ECOLOGY OF THE AFRICAN BLACK OYSTERCATCHER
HAEMATOPUS MOQUINI

by

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ABSTRACT

African Black Oystercatchers Haematopus moquini (Charadriiformes: Haematopodidae) were studied at a number of localities in southern Africa, but principally at Saldanha Bay (33 S,18 E) in the southwestern Cape Province, South Africa. The distribution and abundance of the species throughout its range is described, and considered in the context of the world distribution of oystercatchers. Local movements of adults are analysed, and a conservation plan for the species is outlined. Morphometric differences between the sexes are evaluated. Feeding techniques of the birds are described and are related to the morphologies of specific prey species. Diet of the species on rocky shores is analysed with special reference to the sources of variation, and the implications of the findings for studies of diet in territorial species are considered. An initial assessment is made of the effects of predation by African Black Oystercatchers in modifying intertidal invertebrate and avian communities, and the possibility of oystercatchers influencing genetic structure of prey populations is investigated. The effects of Paralytic Shellfish Poisoning on African Black Oystercatcher populations is examined. Time and energy budgets of nonbreeding birds are assessed, including nocturnal activity, and the causative factors determining activity are considered. An investigation is made into the probable functions of communal roosting in the species. The energetic requirements for chick growth are quantified, and the adaptiveness of early fledging is considered. The bird's basic breeding biology is described, and estimates are made of mortality in relation to the times of hatching and fledging. The conservation implications of human disturbance during the breeding season are discussed, and the importance of island populations to the population as a whole is evaluated in terms of productivity.

Factors that influence nest site selection are investigated with special reference to the rôles of egg and nest crypticity in clutch survival. The distribution and basic biology of other species of oystercatchers in Africa, the European Oystercatcher *H. ostralegus*, and the Canary Islands Oystercatcher *H. meadewaldoi*, are described, and the taxonomic status of the possibly extinct *H. meadewaldoi* is considered in the light of new information about *H. moquini*.

INTRODUCTION

The oystercatchers (Haematopodidae) are a group of birds that have long fascinated ornithologists. They are distributed around much of the world's coasts, and inland in some areas, but are absent from high latitudes, tropical Africa and southern Asia. Despite their panmictic distribution, and the existence of two colour phases, one black and one pied, oystercatchers around the world have undergone very little morphological divergence, and the systematics of the genus are poorly understood.

In comparison with the Palaearctic, Australasia and the Americas, the oystercatcher fauna of Africa is depauperate. Mainland Africa supports only one resident breeding species, the African Black Oystercatcher <u>Haematopus</u> <u>moquini</u>, and one nonbreeding migrant species from the Palaearctic, the European Oystercatcher <u>H.</u> <u>ostralegus</u>.

The African Black Oystercatcher is one of the world's largest Oystercatchers and one of the most geographically restricted and isolated, occurring only along the coasts of South West Africa/Namibia and South Africa.

The earliest mention of its existence appears to be by Étienne de Flacourt in 1648, who described what can only have been this species from Saldanha Bay (33 S, 18 E) in the southwestern Cape. "There are birds like blackbirds, with a very shrill and clear cry, as large as partridges, with a long sharp beak and red legs: they are very good to eat and when they are young they taste like woodcock" (Raven-Hart, 1967).

The unique, and to some eyes, comical, attributes of oystercatchers, both physical and vocal have not escaped the notice of other writers. Lansdowne (1976) writing of the American

Black Oystercatcher H. bachmani comments: "Anyone seeing a black oystercatcher for the first time might be inclined to laugh at its grotesque and rather comic appearance. Its outsize red bill is impossibly bright, the eyes are red-ringed, and the pallid fleshy feet bring to mind a seaside bather who has taken off his shoes and socks. When the bird nods and utters a piercingly loud whinny, the observer is convinced that it is simple as well as strange looking".

Subsequent to the gastronomically-orientated observations of Étienne de Flacourt, our knowledge of the biology of H. moquini advanced little until the publication of regional avifaunal works by Layard (1867), Gurney (1872) and Stark & Sclater (1906). Much early information, particularly with regard to breeding, clearly was culled from a knowledge of the European Oystercatcher and was not always correct. Nothing more of significance was written about the African Black Oystercatcher until 1959, when Hall published on the breeding behaviour of the species, and, in 1977, Summers & Cooper summarized our knowledge of the species' biology. Therefore, up to the point when this study commenced in 1979, the sum total of our knowledge of the species' biology was contained in two publications. In view of this paucity of information, this study, rather than concentrating on one aspect of the bird's biology, attempts to cover a number of facets of the ecology of the African Black Oystercatcher with the aim of describing its ecological rôle and requirements, and providing baseline information on which a conservation-management plan for the species could be formulated, and further experimental study made.

More precisely, the study may be defined as having the following objectives:

1. To describe the distribution, population size and movements of the African Black Oystercatcher and relate these to the practicality of, or need for, conserving the species.
2. To describe the diet and feeding techniques of the species, with special emphasis on the sources of variation in the diet, and to consider the effect that Paralytic Shellfish Poisoning may have on oystercatcher populations.
3. To investigate the impact that African Black Oystercatchers may have on intertidal invertebrate populations (limpets), and to consider whether the birds play a rôle in modifying or regulating invertebrate community structure.
4. To describe the activity rhythms of African Black Oystercatchers and their causative factors, and to consider the functions of social behaviour such as communal roosting.
5. To investigate, experimentally and in the field, the energy requirements for growth and maintenance of African Black Oystercatchers.
6. To investigate those aspects of breeding biology which are inadequately described, with special reference to productivity, its limitation, and related behavioural aspects of the birds' biology such as selection of the nest site.
7. To compare the findings of this study with what is known of the ecology of other species of oystercatchers.

Observations were made over the entire breeding range of the African Black Oystercatcher, but research was concentrated at the islands in and around Saldanha Bay in the southwestern Cape, South Africa, where the species is particularly abundant. Consequently, the study is biased towards the ecology of the species on rocky shores rather than on sandy beaches.

This dissertation consists of a series of papers, all bar one of which have been published or submitted for publication. This format was selected to facilitate rapid communication of the results.

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Part 1. DISTRIBUTION

Part 1.1. Distribution and taxonomy of the Haematopodidae

Oystercatchers Haematopodidae occur along many of the world's coasts, but do not breed in high latitudes, tropical Africa or southern Asia. The distribution of oystercatchers was first mapped by Larson (1957) and subsequently, with little modification, by Heppleston (1973) and Baker (1973). None of these authors differentiated between breeding and nonbreeding distributions. For instance, all plotted the nonbreeding range of *Haematopus ostralegus finschi* of New Zealand, but only the breeding distributions of Palaearctic *H. ostralegus* subspecies. Additionally, Baker (1973) differed from Larson (1957) and Heppleston (1973) in his taxonomic treatment of New World pied forms, ascribing them to *H. palliatus*, not *H. ostralegus*. Other inconsistencies are apparent: both Larson (1957) and Heppleston (1973) mapped the distribution of the doubtfully distinct *H. o. prattii* in Bermuda instead of the Bahamas.

Taxonomic relationships within the Haematopodidae are, without doubt, complex, and to a large extent unresolved. Doubt exists over the validity of western Palaearctic subspecies of *H. ostralegus* (Vaurie, 1965; Heppleston, 1973; A. J. Baker, *in litt*.); the distinctness of the subspecies *prattii* of the Bahamas, and of *pitanay* and *durnfordi* of South America (Wetmore, 1965); the precise range of the American Oystercatcher *H. p. palliatus* in Central America is uncertain.

This paper aims to summarize available information on the breeding and nonbreeding ranges of the species and subspecies of oystercatchers and to consider current systematic treatments. The definition of a species or subspecies in this paper essentially follows the premises of Mayr (1940, 1963) with certain modifications. Mayr (*op. cit*.) considered that populations capable of interbreeding belong to the same species, and subspecies should only be distinguished if they differ in diagnostic morphological characters and inhabit definite geographical subdivisions of the species' range. Mayr's definition encompasses a global situation and Short (1969, 1972) modified this interpretation by pointing out that the existence of hybrids, even reproductively viable ones, was not necessarily indicative of conspecific parents. Parent specificity is only guaranteed when there is a self-perpetuating hybrid zone between the ranges of the "pure" parents.

EVOLUTIONARY CONSIDERATIONS

Attempts have been made to unravel the phylogeny of the Charadriiformes, to which the Haematopodidae belong, based on colour patterns of downy young (Jehl, 1968) and character compatibility analysis (Strauch, 1978). Cracraft (1981) synthesized many of the available studies and attempted a phylogenetic classification of recent birds. The above three studies concluded that the Haematopodidae and the Recurvirostridae (avocets and stilts) were closely related, and Cracraft (1981) included them within the superfamily Haematopodoidea.

Larson (1957) proposed that oystercatchers originated as dark plumaged birds in Eurasia. Emigrants from this stock moved south during the Pleiocene and established themselves as (isolated) new species. Subsequently most of the original northern stock mutated to pied forms, presumably with a selective advantage over black forms, and a second southerly migration of pied birds occurred during the Pleistocene. Pied birds settled as secondary immigrants, sometimes in areas where black forms had already settled, but were able to co-exist owing to evolution in the older black forms. Recent work strongly suggests that melanism in oystercatchers is a derived character that has evolved independently in red-eyed and yellow-eyed lineages of the Old and New World, and that *H. leucopodus*, a pied New World species, is a prototypical oystercatcher and split off earlier from the main lineage (A.J. Baker, *in litt.*).

DISTRIBUTION

Numerous accounts have been published detailing distribution of oystercatchers in various parts of the world. The current state of knowledge is summarized in Table 1. Subspecific names *durnfordi* and *pitanay* have been retained for *H. palliatus*, though it seems likely that all mainland populations of *palliatus* can be referred to the nominate subspecies: whilst there is significant geographic variation, variation on the mainland is clinal with considerable intergrading between populations (A.J. Baker, *in litt.*).

Table 1. Breeding and nonbreeding distributions of the Haematopodidae

TAXON	BREEDING DISTRIBTION	NONBREEDING DISTRIBUTION	STATUS	REFERENCES
Haematopus bachmani American Black Oystercatcher	From western Aleutian Islands (Kiska Is.) and Bristol Bay (Round Is.), Alaska, south to Los Coronados Islands, Baja California, Mexico.	Recorded from Kuril Is., Japan and Pribilof Islands. Majority of wintering population found between southern British Columbia and Baja California.	Common. Rarely hybridizes with H.p. "frazari" in southern part of its range.	Ridgway 1919 Kenyon 1949 A.O.U. 1957 Eley 1976
H.palliatus palliatus x H. bachmani (hybrid species) = H.p. frazari	Coasts of islands of Baja California as far north as Natividad and San Luis Islands, and the west coast of Mexico south to Colima and Guerrero.	Recorded north to southern California (San Diego, Santa Barbara Islands, San Clemente Is. and Ventura County). One record (specimen) from Puerto Jimenez, Costa Rica.	Fairly common. Occasionally hybridizes with H. bachmani in north of its range.	Hellmayr and Conover 1948 Kenyon 1949 Jehl 1978
H.p. galapagensis Galapagos Oystercatcher	Main islands and some smaller islets of the Galapagos Archipelago, apparently absent from Culpepper and Wenman Islands.	As breeding.	Rare: less than 100 pairs.	Ridgway 1919 Hellmayr and Conover 1943 Harris 1974
H.p. pitanay* Peruvian Oystercatcher	Gulf of Panama to Chiloe Is., Chile.	As breeding, but apparently recorded inland on lagoons in the region of Mendoza and Nequén, east of the Andes in Argentina.	Uncommon.	Olrog 1959 Wetmore 1965
H.p. palliatus American Oystercatcher	Fragmented. Breeds Virginia, North and South Carolina, Georgia, Florida, Louisiana, Texas, Yucatan Peninsula, West Indies, locally on coasts of northern Colombia & Venezuela west of the Orinoco estuary, Leeward Islands, Trinidad and Tobago. Amazon delta (Belem) south to Uruguay.	Rare (formerly?) north to Nova Scotia. Not recorded in British Honduras. Rare migrant on coasts of Guatemala and Honduras. Unrecorded in Surinam or Guyana suggesting no interchange between populations south of the Amazon and west of the Orinoco Rivers.	Common, but apparently declining as a breeding species in the north of its range.	Ridgway 1919 O.A.U. 1957 Bent 1962 Wetmore 1965 Haverschmidt 1968 Monroe 1968 Land 1970

