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THE SIZE SELECTION OF CLAMS BY AFRICAN BLACK OYSTERCATCHERS AND KELP GULLS[1]

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Abstract. The selection of prey by two species of shore-dwelling birds was compared with the predictions of a simple optimal diet model. The preferences of African Black Oystercatchers (*Haematopus moquini*) and Kelp Gulls (*Larus dominicanus*) for different size classes of the sand-burrowing bivalve *Donax serra* were examined. Gulls took only large clams, regardless of the availability of the different size classes. This preference is ascribed to the high energy expenditure required for gulls to open clam shells. Oystercatchers, which open bivalve shells relatively easily, took both small and large clams, even when large clams were abundant. The selection of small clams when large clams were abundant appears to have resulted from the lack of discrimination of clam sizes by oystercatchers and the temporal segregation of availability of small and large clams.

Key words: clams; gulls; optimal diet; optimal foraging; oystercatchers; recognition time; size selection.

INTRODUCTION

Simple optimal diet selection models (e.g., Emlen 1966, Schoener 1971, Charnov 1976) assume that animals maximize the net rate of energy gain while foraging. A forager with more energy is assumed to have greater fitness. Two important assumptions of such foraging models are: (1) that animals maximize the average rate of energy intake over a long term, and (2) that searching and exploiting are mutually exclusive. Combining these two assumptions leads to "the principle of lost opportunity" (Stephens and Krebs 1986). Decisions about exploiting items can be assessed by comparing potential gains from exploitation with the potential loss of opportunity to do better.

A third assumption of simple optimal diet models is that the predator chooses prey from a population that is randomly dispersed (Stephens and Krebs 1986). This aspect of these models has frequently been overlooked (e.g., Goss-Custard 1977, Barnard and Stephens 1981, Thompson 1983, Richardson and Verbeek 1986), in spite of the important implications this has for the model's predictions. If prey is not randomly dispersed, then the predator may have to make choices among a different variety of prey categories in each patch.

Shorebirds that feed on clams near Sundays River in South Africa provide an opportunity to test the classic diet model because the abundance of clams of different size classes differs among sites. The biology of the sand-burrowing wedge clam *Donax serra* in the eastern Cape, South Africa is well known (McLachlan and Hanekom 1979, Donn 1987). The size distribution of *D. serra* varies along the 35-km sandy beach east of the Sundays River mouth. There are many small but few large individuals close to the river mouth, an intermediate number of small and large individuals 5–20 km from the river mouth, and many large but few small individuals ≥20 km from the river mouth (Donn 1987) (Fig. 1).

I examined the preferences of nonbreeding African Black Oystercatchers (*Haematopus moquini*) and Kelp Gulls (*Larus dominicanus*) for different sizes of clams and tested whether these birds selected an energetically optimal diet from the different sizes of *D. serra* available at different locations on the beach.

METHODS

Study area

The seven study sites I chose were 2.2, 5.5, 8, 15, 20, 25, and 30 km from the Sundays River mouth. I chose these sites because at least two pairs of oystercatchers were present within 500 m of the transect points. At least two gulls were also present at each of these sites when the foraging behavior of the oystercatchers was observed. The study was conducted over 2 mo (February–March 1988); clam densities did not vary within sites during this period.

Clam availability

I measured the availability of the various size classes of clams as follows: At each study site, I sampled five transect lines 5 m apart and perpendicular to the high-water mark. Along each line, I examined 0.09-m^2 quadrats of sand to a depth of ≈30 cm, at 3-m intervals. Sand was sieved through a 4-mm mesh sieve, which effectively trapped all *Donax serra* >9 mm in length. Quadrats were taken from the center of the *D. serra* zone to the first quadrat containing no clams above and below this zone. Clam length was measured to the

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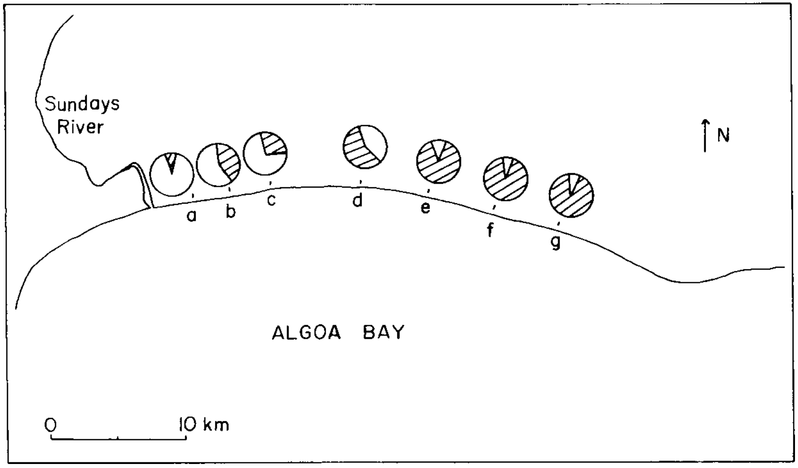

FIG. 1. The study area on the beach east of the Sundays River mouth, eastern Cape, South Africa. The distances of the study sites from the river mouth are: (a) 2.2 km, (b) 5.5 km, (c) 8 km, (d) 15 km, (e) 20 km, (f) 25 km, (g) 30 km. The population structure of *Donax serra* is indicated by pie charts as follows: The unhatched area indicates the proportion of small clams (<30 mm length) and the hatched area the proportion of large clams (>30 mm length) at each study site.

nearest millimetre using vernier calipers. Length of *D. serra* at a nearby beach (in millimetres) was related to tissue dry mass (in milligrams) by the following equation: log(mass) = 3.07 log(length) − 2.1; $r^2 = 0.97$, $P < .001$ (McLachlan and Hanekom 1979).

