Diet of the African black oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation

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The diet of the African black oystercatcher *Haematopus moquini* was investigated throughout the species' range. Variation in diet is related to time, place and sex of the bird. Correspondence analysis, using simple graphical displays, was chosen as the most appropriate technique for describing regional and local variation. Principal prey species on the west coast are mussels *Choromytilus meridionalis* and *Aulacomya ater*, and limpets *Patella granularis* and *P. argenvillei*. The mussel *Perna perna* predominates in the diet on the south and south-east coasts. Less food is taken by night than by day, and at night the nocturnally active *Patella granularis* forms a much greater proportion of the diet than by day. An increasing proportion of mussels and correspondingly fewer limpets are fed to chicks as they grow older. Territorial pairs reduce potential intersexual competition for food by removing prey in differing relative proportions: males take more limpets and whelks while females take a greater proportion of polychaetes and small unshelled items. Diet separation is a function of bill dimorphism. Small prey items generally are not selected, and prey size selection is consistent within prey species and between localities.

S. Afr. J. Zool. 1984, 19: 1 – 11

Die dieet van die tobie *Haematopus moquini* is deur die spesie se hele gebied ondersoek. Variasies in die dieet is verwant aan tyd, plek en geslag van die voëls. Ooreenstemmingsontleding, wat van eenvoudige grafieke gebruik maak, is gekies omdat dit die mees geskikte tegniek is om streek- en plaaslike variasies in die dieet te beskryf. Langs die weskus eet die tobie hoofsaaklik die mosselsoorte *Choromytilus meridionalis* en *Aulacomya ater* en die perdevoetjies *Patella granularis* en *P. argenvillei*. Die mossel *Perna perna* is die belangrikste prooi langs die suid en suidoos kus. Minder kos word gedurende die nag as in die dag ingeneem en gedurende die nag maak die nagtelike *Patella granularis* 'n groter gedeelte van die dieet uit as gedurende die dag. Soos die kuikens ouer word, word hulle toenemende hoeveelhede mossels gevoer en minder perdevoetjies. Territoriale pare verminder moontlike mededinging deur prooispesies in verskillende proporsies te verwyder; mannetjies verwyder 'n groter hoeveelheid perdevoetjies en wulke en wyfies meer wurms en klein ongedopte ongewerwelde diere. Dieetskeiding is 'n funksie van dimorfisme van die bek. Klein prooidiere word oor die algemeen nie uitgesoek nie en die keuse van die grootte van die prooi is dieselfde vir elke prooisoort asook verskillende liggings.

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The African black oystercatcher, *Haematopus moquini*, occurs around the southern African coast from central Namibia to central Transkei, with highest breeding densities at west coast islands (Hockey 1983a). The species' techniques of feeding on certain rocky shore invertebrates have been described (Hockey 1981a) but its diet on rocky shores has been described only for St Croix Island, Algoa Bay, in the southern Cape Province, South Africa (Randall & Randall 1982). The range of the African black oystercatcher spans two major zoogeographic regions, a cool west coast region extending from Cape Point northwards, and a temperate south coast region extending from Cape Point east to Port St Johns (Stephenson 1948). The species rarely straggles into the subtropical east coast region north of Port St. Johns where the intertidal zone is characterized by tropical and subtropical invertebrates (Stephenson 1948; Hockey 1983a).

Few quantitative assessments of oystercatcher diet have been made in areas where more than one prey species is eaten. Diet has been quantified locally for the European oystercatcher *H. ostralegus* (Heppleston 1971; Dare & Mercer 1973), and the American black oystercatcher *H. bachmani* (Webster 1941; Hartwick 1976; Morrell, Huber, Lewis & Ainley 1979). Diet of African black oystercatchers on a sandy shore in Algoa Bay has been described from two stomach samples (McLachlan, Wooldridge, Schramm & Kühn 1980).

The present study was designed to quantify geographical, local, temporal and intersexual dietary variations in the African black oystercatcher. In addition, we identify problems and pitfalls of generalization that frequently arise in diet studies.

Methods

When African black oystercatchers feed chicks, piles (middens) of emptied mollusc shells frequently are created at feeding stations, especially at exposed localities where chicks are fed above the high-water mark. To assess geographical variation in the mollusc component of diet, collections of such middens were made from 96 pairs of birds at 12 localities spanning most of the species' breeding range (Figure 1). No collections were made in Transkei, the extreme easterly limit of the breeding range (Hockey 1983a). Total collections of shells at all middens were made in preference to subsampling as wind often blew light shells such as ribbed mussels *Aulacomya ater* into cracks and depressions, thus producing a non-random distribution of species within middens.

Remains of soft-bodied animals were rarely found at middens. To check the validity of analysing variations in diet based solely on the mollusc component, direct observations of feeding

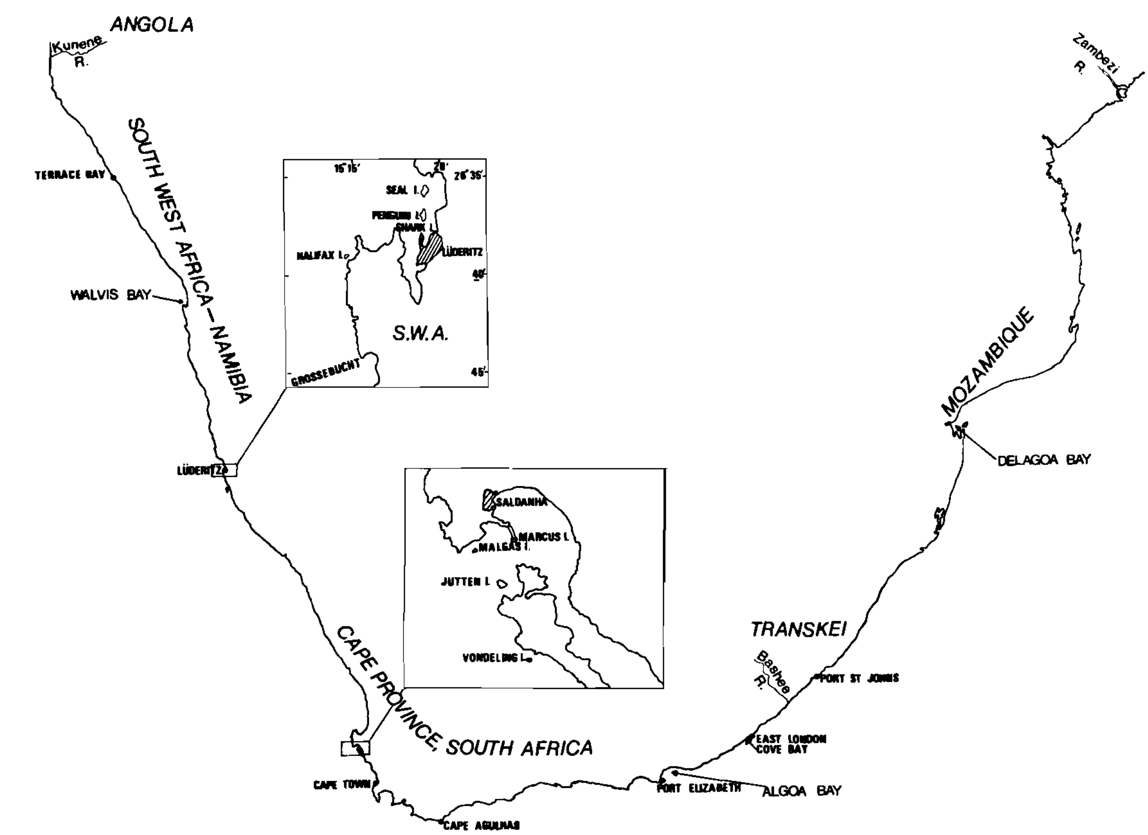

Figure 1 Map of the study area showing localities mentioned in the text.