H.p. durnfordi* Durnford's Oystercatcher	Atlantic coast of Argentina south to Santa Cruz.	As breeding, and north to Uruguay.	Fairly common. Occasionally hybridizes with H. ater where sympatric.	Hellmayr and Conover 1948 Blake 1977 Jehl 1978
H. ater Blackish Oystercatcher	South from Chiclayo, Peru, around the South American coast and at islands, including the Magellanic and Falkland Is., to Chubut, Argentina.	Some northerly movement of southern birds. Recorded as far north as Lambayeque, Peru, on the west coast and possibly Uruguay on the east coast. Also recorded at Juan Fernandez Islands, 800 km off the coast of Chile.	Less numerous than H. leucopodus where the species are sympatric.	Woods 1975 Blake 1977
H. leucopodus Magellanic Oystercatcher	Chiloe Is., Chile, south around the South American coast (some inland when breeding) to Chubut, Argentina. Breeds on islands in the Cape Horn region and in the Falkland Is.	As breeding, but northerly movement of southern birds. Casual to Valirdia, Chile.	Common in suitable habitats.	Humphrey *et al.* 1970 Blake 1977
H. meadewaldoi Meade-Waldo's Black Oystercatcher	Eastern Canary Islands. Coastal, rocky shores. Presence recorded on at least six islands.	As breeding. Sight record from Tenerife, 1968.	Probably extinct.	Appendix 1.3
H. ostralegus ostralegus European Pied Oystercatcher	Iceland, Faeroe Is., and European coasts from the Pechora delta to Scandinavia and south including the Baltic region and British Isles, Atlantic coasts of France and Iberia, the Camargue, north Italy central and southern Yugoslavia, Albania and north Greece, Aegean coast of Turkey. Mainly a coastal breeder, but inland in Sweden, Holland and the British Isles.	Breeding area south of 60°N, but largely absent from the Baltic. North and west coasts of Africa south to Nigeria. Some probably straggle to Red Sea and east African coasts. Vagrant to southern Greenland.	Common. Apparently increasing in many parts of its range. Southerly extension of breeding range over the past 50 years.	Vaurie 1965 Heppleston 1972

H.o. *longipes* Continental Pied Oystercatcher	Eastern and southern Russia eastwards to western Siberia, Turkestan and western Dzungaria. Inland rivers and lakes.	South to breeding range to Persian Gulf, Arabian Sea, the east coast of Africa south to South Africa.	Locally common	Vaurie 1965 Ali and Ripley 1969
H.o. *osculans* Eastern Pied Oystercatcher	Range uncertain. East coast of Kamchatka, Penzhin Gulf at north end of Sea of Okhotsk. West coast of Korea. May breed on Kuril Is., basin of the middle Amur and of Sung-hua and Ussuri and on the coast of Hopeh. May have bred Japan last century.	Coast of China south to northern Kwantung, straggling to Anadyr Estuary, Bering Island, Kuril Is., Sakhalin, Burma, Bangladesh.	Uncommon and scattered.	Vaurie 1965 Dement'ev and Gladkov 1969
H. *moquini* African Black Oystercatcher	Seal Island, Namibia, to Mazeppa Bay, Transkei, South Africa. Favours islands and mixed rocky/sandy shores.	Largely non-migratory. Regular north to Hoanib estuary, Namibia, vagrant northto Lobito, Angola. Casual in Natal.	Estimated world population *ca.* 4 800.	Part 1.2
H. *fuliginosus* Sooty Oystercatcher	Coasts of Australia, from Abrolhos Islands, W. Australia, south and east to Brisbane. (Normally rocky shores and islands.)	As breeding.	Common.	Serventy and Whittell 1962 Condon 1975 McKean 1978
H. *ophthalmicus* Spectacled Oystercatcher	North Australia from Peron Peninsula, W. Australia to Lady Elliott Is. at the extreme south of the Great Barrier Reef. (Rocky coasts and islands.)	As breeding.	Common.	Condon 1975 McKean 1978
H. *longirostris* Australian Pied Oystercatcher	Around the coasts of Australia and Tasmania, also south coast of New Guinea (Utanata R., Orangerie Bay). Prefers sandy and muddy beaches.	As breeding.	Common.	Serventy and Whittell 196 Condon 1975

H. unicolor Variable Oystercatcher	Coasts of North and South Islands, New Zealand.	As breeding.	Fairly common. Black phase commonest throughout range but forms higher proportion of population in the south.	Baker 1973
H.o. finschi South Island Pied Oystercatcher	South Island, New Zealand. An inland breeder.	Coastal South and North Islands, New Zealand. Large flocks at major bays, harbours and estuaries.	Declined from late 19th to mid 20th century. Spectacular irruption and increasing use of inland areas since 1940.	Baker 1973
H. chathamensis Chatham Islands Oystercatcher	Rocky coasts of Chatham Island, Mangere Is., Pitt Is. and Rangatira Is. Found on some sandy beaches at Chatham and Pitt Is.	As breeding.	Rare. Estimated population *ca*. 50 birds.	Fleming 1939 Baker 1973

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* *H. p. pitanay* and *H. p. durnfordi* should probably be considered as nominate *H. p. palliatus*

TAXONOMY

Peters (1934) classified oystercatchers into four species, two with subspecies, namely:

1. *Haematopus ostralegus*
    - *bachmani*[1]
    - *frazari*[2]
    - *palliatus*
    - *prattii*
    - *galapagensis*
    - *pitanay*
    - *durnfordi*
    - *ostralegus*
    - *occidentalis*
    - *malacophaga*
    - *longipes*
    - *osculans*
    - *meade-waldoi*[1]
    - *moquini*[1]
    - *longirostris*
    - *unicolor*[2]
    - *chathamensis*
2. *Haematopus fuliginosus*
    - *fuliginosus*[1]
    - *ophthalmicus*[1]
3. *Haematopus leucopodus*
4. *Haematopus ater*[1]

1 = black forms

2 = variable forms

Heppleston (1973) proposed the following changes to this classification: *H. o. moquini* became *H. moquini*; *H. o. malacophaga* was not a distinct subspecies (he implied, but did not state that it should be included with *H. o. occidentalis* of the British Isles); *H. leucopodus* became *H. o. leucopodus*; *H. o. finschi* be separated from *H. unicolor*, and that *H. unicolor* contained two subspecies, nominate *unicolor* and *reischeki*.

Baker (1973) differed from Peters (1934) and Heppleston (1973) in the following: *bachmani* was accorded specific status; a polytypic *H. palliatus* was recognized in the New World incorporating *frazari*, *palliatus*, *prattii*, *pitanay* and *durnfordi*; a polytypic *H. moquini* was recognized incorporating nominate *moquini* and *meadewaldoi*, and *chathamensis* was accorded specific status.

Heppleston (1973) attributed all pied forms to *H. ostralegus*, as, with the exception of *leucopodus*, did Peters (1934). Baker (1973) attributed New World pied forms, except *leucopodus*, to *H. palliatus*, justification for which was presented earlier by Wetmore (1965).

..."Oystercatchers throughout the world are closely similar in appearance, especially the pied forms. Those of the Old World have the back and rump clear white while the eyes, feet and tarsi are red. In the New World all have dark coloured backs, only the sides of the rump and the uppertail coverts being white. The eye is bright yellow, and the legs and feet are flesh colour or faintly pinkish white. While these are not great differences they are clear cut and constant and therefore sufficient to indicate two species groups, *H. ostralegus* for the Old World and *H. palliatus* for the Americas."

In addition, all red-eyed species (Old World) have several fixed allele differences from all yellow-eyed species (New World) (A.J.

Baker, *in litt*.).

Nearctic and Neotropical Oystercatchers

It appears that no subspecies of the *H. palliatus* species group is sufficiently separable on mensural grounds to satisfy the seventy-five percent rule of Amadon (1949), and all should be referred to the nominate subspecies with the possible exception of *H. p. galapagensis* which is geographically isolated. *H. p. prattii*, identical in coloration to *palliatus*, originally was separated on the basis of different bill shape (Bangs, 1900). The consistency of this character was disputed by Wetmore (1965) and *prattii* was considered synonymous with palliatus by Blake (1977). There are three main plumage characters that have been used in the separation of *H. palliatus* subspecies: the presence or absence of mottling on the breast at the lower limit of the black pectoral area, the amount of white on the shafts and webs of the inner primaries, and the colour of the dorsal surface. Features currently used for separating subspecies are:

palliatus	Head, neck and upper chest uniform black with clearly defined margin to pectoral band. Upperparts pale greyish brown. White patches present on webs of inner primaries. Underwing coverts white (Ridgway, 1919; Murphy, 1925; Hellmayr & Conover, 1948; Blake, 1977).
"*frazari*" (*palliatus* x *bachmani*)	Averages much darker than *palliatus* and chest usually conspicuously spotted or blotched with black, sometimes extending to undertail coverts. May be totally black, as *bachmani*. White patches on

	primaries absent or indistinct. Underwing coverts heavily blotched (Ridgway, 1919; Hellmayr & Conover, 1948; Kenyon, 1949). (*Frazari* in fact has no status as a taxon name since it was erected for a bird which is a hybrid between *bachmani* and *palliatus* and refers to all those birds that are putative hybrids (A. J. Baker, *in litt*.). The name *frazari* is retained here for convenience.)
durnfordi	Very similar to *galapagensis* but has much smaller feet and at least some white on the primaries. Extent of white on remiges, and shaft colour, are variable (Ridgway, 1919; Murphy, 1925; Hellmayr & Conover, 1948; Blake, 1977).
pitanay	Most resembles *palliatus* in having clearly demarcated pectoral band. White subterminal markings on inner primaries are absent or greatly reduced. Darker and greyer on dorsal surface than "*frazari*" (Murphy, 1925; Hellmayr & Conover, 1948; Wetmore, 1965; Blake, 1977).
galapagensis	Similar to "*frazari*" but upperparts more heavily pigmented with less white on wing coverts. Feet are hypertrophied. No white on primaries (Ridgway, 1919; Hellmayr & Conover, 1948).

There is evidence of hybridization between *durnfordi* (*palliatus*) and *H. ater* (Jehl, 1978) and between "*frazari*" and *bachmani* (Kenyon, 1949). On both morphological and ecological grounds, the specific status of *H. ater* seems unquestionable. The fact that "*frazari*" hybridizes with *bachmani* and is a variable form occurring between the ranges of bachmani and pitanay (palliatus) raises the question of whether "frazari" merely represents a 'hybrid zone' (Short, 1969) between populations to the south and north. The distribution maps of Baker (1973) and Heppleston (1973) indicate that the ranges of "frazari" and pitanay (palliatus) are contiguous: distributional evidence contradicts this. The southern limit of "frazari" is the Pacific coast of southern Mexico (c. 18 S), (Table 1) and oystercatchers are then absent south to Panama. There is one record of "frazari" in Costa Rica (Hellmayr & Conover, 1948).

Hellmayr & Conover (1948) considered "frazari" was "clearly the southern representative of H. bachmani". In view of the fact that the two forms are sympatric in part of their ranges, are suspected to interbreed and have no other congeners, there may be a case for retaining bachmani within the H. palliatus species group, based on the species definition of Mayr (1940). However, hybrid phenotypes between bachmani and palliatus ("frazari") are such that backcrossing with parentals is either rare or does not occur at all. Hybrids are therefore at a selective disadvantage and the hybridizing forms must be treated as separate species. There are fixed allele differences between bachmani and palliatus (A. J. Baker, in litt.).