Clams eaten

I determined the diet of the two bird species by collecting the shells of clams eaten by each and measuring them. Both bird species fed almost entirely on *D. serra* while foraging near the Sundays River mouth. Kelp Gulls ate carrion opportunistically, although this was not observed during the part of the tidal cycle when *D. serra* were in the thixotropic zone (where the sand is covered by a light film of water). Shells of clams eaten by oystercatchers (500 per site) and gulls (200 per site) were collected from an area extending 500 m on either side of the transect lines at each of the seven study sites. African Black Oystercatchers removed clams from the thixotropic zone and took them to the high-water mark. Clam flesh was exposed by inserting the bill between the valves to force them open. Clams eaten by oystercatchers were left with the valves intact and spread ≈90° apart. Kelp Gulls removed clams from the thixotropic zone and flew either to the pebble zone above the high-water mark or to a patch of hard sand and dropped the clams from a height of ≈6 m (pebbles) or ≈10 m (hard sand) to break them open. Clams eaten by gulls always had only one valve intact. The only other predator of clams on this beach was the three-spot swimming crab *Ovalipes punctatus*, which crushed both valves of the clam, making these clams distinguishable from those eaten by gulls and oystercatchers (Du Preez 1984).

Overlap in choice of clam sizes by gulls and oystercatchers was measured to determine similarities in selectivity, given the different constraints placed on the feeding strategies of these birds. I used Pianka's (1973) index of diet overlap:

$$\text{overlap} = \sum_{i}^{n} P_{ij} P_{ik} \Big/ \left(\sum P_{ij} \sum P_{ik} \right)^{1/2}, \qquad (1)$$

where P_{ij} and P_{ik} represent the proportion of the i^{th} category of a particular resource dimension (in this case a particular size class of clam) used by the j^{th} and k^{th} species.

Handling time, distance searched, and activity budgets

I determined the handling times and search times for clams of different sizes at the various study sites. Handling time was the time taken from the capture of the clam until the bird returned to the thixotropic zone to feed. Probing rate was the number of instantaneously recorded probes every 10 s, i.e., instantaneous behavior sampling sensu Altmann (1974). An index of search efficiency was determined as the number of *D. serra* taken per unit distance searched rather than the number taken per unit time, because the oystercatchers fed intermittently, frequently standing still for long periods. This index was determined using the following equation, with length of pace expressed in metres:

$$\text{Search efficiency} = \frac{\text{no. of clams taken/min}}{\text{length of pace} \times \text{no. of paces/min}}. \qquad (2)$$

Mean values for each study site were used in this equation. This index was termed "feeding rate" by Goss-Custard (1977). The latter term is incorrect because handling time is not included in the equation, and the word "rate" implies that time is the unit of comparison rather than distance. The index of search efficiency and handling times were determined at the 2.2-, 5.5- and 25-km sites. These sites exhibited the greatest variation in size structure of the *D. serra* population, namely many small clams and few large ones at 2.2 km, many small and large clams at 5.5 km, and few small and many large clams at 25 km. Only adult birds were studied. All statistical tests were analyses of variance (ANOVA) and all mean values are presented ±1 SE, unless otherwise stated. Repeated observations of the same bird were assumed to be independent. I divided the time spent observing birds at each site equally between members of a pair of oystercatchers, and observed at least two gulls from each flock during each foraging bout in order to minimize the effects of individual variation on the interpretation of diet selection.

Diet selection

To provide quantitative support for optimal diet selection, selectivity must depend on the birds' encounter rate with the most profitable sizes of clam. Simple optimal diet models predict that predators will include less profitable prey in their diet when their encounter rate with profitable prey is low, but exclude them, regardless of encounter rate, when it is high (Hughes 1979).

To test this, a modified equation from Charnov (1976) and Thompson and Barnard (1984) was used to calculate the expected rate of energy intake from taking one or more size classes as follows:

$$E_{t(1\,\ldots,\,N)} = \frac{\Sigma\lambda_{(1\,\ldots,\,N)}\cdot E_{(1\,\ldots,\,N)}}{1 + \lambda_{(1\,\ldots,\,N)}(h_{(1\,\ldots,\,N)})}, \qquad (3)$$

where $E_{t_1\,\ldots,\,N}$ is the expected rate of energy intake from clam classes 1 to N, in 10-mm increments from 11–70 mm, where 11–20 mm clams constitute class 1, 61–70 mm clams constitute class 6, and N is any number from 1 to 6. $E_{1\,\ldots,\,N}$ is the median dry mass of clams in each size class; $h_{1\,\ldots,\,N}$ is the median handling time for clams of classes 1 to N; and $\lambda_{1\,\ldots,\,N}$ is the encounter rate with clams of classes 1 to N. $\lambda_{1\,\ldots,\,N}$ was calculated as the reciprocal of the expected travel time between consecutive clams, using the following equation (Barnard and Stephens 1981, Thompson 1983):