were made at Marcus Island, south-western Cape. The diets of two pairs of birds were recorded over several months. The feeding territory of Pair 1 was dominated by beds of *A. ater* on the low shore and by the limpet *Patella granularis* on the mid- and upper shore. Pair 2 defended a territory dominated by black mussels *Choromytilus meridionalis* on the low shore and by *P. granularis* on the mid- and upper shore. Adults of both pairs were individually colour ringed and had been sexed at capture by cloacal examination (Hockey 1981b). Diet was recorded for both members of the pair during the same observation periods. Observations were made from a hide and prey were identified at the moment of capture using a 25 × telescope. Incidental observations of other pairs were made at several localities around the coast to obtain as full a listing of prey species as possible.

Dawn and dusk collections of middens were made at Jutten Island during March 1981 to compare diurnal and nocturnal diets. Twenty-two 'day middens' and 30 'night middens' were collected. Subsamples of commoner molluscs collected at middens were measured (maximum length to the nearest 1 mm) and size distributions of prey were compared between localities. Size distributions of prey captured were compared with size distributions of prey potentially available in the habitat. Only mussels were chosen for this part of the investigation as preliminary research had shown that African black oystercatchers modify limpet populations to such an extent that the classical comparison of size classes taken with size structures of the remaining populations is meaningless in terms of demonstrating selection (Hockey 1983b). Size preferences of mussels during the breeding season (*Perna perna* fed to chicks on the south-east coast) and during the nonbreeding season (*C. meridionalis* taken by adults on the west coast) were assessed.

A novel approach to the analysis of diet was adopted, namely correspondence analysis. Correspondence analysis (Benzecri 1973; Hill 1973, 1974; Nishisato 1980) belongs to the same family of analysis techniques as principal components analysis, canonical correlation analysis, discriminant analysis and factor analysis. All involve finding the eigenvalues and eigenvectors of a matrix computed according to an analysis-specific algorithm. For more thorough discussion of correspondence analysis see Greenacre (1978) or Greenacre & Underhill (1982). Correspondence analysis has the advantage of simultaneously displaying graphically both the variables and object points. Consequently there are two clouds of data points in a state of balance with one another; one representing the objects (middens) and the other the variables (prey species), respectively the rows and columns of the data matrix. Although plotted in two dimensions, these are multidimensional clouds of data. The degree of similarity between objects or variables is related to their separation in the graphical display, similar ones being close together and dissimilar ones farther apart. Variables plotted close to the original are most typical of the greatest number of objects, i.e. prey species close to the origin tend to occur in similar proportions in most middens.

The chief advantage of this type of plot over other types of analysis lies in the object-variable relationship described by the transition formulae (Greenacre & Underhill 1982): if an object has a large score on a particular variable then the object is drawn in the direction of the point representing that variable. Thus, in the display, object points lie in the same direction from the origin as the variables for which they have the highest scores. Objects or variables which differ greatly from the bulk of the data tend to swamp the analysis. These are easily recognized and can be effectively excluded from the analysis and considered as supplementary points (Greenacre & Underhill 1982). This allows analysis of more subtle variation within the majority of the data.

The graphical displays produced by correspondence analysis are supplemented by a series of tables determining the distortion in the display as a whole and which further break down the distortion of each point. These tables show how accurately the multidimensional cloud of data points is projected into two dimensions.

Results

Geographical variation in diet

The mollusc component of the African black oystercatcher diet throughout its range comprised mainly mussels and limpets (Table 1). At sites in Namibia, where mussels are scarce or absent, the diet was dominated by two limpet species, *Patella granularis* and *P. argenvillei*, with *P. granatina* regularly taken in small numbers. Prey species richness in Namibia was low, with a total of 14 prey species recorded and a maximum of 11 prey species at one locality (Possession Island).

In the south-western Cape, the two mussels *Choromytilus meridionalis* and *Aulacomya ater* formed a large proportion of the diet along with *P. granularis*. *Patella argenvillei*, *P. cochlear* and *P. granatina* were recorded regularly (Table 1).

Table 1 Frequency occurrence (%) of 31 mollusc species in African black oystercatcher middens (See Figure 1 for localities. T = trace)

	Namibia					S.W. Cape				S. and S.E. Cape			
Prey species	Seal Island	Shark Island	Halifax Island	Grosse-bucht	Possession Island	Jutten Island	Malgas Island	Saldanha	Vondeling Island	Robberg	St Croix[a] Island	Cove Rock	% of localities where recorded
Choromytilus meridionalis	6,0				0,7	11,4	34,0	56,5	37,9				50,0
Perna perna	0,3					0,2	2,7		1,4	35,0	90,4	70,9	58,3
Aulacomya ater	9,4	1,7			5,0	54,6	19,6	37,6	14,3				58,3
Donax serra						T		5,9	0,4			1,0	33,3
Venerupis corrugatus							0,1						8,3
Haliotis spadicea											T		8,3
Fissurella mutabilis					T						0,1		16,7
F. natalensis												1,8	8,3
Helcion pectunculus					T		T		T				25,0
Cellana capensis												4,7	8,3
Patella cochlear						0,3	0,3		11,0	55,2	1,0	4,2	50,0
P. compressa					0,1	T							16,7
P. granularis	31,2	89,7	58,0	9,1	45,2	25,9	35,7		23,5	3,6	7,2	1,4	91,7
P. argenvillei	51,0		40,1	88,3	47,5	3,4	5,8		9,8	4,4	T	5,1	83,3
P. barbara					0,1	T				0,9	0,9	T	41,7
P. miniata	0,7		0,4		0,3	T	T		T		0,1		66,7
P. concolor												0,2	8,3
P. longicosta											T	6,2	16,7
P. granatina	1,3	6,9	1,1	1,3	0,7	0,3	0,7		0,9				66,7
P. oculus											0,1	4,3	41,7
Siphonaria aspera												T	8,3
S. capensis										0,4			16,7
Turbo sarmaticus												T	8,3
Oxystele sinensis												0,2	8,3
O. variegata				1,3			0,5		0,6				25,0
Burnupena catarrhacta		1,7	0,4		0,3	T	0,2		0,1				50,0
B. lagenaria											T		8,3
Nucella cingulata	0,1					0,2	0,1		T				33,3
N. squamosa						T							8,3
N. dubia										0,4	0,1		16,7
Thais capensis												0,2	8,3
Sample size	695	58	262	143	5394	18901	6597	69	3850	223	3102	1403	40697
Recorded species richness	8	4	5	4	11	15	13	3	14	5	13	15	31

[a]Data from Randall & Randall (1982)

Prey species richness in the south-western Cape was greater than in Namibia with 17 species recorded, and up to 15 species at one locality.