The specific status of leucopodus warrants consideration. Heppleston (1973) suggested that leucopodus was a subspecies of H. ostralegus (= palliatus of this study) for two reasons. If Larson's (1957) hypothesis is correct, then the pied leucopodus should be a secondary immigrant and have evolved from ostralegus stock. He argued that leucopodus closely resembled ostralegus in appearance and that its two adjacent neighbours, pitanay and *durnfordi* (*palliatus*), are both subspecies of *ostralegus* and that competition would occur it they met. As a counter to this, both *pitanay* (*palliatus*) and *durnfordi* (*palliatus*) are populations which nest on the coast, with *pitanay* being characteristically a bird of rocky shores (Johnson & Goodall, 1965), whereas *leucopodus* is a bird of sandy beaches and lagoons which normally breeds inland (Blake, 1977; Miller & Baker, 1980). Additionally, *leucopodus* is behaviourally unique within the Haematopodidae, having developed unusual and elaborate displays and vocalizations associated with breeding (Miller & Baker, 1980). These differences, especially the latter, cast doubt on whether behavioural compatibility between *leucopodus* and either *pitanay* or *durnfordi* would be sufficient for mate recognition and creation or maintenance of a pair bond. *Leucopodus* also has its own taxa of feather lice, further evidence for prototypical status (A. J. Baker, *in litt*.). It differs from other New World oystercatchers in having no brownish dorsal coloration and in having a yellow orbital ring, and underwing coverts of a different colour to the belly, features unique among the Haematopodidae (Miller & Baker, 1980). It is much shorter legged than any form of *H*. *palliatus*. These facts do not adequately explain the allopatry between *leucopodus* and other pied forms but strongly suggest that it is not a member of the *H*. *palliatus* species group.

Haematopus leucopodus, *ater* and *durnfordi* (*palliatus*) occur sympatrically during the breeding season in the Santa Cruz province of Argentina between Puerto Deseado and San Julian (Jehl, 1978). *Haematopus leucopodus* has been reported to hybridize with *ater* in this region (Jehl, 1978) but the evidence is based on only one specimen and is not conclusive. The fact that hybridization has not been reported over the majority of the region where *ater* and *leucopodus* are sympatric, but was recorded in the restricted area where *durnfordi* also occurs, casts further doubt on the significance of this record (see Short, 1969).

Palaearctic Oystercatchers

In the Canary Islands there is a (possibly extinct) black oystercatcher *H. meadewaldoi*. This form, which in the past has been considered a subspecies of both *H. ostralegus* (Peters, 1934) and *H. moquini* (Baker, 1973) recently has been accorded specific status on mensural, plumage and distributional grounds (Appendix 1.3).

Pied oystercatchers occur throughout most of the coastal western Palaearctic, but the subspecific separation of *malacophaga* (Iceland and Faeroes), *occidentalis* (Britain) and *ostralegus* (European mainland) has been questioned. Heppleston (1973) doubted the distinctness of *malacophaga* and mentioned that *occidentalis* is very similar to *ostralegus*. Vaurie (1965) and Prater *et al*. (1977) considered all three as *ostralegus*. Dement'ev & Gladkov (1969) considered *malacophaga* to be synonymous with *occidentalis* but discrete from *ostralegus*, while Baker (1977) found the three to be phenetically very similar and all probably should be referred to as nominate *ostralegus*. Salomonsen (1930), who described the subspecies *malacophaga*, considered the following to be key points in separating the subspecies: *ostralegus*, short wing and thin pointed bill; *occidentalis*, distinguished from *ostralegus* by bill shape; *malacophaga*, long wing and distinctive bill shape. There is considerable overlap in the wing measurements for the three subspecies given by Salomonsen (1930), for *ostralegus* and *occidentalis* combined (240-265 mm), and malacophaga (252-276 mm). Bill length and bill shape have been demonstrated to vary considerably in individual western European oystercatchers, length by up to 10 mm in one year, probably being a function of abrasion dependent on feeding conditions (White & Gittins, 1965). The western European forms are inseparable on plumage characteristics and the extent of overlap in measurements favours the amalgamation of these three forms into one subspecies, H. o. ostralegus. Haematopus o. longipes of the central Palaearctic differs from H. o. ostralegus in having a brownish wash to the dorsal plumage and more white in the wing (Dement'ev & Gladkov, 1969). Prater et al. (1977) note that the groove in the upper mandible is less than half bill length in ostralegus and more than half bill length in longipes. These differences, coupled with its relative geographical isolation, suggest longipes is correctly ascribed subspecific status.

H. o. osculans of the extreme eastern Palaearctic differs from ostralegus and longipes in having black, not white, shafts to the outer three primaries (Prater et al., 1977), and is a very isolated population (Table 1).

Afrotropical Oystercatchers

Only one species of oystercatcher breeds in the Afrotropical region, namely H. moquini of southern Africa. Since meadewaldoi has been accorded specific status, H. moquini should be treated binomially, not trinomially as by Baker (1973) (Appendix 1.3).

Australasian Oystercatchers

The taxonomy of Australasian oystercatchers has been reviewed by

Baker (1974, 1977) and McKean (1978). Regarding the Australian forms, longirostris is phenetically similar to New World forms and differs from ostralegus in wing pattern and lack of an eclipse plumage, and probably warrants specific status (Baker, 1977; McKean, 1978). H. fuliginosus ophthalmicus and H. f. fuliginosus are phenetically similar (Baker, 1977), and both normally are considered as subspecies of H. fuliginosus. McKean (1978) points out that ophthalmicus differs from fuliginosus in bill shape and in having a prominent fleshy red orbital ring, a feature shared with H. moquini of the Afrotropical region. The ranges of the two forms are apparently discrete (McKean, 1978), ophthalmicus having a tropical, and fuliginosus a subtropical distribution. There is no evidence of hybridization, and the assertion (McKean, 1978) that ophthalmicus be accorded specific status provisionally is accepted.

With regard to the New Zealand forms there seems no reason to question the findings of Baker (1974), namely that H. unicolor and H. chathamensis be accorded specific status and that finschi, apparently a Palaearctic element in the Australasian fauna (Baker, 1977) be treated as a subspecies of H. ostralegus. As well as being morphologically similar to other ostralegus subspecies, it is an inland breeder, a behaviour common in nominate ostralegus and longipes.

CONCLUSIONS

In view of the above discussion, I suggest the following classification of oystercatchers:

Nearctic and Neotropical Regions

Haematopus bachmani
H. palliatus palliatus
H. p. galapagensis
H. leucopodus
H. ater
(*H. p. palliatus* x *H. bachmani*)
no valid name

Palaearctic Region

H. meadewaldoi
H. ostralegus ostralegus
H. o. longipes
H. o. osculans

Afrotropical Region

H. moquini

Australasian Region

H. longirostris
H. fuliginosus
H. ophthalmicus
H. unicolor
H. chathamensis
H. ostralegus finschi

Oriental Region

None

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Part 1.2. The distribution, population size, movements and conservation of the African Black Oystercatcher _Haematopus moquini_.

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ABSTRACT

The African Black Oystercatcher *Haematopus moquini* is endemic to southern Africa and occurs as a breeding species between Seal Island, South West Africa/Namibia and Mazeppa Bay, Transkei. Vagrants outside this area are rare farther north than the Hoanib Estuary, South West Africa/Namibia and farther east than Transkei. The present adult population is estimated to be 4 781 birds of which 53 % are located in the southwestern Cape Province, South Africa. Offshore islands support 29 % of the world population and are identified as important breeding localities for African Black Oystercatchers. African Black Oystercatchers face threats from human disturbance, especially from off-road vehicles on the mainland, from introduced mammalian predators at islands and from competition with man for food and bait organisms. Ten islands and seven mainland sites are identified as supporting more than 1 % the world population of the African Black Oystercatcher. These localities, together with their intertidal zones, are recommended for Nature Reserve status.

INTRODUCTION

Marine coastlines are both biologically rich and disturbed ecosystems where the conflicts of conservation and recreation are readily apparent. Shorebirds which occur exclusively, and are therefore dependent entirely on marine coastlines, may conveniently be used as indicators of habitat quality since they are relatively large, easily observed and are at the top of food chains. They may therefore be used to select sections of coastline that are worthy of Nature Reserve status or some form of enhanced protection from detrimental forms of recreation and development. Southern Africa has few coastal Nature Reserves which include protection of the adjoining intertidal zone, an interface between the terrestrial and marine environments utilized by biotic elements of both ecosystems. In southern Africa, as elsewhere in the world, the use of off-road vehicles has proliferated in recent years and this has reduced the remoteness of many stretches of coast.

The African Black Oystercatcher Haematopus moquini, endemic to southern Africa, is restricted as a breeding species to the islands and the coasts of South West Africa/Namibia and South Africa (Summers & Cooper, 1977; Hockey, 1982).

This paper discusses the distribution, population size, movements and conservation of the African Black Oystercatcher throughout the total species range. The findings are used to select sections of the southern African coastline for recommendation as Nature Reserves or as areas where current protection measures should be enhanced.

METHODS

The southern African coastline was divided into five regions on the basis of geography and the extent of current surveys (Summers et al., 1976; Summers & Cooper, 1977; Underhill & Whitelaw, 1977; Whitelaw et al., 1978; Cooper et al., 1980; Hockey, 1982; Western Cape Wader Study Group, unpubl. data), these regions being:

1. The Cunene River to the Orange River (South West

Africa/Namibia).

2. The Orange River to the Olifants River (northern Cape Province, South Africa).

3. The Olifants River to Mossel Bay (southwestern Cape Province).

4. Mossel Bay to the Kei River (southeastern Cape Provinçe).

5. The Kei River to Port Edward (Transkei), (Figs. 1,2).

Counts were made in these areas between 1975 and 1981 by members of the Western Cape Wader Study Group and staff of the FitzPatrick Institute. These data have been supplemented with additional information from remote areas where available. All counts were made during the breeding season (December to February) apart from those in Transkei which were made during October 1980, and some island counts. All African Black Oystercatchers, except fledglings and immatures under parental care, were counted. Age structure rarely was recorded and all birds were considered as adults. Counts were made at low tide as far as possible to reduce effects of tidally influenced movement and to maximise the accuracy of feeding habitat preference. Coastal wetlands normally were counted at the same time as the adjacent coast to avoid errors caused by movements between these areas.

Several counters, of varying expertise, were involved during surveys. However, the African Black Oystercatcher is unmistakable, and misidentification was not a source of error. Shore counts usually were made by observers working in pairs although it was sometimes necessary to work singly. Counts were made on foot or from a moving vehicle. These two techniques have

