.5mm) or smaller (<7.5mm) items. This may indicate an opportunistic approach to foraging as the tide advanced signalling an end to their foraging at that site, with oystercatcher prey choice being governed by species availability.

Oystercatchers did not differ in their chance of having a successful feeding attempt with various prey sizes; surprisingly the birds were no more likely to have a successful feeding attempt when feeding on smaller prey items compared to when feeding on larger items. This differs from Norris and Johnstone's (1998) study on oystercatchers feeding on bivalves on the Burry Inlet estuary, where the probability of a successful feed as a result of an attack decreased with increasing cockle size. However, these results are likely to be a function of the definition of handling used throughout this study. It was difficult for the observer to estimate prey size from one exploratory peck, so prey size could only be estimated when an oystercatcher was continuously attacking an item; throughout this study, handling referred to the sum of the time taken for oystercatchers to free flesh from a prey item previously opened and the amount of time the oystercatchers spent continuously battering or pecking at a rapid rate the same prey item in order to open/dislodge it. Thus the attacks recorded for the prey size data represented items that were handled/ continuously pecked at a rapid rate, and often did not include exploratory pecks or the initial forceful blows that failed to dislodge a limpet or penetrate a mussel. Handling often occurred once the item had been made available and involved retrieving the flesh from the shell, thus the handling of a prey item rarely resulted in a non-successful feed. In comparison, the type of prey, could be distinguished by the observer from a single peck, by the way in which the birds angled their heads for an attack. A peck was likely to be either exploratory, or an attempt to dislodge a limpet or penetrate a mussel and often resulted in a failed feeding attempt, thus the birds appeared to be much more efficient at feeding when the size data was analysed compared to the species data. This is, however, simply a consequence of the way the observational data was collected. Thus analysis of the prey species data is much more sensitive to changes in efficiency than analysis of the size data.

Oystercatchers did not vary their intake rate with the energy present within the area in which they were foraging, in spring, but they did in autumn and winter. As expected, in autumn, oystercatcher intake rate increased with increasing energy available on the shore, which is probably a factor of increased encounter rate. Surprisingly, however, oystercatcher intake rate in winter decreased with increasing energy available. This reduction in intake rate is not due to increased interference as a result of an increase in the density of birds foraging in the most profitable patches (Goss-Custard 1980; Sutherland & Koene 1982), as bird density was always relatively low at less than 4 oystercatchers ha^{-1} (Chapter 3). It may instead be due to the fact that in the winter limpets, which appear to be the birds preferred prey type, were at low densities in comparison to the high densities of mussels (Figure 20 b), thus the overall energy content was high but the prey species the birds are actually feeding on were not that prevalent, thus their intake was reduced. This did not occur in autumn and spring because the birds fed on prey items in a greater relation to their abundance on the shore (Figure 20 a & c).

The intake rates observed for oystercatchers foraging on the rocky shore were within the range of those reported in estuarine environments (Zwarts *et al.* 1996e). With an average intake rate of 60mg AFDM min^{-1}, over a 6 hour foraging period, the overall food consumption by rocky shore oystercatchers appears to be equal to the predicted limit to intake set by the digestive bottleneck (Kersten & Visser 1996a). If the birds are feeding at their maximum capacity, based on the space available in their digestive tract and their internal processing rate, or their natural foraging ability, why are there so few oystercatchers using the rocky shore as a feeding resource? Does foraging on the rocky shore increase risk in the form of bill damage or predation? Can oystercatchers forage on the rocky shore at night to fulfil their energy requirements? If so, is foraging in the dark risky? If not, and they have to feed on supplementary grounds such as fields, is their foraging efficiency reduced due to less experience of foraging, by touch, in soft substrates? Such questions were beyond the scope of this thesis but would be an interesting basis for future work.

In summary, oystercatchers on the rocky shore forage mostly on limpets regardless of the greater abundance of mussels. This is likely to be due to the ease with which limpets can be handled and the energy they provide. Other gastropods are taken the least even though they appear to be the most profitable prey items. This could be because they inhabit crevices that are difficult for oystercatchers to access, or because oystercatchers do not consume the entire flesh, thus reducing their profitability. It may also be that small gastropods, if swallowed whole, incur a large amount of internal handling time and their shells take up valuable space within the gut. Certainly, if the birds are pushed to meet their energy requirements they may need to feed constantly and do not want to be restricted by their digestive bottleneck.

Chapter 5: Effect of Human Disturbance on Oystercatcher Prey Selection on the Rocky Shore

5.1. Introduction

Most animals must balance gaining energy with avoiding predation (Lima *et al.* 1985, Lima & Dill 1990, Lima & Bednekoff 1999b, Caraco *et al* 1980, Dill & Fraser 1984). In theory, the risk of predation should outweigh the potential risk of starvation, as starvation generally occurs due to a frequent failure to meet daily energy requirements whilst one failure to detect a predator can result in immediate death or serious injury (Lima & Dill 1990). For foraging wading birds, however, when energy requirements are high or energy intake restricted by interference and competition from more dominant individuals, short-term trade-offs between energy intake and predator avoidance are apparent, as individuals feed in riskier conditions but where their intake rate is higher (Cresswell 1994a, Hilton *et al.* 1999b). It may be that for large foraging waders, predation events are relatively infrequent (Whitfield 1985, Houston 1996), compared to death by starvation, and so the birds are willing to heighten their predation risk when the potential for starvation is increased.

Disturbance from recreational activities cause birds to lose foraging time to monitoring and then time and energy in fleeing from the potential threat (Coleman *et al.* 2003, de Boer & Longamane 1996, Fitzpatrick & Bouchez 1998, Smit & Visser 1993, see Chapter 4). Many studies have shown that birds subjected to human recreational disturbance increase their vigilance at the cost of time spent foraging (Frid & Dill 2002, Burger & Gochfeld 1998, Fernández-Juricic & Tellería 2000, Fernández-Juricic *et al.* 2003, Smit & Visser 1993). Lost foraging time infers less energy intake, assuming that the birds were foraging at their maximum level. Compensatory mechanisms used to recover lost foraging time, may include extending the foraging period by feeding at night (Robert & McNeil 1988, Goss-Custard & Verboven 1993, Hockey & Underhill 1984, 1987b, Kersten & Visser 1996b) or feeding in supplementary areas, such as fields, at high tide (Heppleston 1971a, Velasquez & Hockey 1992, Caldow *et al.* 1999, Goss-Custard & Durell 1983). If, however, the birds were not feeding at their maximum level prior to disturbance, then any loss of energy intake as a result of disturbance may be offset by increasing foraging intensity (Swennen *et al.* 1989, Stock & Hofeditz 1997, Fitzpatrick & Bouchez 1998), and thus energy intake after the disturbance event has ceased. Foragers have the ability to increase their intake rate and simultaneously reduce their energy expenditure by feeding in patches where prey density is high; a higher encounter rate means fewer steps and shorter bouts of searching in between finding and handling prey items allowing more items to be processed in the allotted foraging period. Alternatively, they could reduce the level of their baseline vigilance (Metcalfe & Furness 1984), feed on larger, more energetically valuable or profitable prey items (Sutherland 1982b, Meire & Ervynck 1986, Cayford & Goss-Custard 1990), or attempt to handle prey items at a faster rate (Swennen *et al.* 1989, Wanink & Zwarts 1996), which could increase the potential for bill damage. In addition, during the actual disturbance event, individuals may attempt to maintain energy intake by changing their prey choice (see Lima & Dill 1990 for review), perhaps by foraging on mainly smaller items that can be consumed quickly in between vigilance scans, or species of prey that require less handling time (Sih 1993). For example, the flesh of most gastropods may simply be plucked from their shells (Feare 1971) in between scans of the environment, whilst the retrieval of mussel flesh requires a greater amount of time and accuracy especially when there is a risk of bill damage (Norton-Griffiths 1967; Hulscher 1996), possibly making it difficult for individuals to effectively handle their prey item whilst simultaneously being vigilant.

Oystercatchers foraging on rocky shores are often subject to harsh environmental conditions. Cold weather and strong winds can make it difficult for the birds to meet their daily energy requirements as their thermoregulatory demands increase, and therefore affect oystercatcher health and increase mortality (Heppleston 1971a, Baillie 1980, Davidson & Evans 1982, Swennen & Duiven 1983, Kersten & Brenninkmeijer 1995, Goss-Custard *et al.* 1996a). The baseline daily energy requirement for free-living oystercatchers at thermo-neutral conditions is estimated at 36g AFDM, if temperatures fall lower than 10°C this value can increase up to 50g AFDM (Kersten & Piersma 1987, Goede 1993). Time budgets in the winter are frequently tight, with oystercatchers feeding at a rate greater than 1mg AFDM s^{-1} having to feed for anywhere up to an estimated 14 hours a day when temperatures are below 10°C, and 10.5 hours a day when temperatures are above 10°C in order to meet their target intake (Zwarts *et al.* 1996d). For oystercatchers on the rocky shore that feed at rates less than 1mg AFDM s^{-1} the time required for feeding may be significantly longer (Chapter 4). The structural complexity of the rocky shore is likely to increase an individual's perceived predation risk by restricting it's view of it's environment and determine that vigilance and foraging are mutually exclusive (Metcalfe 1994), thus forcing the birds to exhibit enhanced levels of vigilance at the cost of foraging. When a potential threat is present energy intake is likely to decline significantly as the birds monitor the threat, and energy expenditure increase as the birds flee from the threat, possibly forcing the birds to extend their feeding time in compensation and putting pressure upon their time budgets (Pfister *et al.* 1992, Urfi *et al.* 1996, Rodgers & Smith 1997, Burger & Gochfeld 1998, Coleman *et al.* 2003).

It is imperative that the birds have a high enough energy intake to support themselves throughout the winter months, and for breeding adults to have acquired enough energy by the spring for migration to their northern breeding grounds (Dare 1977). An increase in human recreational disturbance in coastal areas over recent years, and its extension throughout the winter months, could cause problems for foraging oystercatchers, as time previously dedicated to foraging is traded-off with vigilance (Coleman *et al.* 2003, See Chapter 2). Temporal and energetic costs associated with monitoring and fleeing from a disturbance event place extra pressure on the birds, and unless the birds have some compensatory mechanism, is likely to have a detrimental effect upon them.

The aims of this chapter were to establish whether any reduction in foraging time, due to the increased vigilance expected to be demonstrated by the birds during a disturbance event, was compensated for either at the time of the disturbance or after the disturbance had ceased. The hypotheses were that oystercatchers would compensate for lost foraging time by a) feeding with greater efficiency, or b) by feeding on items that were easier to find/abundant, or c) by feeding on prey items that were easier to handle and consume whilst monitoring the disturbance, or d) by feeding on more profitable prey items after the disturbance event had ceased. It was also hypothesized that e) individuals would allow a disturbance agent to approach to a closer proximity before taking flight if the patch they occupied had a higher energy content.

5.2. Methods

See the Study Site and General Methodology described in chapter 2.

5.2.1. Disturbance and prey selection

A focal bird was observed for 300s and components of its foraging behaviour recorded in real time using a cassette tape recorder. The behaviours recorded included the number and direction of steps, the number of pecks and successful feeding attempts and the proportion of their observed feeding time that the birds spent with their head down/searching, and handling. A peck was defined as one single strike of a prey item. A successful feeding attempt was easily identified as the birds raised their heads and moved their necks in a swallowing motion. Searching/head down referred to the bird being in a head down orientation (length of bill vertical to the shore or at an angle from the shore of <50 deg) when either stationary or moving, and handling was defined as when an individual was continuously either handling or attacking a prey item regardless of success. The size and species of prey items handled or successfully fed upon were also recorded. Prey size was estimated by comparing the length of the prey item to the bill length of the oystercatcher handling it (Goss-Custard *et al.* 1987). Oystercatcher bill length ranges from 65mm to 85mm (Goss-Custard *et al.* 1987) and so a mean of 75mm was the assumed length for all oystercatcher bills. Such a method of size estimation is open to error (Goss-Custard *et al.* 1987), but due to the length of the observation period, the tidal cycle and the need to restrict disturbance, no other method was viable and so a calibration exercise was conducted to highlight observer bias. The calibration exercise (described in chapter 4) indicated the observer's identification of prey species to be nearly 100% accurate and precision of estimation of prey size to lie within 3mm of the actual prey size. The time and position of any incidental disturbance was also noted. Intake rate was calculated using the observed prey size and species successfully eaten and their associated energetic value, see Energy Content of Prey Items as described in Chapter 4.

Six oystercatchers were observed per day, three before (ebb) and three after low tide (flood). The birds observed were divided into three groups within the twelve control days (days with no applied disturbance) and twelve disturbance days (when two controlled disturbance agents were applied). 'Pre-disturbance birds' were those observed before the disturbance was introduced on disturbance days and at the equivalent time on control days (Low Tide (LW) –3hrs and LW +1hr). 'Disturbed birds' were those observed specifically for their reactions during the disturbance event on disturbance days and at the equivalent time on control days (LW –2hrs and LW +2hrs), and 'Post-disturbance birds' were those observed after the disturbance had ceased on disturbance days and at the equivalent time on control days (LW –1hr and LW +3hrs). Preliminary observations showed that birds returned almost immediately to the study site if displaced by a disturbance factor, indicating that post-disturbance behaviour could be reliably observed. As the oystercatchers foraged relatively close together (< 10m between individuals, chapter 2) they were all disturbed when the disturbance factor was applied allowing a comparison to be made between the behaviour of a target bird (disturbed) and those associatively disturbed (post-disturbance birds).