Diet on the south and south-east coasts was dominated (up to 90,4%) by the brown mussel *Perna perna*. At Robberg (34°06'S/23°24'E), *Patella cochlear* formed 55,2% of the diet by numbers and this species was preyed on regularly at all south coast sites. *Patella granularis* and *P. barbara* also were recorded at all south coast sites. Twenty prey species were recorded on the south coast, making it the region with greatest prey species richness: a maximum of 15 species was recorded at one site. Sand mussels *Donax serra* were recorded at some sites, having been carried to chicks from nearby sandy beaches.

Overall, 52 prey species were recorded for African black oystercatchers, 49 from rocky shores and three from sandy shores and estuaries (Table 2).

The first two factors of the correspondence analysis are shown for all middens in Figure 2. 'Factors' are positive or negative associations of prey species and are arranged hierarchically — i.e. factor 1 is the most important. They are determined by the data and are not preconceived by the observer. Ninety-three percent of the inertia (the sum of the eigenvalues) was accounted for by the first four factors: a further four factors accounted for the remaining 7% of the inertia and are not considered further. The first two factors accounted for 62% of the total inertia. [All south coast sites (Robberg, St Croix Island and Cove Rock) were treated as supplementary points and as such did not influence the overall analysis: prey species which are unique to these sites appear at the origin in Figure 2.]

Factor 1 distinguished those middens with a high proportion of *P. argenvillei*, primarily Namibian middens on the left, from those with a high proportion of *A. ater* (south-western Cape) on the right (Figure 2). This distinction accounted for 92% of the inertia in the first factor and for 39% of the total inertia. Factor 2 separated those middens with a high proportion of *A. ater* from those with high proportions of *C. meridionalis* and *Perna perna*. This essentially distinguished Jutten Island from Malgas and Vondeling Islands. Factor 2 accounted for 23% of the total inertia.

Factor 3 (not plotted) separated sites with an association between *Patella granularis* and *P. granatina* from those with a high proportion of *C. meridionalis*, and accounted for a further 17% of the inertia. There is no obvious geographical explanation of this factor. Factor 4 identified those middens with relatively high proportions of *P. cochlear*, namely Vondeling Island, and the supplementary localities of Robberg and Cove Rock.

When data from the three closely proximate south-western Cape islands were considered separately (1980 data only) (Figure 3), further refinements could be made to the interpretation. *Aulacomya ater* was most characteristic of Jutten Island, and *P. cochlear, P. argenvillei* and *C. meridionalis* of Vondeling Island. The Malgas Island data almost formed a subset of the data from the other two islands. Birds from Vondeling Island exhibited the greatest within-island variability in diet in the south-western Cape (Figure 3).

We therefore conclude that *P. argenvillei* was highly characteristic of Namibia (Figure 2) and *A. ater* was highly characteristic of Jutten Island (Figure 3). *Patella granularis, P. granatina* and whelks and winkles emerged close to the origin: the proportions of these species in the diet are thus relatively constant and they exerted little influence on the analysis. Of the major dietary components, *P. argenvillei, A. ater* and *C. meridionalis* exerted the greatest influence on the analysis and hence are the key indicator species of geographic variation in diet on the west coast.

Table 2 Recorded prey species of African black oystercatchers (1 = important prey species, 2 = regular, 3 = uncommon, 4 = rare. [a]sandy shore and estuarine species.)

Order Actinaria (sea anemones)
Bunodactis reynaudi (3)

Class Polychaeta (bristle worms)
Lepidonotus semitectus (3)
Syllis/Trypanosyllis spp. (3)
Pseudonereis variegata (2)
Marphysa depressa (2)
Cirriformia spp. (4)
Scoloplos johnstoni (3)

Order Cirripedia (barnacles)
Octomeris angulosa (4)
Tetraclita serrata (3)
Austromegabalanus cylindricus (4)

Order Isopoda (isopods)
Paridotea spp. (4)

Order Amphipoda (amphipods)
Talorchestia spp.[a] (3)

Class Amphineura (chitons)
Acanthochiton garnoti (3)

Class Pelecypoda (bivalves)
Choromytilus meridionalis (1)
Perna perna (1)
Aulacomya ater (1)
Venerupis corrugatus (4)
Donax serra[a] (1)
D. sordidus[a] (1)
Macoma ? littoralis[a] (3)

Class Gastropoda (gastropods)
Haliotis spadicea (4)
Fissurella natalensis (2)
F. mutabilis (4)
Crepidula porcellana (4)
Helicon pectunculus (4)
H. pruinosus (4)
Cellana capensis (2)
Patella cochlear (2)
P. compressa (4)
P. granularis (1)
P. argenvillei (1)
P. barbara (2)
P. miniata (3)
P. concolor (2)
P. longicosta (2)
P. granatina (2)
P. oculus (2)
Siphonaria capensis (4)
S. aspera (4)
Turbo sarmaticus (3)
Oxystele sinensis (3)
O. tigrina (3)
O. variegata (3)
Argobuccinum pustulosum (4)
Burnupena catarrhacta (2)
B. lagenaria (2)
Nucella squamosa (3)
N. cingulata (3)
N. dubia (4)
Thais capensis (4)

Class Holothuroidea (sea-cucumbers)
Thyone aurea (4)

Class Tunicata (sea-squirts)
Pyura stolonifera (3)

Temporal variation in diet

Comparing diet at Jutten Island between two years, 1980 and 1981, correspondence analysis indicated some interesting differences (Figure 4). In 1980, *A. ater* and *P. cochlear* influenced overall diet composition, whilst in 1981, *C. meridionalis, P. argenvillei* and *Perna perna* were important differentiating species.

At night, a higher proportion of *P. granularis* and a correspondingly lower proportion of *A. ater* and *C. meridionalis* were removed than by day (Table 3). Relative proportions of other prey species varied little. Comparing relative abundance of the three most abundant prey species (other species being lumped) differences between day and night were highly significant (χ^2 = 81,30; d.f. = 3; $p < 0,001$). The mean number of shells in middens created by day was 31,6 and by night was 11,4: on average, therefore, night middens contained some 36% as many prey items as daytime middens.