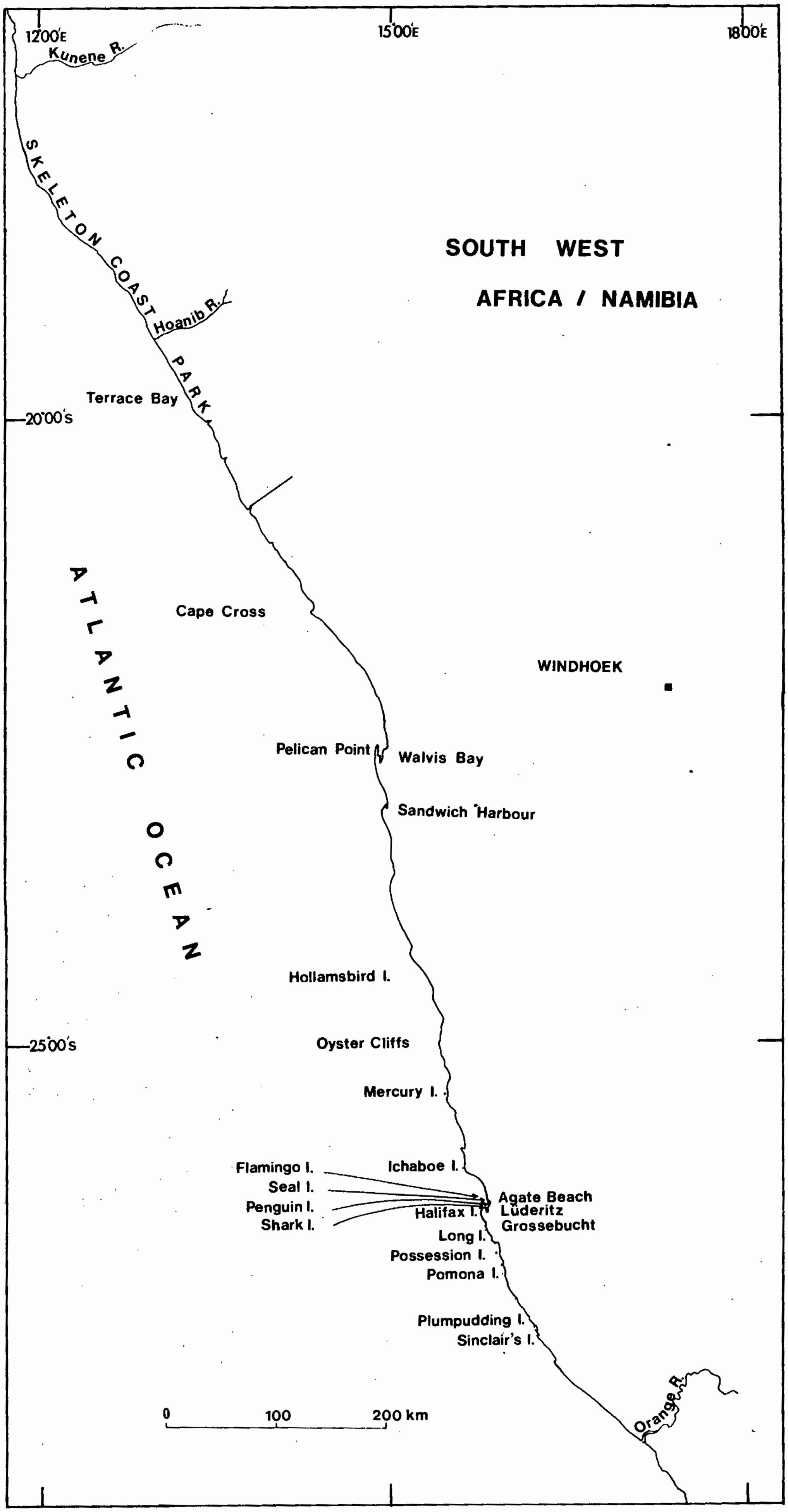
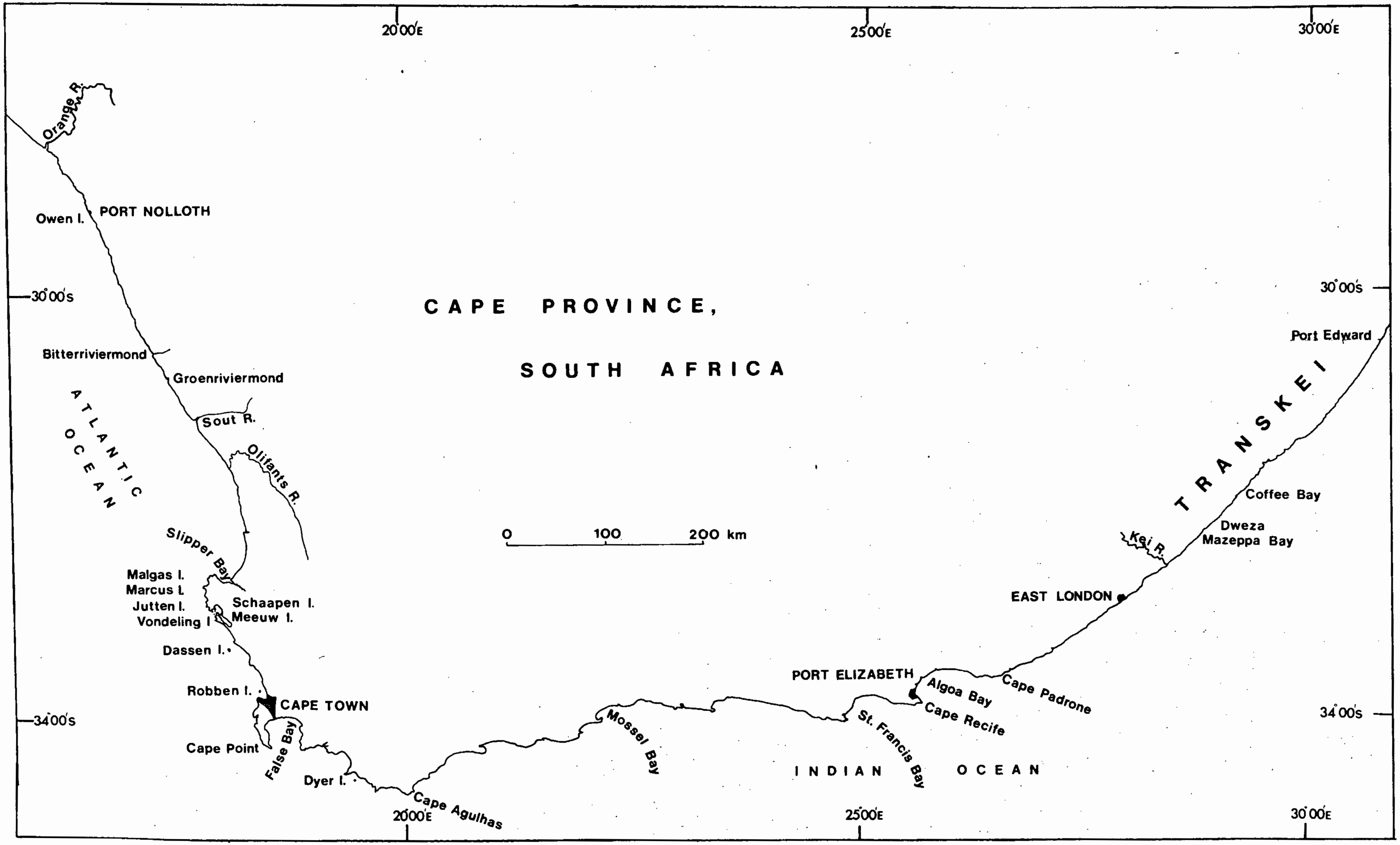


Figure 1. Map of the study area: South West Africa / Namibia

Figure 2. Map of the study area: South Africa and Transkei



been found to be compatible for counting waders (Underhill & Whitelaw, 1977). African Black Oystercatchers are most conspicuous during the breeding season as they are highly vocal, and for this reason the accuracy of counts is high on the mainland where the densities are relatively low. At offshore islands, densities are high and birds breed both along the edges and in the interiors or these sites. The observer therefore causes disturbance by forcing individuals to move into other birds' territories which sometimes leads to aerial chases thus confusing the counter. For this reason, all but the smallest and most inaccessible islands were visited on more than one occasion and mean figures were adopted for calculation of the world population.

Only in the northern Cape Province was less than 70 % coverage of the coastline achieved: oystercatcher density here is low and although it is not possible to put an error estimate on extrapolated figures, such an error is unlikely to affect the overall conclusions. In all areas, except parts of South West Africa/Namibia, extrapolations were made by habitat type to maximise accuracy.

Of the 1 520 km of South West African/Namibian coast, two stretches totalling 408 km (27 %) were not surveyed. A guess was made for the population in the 145 km stretch of coast between Oystercliffs and Agate Beach, and a figure was extrapolated from the survey data for the Lüderitz area for the 263 km from Grossebucht to the Orange River: the entire population of the latter area was assumed to be on rocky shores (Fig. 1). The South West African/Namibian coast was subdivided into six sections on the basis of existing data. Distribution in South West Africa/Namibia was recorded by habitat only in a small area around

Lüderitz and, therefore, habitat preferences were not extrapolated to the rest of South West Africa/Namibia.

Four sections of approximately equal length were recognized in the northern Cape Province. The extent of the survey cover was variable and, therefore, some data had to be extrapolated. Two habitat types were recognized for this purpose: rocky shores and sandy shores/wave cut platforms. Each of the four coastal sections was further subdivided into units of approximately 15 minutes latitude and extrapolations were based on the percentage of each habitat type surveyed within these units. Where habitat type was not known it was deduced from the 1:50 000 topographic maps of the South African Department of Surveys and Mapping.

Complete coverage of the southwestern Cape Province was achieved and the coastline was divided into four sections. Six coastal habitat types were recognized: rocky shores, sandy shores, mixed shores, wave cut platforms, cliffs and man-made habitats. Wetlands were classified as estuaries, lagoons/lakes, saltpans and sewage works. All islands were visited, some on several occasions.

In the southeastern Cape Province, 78 % coverage of the coast was achieved, the majority of the unsurveyed area being cliffs. Four sections were recognized, and because of the high coverage, extrapolations were made by habitat type within these four sections. Five habitat types were recognized: cliff, rocky shore, wave-cut platform backed by cliff, wave-cut platform backed by beach, and sandy shore. Wetlands were subdivided as for the southwestern Cape.

In Transkei, complete coverage of the coast from the Kei River to

Coffee Bay was achieved. So few observations of oystercatchers were made that these are considered individually.

The extent of local movement of adults was assessed by analysing ringing recoveries and controls, and by using populations of individually colour ringed birds trapped as breeding adults at three localities in Saldanha Bay. The distances moved by colour ringed individuals away from the ringing sites were recorded. In addition to casual observations of birds away from the ringing sites, regular checks were made at a number of roost sites along the nearby coast between Ysterfontein (33 21S, 18 09E) and St Helena Bay (32 47S, 18 05E), and at Jutten and Malgas Islands (Fig. 3).

Seasonal habitat shift was assessed in two ways. A complete census of the Saldanha Bay area was made during the nonbreeding season (May 1980) and the breeding season (January 1981) and the distribution of birds in different habitats was compared between the two surveys. In addition, seasonal differences between counts at three islands (Marcus, Malgas and Jutten) were analysed, as were monthly counts made between January 1979 and August 1981 along 15 km of open sandy beach north of Ysterfontein.

The nest record cards (NRC) of the Southern African Ornithological Society were consulted to supplement personal observations and published details of breeding.

RESULTS

Distribution

South West Africa/Namibia

In the northern section from the Cunene River to Cape Cross, no African Black Oystercatchers were observed in September 1975 (Summers & Cooper, 1977), and only one was recorded during a complete survey of the area in December 1980, 7.5 km north of the Hoanib River (J. Cooper, pers. comm.). Additionally, birds have been seen at Terrace Bay: one on 30 September 1978 and two on 1 July 1980 (R. Loutit & A. Berruti, <u>in litt</u>.), and nine were present at the Hoanib estuary between October 1978 and January 1979. (T.G. Cooper, <u>in litt</u>.) (Fig. 1). Between Cape Cross and Sandwich Harbour the species is rare, but flocks of up to 87 have been recorded at Walvis Bay Lagoon and Pelican Point (Underhill & Whitelaw, 1977; J. Cooper, pers. comm.) and up to 150 have been recorded at Sandwich Harbour (Berry & Berry, 1975) though large numbers were not seen here during the 1976/1977 summer survey (Underhill & Whitelaw, 1977). Of 28 birds carefully examined in a flock of 44 at Pelican Point in January 1978, 11 were considered, on the basis of soft part coloration, to be subadult and at least one adult was in primary moult and as such was almost certainly a nonbreeding bird (J. Cooper, pers. comm.).

No birds were seen between Sandwich Harbour and Oystercliffs in February 1976 (Summers & Cooper, 1977) and there are probably very few birds between Oystercliffs and Agate Beach (Lüderitz) since there are no offshore islands in this area to act as "sources" for mainland birds. The mainland density in the Lüderitz area is high, averaging 3.5 birds per km over 46 km, and this is the most northerly known mainland breeding locality (Hockey, 1982). The high density is probably a function of the extensive undisturbed rugged rocky shoreline and the proximity of offshore islands where oystercatcher density is high. Isolated counts between Grossebucht and Van Reenen Bay show that oystercatchers are

TABLE 2

DISTRIBUTION OF AFRICAN BLACK OYSTERCATCHERS ALONG THE COAST AND AT COASTAL WETLANDS OF SOUTH WEST AFRICA/NAMIBIA

LOCALITY	COASTLINE LENGTH (km)	NUMBER OF BIRDS	DENSITY (BIRDS PER KM)
1. Kunene River to Cape Cross	600	c.12	0,02
2. Cape Cross to Sandwich Harbour	236	100	0,42
3. Sandwich Harbour to Oystercliffs	230	0	0,00
4.* Oystercliffs to Agate Beach	145	?20	?0,14
5. Agate Beach to Grossebucht	46	163	3,54
6.++ Grossebucht to Oranjemund	263	c.300	c.1,14
TOTALS	1 520	595	0,39

* No systematic survey data, population guessed.