Disturbance and control days were conducted on alternate, but randomly assigned, sample days in order to limit confounding. The disturbance event was applied mid-way through both the first and second half of the study period and consisted of a single person approaching a focal foraging oystercatcher along a linear path at a constant speed (average 0.9 metres s^{-1}). The start position of the disturber (distance and angle from the observer) was recorded; the disturbance agent's approach began at the edge of the rocky shore where it was sandy, as very few people ventured past this point on to the rocks (pers obs). The observer recorded the focal bird's behaviour as the disturbance agent approached, until the bird took flight, at which point the disturber remained stationary, and their final position was recorded. The amount of time the focal bird spent with its head down, searching and foraging, was used as an indicator of the individual's sensitivity to disturbance (Burger & Gochfeld 1998; Fernández-Juricic & Tellería 2000; Coleman *et al.* 2003). It was assumed that the amount of time devoted to searching and thus feeding would decline as more time was devoted to monitoring a disturbance. The flight initiation distance, defined as the distance from the disturbance factor at which the bird takes flight was also used to measure the response of birds to the disturbance (Madsen, 1998; de Boer & Longamane 1996). The position of the focal bird before it took flight could be calculated by using the estimated stride length of the oystercatcher in conjunction with the number of steps the focal bird took and the observed general direction it moved in. Oystercatcher stride length has previously been estimated at 0.12m ± 0.03 when searching and 0.18m ± 0.05 when attacking a conspecific (Stillman *et al.* 2002), so a median value of 0.15m was considered to be an appropriate estimate of stride length when retreating from a potential threat. The flight initiation distance was used in conjunction with the energy content of each patch (see Energy Content of Site, as described in Chapter 4) to calculate whether the amount of energy available to an individual within patch affected the distance it allowed a person to approach.

5.2.2. Analysis

The bird behaviour recorded during fieldwork was transcribed into a computer using 'The Observer' 4.0 behavioural software (1998, Noldus Technology, Waginengen). The percentage of time birds spent with their head down, and handling; the peck, success and intake rate, and foraging and handling efficiency, on control and treatment days, were calculated from the data. The results were analysed using ANOVA in the statistical package GMAV (EICC, University of Sydney). The percentage data were arc-sine transformed prior to analysis; and before ANOVA, homogeneity of variance was tested by Cochran's test (Underwood 1997). SNK tests were used for post-hoc comparisons.

The proportion of mussels, limpets, snails and other prey items, eaten by the birds on control and treatment days, in autumn, winter and spring, in comparison to their abundance on the shore were analysed using G-tests adjusted by Williams correction (Sokal & Rohlf 1995). A Kolmogorov-Smirnov two-sample test for large samples was used to compare the frequency of successful feeds on different prey sizes in relation to the frequency at which each prey size was found on the shore following procedures in Sokal and Rohlf (1995).

The number of successful feeds on different species and sizes of prey items, on ebb and flow tides, on disturbance and control days, before, during and after the disturbance, were analysed using ANOVA procedures in GMAV. The prey types included in the analyses were limpets, mussels and snails; the size classes were binned into groups of <7.5mm, <15mm, <22.5mm and ≥22.5mm in order to limit heterogeneity of variance. Prior to analysis, data were log transformed, Ln(X+1), and homogeneity of variance tested using Cochran's test (Underwood, 1997). In cases of heterogeneity of variance persisting after transformation, raw data were used (Underwood 1997, Sokal & Rohlf 1995). As the number of samples in this experiment was large, ANOVA is robust against departures from homogeneity of variance (Underwood 1997, Sokal & Rohlf 1995). SNK tests were used for post-hoc comparisons.

Odds ratios (Sokal & Rohlf 1995) were used to compare the probability of a successful feed when feeding on control and treatment days, ebb and flood tides, before, during and after disturbance, on mussels compared to limpets. The Mantel-Haenszel procedure was adopted as a test of homogeneity of odds ratios for replicated 2x2 tables (Sokal & Rohlf 1995). Where homogeneity of odds ratios was not found G-tests were used for comparison (Sokal & Rohlf 1995). Odds ratios were also used to describe the chance of having a successful feed compared to a non-successful feed when foraging on prey size classes of <7.5mm, <15mm, <22.5mm and ≥22.5mm, on control and treatment days, and before, during and after disturbance. The size data were analysed using a RxC test of independence using G-tests (Sokal & Rohlf 1995).

The handling time associated with successfully feeding on mussels and limpets of various sizes, on treatment days (control day data were analysed in Chapter 4), was analysed using ANCOVA procedures in SPSS (SPSS Inc 1989-2000, Chicago). Snails were not included in the analysis as too few were eaten. The data were analysed using tests of homogeneity of slopes and intercepts to see whether the relationship between the size of a prey item and the handling time required to ensure a successful feed was different for mussels and limpets, dependant upon whether it was a treatment or control day. Prior to ANCOVA, Levene's test for homogeneity of variance was conducted; where heterogeneity of variance was found after transformation, ANCOVA was not conducted; the data was interpreted using scatterplots.

The effect that the energy content per m^2 of the patch which the bird occupied, had on the bird's flight initiation distance in autumn, winter and spring, was analysed using regression and ANCOVA procedures in SPSS. Prior to ANCOVA, Levene's test for homogeneity of variance was conducted; where heterogeneity of variance was found after transformation, ANCOVA was not conducted and the data was interpreted using scatterplots.

5.3. Results

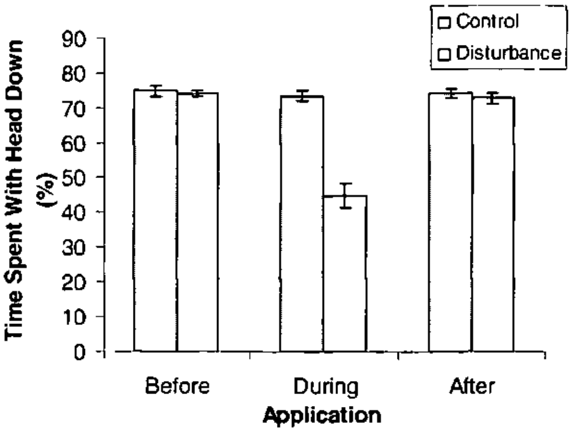
5.3.1. Disturbance and Oystercatcher Behaviour

Oystercatchers spent significantly less time with their heads down/searching, and handling, and had a significantly lower peck rate on disturbance days, during the disturbance period (Table 11). The birds subjected to the disturbance event spent an average 45% and 20% of their foraging time with their head down and handling respectively, compared to an average 74% and 29% as demonstrated by control, pre- and post-disturbance birds (Figure 27 a & b). Peck rate decreased from an average 10 pecks min^{-1} for control, pre- and post-disturbance birds to an average 6 pecks min^{-1} for disturbed birds (Figure 27 c). SNK tests showed that post-disturbance bird behaviour on treatment days did not differ significantly from pre-disturbance bird behaviour (Figure 27 a, b & c, all NS). Success rate and intake rate were not affected by disturbance, but SNK tests showed significant differences between tides (Table 11, $P<0.05$). During ebb tides oystercatchers had 30% more successful feeds and consumed 23% more energy than during flood tides (Figure 27 d & g). Foraging efficiency (the amount of successful feeds in relation to the number of pecks) and the handling efficiency (the amount of successful feeds in relation to the amount of time spent handling) did not vary with disturbance (Figure 27 e & f, respectively, Table 11), as would be expected when peck rate and percentage of time spent handling time was reduced but success rate remained constant. This could also be a factor of large amount of variance in the percentage of time spent handling, as well as the peck and success rates (Figure 27 b, c & d). Foraging and handling efficiency were found to differ between tides (Table 11, Figure 27 e & f), as birds were significantly more efficient at foraging and handling prey items on an ebb tide than on a flood ($P<0.05$), which could be a factor of the size or species of the prey items taken.

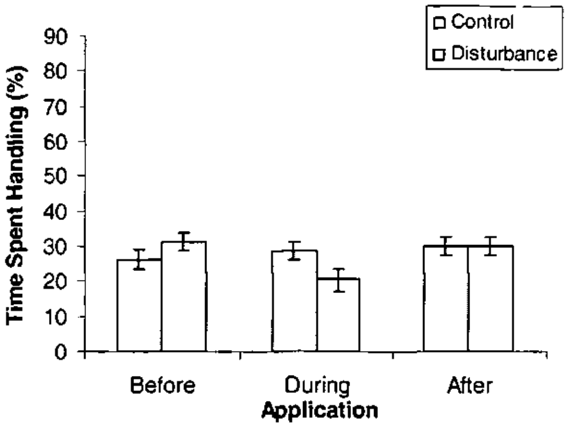
Source	df	Time Spent With Head Down (%)		Time Spent Handling (%)		Peck Rate (Peck/Min)		Success Rate (Successes/Min)	
		MS	F	MS	F	MS	F	MS	F
Tide (Ti)	1	0	0 NS	**429.37**	**4.67***	0.01	1.71 NS	**0**	**4.19***
Treatment (Tr)	1	**1326.12**	**34.16*****	54.05	0.59 NS	**0.03**	**8.20****	0	0.04 NS
Application (Ap)	2	**1282.99**	**33.05*****	**317.07**	**3.45***	**0.02**	**4.87****	0	1.16 NS
Ti x Tr	1	3.3	0.09 NS	26.37	0.29 NS	0	0.9 NS	0	1.04 NS
Ti x Ap	2	57.57	1.48 NS	163.37	1.78 NS	0	1.04 NS	0	2.17 NS
Tr x Ap	2	**1212.96**	**31.24*****	**375.11**	**4.08***	**0.02**	**4.46***	0	1.26 NS
Ti x Tr x Ap	2	6.28	0.16 NS	11.73	0.13 NS	0	0.21 NS	0	0.86 NS
Residual	132	38.82		92.04		0		0	
Total	143								

Source	df	Handling Efficiency (Successes/Handling Time S^{-1})		Foraging Efficiency (Successes/Pecks)		Intake Rate (AFDM(mg)/Min)	
		MS	F	MS	F	MS	F
Tide (Ti)	1	**33.39**	**4.78***	**4.42**	**4.77***	**8079.33**	**3.98***
Treatment (Tr)	1	2.01	0.29 NS	0.13	0.13 NS	1881.43	0.95 NS
Application (Ap)	2	1.82	0.26 NS	0.42	0.45 NS	1390.34	0.70 NS
Ti x Tr	1	14.95	2.14 NS	1.75	1.88 NS	691.24	0.35 NS
Ti x Ap	2	15.59	2.23 NS	0.95	1.03 NS	581.2	0.29 NS
Tr x Ap	2	1.09	0.16 NS	0.18	0.2 NS	3716.66	1.88 NS
Ti x Tr x Ap	2	14.32	2.05 NS	1.02	1.1 NS	1171.03	0.59 NS
Residual	132	6.99		0.93		1977.3	
Total	143						

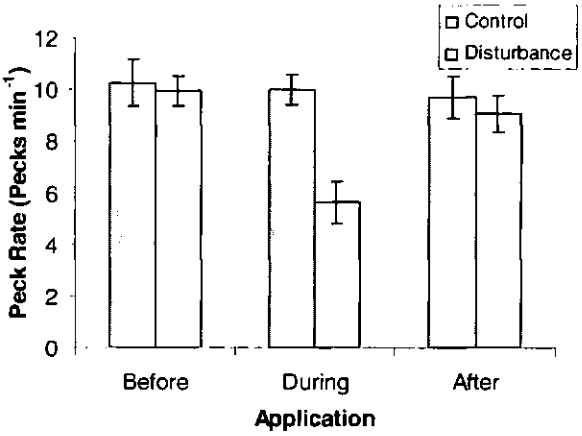
Table 11. Analyses of variance on the behaviour of Oystercatchers on ebb and flood tides (Ti); on control and treatment days (Tr); and before, during and after a disturbance event (Ap) had occurred (NS – Non-significant $P > 0.05$; *$P < 0.05$; **$P < 0.01$ and ***$P < 0.001$). Percentage of time birds spent with their head down and handling, and the proportion of pecks that resulted in a successful feed, were arc-sine transformed prior to analysis. All data were tested for homogeneity of variance by Cochran's test prior to analysis (Head Down: C=0.44, $P < 0.01$; Handling: C=0.22, $P < 0.05$; Peck Rate: C=0.16, NS; Success Rate: C=0.20, NS; Intake Rate: C=0.17, NS; Handling Efficiency: C=0.14, NS; Foraging Efficiency: C=0.18, NS).