$$\lambda_{(1\,\ldots,\,N)} = \frac{1}{100\sqrt{[(1/d_{(1\,\ldots,\,N)})/a]}}, \qquad (4)$$

where $d_{1\,\ldots,\,N}$ is the number of clams of classes 1 to N per square metre and a the mean rate of movement (centimetres per second) at each study site. Rate of movement was determined from the mean stepping rate and the distance covered by a step (measured after the birds had walked in moist, but stable, sand). Eq. 4 measures the maximum encounter rate because it assumes that a bird will encounter each clam in the sand (Barnard and Stephens 1981). However, since it is reasonable that a bird's encounter rate with each size class of clams is a function of the density of that size class, such an estimate is a useful relative measure. Also, both gulls and oystercatchers detect their prey visually from a distance of up to 3 m (D. Ward, *personal observation*), and are, thus, probably aware of the distribution of all prey categories in their search paths.

Clam size classes were ranked in order of profitability and the expected rate of energy intake calculated from taking just the most profitable class, then the two most profitable classes, then the best three, and so on until all six classes were taken into account.

Chesson's (1983) measure of preference, α_i, was used to examine changes in preference for different clam size classes with changes in the availability of large and small clams. This maximum likelihood estimator may be used only if food availability or density (as was the case in this study) does not change appreciably over the experimental period. Chesson's (1983) measure is:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}, \qquad (5)$$

where r_i is the number of items of food type i (in this study, the i^{th} 10-mm size class of clam) in the consumer's diet and n_i is the number of items of food type i in the environment. In order to test the fit of the data to the models, the preferences for different clam sizes were compared to the frequencies of prey available using a G test (Sokal and Rohlf 1969).

Relative availability of clams

The clams orient in the sand with the long axis of their valves at 90° to the surface, so that the posterior surface area is the only part of the clam exposed to vertical probing by birds. Therefore, length of clam relative to posterior surface area (=plan area) was determined in order to give an indication of the chance of a probing bird striking a clam. The plan area of *D. serra* increased allometrically with length ($y = 2.54x^{2.21}$; $r^2 = 0.98$; $P < .001$; $n = 53$). This indicates that large clams may be easier to detect by vertical probing and are thus more readily available to the birds than small clams. I did not include this factor in my measure of expected rate of energy intake (Eq. 3) because the birds usually detected clams of all sizes from several metres away and may not have been affected by it.

Clam burrowing depth has been included in indices of availability in studies of this nature (Richardson and Verbeek 1986, 1987) because large clams have longer siphons than small ones and are likely to be more difficult for the birds to extract because they are buried deeper. However, I found that all clams fed just below the surface, so depth of clam was not included in this measure.

Ease with which clams are broken

Gulls usually dropped clams from ≈6 m (measured by eye relative to a scaffold of known height at the 2.2-

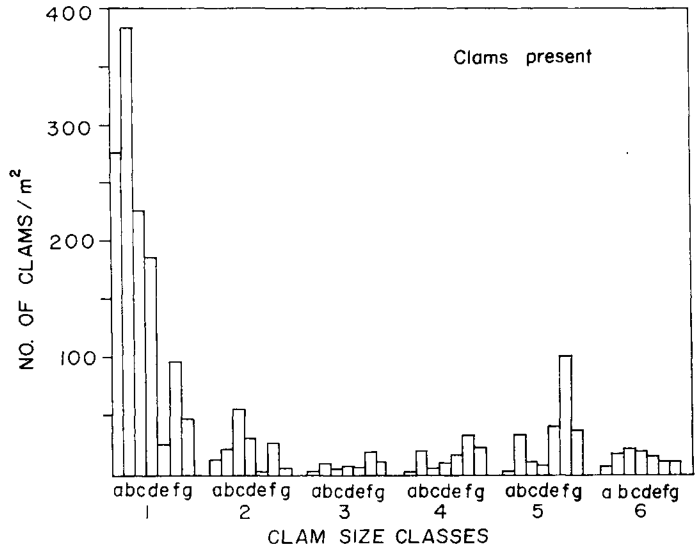

FIG. 2. Mean number of *Donax serra* clams/m² in transects at (a) 2.2 km, (b) 5.5 km, (c) 8 km, (d) 15 km, (e) 20 km, (f) 25 km, (g) 30 km sites. Size classes are in 10-mm length increments, where 1 = 11–20 mm clams and 6 = 61–70 mm clams.

km site) onto a pebble surface. In order to simulate this, clams ranging in size from 10–70 mm in length were arranged in 10-mm categories (20 in each category) and dropped from a 6 m high tower onto a 5 mm thick steel plate to determine whether different sizes of clams broke more easily than others. I did not drop the clams onto the irregular pebble surface because I assumed that the gulls were more accurate than I was, and did not miss the pebbles and allow the clams to land unbroken on the soft sand between pebbles.