There was a change in the relative proportions of prey species fed to chicks as the latter aged (Tables 4 & 5). At Jutten Island (Table 4) there was a higher frequency of mussels and cor-

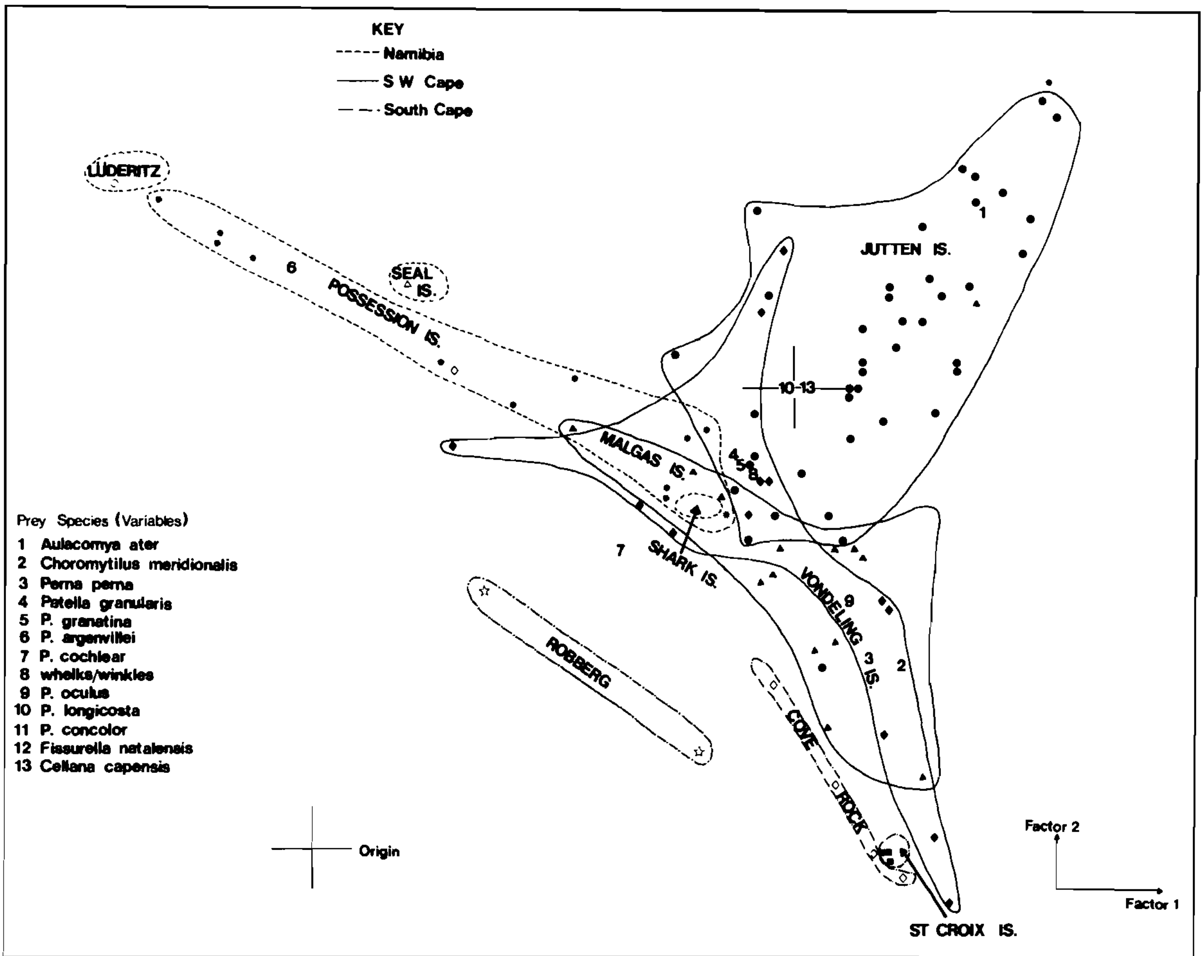

Figure 2 A correspondence analysis plot of 96 African black oystercatcher middens showing relationships of middens to component prey species. Points represent middens, ones with similar species composition being close together. Middens from different localities are represented by different symbols. Envelopes show localities, and numbers represent prey species in the middens.

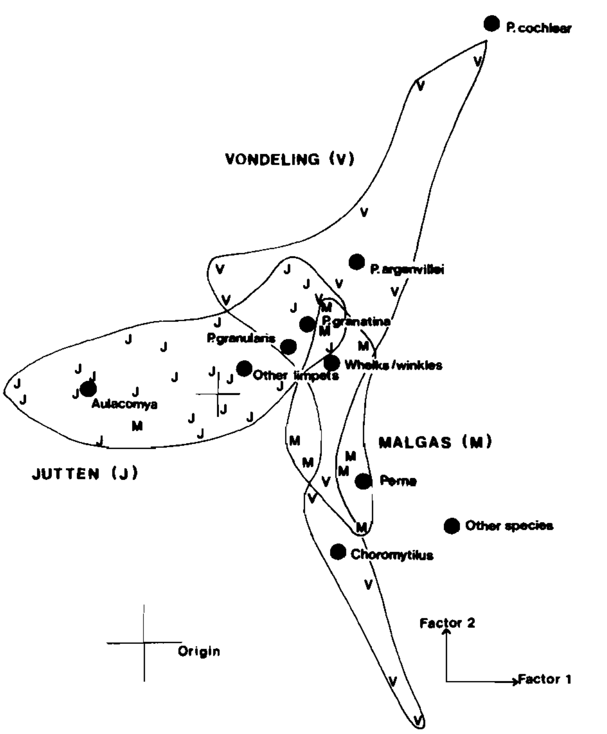

Figure 3 A comparison of African black oystercatcher midden composition at three islands (Jutten, Malgas and Vondeling) in the south-western Cape, South Africa (see text for details).

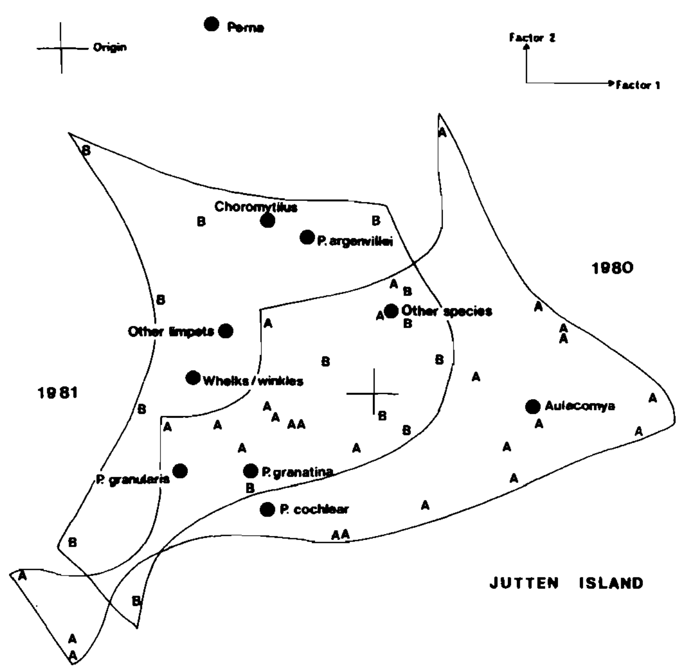

Figure 4 A correspondence analysis plot comparing diet of African black oystercatchers at Jutten Island in 1980 and 1981. A = 1980, B = 1981.

respondingly fewer limpets in middens of older chicks (χ^2 = 362,3 d.f. = 6; p < 0,001). This pattern was repeated at Malgas Island (Table 5) where sequential collections were made at one midden (χ^2 = 114,7; d.f. = 10; p < 0,001).