Time Spent With Head Down (%)
90
80
70
60
50
40
30
20
10
0
Before
During
After
Application
□ Control
□ Disturbance

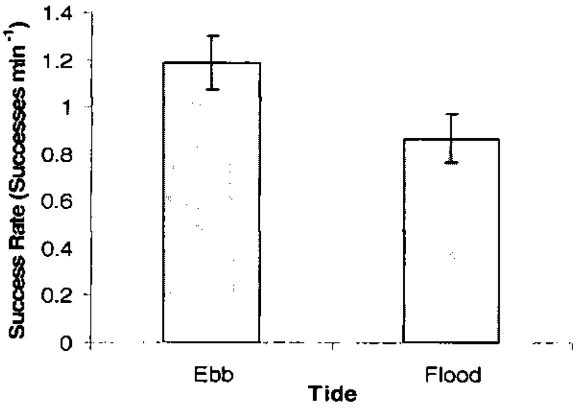
(a)


Time Spent Handling (%)
90
80
70
60
50
40
30
20
10
0
Before
During
After
Application
□ Control
□ Disturbance

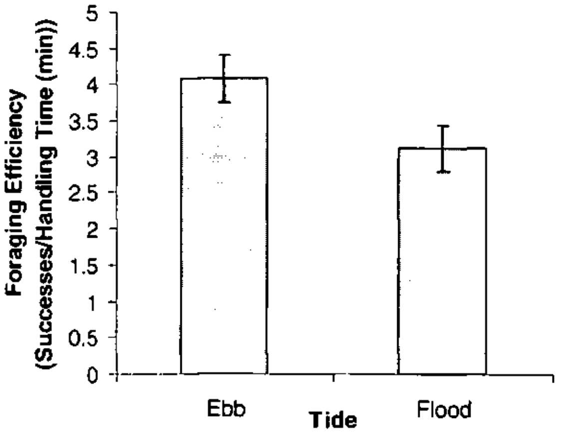
(b)


Peck Rate (Pecks min-1)
12
10
8
6
4
2
0
Before
During
After
Application
□ Control
□ Disturbance

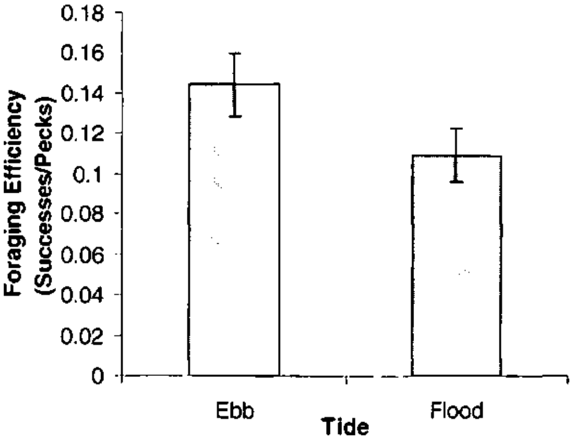
(c)


Success Rate (Successes min-1)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Ebb
Flood
Tide

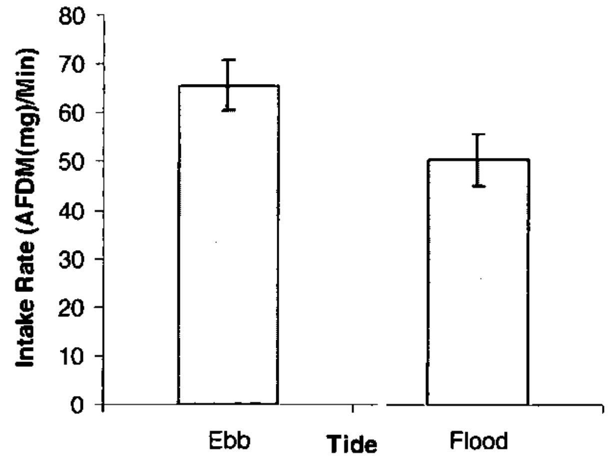
(d)


Foraging Efficiency (Successes/Handling Time (min))
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
Ebb
Flood
Tide

(e)


Foraging Efficiency (Successes/Pecks)
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Ebb
Flood
Tide

(f)



(g)

Fig. 27. The mean percentage of time oystercatchers spent with their head orientated downwards (a), handling prey items (b), and their mean peck rate (c) prior to the experimental disturbance event, during the disturbance, and post-disturbance. The oystercatchers mean success rate (d), and their mean handling (e) and foraging efficiency (f) and their mean intake rate (g) on ebb and flood tides. A total of 144 birds were observed for a 300 second period. Untransformed results are shown (mean ± SE).

5.3.2. Disturbance and Oystercatcher Prey Selection

The number of successful feeds that oystercatchers had on limpets, mussels, snails and other prey types (all other prey types grouped together) on days when disturbance was applied, was significantly different from the abundance of each prey type on the rocky shore in autumn (G_{adj} = 283.472, d.f.= 3, P<0.001; Figure 28 a), winter (G_{adj} = 476.499, d.f.= 3, P<0.001; Figure 28 b) and spring (G_{adj} = 73.658, d.f.= 3, P<0.001; Figure 28 c). In accordance with the control day data analysed in chapter 4, birds observed on disturbance days successfully fed upon more limpets and fewer mussels, than would be expected from their abundance on the shore (Figure 28 a, b & c). On disturbance days in winter and spring, snails were generally eaten relative to their abundance on the shore, however in autumn, slightly more snails were consumed by oystercatchers than was expected (Figure 28 a, b & c).

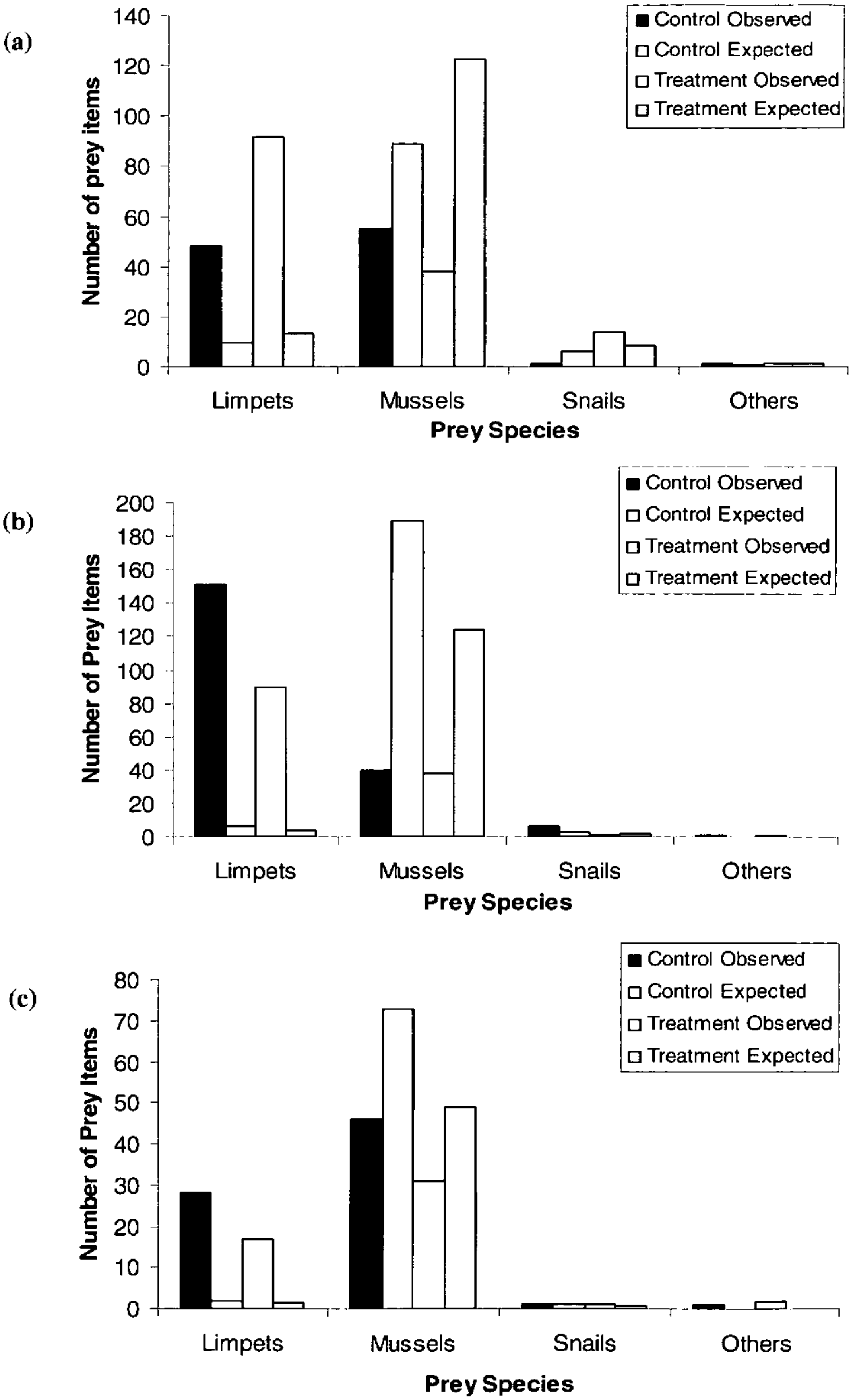


Fig. 28. The mean number of limpets, mussels, snails and other prey items successfully fed upon by oystercatchers (observed) in relation to the number that was expected based on the abundance o each prey type on the shore, in a) autumn, b) winter and c) spring. Data for control and treatmen (disturbance) days are shown. A total of 144 birds were observed for 300s period.

On disturbance days, the prey size distribution for the number of successful oystercatcher feeds was not significantly different from the prey size distribution for abundance, in the autumn ($D = 0.069$, NS, $n_1 = 543$, $n_2 = 125$; Figure 29 a); but the distributions were significantly different in the winter ($D = 0.664$, $P<0.001$, $n_1 = 1961$, $n_2 = 126$; Figure 29 b) and the spring ($D = 0.672$, $P<0.001$, $n_1 = 2307$, $n_2 = 47$; Figure 29 c). These results are in contrast to those found on control days which were analysed in chapter 3, where oystercatchers did not feed on prey sizes relative to their abundance in autumn, winter or spring (Figure 16 a, b & c). However in agreement with control day data oystercatchers observed on disturbance days predominantly fed upon prey items less than 30mm in length in the autumn, items between 11mm and 30mm in length in the winter, and items 21-30mm in length in the spring (Figure 29 a-c).

The number successful feeds that the oystercatchers had on mussels, limpets and snails was found to vary ($F_{(4,396)}=18.00$, $P<0.001$) dependant on whether the tide was ebbing or flooding, and the time in relation to low tide (before, during and after was used as a representation of temporal change in tidal state, in addition to indicating how disturbed the birds were) (Figure 30 a). There was no significant interaction between tide, disturbance, application and the prey species eaten (Table 12). SNK tests showed that oystercatchers feeding on the rocky shore fed predominantly on mussels ($P<0.01$), then on limpets ($P<0.01$) and the least amount on snails as the tide began to ebb at the beginning of the observation period; as the tide retreated mussels and limpets were taken equally over snails ($P<0.01$), until just before low tide when the birds fed mostly on limpets ($P<0.01$) over mussels and snails; this transition from feeding predominantly on mussels to limpets was mirrored almost exactly as the tide advanced (Figure 30 a). Birds fed more on limpets than on mussels and snails ($P<0.01$) up until just before the shore was completely flooded, when they switched to feeding on mussels over limpets and snails ($P<0.01$). Snails were generally the least favoured prey type (Figure 30 a). These results are similar to those observed for the effects of tide on control days (Figure 22 a, Table 9).