Prey profitability

A value of 19.0 × 10³ J/g dry mass was used to calculate the gross energy content of each size class of clam (McLachlan and Hanekom 1979). Energy costs and benefits of prey selection were calculated using handling times, a basal metabolic rate of 4.6 J/s for oystercatchers and 4.8 J/s for gulls (from Lasiewski and Dawson's [1967] allometric equation for metabolic rate against body size), an assimilation efficiency of 75% (Ricklefs 1974), and multipliers of 9 × BMR for flying, 4 × BMR for searching, and 2 × BMR for other parts of the handling process (Zach 1978, Richardson and Verbeek 1986). Time and energy expended in flight were assumed to be independent of the size of the clam being carried. This is reasonable because even the largest clams were <5% of a gull's body mass (see also Richardson and Verbeek 1986, 1987).

RESULTS

Transects

The transects at the seven study sites along the beach revealed a similar trend to that found by Donn (1987). However, *D. serra* was most abundant at the 25-km site rather than at the 20-km site, as in Donn's (1987) study. *D. serra* is not an intertidal migrant and was found in a band between 18 and 33 m below the mean spring high tide mark. *D. serra* had a bimodal size distribution (Fig. 2) at all study sites, with very few individuals in the 31–40 mm valve length range.

Smaller *D. serra* were found at all tidal elevations on the beach at all sites (e.g., at 5.5-km site; Fig. 3). This trend has been consistent in monthly sampling at this beach over a period of 3 yr (T. E. Donn, *personal communication*). Due to this stratification, large clams were not available to the birds (which feed only when the sand is thixotropic) at some stages of the tide, whereas small clams always were available. As a result, one assumption of the optimal diet model, viz., that

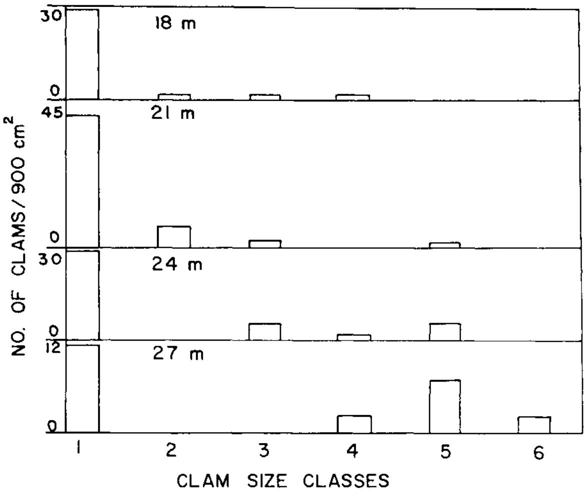

FIG. 3. Stratification of *Donax serra* clams up the beach on transect 1 at the 5.5 km site. Sampling quadrats were 30 × 30 cm. Distances are from the mean high water mark. Size classes are as in Fig. 2.

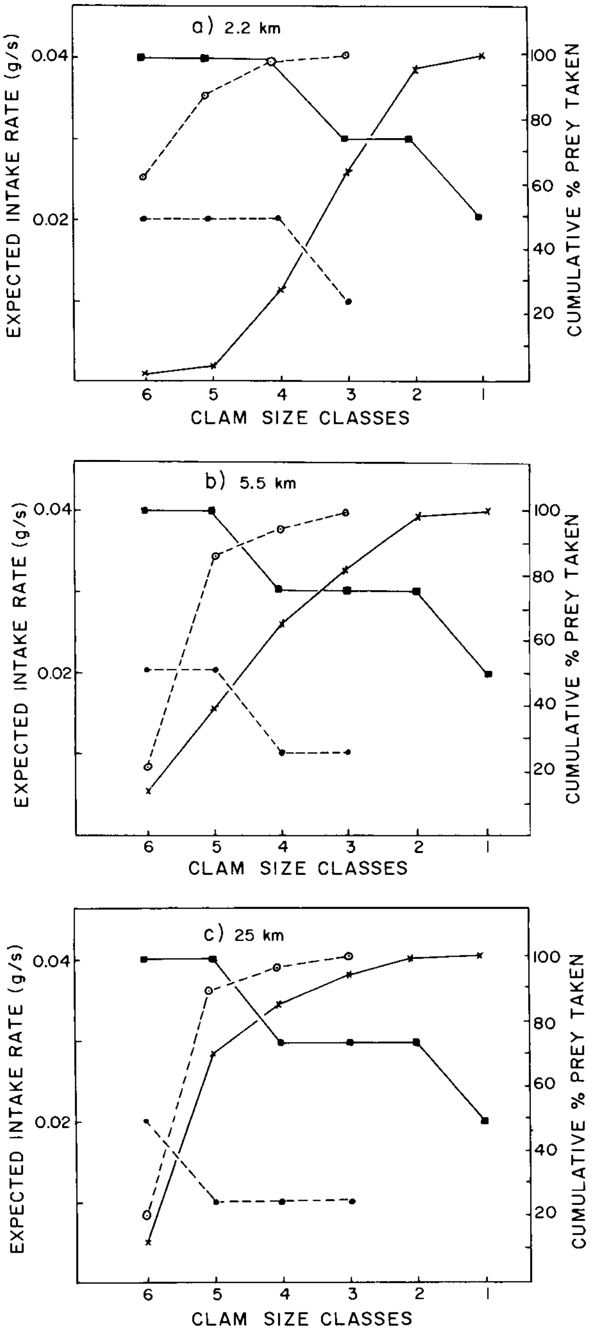

FIG. 4. Expected rate of intake and actual cumulative % of clams taken by oystercatchers and gulls from the different clam size classes at sites (a) 2.2 km, (b) 5.5 km, and (c) 25 km from the river mouth. Broken lines = gulls; solid lines = oystercatchers; ● = expected rate of energy intake (including search + handling time) for gulls; O = cumulative % intake for gulls; ■ = expected rate of intake for oystercatchers; X = cumulative % intake for oystercatchers. Note reverse order of size classes in horizontal scale.

prey are randomly distributed, was not met. Nonetheless, I decided to test the optimal diet model because small clams were randomly distributed within the zone containing the large clams (>30 mm length, the expected preferred prey). This means that the birds still had to make choices among items in a random distribution within the zone where their preferred (large) prey were present.