Sex-related differences in diet

A total of 620 prey items was recorded for Pair 1 (male 328,

Table 3 Numbers and relative proportions (%) (in parentheses) of prey species in feeding piles at Jutten Island by day and night

	Prey species										
	Choromytilus meridionalis	*Aulacomya ater*	*Perna perna*	*Donax serra*	*Patella granularis*	*P. cochlear*	*P. argenvillei*	*P. miniata*	*P. granatina*	No. of shells	No. of middens sampled
Day	105	416	3	0	149	5	8	0	9	695	22
	(15,11)	(59,86)	(0,43)		(21,44)	(0,72)	(1,15)		(1,29)		
Night	34	128	3	2	165	3	5	2	0	342	30
	(9,94)	(37,43)	(0,88)	(0,58)	(48,25)	(0,88)	(1,46)	(0,58)			

Table 4 Relative proportions (%) of principal prey species collected at middens of chicks of differing ages at Jutten Island

Age of chick when midden collected (days)	Prey species			Sample size
	Aulacomya ater	*Choromytilus meridionalis*	*Patella granularis*	
10 – 19	51,6	8,6	39,8	1091
20 – 29	57,8	6,8	35,3	2544
30 – 39	65,2	11,9	22,9	5179
40 – 49	53,1	17,1	29,8	3743
Totals	58,9	12,1	29,0	12557

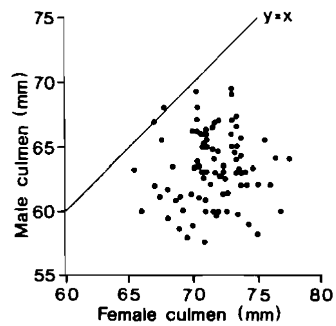

Figure 5 The relationship between male and female exposed culmen lengths of 85 pairs of African black oystercatchers from rocky environments in the south-western Cape, South Africa.

female 292) (Table 6). The differences in diet between male and female were highly significant (χ^2 = 303,73; d.f. = 8; $p < 0{,}001$). Most of the variation was accounted for by *P. granularis* and *Burnupena catarrhacta* which were favoured by the male. The male also removed a smaller proportion of *A. ater* than the female (χ^2 = 12,98; d.f. = 1; $p < 0{,}001$).

Pair 2 preyed on a smaller suite of species, reflecting a lower invertebrate diversity in beds of *C. meridionalis* (Hockey & Branch, in prep.), but there was still a significant difference in diet (χ^2 = 35,19; d.f. = 6; $p < 0{,}001$). The difference was accounted for almost entirely by the greater proportion of *P. granularis* taken by the male: 30,6% as compared with 5,1% taken by the female. The male of Pair 2 fed exclusively on molluscs and barnacles, whereas the female included some polychaetes and small unshelled items in the diet.

Overall, the pair foraging in the *A. ater* dominated area consumed 71,5% molluscs by number and the pair in the *C. meridionalis* dominated area took 95,9% molluscs.

Bill shape in African black oystercatchers is sexually dimorphic, with females having longer and more pointed bills on average, but with some sexual overlap (Hockey 1981b). Within pairs, however, the bill of the female is almost invariably longer than that of the male (Figure 5).

Prey size selection

African black oystercatchers avoided selecting small mussels both when feeding chicks (χ^2 = 592,6; d.f. = 25; $p < 0{,}001$) and during the nonbreeding season (χ^2 = 180,6; d.f. = 29; $p < 0{,}001$) (Figure 6). Size selection for the limpets *P. granularis* and *P. argenvillei* was consistent between localities (Figures 7 & 8). Most *P. granularis* selected were between 25 mm and 40 mm in length, corresponding to limpets 1 – 2 years old (see Branch 1975).

During 1980, larger *C. meridionalis* were selected at Vondeling Island than at nearby Malgas and Jutten Islands (Figure 9), but this trend was not evident in predation on the other abundant mussel, *A. ater* (Figure 10).

Discussion

Comparison with other species

Only one comparable quantitative analysis of oystercatcher diet on a rocky shore exists: the American black oystercatcher *Haematopus bachmani*, preys mainly on limpets (44,3%), mussels (29,4%) and small unshelled items (22,4%) at Cleland Island, British Columbia (Hartwick 1976). The remainder of the diet comprises nereid worms, 'snails', crabs, chitons and 'worms'. The variable oystercatcher, *Haematopus unicolor*,

Table 5 Relative proportions (%) of principal prey species in a midden at Malgas Island collected on three occasions (two chicks)

Age of chicks at collection (days)	Prey species						Sample size
	Aulacomya ater	*Choromytilus meridionalis*	*Perna perna*	*Patella granularis*	*Patella argenvillei*	Other	
13	14,5	22,6	1,7	55,1	4,4	1,7	296
24	25,7	40,2	2,3	24,7	6,5	0,6	612
51	20,2	45,2	1,1	25,4	7,2	0,9	566
Totals	21,3	38,6	1,7	31,1	6,4	0,9	1474

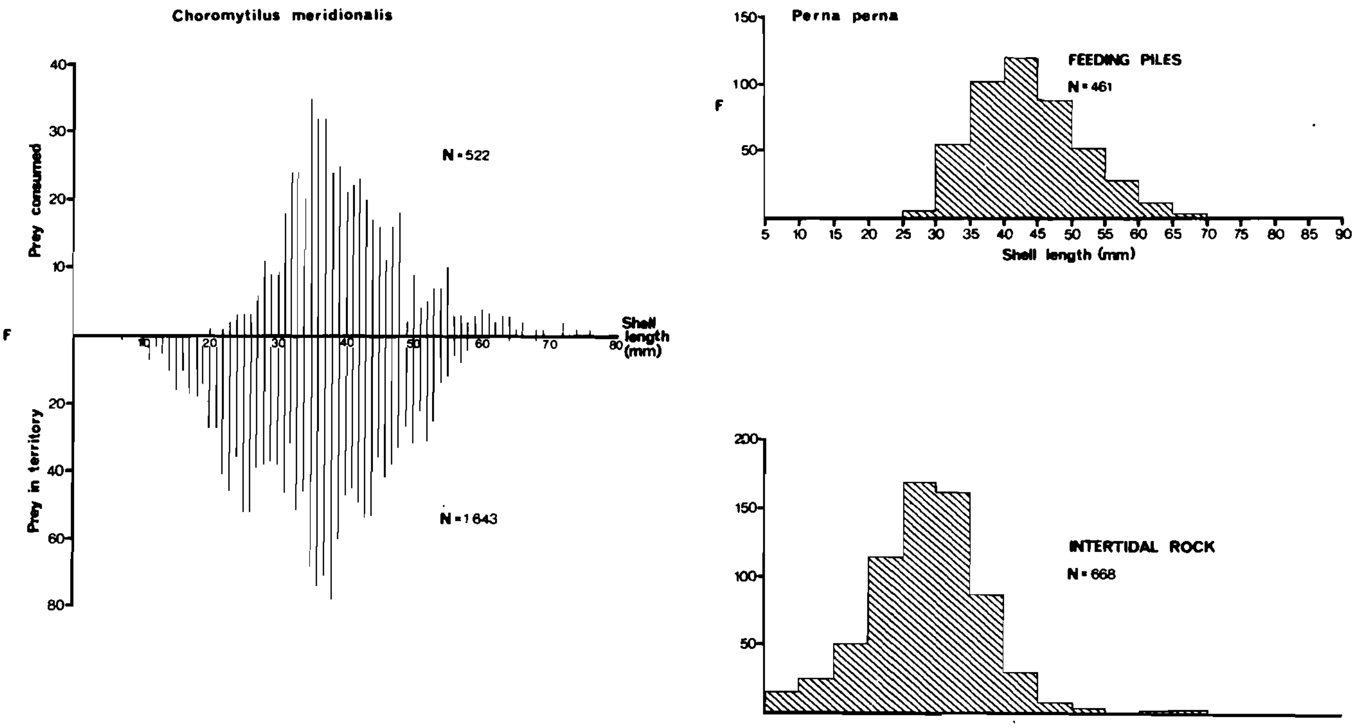

Figure 6 Prey size selection (mussels) by African black oystercatchers. (a) Items eaten by adults during the nonbreeding season (*C. meridionalis*, west coast). (b) Items fed to chicks (*P. perna*, south-east coast).