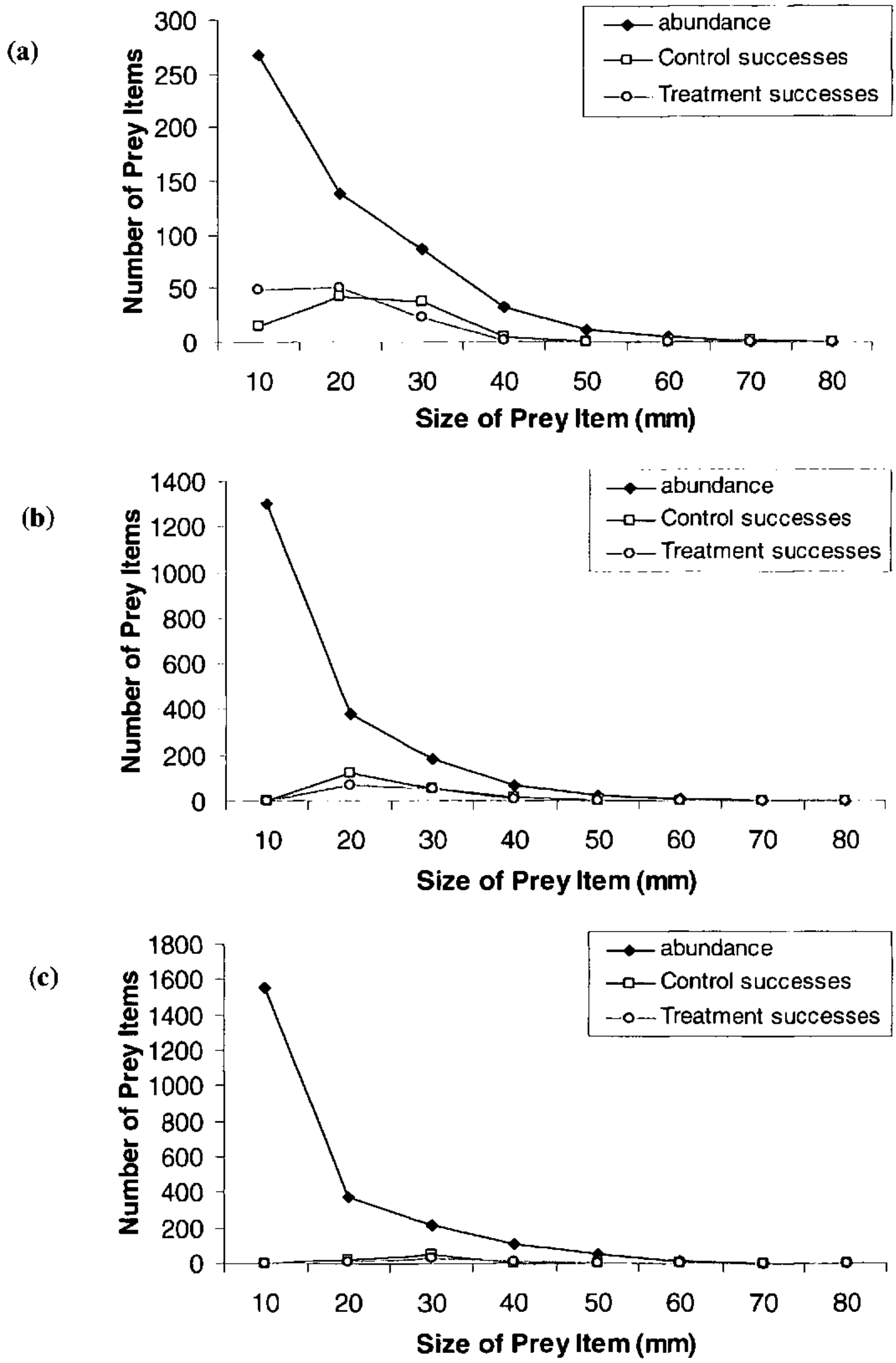


Fig. 29. The distribution of the mean number of each prey size found per m^2 on the shore and the distribution of the mean number of successful feeds the birds had on each prey size, on control and treatment (disturbance) days, in the a) autumn, b) winter and c) spring. A total of 144 birds were observed for 300s period.

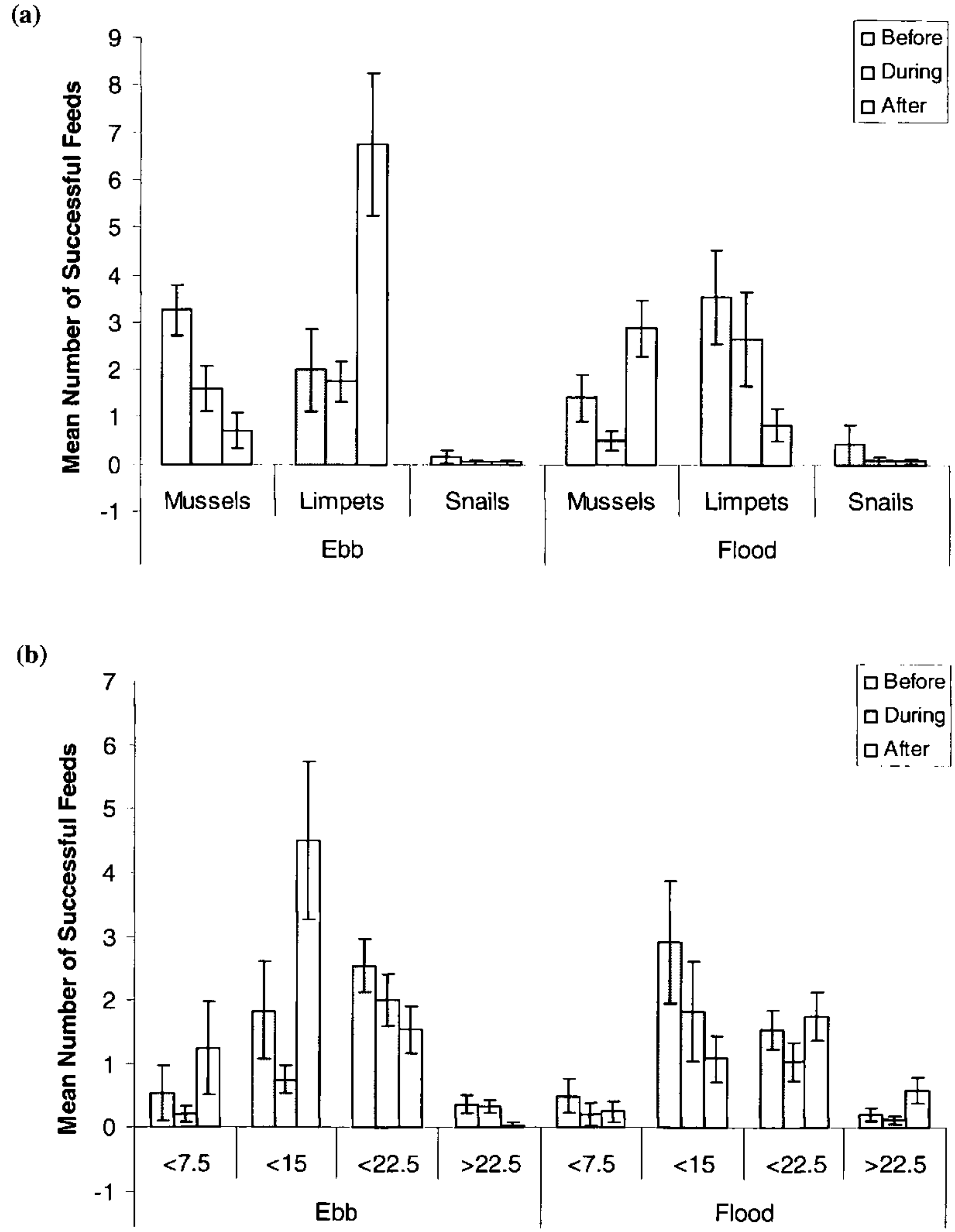


Fig. 30. The mean number of successful feeds/ 300s on mussels, limpets and snails, on ebb an flood tides (a). The mean number of successful feeds/ 300s on prey items <7.5mm, <15mm <22.5mm, and ≥22.5mm in length, on ebb and flow tides (b). A total of 144 birds were observe for a 300 second period each. Untransformed results are shown (mean ± SE).

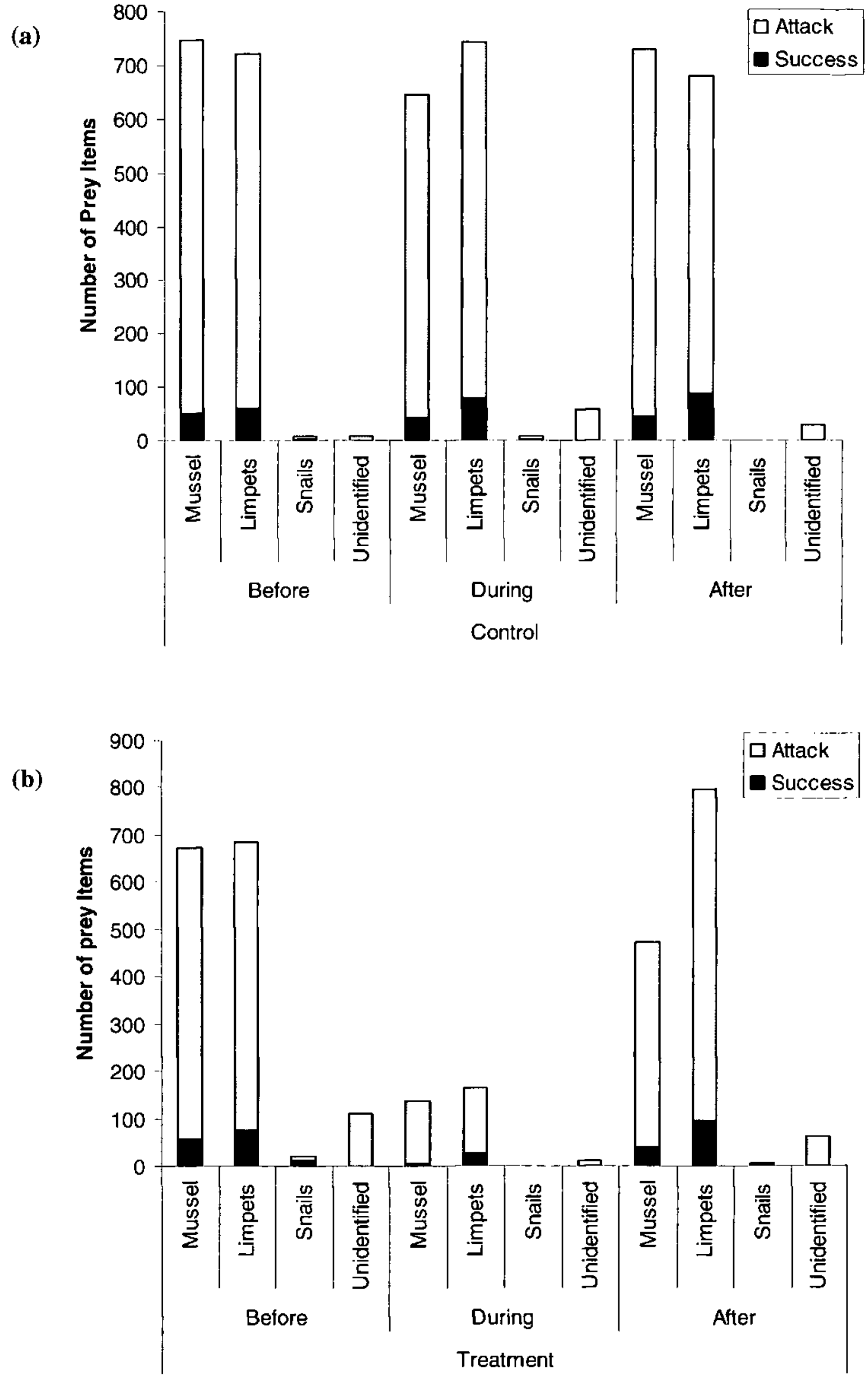
		Species	
		Number of Successful Feeds	
Source	df	MS	F
Tide (Ti)	1	1.095	2.28 NS
Treatment (Tr)	1	1.027	2.14 NS
Application (Ap)	2	1.19	2.48 NS
Species/Size (Sp)	2	**23.22**	**48.41*** **
Ti x Tr	1	0.02	0.04 NS
Ti x Ap	2	0.05	0.11 NS
Ti x Sp	2	0.49	1.03 NS
Tr x Ap	2	**1.91**	**3.96***
Tr x Sp	2	0.33	0.7 NS
Ap x Sp	4	0.57	1.18 NS
Ti x Tr x Ap	2	0.1	0.2 NS
Ti x Tr x Sp	2	0.26	0.53 NS
Ti x Ap x Sp	4	**8.64**	**18*** **
Tr x Ap x Sp	4	0.25	0.51 NS
Ti x Tr x Ap x Sp	4	0.35	0.72 NS
Residual	396	0.48	
Total	431		

		Size (mm)	
		Number of Successful Feeds	
Source	df	MS	F
Tide (Ti)	1	15.02	2.72 NS
Treatment (Tr)	1	5.64	1.02 NS
Application (Ap)	2	**18.11**	**3.28***
Species/Size (Si)	3	**121.95**	**22.07*** **
Ti x Tr	1	1.46	0.26 NS
Ti x Ap	2	12.69	2.30 NS
Ti x Si	3	2.65	0.48 NS
Tr x Ap	2	**20.51**	**3.71***
Tr x Si	3	12.01	2.17 NS
Ap x Si	6	5.95	1.08 NS
Ti x Tr x Ap	2	1.75	0.32 NS
Ti x Tr x Si	3	3.76	0.68 NS
Ti x Ap x Si	6	**26.64**	**4.82*** **
Tr x Ap x Si	6	3	0.54 NS
Ti x Tr x Ap x Si	6	5.76	1.04 NS
Residual	528	5.53	
Total	575		