++ No systematic survey data, population extrapolated from section 5.

present between Grossebucht and the Orange River (Cooper et al., 1980) and the population in this region is estimated at 300 birds. The density on seven km of mixed shore on the mainland south of Pomona Island was similar to the density of birds on exposed shores in the Luderitz area (Summers & Cooper, 1977; Hockey, 1982) (Table 2).

African Black Oystercatchers are known to occur at 18 islands off the coast of South West Africa/Namibia, and at five of these islands the mean population exceeds 20 birds (Seal 97, Penguin 55, Halifax 71, Possession 281 and Pomona 24) (Table 3.). Seal Island is the most northerly recorded breeding locality of the species (Cooper et al., 1980). Breeding has been recorded at the following islands: Seal, Penguin, Shark, Halifax, Possession (pers. obs.), Pomona (P. D. Shaughnessy, NRC) and Sinclair (Rand, 1950). Although birds are resident at Ichaboe Island, no breeding has been recorded (B. Smith, in litt.) nor has breeding been recorded at Plumpudding Island though suitable habitat exists: birds were suspected, but not proven breeding here in January 1980 (R. Wilson, pers. comm.). There is suitable breeding habitat at Flamingo Island, but at low tide a mudbank is exposed, allowing access to terrestrial mammalian predators and four wheel drive vehicles. This may be sufficient disturbance to preclude breeding. Oystercatchers have not been recorded at Hollamsbird Island (Rand, 1952).

The northern Cape Province

African Black Oystercatchers are scarce in the northern Cape Province and data suggest that their distribution is patchy. In January 1980, 63 % of the estimated population of 147 birds was located at only five sites (Table 4). There were 19 at the Orange

TABLE 3

COUNTS OF AFRICAN BLACK OYSTERCATCHERS AT ISLANDS OFF THE COAST OF SOUTH WEST AFRICA/NAMIBIA

SLAND		COUNTS								
		Summer 1978 (Cooper *et al.* 1980)	Summer 1980 (R. Wilson *in litt.*)	March 1981 P.A.R.H.	Others (P.D. Shaughnessy *in litt.*)		Min.	Max.	Mean	No. of counts
ercury	25°43'S, 14°50'E	2	1		2	15.03.77	1	2	2	3
chaboe	26°17'S, 14°56'E	7	2		2	17.05.77	2	7	4	3
arshall Rocks	26°21'S, 14°58'E				0	24.01.78	0	0	0	1
taple Rocks	26°21'S, 14°59'E	0					0	0	0	1
umfudgeon Rocks	26°30'S, 15°07'E				2	11.01.78	2	2	2	2
lamingo	26°35'S, 15°10'E			10			10	10	10	1
eal	26°36'S, 15°10'E	77	110	117	85	18.05.77	77	117	97	4
enguin	26°37'S, 15°10'E	27	52	80	61	18.05.77	27	80	55	4
hark	26°38'S, 15°09'E	8		10	6	15.05.77	6	10	8	3
alifax	26°39'S, 15°05'E	106	31	52	96	19.05.77	31	106	71	4
orth Long	26°49'S, 15°07'E	0			3	21.07.77	0	3	2	2
ady's Rocks	26°51'S, 15°09'E				0	24.01.79	0	0	0	1
orth Isle	27°00'S, 15°11'E	5					5	5	5	1
ossession	27°01'S, 15°12'E	209	245	335	333	21.01.77	209	335	281	4
lbatross Rocks	27°07'S, 15°14,E	2			4	20.01.77	2	4	3	2
omona	27°11'S, 15°15'E	29	20		22	1949	20	29	24	3
lumpudding	27°38'S, 15°31'E	5	10				5	10	8	2
inclair	27°40'S, 15°31'E	0	4		10	13.01.77	0	4	2	3
					TOTALS		397	724	574	

TABLE 4

DISTRIBUTION AND ABUNDANCE OF AFRICAN BLACK OYSTERCATCHERS IN THE NORTHERN CAPE PROVINCE, SOUTH AFRICA. PRIMARY DATA SOURCE: FITZPATRICK INSTITUTE, UNPUBLISHED DATA.

REGION	Total coastline length (km)	% surveyed	SURVEYED AREA				EXTRAPOLATED AREA			
			ROCKY		SANDY		ROCKY		SANDY	
			km	N	km	N	km	N	km	N
28°37'S - 29°15'S	86,5	25,3	9,0	5	12,2	4	32,2	8	33,1	0
29°15'S - 30°15'S	128,6	30,1	5,6	0	32,3	0	20,4	0	70,3	0
*(30°15'S - 31°00'S	100,5	41,8	19,4	2	2,6	0	33,1	2	10,9	0
(30°30'S - 30°45'S (							25,5		9,0	c.25 (unknown shore type)
31°00'S - 31°42'S	97,2	87,1	56,8	20	29,4	30	4,0	1	7,0	10
TOTALS	412,8	45,4	90,8	27	76,5	34	115,2	11	130,3	10 (+25)

	OVERALL NUMBERS OF OYSTERCATCHERS				
	Mainland coast	Density (birds per km)	Coastal wetlands	Islands	TOTAL
28°37'S - 29°15'S	17	0,20	19	0	36
29°15'S - 30°15'S	0	0,00	0	14	14
30°15'S - 31°00'S	29	0,29	0	0	29
31°00'S - 31°42'S	61	0,63	7	0	68
TOTALS	107	0,26	26	14	147

* Includes 25 birds seen between 30°30'S and 30°45'S by C. Rawlston where no habitat was specified. Extrapolated figures apply to areas 30°15'S to 30°30'S and 30°45'S to 31°00'S which were surveyed by the FitzPatrick Institute.

River estuary (28 37S,16 28E), 11 at Owen Island (29 16S, 16 52E), 18 on 6.5 km of coast between Strandbaai (32 12S, 17 48E) and Sout River (31 14S, 17 51E), c. 25 between Bitterriviermond (30 36S, 17 26E) and Gert Josef (30 45S, 17 32E) (20 km) and 29 between Elephant Rock (30 36S, 17 26E) and the Olifants River (30 45S, 17 32E) (6.5 km) (Fig. 2).

There are no breeding records from the northern Cape Province, but a pair of birds was seen displaying as though they had chicks near Groenriviermond (30 50S, 17 34E) on 19 January 1980 (J. Cooper pers. comm.). A pair has been recorded breeding on the south bank of the Olifants River (M. Waltner, in litt.). It is likely that some birds breed along the stretch of coast south of Bitterriviermond, since birds were seen here in pairs during January 1980 (C. Rawlston, in litt.). The majority of northern Cape birds, however, may be non-breeders, since groups of birds at several widely scattered localities were moulting in mid-January (J. Cooper, pers. comm.), whilst adult primary moult normally starts between mid-March and May (Summers & Cooper, 1977).

The southwestern Cape Province

The southwestern Cape supported the greatest numbers of African Black Oystercatchers of the regions surveyed, both along the coastline and at wetlands and islands. Of the 1 602 birds recorded on the coast, 875 (55 %) were in the section between Slipper bay and Cape Point (Table 5, Fig. 2). In this section, the 70.9 km (21 %) of heavily disturbed shoreline around Cape Town, between Bloubergstrand and Noordhoek, supported only four oystercatchers. The remaining 871 were, therefore, distributed over 271.1 km of shore, with a density of 3.21 birds per km. The mean density of birds in the other three sections was 1.04 birds

TABLE 5

THE SUMMER COASTAL DISTRIBUTION OF AFRICAN BLACK OYSTERCATCHERS IN THE SOUTHWESTERN CAPE PROVINCE, SOUTH AFRICA. PRIMARY DATA SOURCE: WESTERN CAPE WADER STUDY GROUP, UNPUBLISHED DATA.

DOMINANT HABITAT TYPE		1)Olifants River to Slipper Bay	2)Slipper Bay to Cape Point	3)Cape Point to Cape Agulhas	4)Cape Agulhas to Mossel Bay	TOTALS
ROCKY	Coastal length(km)	23,7	136,5	121,9	72,4	354,5
	No. of birds(N)	35	352	143	98	628
	Density (D) (birds km^{-1})	1,48	2,58	1,17	1,35	1,77
SANDY	Km	117,5	146,4	104,4	149,1	517,4
	N	87	318	62	153	620
	D	0,74	2,17	0,59	1,03	1,20
EVENLY MIXED	Km	0,0	36,5	22,3	3,5	62,3
	N	-	206	47	5	258
	D	-	5,64	2,11	1,43	4,14
WAVE-CUT PLATFORM	Km	4,7	0,0	6,1	0,0	10,8
	N	16	-	10	-	26
	D	3,40	-	1,64	-	2,41
CLIFF	Km	0	13,1	0	70,0	83,1
	N	-	0	-	68	68
	D	-	0,00	-	0,97	0,82
MAN-MADE	Km	0	9,5	3,1	0,7	13,3
	N	-	0	1	1	2
	D	-	0,00	0,32	1,43	0,15
TOTALS	Km	145,9	342,0	257,8	295,7	1041,4
	N	138	876	263	325	1602
	D	0,92	2,56	1,02	1,10	1,54

per km, with a range of 0.92 to 1.10 birds per km (Table 5).

Where evenly mixed rocky/sandy shore occurred, densities were consistently higher than on other shore types. In the section between the Olifants River and Slipper Bay, wave-cut platforms were preferred. In all four sections, rocky shores supported higher densities than sandy shores. Densities were lowest in man-made and cliff-dominated habitats.

A further 788 (31 %) birds occurred at offshore islands and densities were very much higher at islands than at any mainland sites: (Malgas = 41.3 birds per km, Marcus 68.3, Jutten 70.0, Vondeling 45.9 and Dassen 25.7) (Table 6). Lower densities occurred at the sheltered islands of Schaapen and Meeuw in Saldanha Bay, and at Robben Island which is inhabited, and therefore more heavily disturbed.

One hundred and thirty-three birds were counted at 78 coastal wetlands (Table 7). At all types of wetlands, oystercatchers were present at less than 20 % of sites. Eighty-one birds (61 % of the wetlands' population) were present at lagoons and lakes. This total included 44 birds at Langebaan Lagoon, a large tidal inlet south of Saldanha Bay, and 20 birds at Rietvlei, on the mainland opposite Robben Island.

The total population of 2 523 African black Oystercatchers in the southwestern Cape is 419 less than the population estimated in summer 1975/1976 (Summers & Cooper, 1977). However, the survey data from which the earlier figure was estimated was far less complete than the current survey and the discrepancy between the two figures cannot be considered as indicative of a population decrease.

TABLE 6

COUNTS OF AFRICAN BLACK OYSTERCATCHERS AT ISLANDS OFF THE COAST OF THE SOUTHWESTERN AND SOUTHEASTERN CAPE PROVINCE, SOUTH AFRICA.