Diet selection

At the 2.2-, 5.5-, and 25-km sites, expected profitability (Eq. 3) to oystercatchers did not increase as more size classes of clams were added to the simulated diet (Fig. 4a–c). This indicates that there would be no advantage to taking size classes in addition to the largest class when their encounter rate with class 6 (61–70 mm) is high. There is, however, no disadvantage to taking classes 5 and 4 (2.2-km site) and class 5 (5.5- and 25-km sites), in addition to class 6, because there is no drop in the predicted harvest rate. Oystercatcher diets did not correspond well with predictions at the 2.2- and 5.5-km sites (cumulative percentage of clams eaten = 28 and 40% of diet in clam size classes with highest expected intake rate, respectively), but represented a fairly good fit to predictions at the 25-km site (51–70 mm clams constituted 71% of diet).

Selection by gulls of clam sizes producing the highest expected intake rates at the 2.2-km and 5.5-km sites represented excellent (98%) and very good (81%) fits to the predictions, respectively (Fig. 4a, b). However, at the 25-km site (Fig. 4c), the clam size class with the highest expected intake rate (61–70 mm length) constituted only 19% of the diet.

There was a significant difference between the sizes of clams available and those taken by gulls and oystercatchers at all sites ($P < .05$, Kolmogorov-Smirnov test), both species showing a preference for larger clams. However, at all sites, there was no significant difference ($P > .05$, Kolmogorov-Smirnov test) between the size distribution of clams consumed by gulls and oystercatchers and that of clams available in the three largest size classes (10-mm increments). There was no significant change in the mean size of prey taken by gulls among study sites (Fig. 5). Oystercatchers, on the other hand, took more small clams when large clams were scarce (Fig. 6). Oystercatchers never specialized on large clams, even where these were abundant (20-, 25-, and 30-km sites).

Preference measure

According to the predictions of the optimal diet model (Stephens and Krebs 1986), the birds should include nonpreferred items in the diet only when the preferred prey size is rare. When the preferred prey is abundant, nonpreferred items should be excluded regardless of their relative abundance. Accordingly, I predicted that there should be no significant change in the preference values (Eq. 5) among the 5.5-, 15-, 20-, 25- and 30-km sites, where large clams are abundant and densities of small clams vary. Conversely, there should be a significant difference between the 2.2- and 8-km sites (where large clams are rare) and the other five sites. However, the gulls and oystercatchers showed signif-

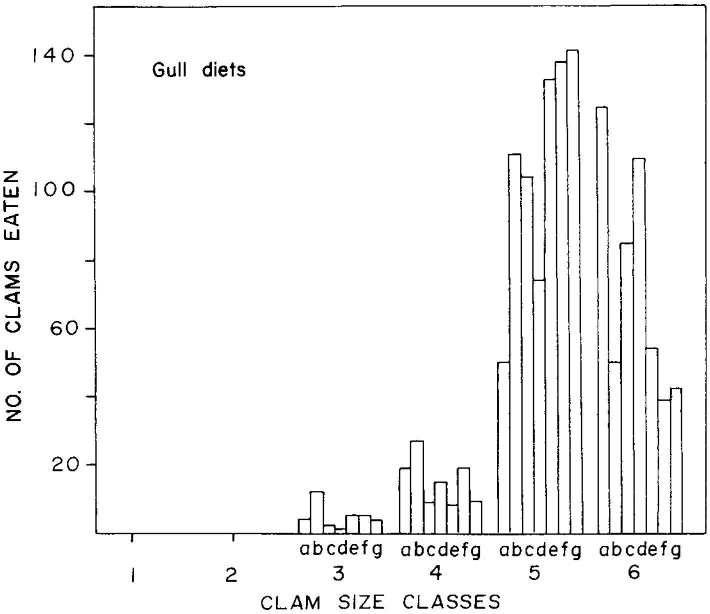

FIG. 5. Distribution of clams of different size classes taken by gulls at sites (a) 2.2 km, (b) 5.5 km, (c) 8 km, (d) 15 km, (e) 20 km, (f) 25 km, and (g) 30 km from the river mouth. Size classes as in Fig. 2.

icant changes in prey preferences (Table 1) among all combinations of sites ($P < .05$). This indicates that the densities of the nonpreferred small clams did affect the selection of preferred large clams.

Energy costs and benefits of prey selection

In order to maintain a positive energy balance, gulls should not take clams that are <30 mm in length, while oystercatchers should not take clams <20 mm (Fig. 7). Gulls only took clams that fulfill this requirement, while oystercatchers sometimes did not.