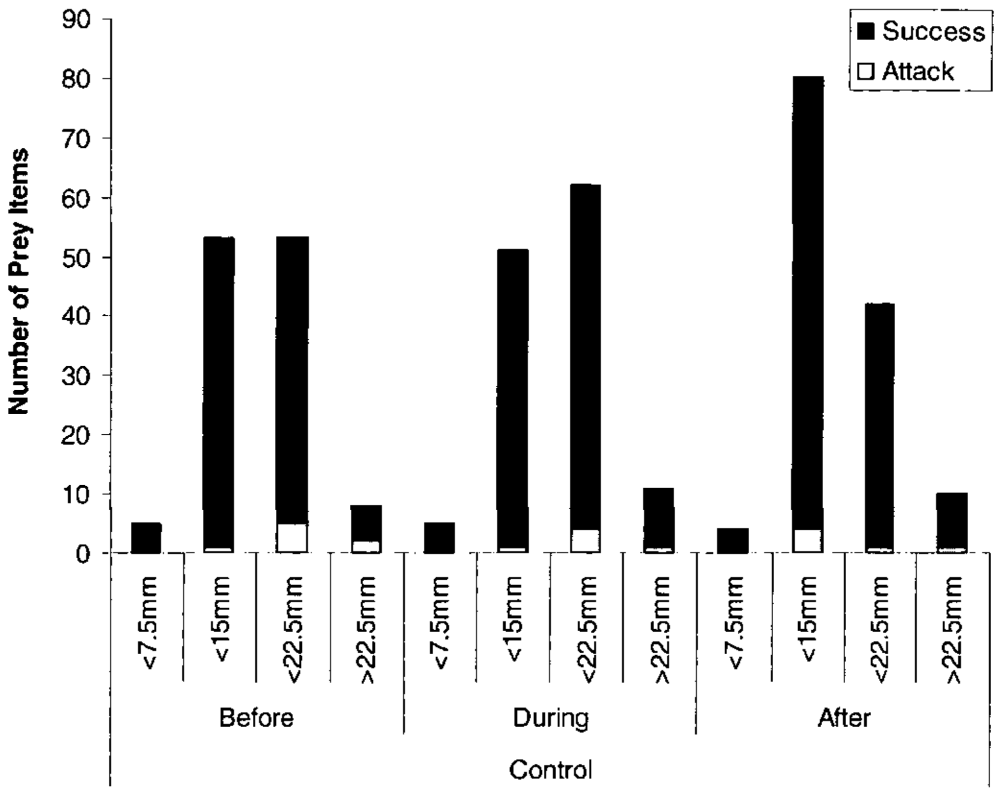
Table 12. Analyses of variance on the number of successful feeds on different prey species (Sp) and sizes (Si), on ebb and flood tides (Ti); on control and treatment days (Tr); and before, during and after a disturbance event (Ap) had occurred (NS – Non-significant $P > 0.05$; $*P < 0.05$; $**P < 0.01$ and $***P < 0.001$). Species were limpets, mussels, and snails; sizes were binned into groups of <7.5mm, <15mm, <22.5mm and ≥ 22.5mm, to reduce heterogeneity of variance. All data were tested by Cochran's homogeneity of variance test prior to analysis; if heterogeneity of variance existed the data was log transformed (Ln (x+1)) (Species: C=0.079, NS; Size: C=0.218, $P<0.01$).

In addition, the number of successful feeds that oystercatchers had on prey items of various sizes also differed with ebb and flood tides and the extent to which the shore was exposed ($F_{(6,528)}=4.82$, $P<0.001$) (Figure 30 b). There was no significant interaction between tide, disturbance, application and the prey size eaten (Table 12). SNK tests showed that oystercatchers generally fed on all the prey sizes similarly, although prey items 15-22.5mm in length were taken more than prey items <7.5mm and >22.5mm in size ($P< 0.05$) until just before low tide, when prey items between 7.5mm and 15mm were most prominently fed upon ($P<0.01$) over the other sizes (Figure 30 b). As the tide began to advance the birds were feeding on more 7.5-15mm sized prey items than the other sizes (majority $P<0.01$), whilst at mid flood they generally fed on all prey sizes to a similar extent although more 7.5-15mm sized prey items were taken than <7.5mm sized prey items ($P < 0.05$). All prey sizes were fed upon equally as the tide was almost completely flooded (all NS) (Figure 30 b). Ultimately, oystercatchers on the rocky shore did not change their prey selection as a result of disturbance but as noted in chapter 3, did change their prey selection with regards to tidal state (Figure 22 b, Table 9).

On control days, oystercatchers fed more successfully upon limpets than mussels before (odds ratio of 1.74), during (odds ratio of 1.16) and after (odds ratio of 3.71) a disturbance would have been applied (Figure 31 a); however, only the before and after results were significantly different from the null ratio of 1 ($G_{adj} = 7.8$, $P<0.01$ and $G_{adj} = 33.51$ $P<0.001$, respectively). On a disturbance day, only during a disturbance did oystercatchers feed significantly ($G_{adj} = 25.60$ $P<0.001$) more successfully on limpets than mussels (odds ratio of 4.23) (Table 13). Whilst birds observed before and after disturbance were 2% and 63% respectively, more likely to have a successful feed when feeding on mussels compared to limpets (Figure 31 b), however neither of these results were significantly different from the null ratio of 1 (Table 13). In accordance with the results found in


(a)
800
700
600
500
400
300
200
100
0
Number of Prey Items
□ Attack
■ Success
Mussel
Limpets
Snails
Unidentified
Mussel
Limpets
Snails
Unidentified
Mussel
Limpets
Snails
Unidentified
Before
During
After
Control
(b)
900
800
700
600
500
400
300
200
100
0
Number of prey Items
□ Attack
■ Success
Mussel
Limpets
Snails
Unidentified
Mussel
Limpets
Snails
Unidentified
Mussel
Limpets
Snails
Unidentified
Before
During
After
Treatment

(c)



(d)

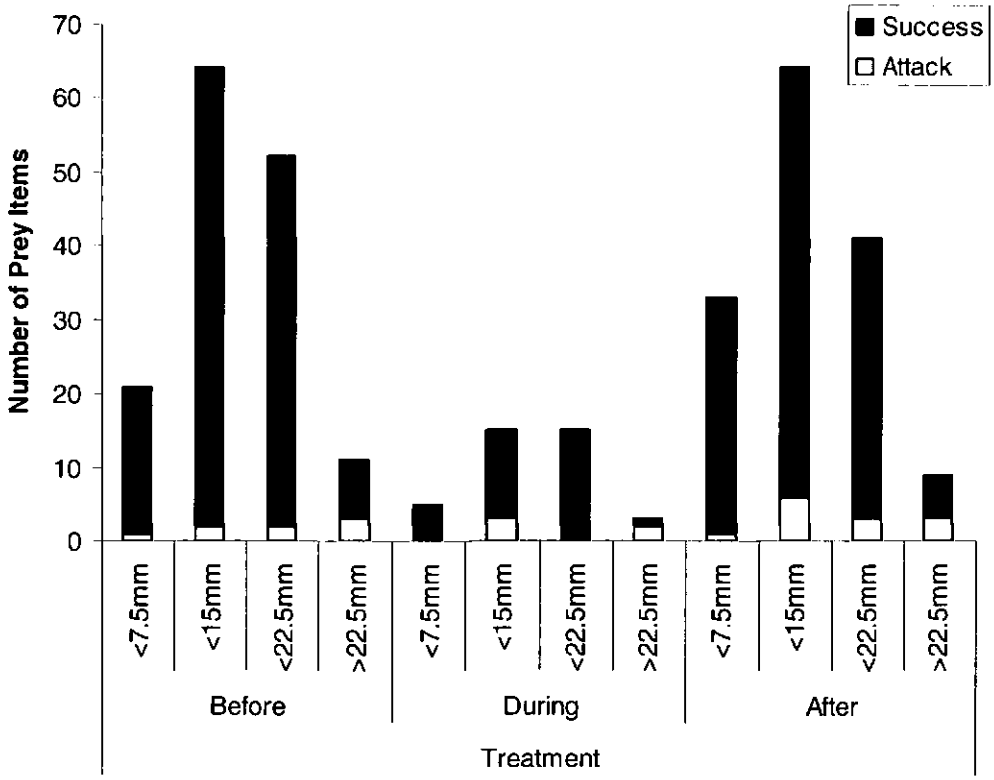


Fig. 31. The foraging success of oystercatchers feeding on various species (a&b) and sizes (c&d) of prey item, on control and disturbance days, before, during and after the treatment (disturbance) was actually (treatment/ disturbance day), or would have been (control day), applied. A total of 144 birds were observed for a 300 second period. The number of attacks and successful feeds are shown. For the species data attacks included handled and pecked prey items, each handled item was recorded as being attacked only once. For the size data, attacks refer to items handled by the oystercatcher only, each handled item was recorded as being attacked only once.

Odds of Having a Successful Feed

			Odds Ratio (ω)	G-Test (Gadj)
Control	Before	Mussel	0.5747	__7.8014**__
		Limpet	1.7401	
	During	Mussel	0.8591	0.4152 NS
		Limpet	1.1641	
	After	Mussel	0.2697	__33.5105***__
		Limpet	3.7081	
Treatment	Before	Mussel	1.0157	0.0049 NS
		Limpet	0.9846	
	During	Mussel	0.2363	__25.6014***__
		Limpet	4.2316	
	After	Mussel	1.6308	3.7255 NS
		Limpet	0.6132	
Control	Before	<7.5mm	1.5	-0.7117 NS
		<15mm	1.3043	
		<22.5mm	0.4722	
		>22.5mm	0.3333	
	During	<7.5mm	6	-1.3207 NS
		<15mm	50	
		<22.5mm	14.5	
		>22.5mm	10	
	After	<7.5mm	5	-1.3144 NS
		<15mm	19	
		<22.5mm	41	
		>22.5mm	9	
Treatment	Before	<7.5mm	20	0.039 NS
		<15mm	31	
		<22.5mm	25	
		>22.5mm	2.67	
	During	<7.5mm	1.25	-2.8255 NS
		<15mm	12	
		<22.5mm	5	
		>22.5mm	0.3333	
	After	<7.5mm	0.5333	1.7597 NS
		<15mm	9.6667	
		<22.5mm	12.6667	
		>22.5mm	2	

Table 13. Odds ratios for the number of successful and non-successful feeding attempts, before during and after disturbance on control and treatment days, on mussels and limpets, and on prey sizes of <7.5mm, <15mm, <22.5mm and ≥22.5mm. The odds ratios were tested for independence using G-tests, with the Williams correction (NS – Non-significant $P > 0.05$; *$P < 0.05$; **$P < 0.01$ and ***$P < 0.001$). Size data was analysed with *RxC* tables for tests of independence using G-tests.

chapter 4, oystercatchers were much more likely to have a successful feed when foraging on limpets as opposed to mussels, and did not differ significantly in their chance of having a successful feed with different prey sizes on control (Figure 31 c) or treatment (Figure 31 d) days (Table 13).

The time taken to handle and successfully feed upon limpets and mussels of various sizes on control and treatment days was LN transformed prior to analysis. The time taken to handle and successfully feed upon mussels, did not differ significantly between control and treatment days (Homogeneity of Slopes: $F_{(1,221)} = 0.030$, NS; Homogeneity of Intercepts: $F_{(1,222)} = 0.132$, NS) and so the data were pooled. The time taken to handle and successfully feed upon mussels increased with mussel size ($F_{(1,222)} = 43.013$, $P<0.001$). In comparison a disturbance event did affect the time taken to successfully feed upon limpets of various sizes (Homogeneity of Slopes: $F_{(1,408)} = 3.196$, NS; Homogeneity of Intercepts: $F_{(1,409)} = 8.013$, $P<0.01$). The birds took slightly longer to successfully feed upon a limpet when observed on a day when disturbance was applied compared to when feeding on a control day (Figure 32 b). The time oystercatchers took open, handle and successfully feed upon limpets increased on both disturbance and control days as the sizes of the limpets attacked increased (Figure 32 b). Therefore it must be assumed that a disturbance causes a reduction in the profitability of limpets but not of mussels.

There was no significant relationship found between the AFDM/m^2 of the area in which the bird was located and the distance the bird allowed a disturbance agent to approach before taking flight ($R^2 = 0.010$, $F_{(1,22)} = 0.228$, NS) (Figure 33).