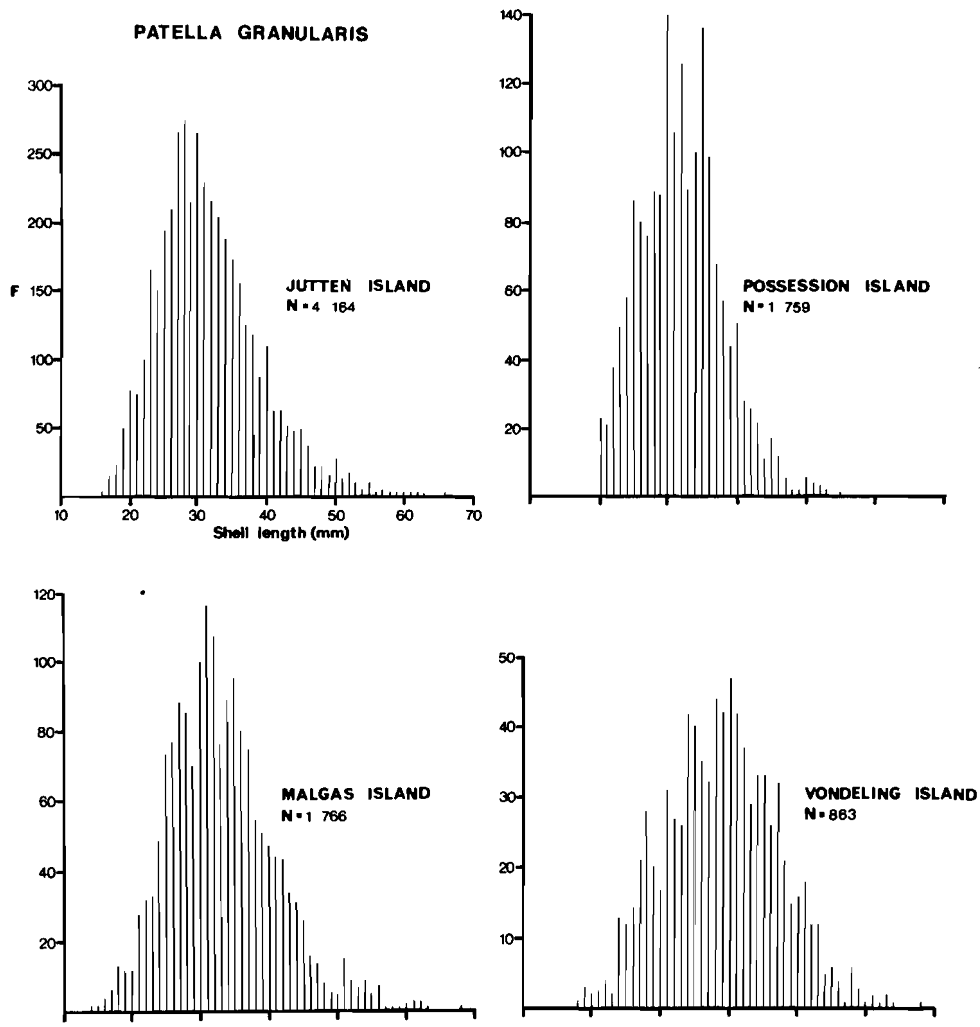

Figure 7 *Patella granularis:* size selection by African black oystercatchers at four west coast islands.

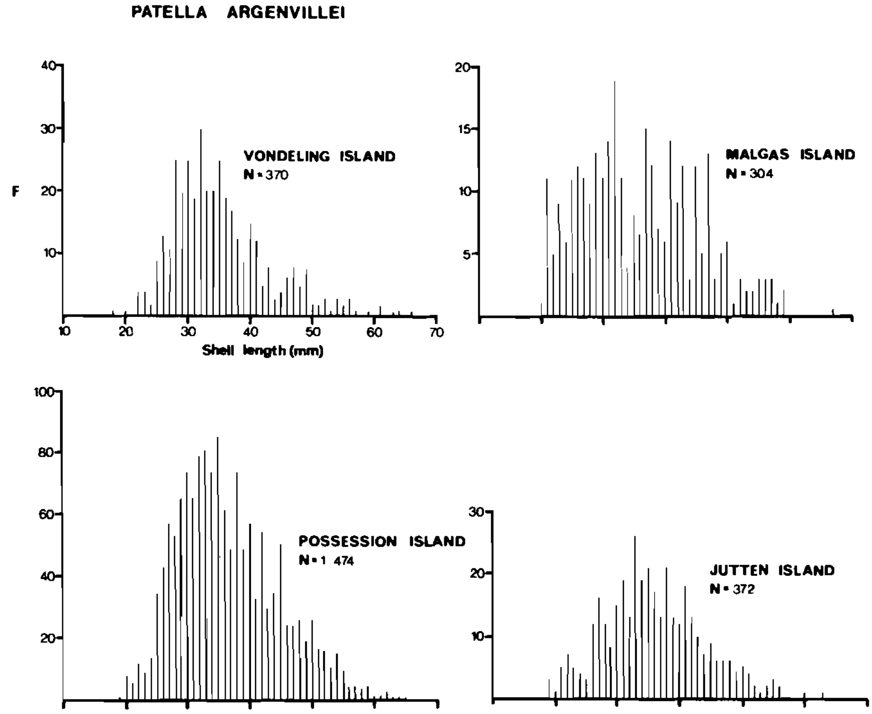

Figure 8 *Patella argenvillei:* size selection by African black oystercatchers at four west coast islands.