Handling times

There was a weak but significant correlation between prey size and handling time in oystercatchers ($r^2 = 0.29$, $y = 0.94x + 2.17$, $P < .05$, $n = 76$), but not in gulls.

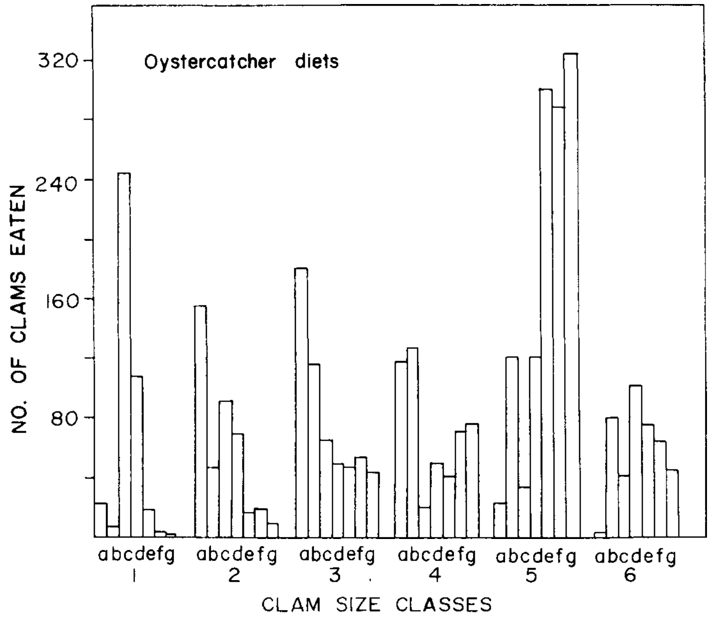

FIG. 6. Distribution of clams of different size classes taken by oystercatchers at sites (a) 2.2 km, (b) 5.5 km, (c) 8 km, (d) 15 km, (e) 20 km, (f) 25 km, and (g) 30 km from the river mouth. Size classes as in Fig. 2.

TABLE 1. Preference values (α_i) for different size classes (lengths) of clams of African Black Oystercatchers and Kelp Gulls, comparing the proportion of shells of each 10-mm size class taken with the proportion of that size class available. This measure is scaled so that $\Sigma\ \alpha_i$ equals 1.

Sites (distance from river mouth, km)	Clam size classes (mm)					
	10–20	21–30	31–40	41–50	51–60	61–70
			Oystercatchers			
2.2	0.0001	0.0226	0.5540	0.3581	0.0643	0.0009
5.5	0.0006	0.0713	0.4456	0.2107	0.1162	0.1556
8	0.0326	0.0507	0.5994	0.1557	0.1029	0.0587
15	0.0153	0.0604	0.1940	0.1484	0.4421	0.1398
20	0.0182	0.3631	0.2421	0.0642	0.1846	0.1278
25	0.0016	0.0365	0.3767	0.1108	0.1470	0.3274
30	0.0011	0.1571	0.2195	0.1664	0.2591	0.1967
			Gulls			
2.2			0.0474	0.2252	0.5927	0.1347
5.5			0.1572	0.1516	0.3636	0.3275
8			0.0348	0.1342	0.6034	0.2276
15			0.0085	0.0951	0.5775	0.3189
20			0.1200	0.0596	0.3883	0.4321
25			0.1044	0.0887	0.2101	0.5968
30			0.0442	0.0647	0.3356	0.5556

The difference between handling time by oystercatchers ($\bar{X}$ = 55.04 ± 3.53 s) and by gulls ($\bar{X}$ = 141.84 ± 9.39 s) was highly significant ($P < .001$).

Foraging efficiency and searching patterns

In addition to examining the diet selection of oystercatchers and gulls in terms of an optimal diet model, I compared the efficiency of predation, and the ability of the birds to alter their feeding patterns according to changes in prey availability, among sites and between species.

The number of clams taken by oystercatchers per 5 min of foraging did not differ significantly ($P > .05$) among sites (Table 2). When foraging efficiency was measured as the number of clams caught per unit distance searched (Eq. 2), then the oystercatchers at 2.2 km were most successful, followed by the oystercatchers at the 25-km site and then those at the 5.5-km site (Table 2). However, when success was measured in terms of dry mass of clam consumed per unit distance searched, oystercatchers were most successful at the 25-km site (Table 2). There was no significant difference in capture rate by gulls between 5.5- and 25-km sites (Table 2). Capture rate was not measured at the 2.2-km site because foraging by gulls was infrequent there. Gulls caught fewer clams than did oystercatchers at the 5.5- and 25-km sites because they selected only large clams.