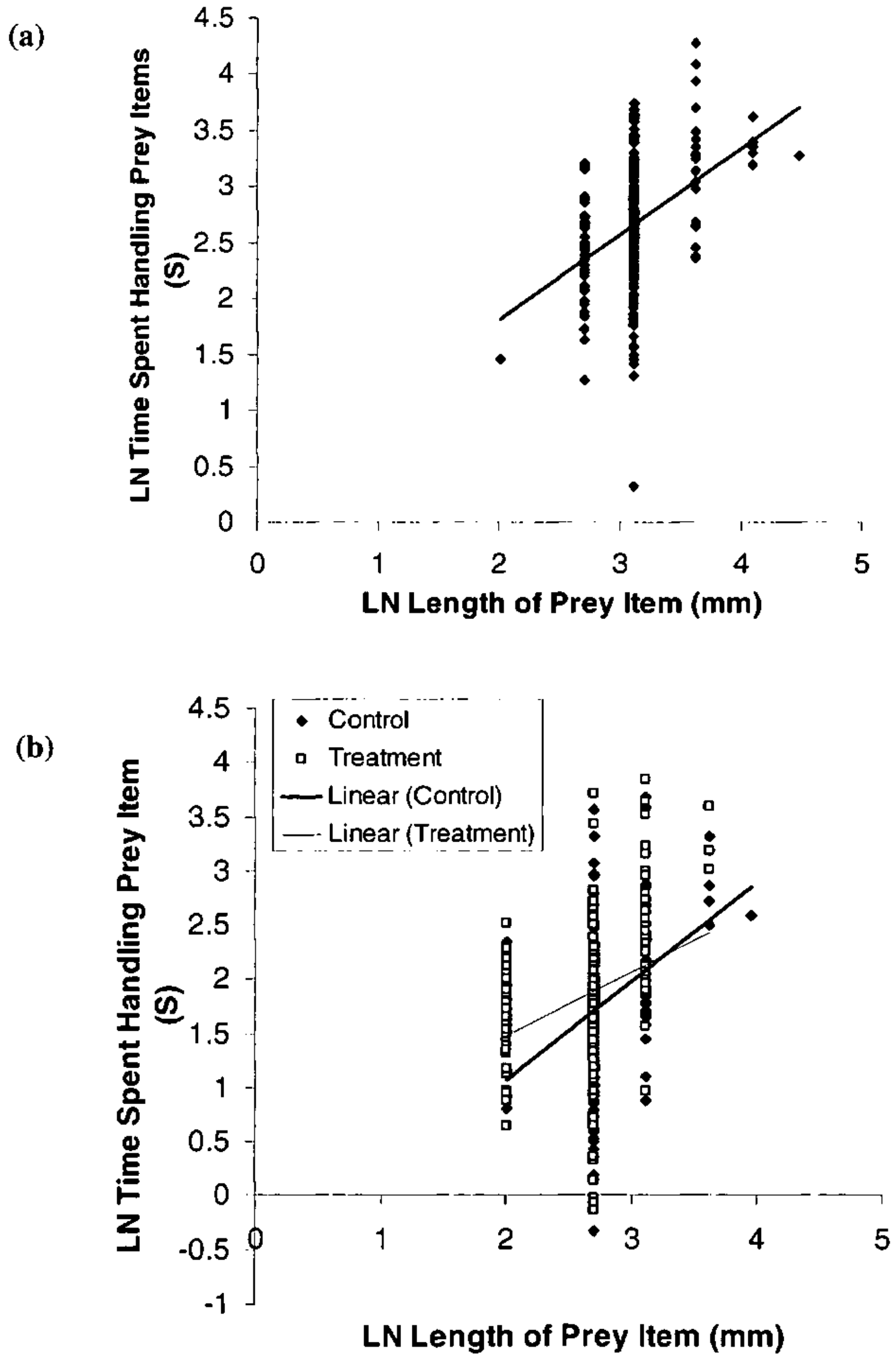


Fig. 32. The relationship between the LN length of a prey item and the $\log_e$ handling time (seconds) required to successfully feed upon it. Data for a) mussels and b) limpets handled on control and treatment days are shown. Snails were not included in the analysis due to the fact that they could be swallow whole and thus often were not handled, providing very few data points. **Mussels** overall: $y = 0.766892x + 0.265578$, $R^2 = 0.16232$, $F_{(1,223)} = 43.21207$, $P < 0.0001$; **limpets - control day:** $y = 0.915554x - 0.776373$, $R^2 = 0.15454$, $F_{(1,211)} = 38.56865$, $P < 0.0001$ and treatment day: $y = 0.585191x + 0.305090$, $R^2 = 0.12579$, $F_{(1,197)} = 28.34740$, $P < 0.0001$.

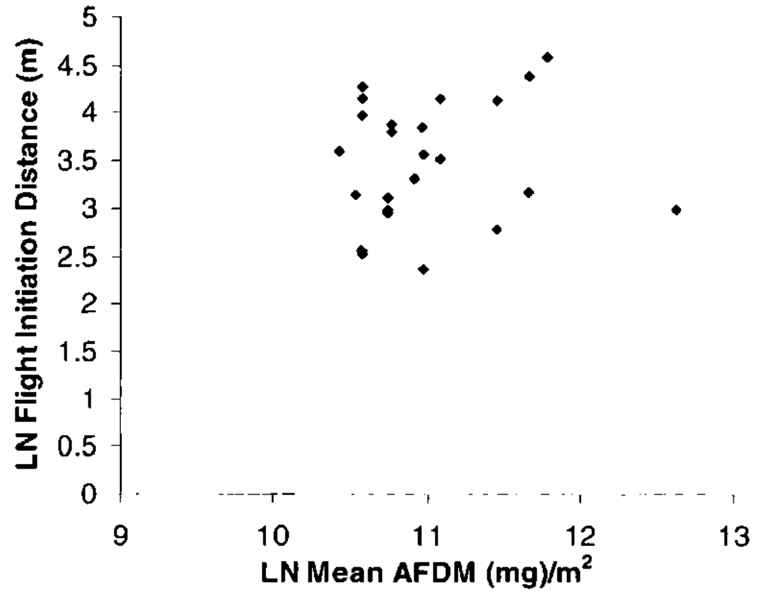


Fig. 33. The relationship between the mean AFDM (mg)/m^2 of the area the oystercatchers were feeding in and the distance they would allow a disturbance agent to approach before taking flight (FID).

5.4. Discussion

5.4.1. Effects of Human Disturbance on Bird Behaviour

The disturbance agent significantly reduced the time that oystercatchers spent foraging. In accordance with other studies the birds spent less time with their head down, foraging and handling prey items, and their peck rate was significantly reduced, as they traded-off vigilance against foraging behaviour (de Boer & Longamane 1996, Smit & Visser 1993). However, the effects of disturbance were only relatively short-term, as post-disturbance birds returned to feeding at pre-disturbance levels within one hour (see Chapter 2). In contrast to studies by Swennen *et al.* (1989) and Burger and Gochfeld (1998), the birds did not increase their foraging intensity after a disturbance event to compensate for lost foraging time, nor did they retain an elevated state of vigilance and depressed foraging activity. Also, disturbances did not result in a significant decline in success and intake rate, suggesting that whilst the number of successful feeds and energy intake may be limited due to a lack of foraging activity, the birds do not become any less efficient at feeding when being disturbed. In fact, if peck rate and the percentage of time spent handling were reduced as a result of disturbance, but success rate remained constant, an increase in foraging and handling efficiency would be expected, however no such result was found. Certainly, individual oystercatchers have been observed decreasing their handling time, and thus increasing profitability, by removing the flesh from shelled prey items at a faster rate (Wanink & Zwarts 1996). The lack of change in foraging efficiency observed in this study, however, could be due to the effects of combining the large amounts of variance in the percentage of time spent handling, success and peck rate data when calculating foraging and handling efficiencies. Success rate, intake rate, foraging and handling efficiency did differ between tides however, with the birds being significantly more efficient at handling and foraging, and having 30% more successes and a 30%

increase in intake rate on an ebb, compared to a flood tide. Ultimately it seems that oystercatcher intake rate is very variable and thus it may be difficult to identify changes in intake rate as a response to a disturbance event, alternatively there simply may be no effect of disturbance on intake rate because the birds have some mechanism for compensation.

5.4.2. Disturbance, Prey Choice and Prey Abundance

In agreement with control day results, oystercatchers did not feed on prey species according to their abundance on the rocky shore when disturbed in autumn, winter, or spring. Instead oystercatchers ate more limpets and fewer mussels than was expected, which could be a factor of the ease with which limpets can be handled (see chapter 4 for discussion of results). On disturbance days in the autumn oystercatchers ate slightly more snails than expected. This could be because snails could be rapidly consumed in between scans of the environment, which may become more frequent in response to the increased predation risk associated with human disturbance (Fitzpatrick & Bouchéz 1998, Coleman *et al.* 2003). This leads to the question of why oystercatchers don't consume snails to a greater extent throughout winter and spring? This may be a factor of prey availability. There is some evidence to suggest that *Nucella lapillus* are only attacked by oystercatchers when distributed singly on the shore, during the winter *Nucella lapillus* move into aggregations in pools and crevices and so may be unavailable to the birds (Feare 1971).

On disturbance days in the autumn the birds took prey sizes relative to their abundance on the shore, with items less than 30mm in length being eaten the most. Prey sizes were not, however, eaten relative to their abundance in winter when, as on control days more prey items 11mm-30mm in length were taken, or in the spring when items approximately 21mm-30mm in length were taken the most. The large number of smaller prey items taken, is probably a factor of the small amount of potential food present on the shore in the autumn, in comparison to in the winter and the spring (see chapter 4, Figure 18 a), thus the birds possibly took what was available when subjected to a disturbance, due to a lack of choice, time, and the need to meet their energy requirements. In the autumn, temperatures are such that energy expenditure should be relatively low, and the birds, not that energetically stressed (Kersten & Piersma 1987); thus oystercatchers could afford to feed upon smaller prey items that may limit the potential for bill damage. The extent to which temperatures will drop over the winter, however, is unpredictable and so the birds may attempt to store energy in preparation for the oncoming months (Evans & Smith 1975, Davidson 1981). In addition, human recreational activities are still frequent in the autumn, thus the potential for the birds to lose foraging time is still significant.

As discussed in chapter 4, there are possible restrictions to the conclusions that can be reliable drawn from the prey abundance/ prey choice data due the methods used for sampling the shore. The proportion of each prey type/prey size available to the foraging birds may change with state of the tide, and so at times oystercatchers may actually be feeding on the most abundant prey (see chapter 4, section 4.4.2. for discussion).

5.4.3. Effects of Human Disturbance on Oystercatcher Prey Choice

A disturbance event was found to have no significant effect on the prey selection of oystercatchers. Theory predicts that prey choice should vary dependant upon predation risk and the handling times associated with prey items (Sih 1993), however, contrary to expectation oystercatchers did not take smaller items or species that would be easier to handle whilst monitoring the disturbance agent, nor did they take larger items after a disturbance event had ceased, to compensate for lost foraging time. It could be that the oystercatchers were unable to compensate for lost foraging time as they were already feeding at their optimal rate (Meire 1996), or lacked the capacity to alter their prey choice.

Oystercatchers did vary, however, in their prey selection as the tide retreated and flooded, which is likely to be related to availability on the rocky shore (de Vlas *et al.* 1996, See Chapter 4 for discussion). Alternatively, it could simply be that a single and short pulse of high predation risk causes the birds to respond significantly (Lima & Bednekoff 1999b) but doesn't disrupt the birds long enough to warrant compensatory behaviour, or that the birds extend the total time they spend feeding (Urfi *et al.* 1996) possibly at night or on supplementary feeding areas at high tide (Heppleston 1971b, Goss-Custard & Durell 1983, Vélasquez & Hockey 1992, Goss-Custard & Verboven 1993, Quinn & Kirby 1993). Prolonged disturbance may cause the birds to react in a very different way (Lima & Bednekoff 1999b).

5.4.4. Effects of Disturbance on Foraging Efficiency Associated with Different Prey Types

During a disturbance event, the birds were significantly more likely to have a successful feeding attempt when feeding on limpets in comparison to mussels, which is probably a factor of the ease with which limpets can be handled. On disturbed days however, the birds did spend a significantly longer time handling limpets compared to on control days (Figure 32 b), whilst the handling time required to successfully feed on mussels remained the same. This is likely to be a factor of the time at which disturbance is applied. At mid ebb or flood, when the disturbance event was applied, the birds were found to eat predominantly limpets, as opposed to mussels that were mainly taken before a disturbance on an ebb and after a disturbance on a flood; and so any increase in the handling time required to successful feed on a prey item as a result of disturbance, may appear to be associated with specifically with prey type. Oystercatchers did not differ in their chance of having a successful feeding attempt with various prey sizes on control (see Chapter 4, Figure 23 b) or disturbance days; surprisingly the birds were no more likely to have a successful feeding attempt when feeding on smaller prey items compared to when feeding on larger items (Zwarts *et al.* 1996d, See Chapter 4 for discussion), however this may be a factor of the definitions used for foraging behaviour throughout this study.

The flight initiation distance did not vary with the energy content of the area in which the birds were feeding; oystercatchers did not allow people to approach more closely when occupying a patch of high prey density. It could be that the birds consider a disturbance event to be a great enough threat to warrant a response at a specific distance regardless of the food available in the patch, or that they are equally reluctant to take flight in response to disturbance due to energetic and temporal costs. Alternatively, it may be that the flight initiation distance doesn't mean that much in terms of energetic and temporal costs to oystercatchers foraging on the rocky shore, as oystercatchers taking flight as a result of disturbance often flew only a short distance to another part of the same rocky shore area and did not leave the site completely. Thus their feeding site was not often completely lost to human disturbance, possibly causing them to behave independently of the quality of their feeding patch. Also, the amount of food present does not mirror exactly the food available to the birds, and so in terms of availability, patches may be of a much lower quality than prey density would suggest (Meire & Ervynck 1986, Norris 1999, Silva *et al.* 1999, Gawlik 2002).