ISLAND		COUNTS Summer 1975/76 (Summers et al. 1976)	Summer 1980/81 (Underhill in litt.)	Incidental Counts PARH.	R.K.Brooke	Min.	Max.	Mean	No. of counts
Bird (Lamberts Bay)	32°05'S, 18°18'E	2	0			0	2	1	2
Malgas	33°03'S, 17°56'E	62	66	82 53	06-11-79 10-12-79	53	82	66	4
Marcus	33°03'S, 17°58'E	136	105	132 120	21-03-80 04-11-80	105	136	123	4
Jutten	33°05'S, 17°58'E	175	196	145 185	10-12-79 19-04-80	145	196	175	4
Schaapen	33°05'S, 18°02'E	26	19	24 23	20-11-79 08-05-80	19	26	23	4
Meeuw	33°05'S, 18°01'E	4	11	15	08-05-80	4	15	10	3
Vondeling	33°09'S, 17°59'E	91		85 57	07-03-80 13-05-81	57	91	78	3
Dassen	33°26'S, 18°05'E	223		202 222 236	03-06-79 01-09-79 05-09-79	202	236	221	4
Robben				40	18-08-77	40	40	40	1
Seal (False Bay)	34°08'S, 18°35'E			'Present' 0	20-10-78 18-06-79	0	?2	1	2
Geyser	34°41'S, 19°25'E		1			1	1	1	1
Dyer	34°41'S, 19°25'E		54	44	16-06-79	44	54	49	2
Seal (Mossel Bay)	34°09'S, 22°07'E		0			0	0	0	0
St. Croix	33°48'S, 25°46'E			14 18	01-06-70 19-01-79	14	18	16	2
Bird Island Group	33°50'S, 26°17'E		14			14	14	14	1
					TOTALS	698	913	818	

TABLE 7

THE SUMMER DISTRIBUTION OF AFRICAN BLACK OYSTERCATCHERS AT COASTAL WETLANDS IN THE SOUTHWESTERN CAPE PROVINCE, SOUTH AFRICA

	ESTUARIES			LAGOONS/LAKES			SEWAGE WORKS/SALT PANS			TOTALS	
	Sites surveyed	Sites present	No.of birds	Sites surveyed	Sites present	No.of birds	Sites surveyed	Sites present	No.of birds	No.of sites	No.of birds
Olifants River to Slipper Bay	2	2	14	2	0	0	2	1	6	6	20
Slipper Bay to Cape Point	3	0	0	10	2	64	6	0	0	19	64
Cape Point to Cape Agulhas	5	0	0	21	4	15	7	1	15	41	30
Cape Agulhas to Mossel Bay	6	2	17	5	1	2	1	0	0	12	19
TOTALS	16	4	31	38	7	81	16	2	21	78	133

The southeastern Cape Province

Seven hundred and eighty-three birds were estimated to be present along a coastline of 746.6 km (Table 8). The highest densities being between the Tsitsikama River and Cape Padrone (Fig. 2). Densities of birds were consistently highest along wave-cut platforms backed by beach, though the greatest numbers of birds occurred on sandy beaches. The largest concentrations of birds were found along two stretches of sandy beach. In St Francis Bay, the 36.8 km of beach between the Kabeljous River and the Maitland River supported 132 birds in January 1979 (3.6 birds per km) and 135 birds in August 1980 (3.7 birds per km). In Algoa Bay, the beach between Sunday's River and Woody Cape (36 km) supported 68 birds in January 1979 (1.89 birds per km) and 92 birds in August 1980 (2.56 birds per km). In August, 21.7 % (20 birds) of the Algoa Bay population were first year birds (pers. obs.).

Between East London and the Kei River (63 km), the density was 0.76 birds per km in January 1979, a lower density than the 0.95 birds per km averaged for this section. In general however, the birds were evenly distributed along the southeastern Cape coast. The only islands in the southeastern Cape are the St Croix and Bird Island groups. St Croix supported 18 oystercatchers in January 1979, and in the Bird Island group, Bird Island supported eight birds, Seal Island four, and Stag Island, two (A. Batchelor, pers. comm.).

Seventy-seven coastal wetlands were surveyed in the southeastern Cape and 40 localities held a total of 104 birds (Table 9). Birds were found more frequently at estuaries (32 %) than at lagoons (18 %) or at sewage works or saltpans (17 %).

TABLE 8

THE SUMMER COASTAL DISTRIBUTION OF AFRICAN BLACK OYSTERCATCHERS IN THE SOUTHEASTERN CAPE PROVINCE, SOUTH AFRICA, MODIFIED FROM UNDERHILL *et al*. 1980

SHORE TYPE	CLIFF				ROCKY SHORE				WAVE CUT PLATFORM BACKED BY CLIFF			
	Extent (km)	% surveyed	Density birds km^{-1}	Total	Extent (km)	% surveyed	Density birds km^{-1}	Total	Extent (km)	% surveyed	Density birds km^{-1}	Total
1. Kleinbrak River to Tsitsikama River	159,9	30	0,9	144	17,3	100	0,8	14	0,0	-	-	-
2. Tsitsikama River to Cape Recife	0,0	-	-	-	72,5	78	0,9	65	0,0	-	-	-
3. Cape Recife to Cape Padrone	0,0	-	-	-	0,0	-	-	-	0,0	-	-	-
4. Cape Padrone to Kei River	1,3	100	0,0	0	5,3	100	1,5	8	15,0	100	0,1	2
TOTALS	161,2	30	0,9	144	95,1	83	0,9	87	15,0	100	0,1	2

SHORE TYPE	WAVE CUT PLATFORM BACKED BY BEACH				SANDY SHORE				SUMMARY TOTAL	EXTENT(km)	BIRDS km^{-1}
1. Kleinbrak River to Tsitsikama River	16,5	100	1,6	26	62,8	100	0,6	38	222	256,5	0,87
2. Tsitsikama River to Cape Recife	5,2	100	1,9	10	74,5	98	1,6	119	194	152,2	1,27
3. Cape Recife to Cape Padrone	3,3	100	1,8	6	98,8	77	1,4	138	144	102,1	1,41
4. Cape Padrone to Kei River	52,8	96	1,6	84	161,3	94	0,8	129	223	235,7	0,95
TOTALS	77,8	97	1,6	126	397,4	91	1,1	424	783	746,5	1,05

TABLE 9

THE SUMMER DISTRIBUTION OF AFRICAN BLACK OYSTERCATCHERS AT COASTAL WETLANDS IN THE SOUTHEASTERN CAPE PROVINCE, SOUTH AFRICA

	ESTUARIES			LAGOONS/LAKES			SEWAGE WORKS/SALT PANS			TOTALS	
	Sites surveyed	Sites present	No.of birds	Sites surveyed	Sites present	No.of birds	Sites surveyed	Sites present	No.of birds	No.of sites	No.of birds
1. Kleinbrak River to Tsitsikama River	8	2	15	11	2	16	1	0	0	20	31
2. Tsitsikama River to Cape Recife	4	3	33	4	1	1	1	0	0	9	34
3. Cape Recife to Cape Padrone	4	2	16	2	0	0	8	2	7	14	23
4. Cape Padrone to Kei River	21	5	12	11	2	4	2	0	0	34	16
TOTALS	37	12	76	28	5	21	12	2	7	77	104

Within habitat density variations were greatest on sandy beaches (0.6 - 1.6 birds per km) and this probably reflects variation in the extent of disturbance and the abundance of the two principal prey species, the sand mussels *Donax serra* and *D. sordidus* (McLachlan *et al*., 1980).

Transkei

During October 1980, African Black Oystercatchers were observed at only three localities between the Kei River and Coffee Bay (Fig. 2). Two birds (adults) at Sandy Point (32 34S, 28 33E), two (1 adult, 1 immature) at the Ngqwana River (32 29S, 28 38E) and 19 at Dwesa Nature Reserve, (32 18S, 28 49E). The 19 birds at Dwesa comprised eight adults, four second year birds and seven first year birds. Seventeen birds were seen at the roost site near Dwesa Camp on 12 October 1980, and at low tide, 16 birds were recorded foraging along three km of shore between Nqabara Point and the Dwesa camp. Dwesa Nature Reserve extends from the Nqabara River to the Bashee river (19.4 km) and was proclaimed in 1975. It is the only area in southern Transkei where the normally heavy exploitation of intertidal invertebrates by man is restricted. In 1977, only two oystercatchers were present in the Reserve (Siegfried, 1977). The increase of 850 % in the subsequent three years implies that reduced disturbance and/or enhanced food supply has enabled oystercatchers to breed successfully, and the current density may be indicative of the population Transkei could support were disturbance and competition with man for food to be reduced. No breeding has yet been proven at Dwesa and the most easterly breeding record is currently Mazeppa Bay, Transkei (32 29S, 28 39E) (Summers & Cooper, 1977).

Extralimital records

East of Transkei there are only six records which unequivocally refer to African Black Oystercatchers, all in Natal, South Africa, the most northerly being a single bird at Dawson's Rocks (28 38S, 32 18E) on 31 July 1981 (Clancey, 1964; Sprawson, 1969; Cyrus & Robson, 1980; D. Roberts, <u>in litt</u>.). There are records of black oystercatchers from Beira, Mozambique, and from the Dahlak Archipelago in the southern Red Sea, both of which are indeterminate (Appendix 1.3). On the west coast there are two acceptable records from Angola, the most northerly being of two birds at Lobito (12 35S, 13 25E) in May 1973 (Summers & Cooper, 1977; Appendix 1.3). There is one more northerly record from the west coast of Africa, in Gabon, but this record is unsatisfactory (Appendix 1.3). The northerly limit of the normal nonbreeding distribution may be considered as the Hoanib estuary, South West Africa/Namibia.

The World Population

The world population of African Black Oystercatchers is estimated at approximately 4 800 birds (Table 10). Fifty-three percent of the population is confined to the southwestern Cape. The majority of the population (63 %) occurs on the mainland coast, and a further 29 % is at offshore islands. Only 13 % of the population is located outside South Africa: South Africa controls almost all the islands off the coast of South West Africa/Namibia. Only 7 % of the population is at coastal wetlands, and breeding has only been recorded at one wetland site: the Strandfontein Sewage Works near Cape Town.

In the Cape Province, the manner in which habitat data were recorded does not allow direct comparison of habitat preference between regions. However, on the mainland, mixed rocky/sandy

TABLE 10

THE WORLD DISTRIBUTION AND POPULATION OF AFRICAN BLACK OYSTERCATCHERS

LOCALITY	MAINLAND COAST	COASTAL WETLANDS	ISLANDS	TOTAL
South West Africa/Namibia	506	89	574	1 169
Northern Cape Province	107	26	14	147
Southwestern Cape Province	1 602	133	788	2 523
Southeastern Cape Province	783	104	30	917
Transkei	25	0	-	25
TOTALS	3 023	352	1 406	4 781

shores and wave-cut platforms backed by beach are preferred habitats during the breeding season. Only in the southwestern Cape is there a considerable difference between densities on rocky and sandy shores. This difference is most noticeable in the area between Cape Point and Cape Agulhas and this may reflect a relative paucity of the preferred sandy shore prey, Donax spp. in this area.

Local and seasonal movements of adults

Fifty-eight African Black Oystercatchers were ringed as breeding adults at Marcus Island between January 1976 and March 1979. Between March 1979 and March 1981, 21 of these were retrapped as breeding adults at Marcus Island and seven were recovered dead. Only one of the latter had moved from the island and was recovered six km away in Saldanha during the nonbreeding season (August), seven months after being ringed. The ring number of one adult was read in the field at Marcus Island in June 1980: this bird was ringed (mist-netted) 44 months earlier (October 1976) at the Olifants River mouth (31 42S, 18 11E), 195 km away (distance measured headland to headland). However, this bird was not originally trapped as a breeding adult and it may not have been accurately aged at the time of capture since second year birds are very similar in appearance to adults (pers. obs.). Juvenile birds are known to disperse over distances in excess of 300 km (Part 5.2) and this is considered the most likely explanation of this record.