Where large prey were most abundant (5.5- and 25-km sites), oystercatchers paced faster than where there were mostly small prey available (2.2-km site; Table 2). At the 2.2-km site, oystercatchers frequently employed a stitching pattern of foraging (like a sewing machine), contributing to the slow pacing rate there and high probing rate. The difference in probing rate between 2.2- and 25-km sites was significant ($P < .01$), although there was no significant difference ($P > .05$) between probing rates at 2.2- and 5.5-km sites and between the 5.5- and 25-km sites (Table 2). Oystercatchers spent significantly ($P < .001$) more time foraging on flow tides ($\bar{X}$ ± 1 SE = 63.28 ± 2.06 min) than on ebb tides (44.67 ± 1.97 min). Gulls made no significant change ($P < .05$) in pacing rate (3.95 ± 0.14 s/10 paces) or search pattern among the 2.2-, 5.5- and 25-km sites. There was no significant difference ($P <$

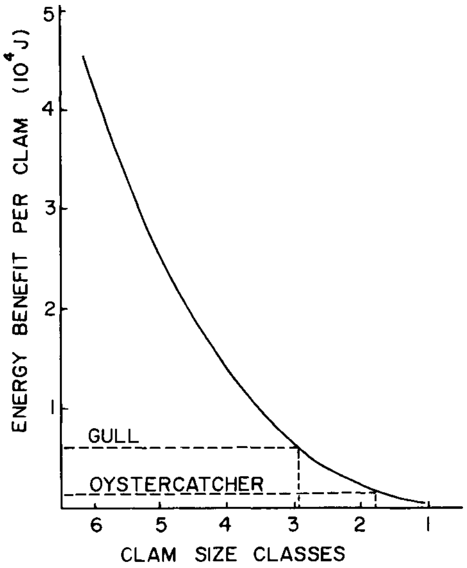

FIG. 7. Energy benefit per clam, calculated as dry mass multiplied by the energy value (McLachlan and Hanekom 1979). Broken lines indicate the points where cost of foraging = energy benefit per clam. Note reverse order of size classes in horizontal scale.

TABLE 2. Foraging patterns and foraging success of African Black Oystercatchers and Kelp Gulls. n = number of hours of observation of each species at each site. Data are means ± 1 SE.

	Distance from river mouth (km)		
	2.2 (n = 137)	5.5 (n = 165)	25 (n = 142)
Pacing speed (s/10 paces)			
Oystercatchers	7.2 ± 0.6	4.23 ± 0.3	4.0 ± 0.25
Gulls	4.03 ± 0.11	3.75 ± 0.16	4.08 ± 0.21
Time spent probing (no. pecks/30 instantaneous observations)			
Oystercatchers	14.37 ± 0.8	12.4 ± 0.91	11.1 ± 0.11
No. of clams taken/min search time			
Oystercatchers	1.7 ± 0.9	1.68 ± 0.13	2.09 ± 0.27
Gulls	···	0.39 ± 0.08	0.56 ± 0.11
No. of clams taken/m searched			
Oystercatchers	0.035	0.02	0.024
Gulls	···	0.002	0.003
No. of grams of clam taken/m searched			
Oystercatchers	0.015	0.02	0.036
Gulls	···	0.002	0.003

.01) in the time spent foraging by gulls on ebb and flow tides (41.13 ± 4.89 min).

Overlap between gulls and oystercatchers in use of the 10-mm clam size classes was high where large clams were abundant. Using Pianka's (1973) measure, in which 1 = complete overlap and zero = none, overlaps at the river sites were 0.12 at 2.2 km, 0.78 at 5.5 km, 0.59 at 8 km, 0.75 at 15 km, and 0.96 at each of the 20-, 25-, and 30-km sites. In spite of the high overlap in prey sizes taken by the two species, interspecific aggression was rare (18 cases in 624 h of observation, 11 initiated by oystercatchers). This indicates that there was little competition for clams between species, probably because there was little depletion of the clam population by the birds.

Clam dropping

Gulls flew $\approx$100 m on a round trip to the pebble zone to drop clams. It took gulls a mean of 3.32 ± 0.42 drops to break a clam. On average, 18 of the 20 clams in each of the 10-mm size categories dropped from the tower broke on the first drop; the rest broke on the second drop.

DISCUSSION

Is gull and oystercatcher foraging consistent with the assumptions of an optimal diet model?

The mean size of clams selected by both Kelp Gulls and African Black Oystercatchers was significantly larger than the mean size of clams available to them. Kelp Gulls selected only large clams (size class 3 or larger). Several studies of shell-dropping behavior in birds (e.g., Siegfried 1977, Zach 1978, Maron 1982) have shown that birds prefer large clams partly because these are easier to break. Gulls in this study may not have selected large clams for this reason, because all size categories broke equally easily in my tests. Kelp Gulls selected clams that constituted excellent and very good approximations to an optimal diet at the 2.2- and 5.5-km sites, but did not at the 25-km site (Fig. 4a–c).

Comparison of the preferences of gulls for different size classes of clams among sites revealed that gulls did not perform according to the predictions of the optimal diet model because they changed preferences among sites depending upon whether preferred (large) clams were abundant. Gulls discriminated between large and small clams but not between clams of adjoining size classes. This lack of discrimination may have caused the lack of absolute congruence between expected and actual intakes at the 5.5-km and the 25-km sites. Gulls, unlike oystercatchers, always took clams that ensured a net energy gain (Fig. 7).

Oystercatchers selected a diet that was similar to the expected optimal diet at the 25-km site only. They also displayed preferences for different size classes that were inconsistent with optimality predictions, and did not discriminate between clams of adjoining size classes. Oystercatchers, unlike gulls, changed their searching speed and pattern with changing prey availability, indicating flexibility in foraging.