In summary, oystercatcher foraging behaviour was affected by disturbance, as birds suffered a decline in peck rate, the percentage of time spent handling and the percentage of time spent with their head down, searching (Smit & Visser 1993, Fitzpatrick & Bouchez 1998, Coleman *et al.* 2003). A decline in foraging activity resulted in a decline in overall energy consumption; however success and intake rates were not significantly affected by disturbance, although this could be due to the large amount of variance in the data. The large amount of variance in intake rate highlights the fact that the effects of disturbance on foraging and/or handling efficiency differs with the individual and is likely to be state dependant (Lima 1999). An individual's age, health, dominance, natural ability to handle prey items, experience of feeding on the rocky shore and previous experience of disturbance, are all factors likely to affect the bird's response to disturbance. The effects of disturbance on foraging activity were not compensated for by changes in prey selection, either during or after the disturbance event; prey selection did however change with tidal state and this is likely to be a factor of prey availability (de Vlas *et al.* 1996, Ens *et al.* 1996c). It is possible that oystercatchers are restricted by the low density of larger prey items, and so do not have the means to increase their intake rate after being disturbed in order to compensate for lost foraging time as they are already feeding at their maximal level (Meire, 1996). The estimated overall energy intake for the 6 hours that oystercatchers could forage on the rocky shore (Chapter 4) was significantly lower than the estimated minimum daily amount of energy required by free-living Oystercatchers at thermo-neutral conditions (Kersten & Piersma 1987), and so it would seem important that the birds forage for as long as possible to meet their energy requirements. Supplementary feeding areas at high tide (Heppleston 1971a, Velasquez & Hockey 1992, Caldow *et al.* 1999, Goss-Custard & Durell 1983), and foraging at night (Goss-Custard & Verboven 1993, Hockey & Underhill 1984, Goss-Custard & Durell 1987b, Kersten & Visser 1996b) are likely to be important parts of the birds' foraging regime. Such compensatory mechanisms, however, may have their drawbacks in terms of rates of energy gain, time budgets and predation risk. A disturbance event/ predation threat, may cause the birds to extend their foraging period at the cost of other important behaviours such as preening and roosting, or alternatively simply cause them to change the order in which they conduct these behaviours (Caldwell 1986). For instance, if disturbance is frequent, birds may choose to preen (a behaviour that may be easily interspersed with vigilance) or roost (evidence suggests birds can regularly peek when sleeping, with minimal cost to their resting time, or demonstrate sleep-vigilance (Lendrem 1983b, Gauthier-Clerc *et al.* 1998, 2000) instead of foraging over low tide. The birds could then feed when disturbance was less frequent, without serious repercussions for their time-budgets (Goss-Custard & Verboven 1993). However if the night-time/ supplementary ground intake rate is less than that during the day/ on the shore, it may take the oystercatchers significantly longer to meet their energy requirements (Drinnan 1958b, Heppleston 1971b, Zwarts & Drent 1981, Sutherland 1982 b & c, Goss-Custard & Durell 1987b). Ultimately the oystercatchers observed on the rocky shore fed at much lower levels than would be expected in order for them survive the winter months, thus any disturbance event that causes the birds to increase their energy expenditure and lose foraging time could have serious implications for oystercatcher health.

Chapter 6: Discussion of the foraging behaviour of oystercatchers on the rocky shore and their response to human disturbance.

6.1. Introduction

The aims of the work presented in this thesis were to observe the behaviour and prey selection of the Eurasian oystercatcher Haematopus ostralegus whilst foraging on the rocky shore, and to ascertain the effects of human recreational disturbance on the oystercatcher's foraging behaviour and prey selection. The primary questions addressed were: a) How do oystercatchers respond to recreational disturbance and does their response vary with the type of disturbance they are subjected to (Chapter 2)? b) How do oystercatchers forage on the rocky shore and how does this vary with changes in their environment (Chapter 3)? c) What do oystercatchers eat on the rocky shore and what factors dictate prey choice (Chapter 4)? d) Do oystercatchers use compensatory mechanisms to reduce the energetic costs of their response to human disturbance (Chapter 5)? The main results from this study and the potential implications for oystercatcher health will be discussed, and comparisons will be made between foraging by oystercatchers in estuarine and rocky shore environments.

6.2. Foraging on the Rocky Shore

The foraging behaviour of the oystercatcher in relation to food density and availability, and environmental variation, has been documented extensively over the last 30 years (see Goss-Custard 1996 for overview and references therein). Understanding oystercatcher foraging behaviour is important for predicting the possible effects of habitat loss as a result of human activities on shorebird populations (Goss-Custard *et al.* 1996c), so that effective conservation and management strategies may be devised. The majority of the work conducted has focussed on the foraging behaviour of oystercatchers in estuarine environments, thus relatively little is known of their foraging behaviour in different systems (see Feare 1971, Hartwick 1976, Frank 1982, Hockey & Underhill 1984, Coleman *et al.* 1999, for exception). Approximately a quarter of the European oystercatcher population in Britain is reported to frequent non-estuarine over-wintering sites (Rehfisch *et al.* 2003), and numerous species of oystercatcher world-wide use rocky shores as their primary feeding site (Hartwick & Blaylock 1979, Hockey 1983, see Hockey 1996 for overview). As discussed in Chapter 2, animals will vary in their response to human disturbance temporally and spatially; and the variation in an animal's response may be an indication of its vulnerability to starvation or predation. It would seem essential therefore to have an understanding of oystercatcher foraging in alternative coastal habitats when analysing the impacts of human disturbance on coastal areas in general, instead of basing predictions upon the effects in one particular type of habitat.

Two obvious differences between estuarine and rocky shore environments are their structural complexity and the dimensional distribution of the biota. Both of these factors are likely to have implications for oystercatcher foraging behaviour. The complex structure of the rocky shore environment will limit the effectiveness of peripheral vision in the detection of potential predators (Metcalfe 1984b), and may prevent oystercatchers from monitoring the behaviour of conspecifics as an anti-predator strategy. Furthermore, oystercatchers may be restricted from viewing others in order to locate food or avoid interference. Foraging and vigilance on the structurally complex rocky shore will therefore, generally be mutually exclusive behaviours, forcing the birds to trade-off energy intake with predator avoidance. The strength of this trade-off may be site-dependant, as different rocky shore sites will vary in the level of their structural complexity. In this study oystercatchers increased their vigilance at the cost of time spent foraging when their perceived predation risk was increased, however when feeding on a less structurally complex rocky shore the oystercatchers were able to retain their undisturbed peck rate (Chapter 2). This suggests that when feeding on a rocky shore of a lower structurally complexity certain aspects of foraging behaviour, namely pulse activities (i.e. pecks), may be interspersed with vigilance, without altering the oystercatcher's perceived risk of being preyed upon (Fitzpatrick & Bouchéz 1998). Where rocks are lower in height an individual may be able to have its head angled slightly downwards facilitating feeding but simultaneously allowing it to monitor the environment by looking over the rocks (Lima & Bednekoff 1999a, Bednekoff & Lima 2005). The movement of the head downward in order to strike a prey item may restrict its view but only for a very short period and thus the approaching threat may be effectively monitored.

In estuarine ecosystems, organisms are buried at various depths affecting their availability to the birds. Furthermore, environmental factors have been shown to have a major influence on prey availability in estuarine environments (Goss-Custard 1969, Evans 1976, Pienkowski 1981, 1983, Zwarts *et al.* 1996a). Cold temperatures, and strong winds and sunny weather which can increase desiccation rates, may cause some organisms to bury deeper in to the substrate for refuge (Pienkowski 1981), placing them out of reach of an oystercatcher's bill. Reduced prey availability in response to environmental conditions is likely to be slightly less of an issue, however, to birds foraging on the rocky shore. In rocky shore ecosystems organisms are generally distributed in a more 2-dimensional fashion resulting in the majority of prey items present being visible with the exception of cover by seaweed and mussel beds. Limpets and mussels may clamp down upon the rock and close their valves tighter respectively, in colder, windier weather, whilst dogwhelks may retreat into crevices in the rock (Feare 1971); the probability of an oystercatcher successfully feeding upon rocky shore organisms however, may be slightly higher compared to estuaries, simply due to the fact that the oystercatchers are capable of reaching the majority of prey items. Certainly, during this study, the type of weather had no significant effect upon foraging behaviour; and higher wind speeds and colder temperatures had no detrimental effect upon oystercatcher success rate (Chapter 3). This suggests that prey availability on the rocky shore was unaffected by these elements of environmental variation, especially as oystercatchers actually increased their success rate in the winter indicating that the birds became more efficient at feeding in colder temperatures as their energy requirements increased (Chapter 3). An additional environmental variation to consider is tidal movement; although foraging intensity was unaffected the oystercatchers' prey choice was found to significantly vary with the movement of the tide (Chapter 4), which is likely to be a factor of prey availability (de Vlas *et al.* 1996, Zwarts *et al.* 1996a).

The rocky shore appears to be abundant with potential oystercatcher prey and yet few oystercatchers, compared to in British estuaries (Goss-Custard *et al.* 1982b) forage there (Chapter 3). This could be due to a greater perceived risk of being successfully preyed upon as a result of reduced visibility (Metcalfe 1984b); or because a higher base level of vigilance, at the cost of foraging, is required when feeding in a potentially riskier area. There may also be other risks associated with rocky shore feeding. Virtually all of the oystercatcher's rocky shore prey items are hard shelled, thus hammering, stabbing or prising techniques are required in order to access the flesh of the oystercatcher's primary prey types (Norton-Griffiths 1967, Feare 1971, Hulscher 1982, Hulscher 1985, Hulscher 1996 for review, Coleman *et al.* 1999, 2004). Oystercatchers can suffer from bill damage as a result of the particularly vigorous handling or attacking of prey (Hulscher 1988 loc cit Hulscher 1996). The risk of bill damage on the rocky shore may be significantly greater than when feeding on the estuary, as the oystercatcher's bill makes contact both with the hard surface of the substrate and with the prey. Bill damage can lead to starvation particularly in cold temperatures (Swennen & Duiven 1983), thus oystercatchers may be reluctant to forage where their risk of bill damage is potentially greater.

The average calculated energy intake rate of oystercatchers foraging on the rocky shore was approximately 60mg AFDM min^{-1} (Chapter 4). This is at the lower scale of energy intake rates observed for the Exe estuary oystercatchers which are often subject to competition and interference (Ens & Goss-Custard 1984) and below the mean interference-free intake rate observed (Goss-Custard & Durell 1988), and thus may explain why the rocky shore is not utilised by a greater number of oystercatchers. The predicted average energy intake for oystercatchers feeding on the rocky shore, for the 6 hours over which the rocks were exposed, is approximately 21g AFDM (Chapter 4); this is just over half the 36g AFDM estimated to be required by oystercatchers at thermo-neutral conditions, and marks a deficit of even greater proportions when temperatures decrease (Kersten & Piersma 1987, Swennen *et al.* 1989, Goede 1993). The reported low energy intake rate is mainly a factor of prey choice, as oystercatchers appeared to select relatively small prey items (Chapter 4). This is likely to be factor of prey abundance; however it may also be that oystercatchers were attempting to limit the probability of bill damage by choosing items that were smaller and thus easier to handle. Certainly, other studies have suggested that the intake of smaller prey items than expected by oystercatchers feeding on estuaries may be due to factors such as reduced parasitic load or the reduced risk of bill damage (Norris 1999). Thus, oystercatchers feeding on the rocky shore may not always be feeding at their maximum rate (based on foraging efficiency and feeding on the largest prey items), but instead feeding at a potentially optimal rate (the balance between factors such as the risk of bill damage and prey profitability) (Norris & Johnstone 1998, Norris 1999, Johnstone & Norris 2000). Oystercatchers may then be able to increase their intake rate in extreme circumstances at the cost of other factors such as reducing bill damage (Swennen *et al.* 1989), which may partly explain the increase in success rate in the winter months compared to success rate in autumn and spring (Chapter 3).

The low energy intake rate of oystercatchers explains why very few were observed roosting over low tide. An intake rate of 60mg AFDM min^{-1} means that an oystercatcher can feed for almost 9 hours before being forced to take a digestive pause, thus it was possible for the birds to feed constantly over the 6 hour period they were present on the rocky shore (Kersten & Visser 1996a). Such low energy intake rates suggest that night-feeding or foraging on supplementary grounds at high-tide, either at night or during the day are likely to form an important part of the oystercatcher's feeding strategy (Heppleston 1971a, Goss-Custard & Durell 1983, Quinn & Kirby 1993, Caldow *et al.* 1999). In order to meet its absolute lowest energy requirements at thermo-neutral conditions an individual feeding on the rocky shore would have to forage for approximately 10 hours, not including time required for digestive pauses. This means that if foraging on the rocky shore, when uncovered, at night oystercatchers would have to be feeding at approximately the same rate as they did during the day. There is a lot of confusion about oystercatcher foraging efficiency at night versus day in estuaries (see Hulscher 1996 for review). Some studies have shown no real difference between day- and night-time foraging (Swennen 1990, Leopold *et al.* 1989), whilst others have shown a reduction in foraging efficiency at night (Goss-Custard & Durell 1987b, Sutherland 1982b). It may be assumed that oystercatchers feeding on the rocky shore, as visual feeders, would find foraging at night extremely difficult; African black oystercatchers (*H. Moquini*) do, however, forage nocturnally on the rocky shore albeit less successfully (Hockey & Underhill 1984). This may be possible due to moonlight providing some illumination of their foraging ground. Without moonlight, however, nocturnal foraging may be significantly more difficult and the risk of bill damage significantly increased. Alternatively, the use of supplementary feeding areas at night or during the day may increase an oystercatchers perceived predation risk. Supplementary feeding areas are also likely to be areas of lower profitability which has implications for energy intake, otherwise oystercatchers would be expected to constantly utilise such areas. Understanding how rocky shore oystercatchers fulfil their energy requirements when their day-time energy intake rates are so low, would be an interesting basis for future work.