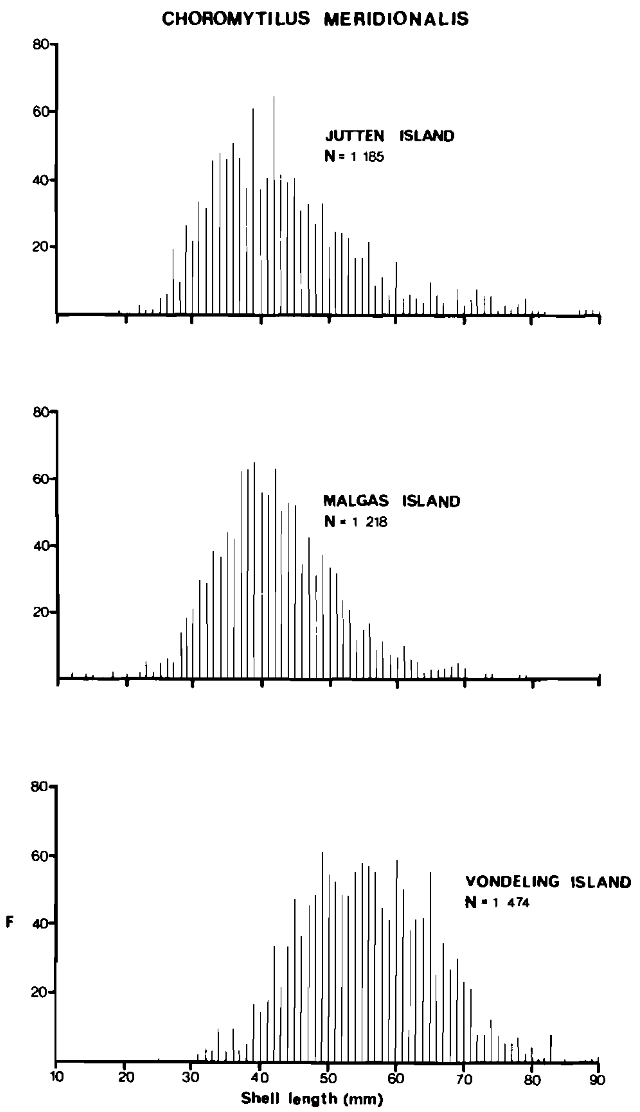

Figure 9 *Choromytilus meridionalis*: size selection by African black oystercatchers at three islands in the south-western Cape.

Table 6 Percentage frequency analysis of diet by sex in two pairs of African black oystercatchers (See text for descriptions of foraging areas)

Prey species	Male %	Female %	Sample *N*
Pair 1			
Choromytilus meridionalis	16,2	16,5	101
Aulacomya ater	10,4	21,9	98
Patella granularis	16,8	1,0	58
Burnupena catarrhacta	52,7	6,2	191
Nucella cingulata	0,3	1,0	4
Pseudonereis variegata	1,5	12,3	41
Small polychaetes	0,3	21,2	63
Small unshelled items	1,5	18,5	59
Actinaria spp.	0,3	1,4	5
Total number of prey items	328	292	620
Pair 2			
Choromytilus meridionalis	67,5	87,3	279
Aulacomya ater	0,5	0,0	1
Patella granularis	30,6	5,1	72
Barnacles	1,4	1,3	5
Large polychaetes	0,0	0,6	1
Small polychaetes	0,0	4,4	7
Small unshelled items	0,0	1,3	2
Total number of prey items	209	158	367

of New Zealand eats principally mussels and limpets on rocky shores, but includes other pelecypods and gastropods in the diet. It also eats chitons, decapods, amphipods and isopods on rocky shores (Baker 1974). European oystercatchers, *H. ostralegus*, in Britain preferentially feed on mussels, cockles and nereid worms in estuarine habitats. Smaller gastropods (*Littorina* spp.), decapods, isopods, amphipods and other polychaetes also are eaten (Heppleston 1971; Dare & Mercer 1973).

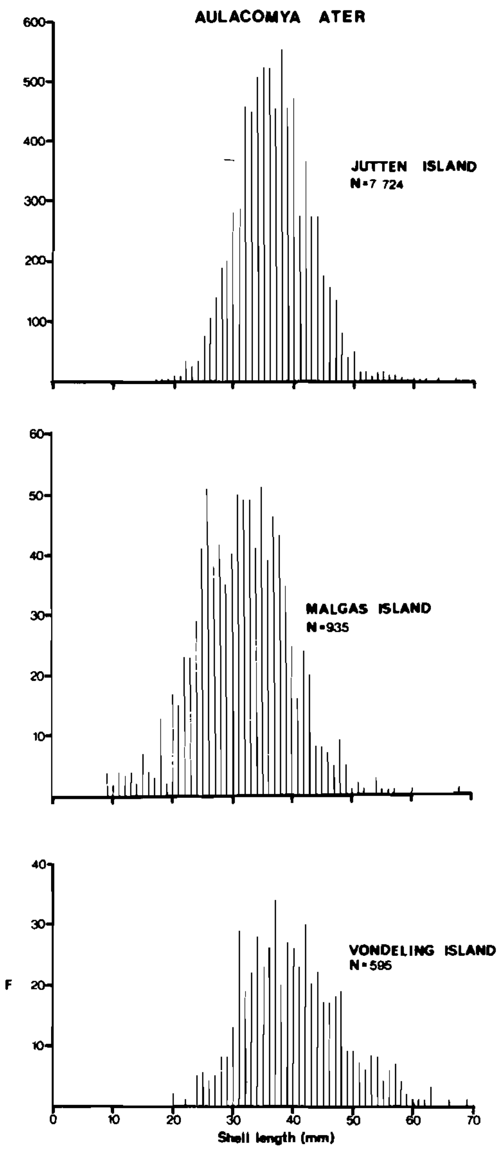

Figure 10 *Aulacomya ater*: size selection by African black oystercatchers at three islands in the south-western Cape.

Geographical considerations

African black oystercatchers, when feeding chicks, remove mollusc prey species in the same relative abundance as they occur on the shore, though there is some selection for limpets and away from siphonarians (false limpets) (Randall & Randall 1982). Data presented in this study therefore reflect the relative abundance of prey species on a geographical basis. *Choromytilus meridionalis* and *A. ater* were clearly the dominant rocky shore bivalves on the west coast and *Perna perna* was dominant in the south and east during the course of this study. *Patella granularis* and *P. argenvillei* became increasingly dominant in the west and north and *P. miniata* and *P. granatina* were evenly but relatively sparsely distributed along the west and south coasts.

The siphonarians *Siphonaria capensis* and *S. aspera* occur commonly throughout the study area, though *S. aspera* is absent from Namibia (Day 1974). However, they were eaten only at south coast sites, and then so infrequently as to be an insignificant component of the diet. Siphonarians adhere weakly to the rock, they are also common and obvious components of the upper intertidal fauna. When disturbed, however, they exude a glutinous white secretion which may be chemically noxious and act as a deterrent to potential predators. No other intertidal predators are known to eat siphonarians regularly (Branch 1981).

Although there is geographical variation in prey species taken by African black oystercatchers, the types of prey taken are similar throughout the range. In the south-western Cape, a greater degree of dietary overlap might have been expected at the three islands considered (see Figure 3). The islands lie within 12 km of one another, yet variability of the diet at Vondeling Island clearly is greater than at Jutten Island, which in turn shows greater variability than Malgas Island. The physical natures of the islands themselves provide an explanation for this. Vondeling Island is elongate, with one shore highly exposed and wave action on the other shore heavily damped by extensive kelp (*Ecklonia* and *Laminaria*) beds. Jutten Island is larger and more oval shaped with less extensive kelp beds on the sheltered shore. Sampling at Jutten Island may have been biased in favour of exposed sites as much of the sheltered shore consists of boulders where middens are less commonly found. Malgas Island is almost circular and the sheltered side is regularly disturbed by humans; oystercatchers breed only in the more exposed areas. It seems that greater variability of diet probably reflects greater within-site variability in exposure.

Temporal variation in diet

When Jutten Island was sampled intensively in two successive years, the overlap in diet compositions of pairs between the two years, as indicated by correspondence analysis, was barely 50% (Figure 4). To check whether this is a true reflection of temporal variation in diet or merely an artifact of sampling different pairs in the two years it would be necessary to sample exactly the same pairs of birds on the same territories over more than one year.