It may be argued that the gulls were more selective than the oystercatchers because the gulls also eat carrion and can thus afford to be selective. By this argument, oystercatchers, which specialize on clams, are forced to eat small clams to maintain a positive energy budget. This scenario is unlikely because: (1) the gulls spent most of their day loafing between bouts of foraging on clams (i.e., they did not take clams to supplement their carrion diets, but rather the reverse); (2) even if gulls were majoring on carrion, those birds that selected the optimal clam sizes had a greater expected return to fitness than those that did not because they would have been maximizing energy intake per unit cost; and (3) oystercatchers spent most of their day inactive between clam-foraging bouts, and avoided many other potential prey species that are available to them on this beach (Wendt and McLachlan 1985), i.e., they did not appear to have been forced to eat small clams.

Several other factors have been shown to affect the foraging strategies of birds feeding on bivalves, viz., aggression and dominance (e.g., Goss-Custard and Durell 1988), age differences (e.g., Richardson and Verbeek 1987), and methods of opening bivalves (Goss-Custard and Sutherland 1984). All the gulls and oystercatchers in this study were adults, interspecific aggression was rare, intraspecific dominance effects were not apparent, and all individuals of each species opened clams in the same way. Therefore, it is unlikely that any of these factors played a role in the size selection of clams.

I have assumed that the birds maximize their rate of net energy intake. It is possible that the birds attempt to optimize the intake of some other nutrient or that energy intake is optimized subject to nutrient constraints (Pulliam 1975). However, these factors may also be allometrically scaled to body size (McLachlan and Hanekom 1979, Richardson and Verbeek 1986, 1987), and energy maximization will usually involve the simultaneous maximization of the intake of other nutrients (although see Belovsky 1978 for a counter example).

Comparison with previous studies

Richardson and Verbeek (1986) found that Northwestern Crows *Corvus caurinus* selected sizes of littleneck clams *Venerupis japonica* that maximized the net long-term rate of energy intake at a single site. Northwestern Crows, like Kelp Gulls, extract flesh from clams by dropping them. It is likely that the greater similarity between expected and actual diets in gulls and crows than in oystercatchers is a result of stronger selection pressure on the two former species, which expend considerable amounts of time and energy (and thus incur large missed opportunity costs) while foraging. Richardson and Verbeek (1986) also found, as I have, that the birds did not select clams in the all-or-none manner predicted by some optimal diet models (e.g., Krebs and McCleery 1984, Stephens and Krebs 1986). They suggested that this was not an unexpected result, because the prediction is based on the assumption that predators are unerring in their choices and do not vary in their ability to detect, capture, and handle prey. A study by Hulscher (1982) on European Oystercatchers (*Haematopus ostralegus*) feeding on *Macoma* mussels, as well as other studies of the foraging behavior of Pied Wagtails (*Motacilla alba*; Davies 1977), Redshanks (*Tringa totanus*; Goss-Custard 1977) and European Swallows (*Hirundo rustica*; Turner 1982), for example, showed that these species also took unprofitable prey.

Why the model failed to predict the birds' diet

Recognition time.—Partial preferences for less profitable prey can occur as an effect of errors of discrimination by the predator (Hughes 1979, Getty 1985), as may have been the case in this study. In addition, Lucas (1983) has shown that animals, such as intertidal animals, with a time constraint on foraging, will show decreased diet selectivity towards the end of a foraging bout.

Oystercatchers and gulls in this study have two constraints that may affect their ability to discriminate between different sizes of prey: (1) they only remove clams in the middle part of the tidal cycle, i.e., when the waves are just washing over the zone 18–33 m from the mean high water mark; and (2) clams are removed only when the sand is thixotropic.

This reduced time for searching and capturing clams leaves a short time for the birds to assess the size of the clam and seize it before the next wave washes over them. A bird that hesitates during this period is likely to be left with no clam at all. This beach has strong wave action (average wave height = 2–3 m; Wendt and McLachlan 1985), placing the birds at considerable risk while removing clams. On stormy days, the birds rarely fed on clams, possibly because of this factor. An extreme case of the effects of improper discrimination was the selection by oystercatchers of clams <20 mm in length, whose consumption causes a small net energy debt (Fig. 5). As the selection of these small clams was rare this behavior will not be selected against strongly.

Temporal segregation of prey availability.—It is apparent from the size selection of clams by oystercatchers in this study that the intertidal segregation of size classes of clams influences foraging choices. For this reason, simple optimal diet models (Schoener 1971, Pulliam 1974, Charnov 1976) cannot explain the pattern observed, because they are based on the assumption that the prey are randomly dispersed. Because clams were distributed in diminishing order of size up the beach (Fig. 3), oystercatchers and gulls would not encounter large clams when small clams were available to them closer to the high-water mark. Therefore, oystercatchers lose nothing by taking small clams (as long as they are >20 mm in length) and stand to gain by reducing total time spent feeding. This hypothesis is supported by the observation that oystercatchers spent more time foraging on a flow tide than on an ebb tide. This suggests that the less profitable prey sizes were taken after the birds were unable to obtain a sufficient number of the more profitable large clams.

Optimal diet models assume a constant search mode (Stephens and Krebs 1986). Oystercatchers changed their search mode slightly at the 2.2-km site, making a comparison between their behavior there and at the other two sites difficult. As a result of this change and the biologically more significant temporal segregation of prey availability, the optimal diet algorithm is not relevant for oystercatchers feeding on this beach.

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