6.3. Human Disturbance

Human disturbance is becoming increasingly frequent along the coastal areas of Britain which could have implications for the organisms that inhabit such areas, especially at times when individuals are most vulnerable to starvation (Cayford 1993). It is therefore important to understand and attempt to quantify the effects of human disturbance on animals for the conservation and management of disturbed habitats. The costs of human disturbance to an individual may be significantly greater when the habitat is of greater structural complexity and so vigilance is traded off with foraging (Metcalfe 1984b), when the individual is most vulnerable to starvation due to a low foraging rate or high energy expenditure (Stillman & Goss-Custard 2002), and when suitable, nearby alternative foraging areas are unavailable (Gill *et al.* 2001). When the structure of the habitat is more complex individuals are forced to decrease their foraging activity in order to monitor the approaching disturbance factor (Chapter 2 & 5). Whilst individuals that already have trouble meeting their energy requirements either due to environmental conditions or a lower foraging efficiency (Swennen & Duiven 1983), may suffer an energy deficit as a result of the temporal and energetic costs of monitoring and avoiding the potential threat. Lastly, individuals that have an alternative foraging site of similar quality nearby have the option of retreating to the undisturbed site when disturbance becomes too frequent, thus limiting the temporal costs of disturbance (Gill *et al.* 2001). Of course, the more frequent the occurrence of non-lethal disturbance the more habituated individuals will become, thus delaying their response to the disturbance (Smit & Visser 1993, Klein *et al.* 1995, Rees *et al.* 2005). Ultimately, however, an approaching disturbance factor will elicit a behavioural response from a wild animal, until eventually the animal employs avoidance tactics. Individuals that have no alternative foraging site of a similar quality, however, may be forced to endure the temporal costs of disturbance, expend extra energy retreating to a site that is a greater distance away, or suffer a reduction in energy intake when displaced to a lesser quality site or where intake rates may be limited by interference and competition (Bell & Austin 1985, Yalden 1992, Goss-Custard & Verboven 1993, Gill *et al.* 1996, Gill & Sutherland 2000).

Although animals may respond to approaching human disturbance and an actual predator in a similar way (i.e. monitoring and then avoiding the potential threat), the rate of change in their behaviour to predominantly vigilance/avoidance behaviour may be significantly lower when subjected to human disturbance than if subjected to an actual predator threat. There is some evidence that in places where and at times when, the shooting of waders occur, shorebirds show a greater response to human disturbance than in places where and at times when humans pose no actual and immediate threat to shorebird health (Hockin *et al.* 1992, Madsen 1998). It is questionable therefore how analogous human disturbance is to a predation threat for those animals to which humans pose no real predatory threat. Furthermore, the primary predator of the oystercatcher is the peregrine (Whitfield 1985, Quinn 1997); an aerial predator that is likely to elicit a very different behavioural response from oystercatchers compared to a terrestrial predator. Of course, dogs on the rocky shore may be considered a real predator threat to foraging oystercatchers and so would be expected to induce a greater behavioural response from the birds (Thomas *et al.* 2003). The fact that the birds observed throughout this study showed no significant difference in their response to the model dog compared to other types of experimental human disturbance may simply be due to the fact that the aspects of dog behaviour that make the dogs most threatening and thus are most influential in shaping the oystercatchers' response were the aspects of dog behaviour that were actually controlled for (i.e. the speed and randomness of approach) (Chapter 2).

At no point during the time for which oystercatchers were observed at any of the sites, was an actual predatory attack from a peregrine witnessed, suggesting that predatory attacks on oystercatchers were infrequent. This is likely to have implications for the response of oystercatchers to human disturbance. When predatory attacks are infrequent individuals are likely to respond to a greater extent when confronted by a potential threat as usual low levels of vigilance allow for greater energy intake, so that when a threat does occur the individual has the time and energy available to respond in a way that will heighten the probability of successfully avoiding predation. As previously discussed, to oystercatchers human disturbance may not be analogous to a predator attack, however human disturbance is still obviously perceived to be a threat. If frequently responding to actual predatory attacks individuals may dampen their response to potentially lower risk threats such as human disturbance so as to conserve energy and reduce temporal costs. Future studies on the vulnerability of shorebird populations to human disturbance may therefore be more appropriate if looking at those species that are smaller and thus more vulnerable to natural predators; species that may already be pushed for time and energy.

The effect of human disturbance on the overall foraging behaviour of the oystercatcher was similar at each of the three rocky shore sites used during this study; the overall time oystercatchers spent foraging significantly decreased when the birds were subjected to a disturbance (Chapter 2 & 5, Goss-Custard & Verboven 1993, Smit & Visser 1993, Lambeck *et al.* 1996, Verhulst *et al.* 2001). The effects of human disturbance on components of oystercatcher foraging behaviour however, did vary spatially (Chapter 2 & 5). At Par oystercatchers suffered a decline in time spent handling but not in peck rate, whilst at Looe oystercatchers suffered a decline in handling time and peck rate as a result of disturbance (Chapter 2). Oystercatchers in Looe and Par suffered a decline in their number of successful feeds due to the reduced time they spent foraging, however the chance of their having a successful feeding attempt (i.e. their foraging efficiency) was unaffected by disturbance (Chapter 2). This contrasts with studies by Coleman *et al.* (2003) and Fitzpatrick and Bouchéz (1998) where oystercatchers became less efficient when feeding in soft substrata and more efficient when feeding on a structurally uncomplex rocky shore respectively, when subjected to a moderate level of human disturbance. At Trebetherick, although the time oystercatchers spent foraging and handling prey and their peck rate declined when the birds were being disturbed, the oystercatchers' success and energy intake rates did not vary significantly as a result of human disturbance (Chapter 5). This appears to suggest that their foraging efficiency actually increased as a result of disturbance (Fitzpatrick & Bouchéz 1998). The most likely explanation however, is that individual oystercatchers vary significantly in their success and energy intake rates based on factors such as their age, experience of feeding on the rocky shore, how hungry they are, environmental conditions etc; and thus such variation made it impossible to establish the effects of disturbance. This work highlights the fact that in the response of oystercatchers to human disturbance there is considerable variation, also aspects of individual foraging behaviour vary within and between sites, which is an important consideration for conservation and management strategies.

The effects of human disturbance on the foraging behaviour of oystercatchers appeared to be only very short-term as the birds returned to feeding at their pre-disturbance levels almost immediately (Chapter 2). If we consider that disturbance generally limits energy intake due to time lost from foraging, then the oystercatchers' rapid return to feeding could indicate a reluctance to lose any more foraging time than absolutely necessary due to high energy demands (Gill *et al.* 2001, Stillman & Goss-Custard 2002). Oystercatchers did not attempt to limit the effects of disturbance by altering their prey choice when actually being disturbed; nor did oystercatchers attempt to compensate for lost foraging time by either increasing their foraging intensity, or by altering their prey choice in order to gain more energy after the disturbance had ceased (Chapter 5, Meire 1996, Urfi *et al.* 1996). These results could indicate that the birds were feeding at their optimal rate and were reluctant to increase their foraging intensity at the cost of vigilance due to the heightened risk of their being successfully preyed upon. Alternatively, they may have been reluctant to increase their handling rate or alter their prey size selection due to the risk of bill damage. It is most likely, however, that a significant but short-lived increase in the birds' perceived predation risk simply does not disturb the birds, and thus reduce energy intake, for long enough to warrant compensatory behaviour (Urfi *et al.* 1996). In fact, the short period of time that the birds were disturbed for may simply be used as a digestive pause in their foraging activity, and so prolonging the time they will be able to constantly feed for prior to being restricted by their digestive bottleneck (Zwarts *et al.* 1996d). Furthermore, it is extremely unlikely that any of the birds observed throughout this study were able to meet their energy requirements in one period of shore exposure, thus increasing the likelihood of night foraging and feeding in supplementary areas where compensatory mechanisms may take the form of prolonged feeding activity (Heppleston 1971a, Goss-Custard & Durell 1983, Caldow *et al.* 1999, Urfi *et al.* 1996). Ultimately, only if birds were frequently subjected to disturbance, and thus feeding was significantly restricted, would compensatory mechanisms need to be employed either immediately after the disturbance had ceased or at a later time or place. Establishing the level of disturbance necessary a) for compensatory mechanisms to be employed and b) to cause the birds to completely abandon the feeding site, would be an interesting focus for future work.

In formulating this work, there was an expectation that variations in oystercatcher foraging behaviour in response to human disturbance would have implications for rocky shore assemblages. Oystercatcher predation upon limpets has been found to modify algal abundance over the scale of shores in the USA and South Africa (Bosman & Hockey 1988, Wootton 1992). As oystercatchers are selective of the species (Hahn & Denny 1989) and the distribution of the limpets (Coleman *et al.* 1999) they attack dependant upon associated handling times (Hahn & Denny 1989, Coleman *et al.* 2004), it was expected that disturbance would modify handling time decisions and thus influence prey selection. As oystercatchers did not vary their prey selection when disturbed (Chapter 5) these expectations were not supported. Thus, whilst disturbance by human activities may influence oystercatcher behaviour, there may be only a very small impact upon rocky shore assemblages.

6.4. Conservation Implications

Much work over the years has been aimed at understanding the factors that affect shorebird vulnerability to starvation with a view to conserving and managing visiting and resident shorebird populations. Shorebirds will vary in their susceptibility to starvation spatially and temporally dependant upon factors such as interference and competition (Goss-Custard 1980, see Ens & Cayford 1996 for overview), environmental factors which dictate energy requirements (Kersten & Piersma 1987, Goede 1993, Wiersma & Piersma 1994), foraging efficiency (Goss-Custard & Durell 1988, Caldow *et al.* 1999, Stillman *et al.* 2000b), and the energetic value of prey, prey density and availability (see Goss-Custard *et al.* 1996a for overview). More recently, the effects of habitat loss and disturbance by human activities on the health of shorebird populations have become increasingly important, as human activities in coastal areas have become more frequent and now occur continuously throughout the year. This puts extra pressure on shorebirds that may already be struggling to survive the winter months and on resources where individuals may congregate after being excluded from their original feeding ground by disturbance factors. Gaining knowledge about shorebird foraging behaviour is therefore important for predicting the effects of disturbance and habitat loss on shorebird populations.

Animals that feed in structurally complex areas may be particularly vulnerable to starvation, as they are forced to trade-off vigilance and foraging (Chapter 2); although the extent of this trade-off is likely to vary dependant upon the structural complexity of the area in which they are feeding (Chapter 2, Bednekoff & Lima 2005). For animals that inhabit areas where predation risk is increased as a result of high predator abundance and frequent attacks, and where individuals feeding as isolates are solely responsible for detecting predators, meeting energy requirements may be difficult especially during the colder periods of the year. Frequent disturbance by human activities will apply added pressure to individuals as they lose even more time from foraging to monitoring (Chapter 2), and expend additional energy avoiding, disturbance factors. It would seem important therefore to limit the frequency of disturbance in such habitats.

For those individuals that have alternative foraging grounds nearby that they are able to utilise if disturbance levels become too high, disturbance may have a limited effect upon their health (Gill *et al.* 2001). Individuals that do not have alternative foraging sites of a reasonable quality to which to retreat may be forced to remain at a site where their energy intake is limited by the presence of people, which could have serious implications for their health. An additional consideration is the size of the individuals foraging site. When foraging in an area that is very large individuals that are displaced from one area of the shore may simply redistribute themselves to another area of the same shore, however those that are inhabiting a smaller foraging area are displaced completely from the site when disturbed, incurring temporal and energetic costs to the birds.

Human activities can have a major effect on the behaviour of animals. It has generally been accepted the response of individuals to human disturbance will vary dependant upon the nature of the activity. The duration and frequency of disturbance events however, are far more likely to have a greater impact upon the health of animals. Individuals naturally vary in their foraging behaviour and energy intake rate based on numerous individual, temporal and spatial factors; subsequently they will vary in the extent to which they respond to human disturbance which has implications for their risk of starvation. Where potential constraints to energy intake rates exist (such as the risk of bill damage, inexperience of foraging, interference, competition, and prey availability) individuals may struggle to meet their energy requirements and be more likely to suffer a greater decline in health when prevented from feeding or forced to expend extra energy as a result of human activities.

6.5. Future Work

Although much work has been conducted over the years on the immediate response of animals to human disturbance very little is known about the actual costs to the health of individuals that are frequently disturbed, and the compensatory mechanisms that must be employed if the individuals are to avoid starvation. During this study oystercatchers appeared not to be disturbed enough to warrant compensatory behaviour. It could be, however, that oystercatchers compensated for any reduction in energy intake by extending the time they spent foraging at night or on supplementary feeding grounds, compensatory behaviour that potentially went unobserved; this needs further investigation. Knowledge of the behaviour and energy intake rates of rocky shore oystercatchers when foraging on supplementary feeding areas and feeding at night may give a greater indication of the potential effects of disturbance on oystercatcher health.

It is also important for conservation purposes to understand the level of disturbance that may be tolerated before an oystercatcher's energy intake is reduced to the detriment of the oystercatchers' health or before an individual is forced from their foraging area. Furthermore, the suggestion that the structural complexity of an animal's foraging site has a significant influence upon both its undisturbed and disturbed foraging behaviour and energy intake, needs to be confirmed.

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