Although annual variations in diet were suggested but could not be proved, there were clear differences between day and night. By night the limpet *P. granularis* is twice as important in the diet as by day. *Patella granularis* is primarily a nocturnal forager but is also active by day under humid conditions (Branch 1971). It feeds almost exclusively when exposed. When mobile, limpets are more easily dislodged from the rock which probably accounts for the greater proportion in the diet at night. Another intertidal predator of limpets, the giant clingfish, *Chorisochismus dentex*, takes only active individuals (Stobbs 1980). It is possible that adult oystercatchers preferentially forage higher up the shore at night in order to remain closer to the chicks during the period of maximum predation risk (Hockey 1982). Following the breeding season, oystercatchers spend proportionally more time foraging in the upper balanoid zone at night than by day (P. Ryan, unpubl. data). However, the presence of low shore limpet species such as *P. cochlear* and *P. argenvillei* in the diet at night indicates that some foraging is done low on the shore.

Less food is brought to the chicks by night than by day: this parallels the observation that adults feed for less time at night than during the day in the nonbreeding season (Hockey 1982). The increasing proportion of mussels brought to older chicks agrees with the findings of Hartwick (1976) for *H. bachmani*.

Sex-related variation in diet

Sex-related differences in diet have not been reported in any other species of oystercatcher. All species of oystercatchers exhibit sexual dimorphism in bill dimensions, females having on average longer and more pointed bills than males (Hockey 1981b). The internal anatomy of the bill is the same in both sexes of *H. ostralegus* (Heppleston 1970). Baker (1975) suggested that since there is sexual overlap in bill length but within pairs the dimorphism is consistent, it is associated with sex recognition and pair formation. African black oystercatchers display within-pair bill dimorphism (Figure 5) and it appears that this dimorphism performs an additional function in raising the efficiency of exploitation of resources within a territory by reducing intersexual competition for food. Although males and females take similar proportions of mussels, males, with their more robust, chisel-shaped bills favour limpets, and the longer-billed females select worms whose capture necessitates probing into mussel beds (Hockey 1981a). There are some sites, such as Possession Island, where mussels are largely absent and females are obliged to feed on limpets. A greater degree of dietary separation was recorded in a complex *A. ater* dominated habitat than in a relatively simple *C. meridionalis* bed. By raising the efficiency of resource exploitation in the feeding area, African black oystercatchers theoretically can defend smaller territories than if both members of the pair consume invertebrates in similar proportions. A tentative test of this hypothesis is to compare densities of birds at islands with and without extensive mussel beds. The breeding season densities of birds (number per km of shore) at four islands with mussel beds are: Marcus 75, Malgas 60, Jutten 63 and Vondeling 51. The density at Possession Island, where mussels are scarce, is 53. These figures do not allow acceptance of the hypothesis, but highest densities of birds were recorded at the two sites where *A. ater* is an important prey species, namely Marcus and Jutten Islands.

Prey size selection

Prey size selection is consistent within prey species and between localities. During the nonbreeding season at Marcus Island, the modal size of *C. meridionalis* taken was the same as the modal size of mussels potentially available but smaller mussels were avoided: during the breeding season at Cove Rock, the modal size of *Perna perna* fed to chicks was considerably larger than the modal size of available mussels (Figure 6). An analogous observation was made at Cleland Island where limpets fed to chicks of *H. bachmani* were larger than those consumed by adults (Hartwick 1976). The tendency of *H. ostralegus* to carry larger food items to the chicks, in this instance nereid worms, was noted by Lind (1965).

One inconsistency in within-species size selection was noticed: at Vondeling Island during 1980, African black oystercatchers took larger *C. meridionalis* than at nearby Malgas and Jutten Islands. This may reflect either an unseasonal spatfall at Vondeling Island or a different growth rate of *C. meridionalis* at this site. Growth rates of *C. meridionalis* vary greatly depending on local conditions (Griffiths 1981).

Comparison of size selection for limpets and mussels by African black oystercatchers with *H. bachmani* and *H. ostralegus* shows that the African black oystercatcher selects similar sized mussels to *H. bachmani* and larger mussels than *H. ostralegus*. Limpets selected by African black oystercatchers are larger on average than those taken by the other two species (Table 7). This may reflect either the more robust bill of the African black oystercatcher or the generally lower growth coefficients and smaller sizes of northern hemisphere limpets (Branch 1981).

Conclusions

The diet of African black oystercatchers varies with regard to several factors. There is variation on a regional and local scale resulting from invertebrate distribution patterns and local topography, diurnal and nocturnal diet composition (and the extent of feeding) differs and there is some evidence of annual variation in diet. Males and females eat species in differing proportions, chick diet is age dependent, and sizes of prey selected by adults differ from those fed to chicks. Indeed, prey size selection is the only aspect of diet studied that was consistent within and between localities, and hence pairs of birds.

The implications of these findings for diet studies of waders and territorial species, and probably other species, are impor-

Table 7 A comparison of the modal size classes of mussels and limpets eaten by three species of oystercatcher ([a]mean size)

	Limpets			Mussels		
Oystercatcher species	species	modal size (mm)	source	species	modal size (mm)	source
Haematopus bachmani	*Acmaea pelta*	26[a]	Webster 1941	*Mytilus edulis*	45 – 50	Hartwick & Blaylock 1979
	A. digitalis	25[a]	Webster 1941			
	A. mitra	23[a]	Webster 1941	*M. edulis*	41[a]	Webster 1941
	Acmaea spp.	10 – 20 (13)[a]	Hartwick 1976	*M. californianus*	40[a]	Webster 1941
				Mytilus spp.	40 – 60 (49)[a]	Hartwick 1976
Haematopus ostralegus	*Patella vulgata* + *P. aspera*	20 – 25	Feare 1971	*M. edulis*	20 – 35	Heppleston 1971
				M. edulis	25[a]	Norton-Griffiths 1967
	Patella spp.	27 – 31	Harris 1965			
				M. edulis	39[a]	Norton-Griffiths 1967
Haematopus moquini	*P. granularis*	25 – 35	this study	*Perna perna*	35 – 45	Randall & Randall 1982
	P. granularis	35 – 45	this study			
	P. argenvillei	30 – 40	this study	*Perna perna*	40 – 45	this study
	P. cochlear	25 – 35	this study	*Choromytilus meridionalis*	35 – 45	this study
	P. longicosta	35 – 40	this study			
	Cellana capensis	25 – 30	this study	*C. meridionalis*	50 – 60	this study
				Aulacomya ater	30 – 40	this study

tant. Before any extrapolation from specific data to a general description of diet can be made, the above sources of variation must be taken into account and built into the calculation. An additional important factor not considered in this paper, but of special importance in the study of migrant waders, is that of seasonal variation in diet.

There are several attributes of correspondence analysis that make it a valuable tool in this type of diet study. The facility to present graphically both objects and variables simultaneously, and their relations to one another, allows a meaningful biological interpretation of the data. Similarly, subtle variations, which may be obscured by a less sensitive technique, are apparent. In this study, correspondence analysis has identified those prey species which form predictable and unpredictable proportions of the diet throughout the species' range and may therefore be suitable for a geographical study of the impact of predation on populations of particular prey species.

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