Between March 1979 and March 1981, 178 breeding adults were colour coded (three colours) at Marcus Island, along the island causeway and at the adjacent Hoedjies Point. All resightings away from the ringing area were recorded (Fig. 3). Only resightings of Marcus

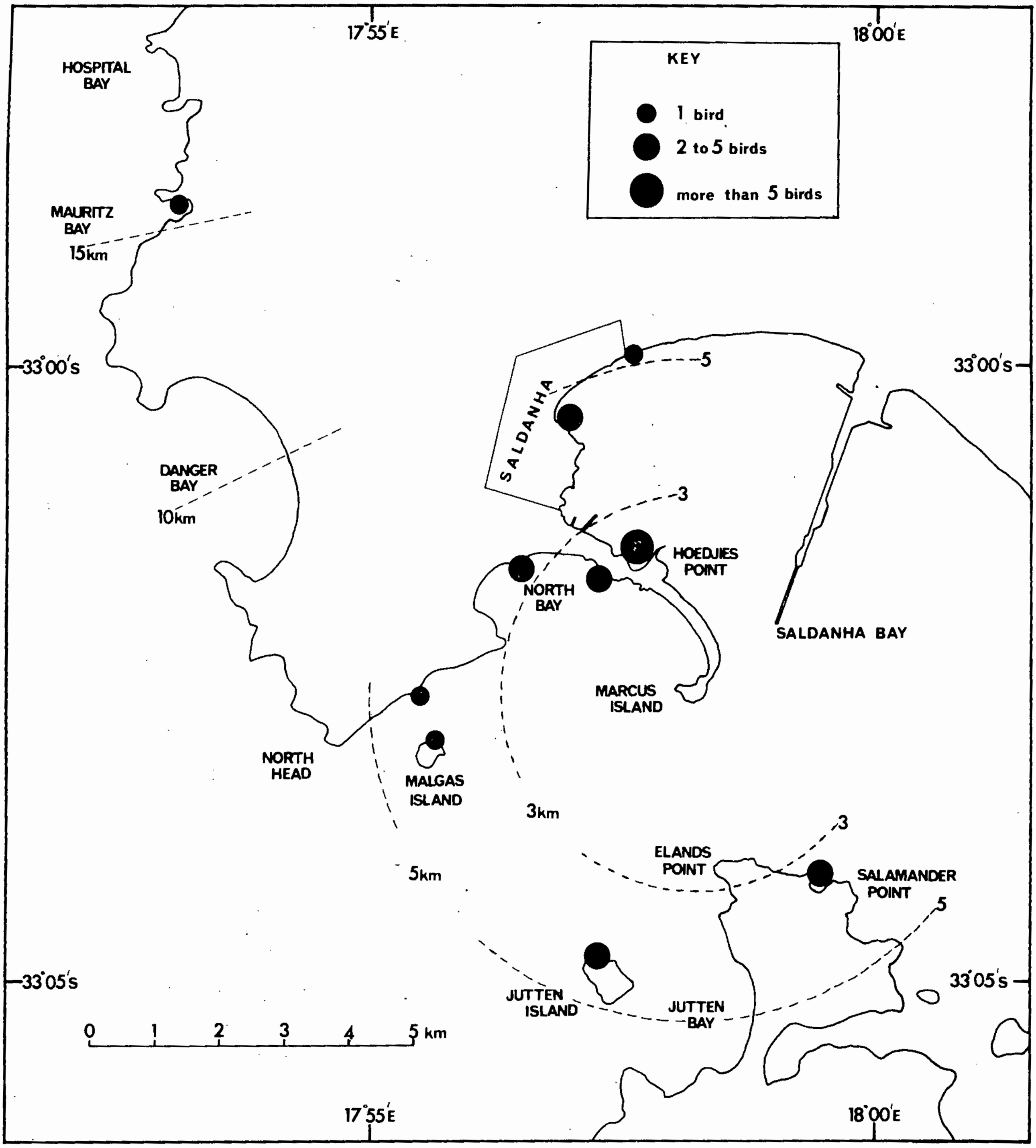


Figure 3. Map of the Saldanha Bay area depicting movements of colour ringed adult African Black Oystercatchers away from Marcus Island

Island birds are plotted, with two exceptions, a causeway-ringed bird that was resighted at Malgas Island and at North Bay. The figure records only different individuals since some birds regularly were resighted at the same locality. Movements between Marcus Island and the causeway and vice versa are not plotted for two reasons: birds that breed on the causeway regularly forage in defended territories at the island and, when the causeway floods during storms, the roost that normally gathers on the island moves to the flooded area.

Some breeding adults were ringed at Malgas Island and individuals were recorded at Marcus Island (once) and along the shoreline between North Bay and North Head (regularly). Only one adult was sighted more than five km from its ringing site, a single female seen at Mauritz Bay, 15 km away, in May and June 1981 (Fig 3). The bird was ringed at Marcus Island in January 1980, but neither it, nor its mate, was seen on the island subsequent to 20 May 1980. This represents the maximum proven displacement of an adult African Black Oystercatcher from its breeding site. Adult African Black Oystercatchers are, therefore, non-migratory and undergo only small local movements.

Summers & Cooper (1977) suggested that there was a shift towards sandy beaches during the breeding season. This was borne out by the results of monthly counts on the beach at Ysterfontein where numbers clearly are highest during the breeding season (November to March) (Fig. 4). Summer numbers may be even higher than suggested by Fig. 4, since birds incubating among dunes behind the beach probably were overlooked. More detailed seasonal habitat shifts in Saldanha Bay (Fig. 5) during the breeding season are presented in Table 11. There was a shift towards exposed islands

TABLE 11

SEASONAL VARIATION IN THE DISTRIBUTION OF AFRICAN BLACK OYSTERCATCHERS IN SALDANHA BAY

			MAY 1980		JANUARY 1981	
HABITAT	+LOCALITY No.	Shore length (km)	No.of birds	Density (birds km^{-1})	No.of birds	Density (birds km^{-1})
ISLANDS:						
Exposed	4	1,8	83	46,1	105	58,3
	5	1,3	40	25,0	66	41,3
	18	2,5	184	73,6	196	78,4
TOTALS		5,6	307	52,0	367	65,5
Sheltered	12	2,0	23	11,5	19	9,5
	13	1,1	15	13,6	11	10,0
TOTALS		3,1	38	12,3	30	9,7
MAINLAND:						
Rocky shores	1	3,6	25	6,9	7	1,9
	3	4,6	72	15,7	30	6,5
	10	1,0	10	10,0	(+Loc.11=34)	
TOTALS		9,2	107	11,6		(4,5)
Sandy shores	8	4,2	5	1,2	(13 (	(1,5 (
	9	4,7	0	0,0		
	14	2,5	4	1,6	11	4,4
	16	2,3	17	6,5	14	6,1
TOTALS		13,7	26	1,9	38	2,8
Mixed shores,	15	7,0	36	5,1	14	2,0
predominantly rocky	17	3,2	21	6,6	21	6,6
TOTALS		10,2	57	5,6	35	2,5
Mixed shores,	2	2,7	42	15,6	6	2,2
predominantly sandy	11	5,6	10	1,8	(+Loc.10=34)	
TOTALS		8,3	52	6,3		(2,2)
Evenly mixed shores	6	1,0	17	17,0	33	33,0
Urban mixed shores	7	2,3	1	0,4	0	0,0
ALL MIXED SHORES		21,8	127	5,8		(5,3)
OVERALL SUMMARY		53,4	605	11,3	580	10,9

+see Fig 5.

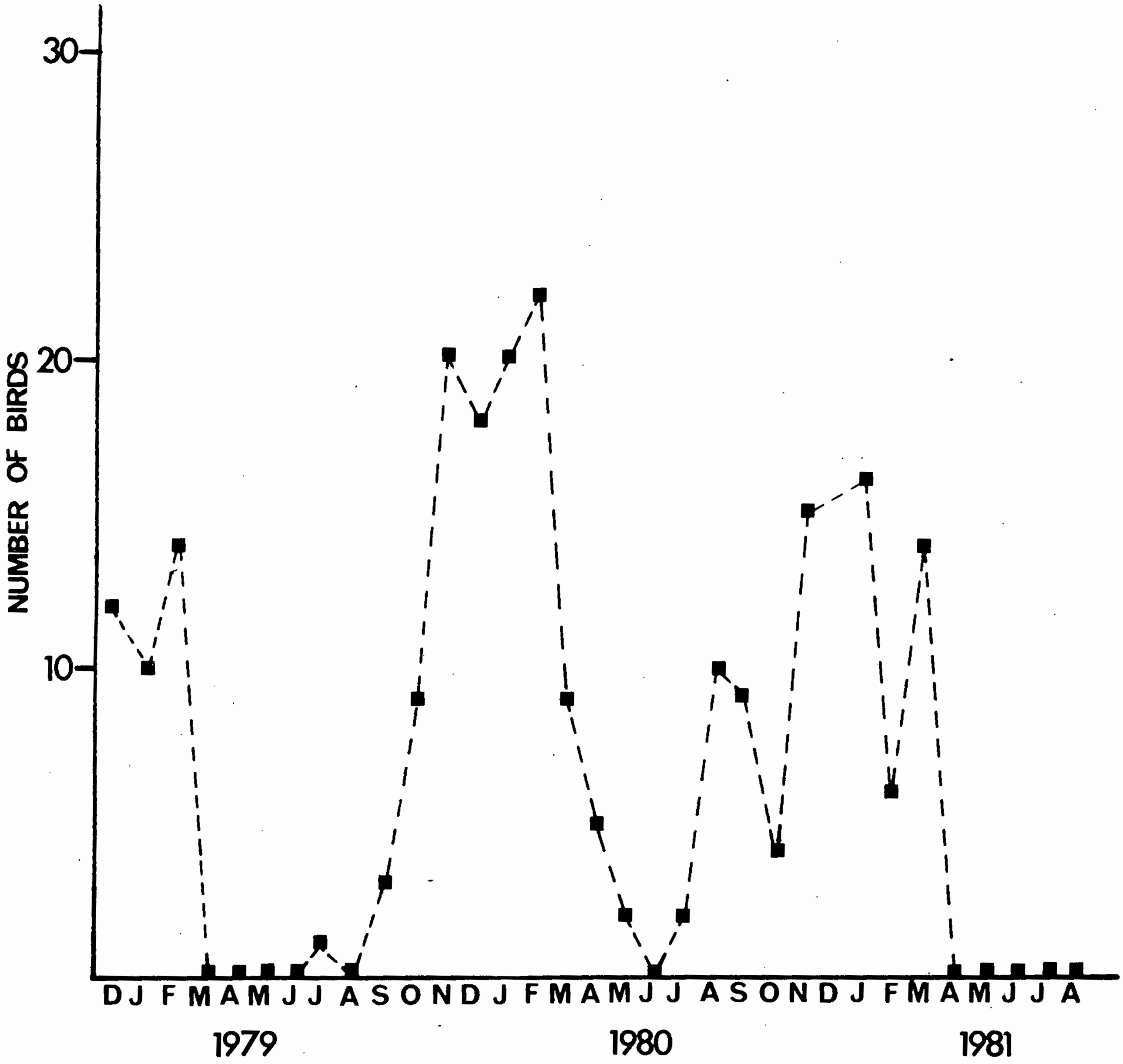


Figure 4. Monthly counts of African Black Oystercatchers along 15 km of sandy beach north of Ysterfontein, southwestern Cape

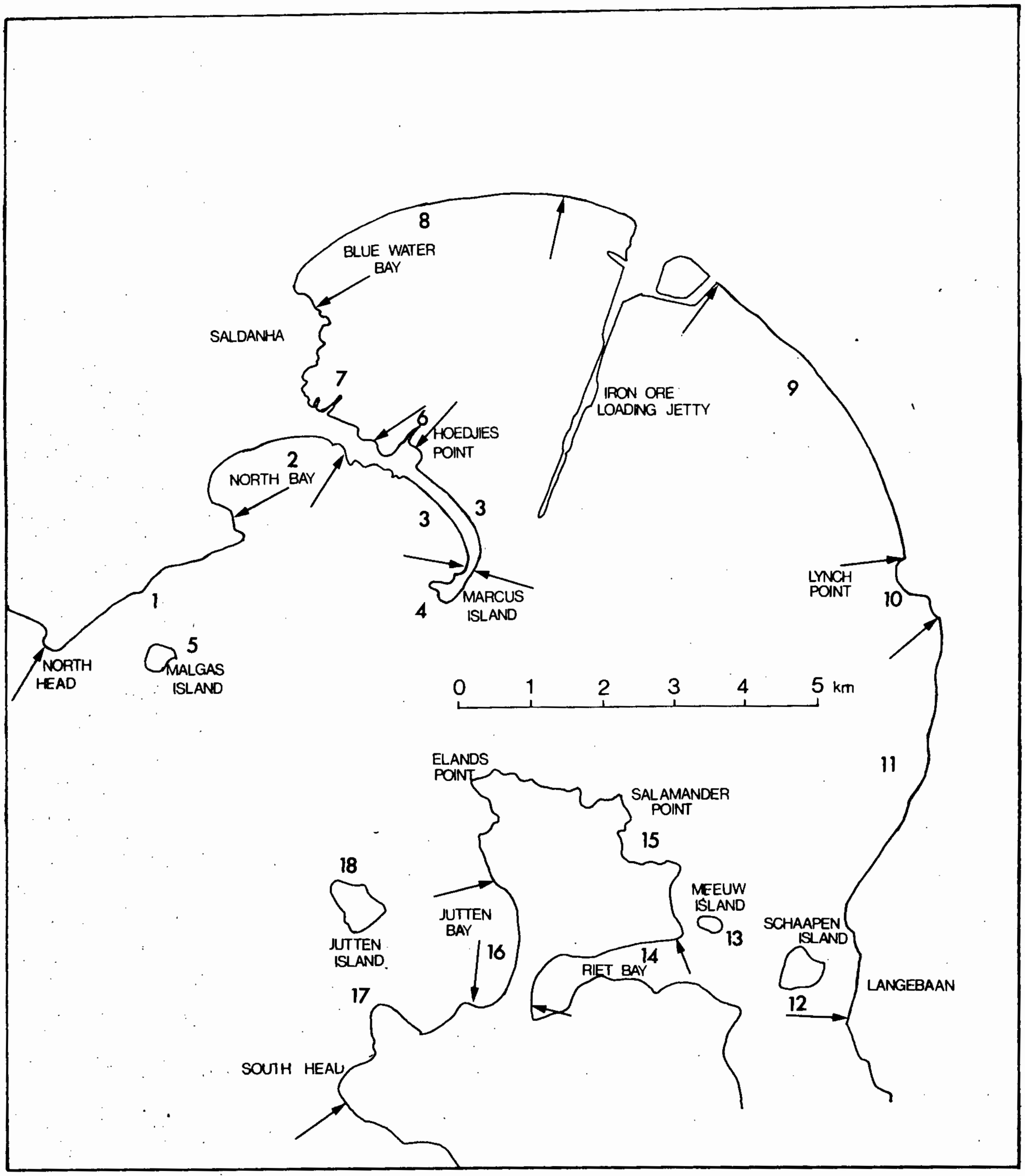


Figure 5. Map of Saldanha Bay showing areas censused seasonally for African Black Oystercatchers

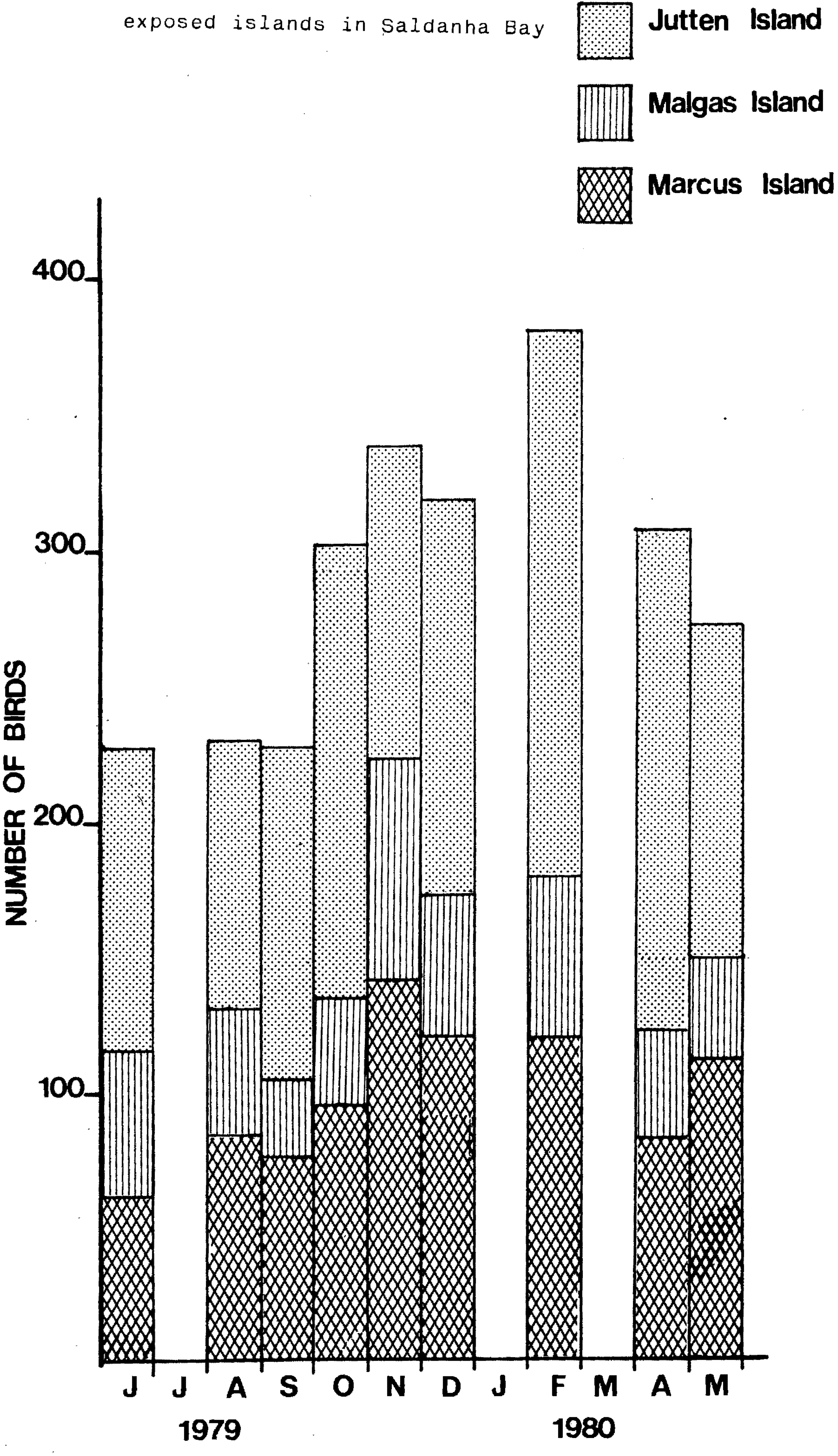
and mainland sandy shores during the breeding season, and a corresponding density decrease occurred at sheltered islands and at mainland rocky shores. Counts made between June 1979 and May 1980 at Marcus, Malgas and Jutten Islands demonstrate clearly the shift towards exposed islands in the breeding season (Fig. 6). Accurate counts during the breeding season are difficult as birds nest inland on the islands (Part 5.3) and no total counts were attempted during January and March 1980 to avoid unnecessary disturbance. There is, however, a clear increase in numbers prior to the peak egg-laying period, in December and January. Therefore birds prefer to breed on exposed rocky islands and on sandy beaches. Densities apparently remain constant on mixed shores throughout the year. This probably reflects the availability of rocky areas for feeding and sandy areas for breeding, thus obviating the need for seasonal movements by these individuals to satisfy breeding requirements.

CONSERVATION

The population of less than 5 000 birds renders the African Black Oystercatcher southern Africa's second rarest endemic coastal breeding species, after the Damara Tern _Sterna balaenarum_ (FitzPatrick Institute, unpubl. data). Apart from a few breeding records from the Lüderitz area, South West Africa/Namibia, the known mainland breeding distribution extends from the Olifants River in the western Cape to Mazeppa Bay, Transkei. The species also breeds on most of the offshore islands from Seal Island, South West Africa/Namibia to Bird Island, Algoa Bay.

Ten islands and seven mainland areas have been identified as each supporting more than 1 % of the world population (Table 12). The

Figure 6. Monthly counts of African Black Oystercatchers at three exposed islands in Saldanha Bay



RAMSAR Convention (Smart, 1976) states that a wetland should be considered of international importance if it regularly supports 1 % or more of the flyway or biogeographical population of at least one species of waterfowl. The 1 % level has been chosen on this basis. The current conservation status of these sites is listed in Table 12. These sites are recommended for Nature Reserve status.

Summers & Cooper (1977) identified two main threats to African Black Oystercatchers: human disturbance in breeding areas and the introduction of mammalian predators to offshore islands. Human disturbance is mostly unintentional, but large numbers of off-road vehicles now allow ready access to remote beaches which were previously undisturbed, and increase pressure on dune areas which are favoured breeding sites. The African Black Oystercatcher has been shown to be a largely sedentary species when adult and protection of breeding sites throughout the year will also protect feeding areas.

Mammalian predators are recorded from three islands. Bird Island (Lambert's Bay) is now connected to the mainland and has large numbers of rats _Rattus norvegicus_: oystercatchers do not breed there. Feral cats _Felis catus_ were introduced to Dassen Island and one is known to have killed an adult oystercatcher (Summers & Cooper, 1977): Dassen Island has a lower oystercatcher density than other islands off the western Cape coast. A causeway connecting Marcus Island to the adjacent mainland was completed in February 1976 and this has allowed mammalian predators access to the island (Summers & Cooper, 1977). During the 1979/1980 breeding season at least 10 oystercatchers were killed (Part 4.3), representing 8 % of the breeding population. Strong

TABLE 12

AREAS SUPPORTING MORE THAN 1 % OF THE WORLD POPULATION OF AFRICAN BLACK OYSTERCATCHERS

LOCALITY		COASTAL LENGTH(km)	No. of birds	% of world population	Current conservation status
ISLANDS	Seal, SWA		97	2,03	Landing regulated by permit
	Penguin		55	1,15	"
	Halifax		71	1,49	"
	Possession		281	5,88	"
	Malgas		66	1,38	"
	Marcus		123	2,57	"
	Jutten		175	3,66	"
	Vondeling		78	1,63	"
	Dassen		221	4,62	"
	Dyer		49	1,02	"
MAINLAND AREAS					
Agate Beach to Grossebucht		46,0	163	3,41	Unprotected
Sandy Point (32°45'S,18°01'E) to Mauritz Bay (32°58'S,17°53'E)		66,3	239	5,00	8,5km protected at Columbine Nature Reserve
Saldanha Bay		44,7	173	3,62	Controlled access to 20,4 km
Ysterfontein (32°21'S,18°09'E) to Skulp Bay (33°35'S,18°21'E)		42,9	108	2,26	Unprotected
Cape of Good Hope Nature Reserve		38,6	96	2,01	Protected
St. Francis Bay (Kabeljous River to Maitland River)		36,8	68	1,42	Unprotected
Algoa Bay (Sundays River to Woody Cape)		36,0	123	2,57	Unprotected
TOTALS		311,3 (mainland only)	2 186	45,72	

circumstantial evidence suggests that the predators were Cape Foxes *Vulpes chama* which have been trapped on the island. Construction of a predator-proof barrier was completed in July 1981 and has proved largely effective in controlling predators. Oystercatcher breeding production at Marcus Island decreased after the causeway was completed, but increased dramatically following completion of the predator proof barrier (Cooper, Hockey & Brooke, in press).

An additional threat to local oystercatcher populations is the exploitation of intertidal invertebrate resources by man for both food and bait. This problem is most pronounced at the eastern edge of the species'range, especially in Transkei. The Dwesa situation, discussed earlier, suggests that such exploitation and concommitant disturbance may be a factor limiting the species' eastern distribution. Island breeding sites, with the exception of Shark Island at Lüderitz, which is connected to the mainland by a causeway and is a high intensity recreation area, all currently are afforded some measure of protection. They are administered by the Sea Fisheries Research Institute and landing is controlled by permit. Oystercatcher breeding production at these islands is greater than on the mainland (Part 5.2) and, with the exceptions mentioned above, they are free from the three major threats. Guano scraping still continues at some of these islands, but this is done outside the breeding season and is not thought to affect oystercatchers, though other species such as Jackass Penguins *Spheniscus demersus* may be adversely affected (Siegfried *et al*., 1976).

A very small fraction of the mainland population occurs within proclaimed Nature Reserves or National Parks. Of the seven important mainland localities, only one is protected (the Cape of

Good Hope Nature Reserve) and a small section (8.5 km) of another falls within the Columbine municipal Nature Reserve. However, these Nature Reserves extend only to the high water mark and intertidal exploitation is limited only by legal daily removal quotas of certain species. In the case of oystercatchers, which forage intertidally, protection of the marine as well as the terrestrial environment is important.

The monitoring of population changes is not easy in a long-lived species with a low rate of recruitment, particularly when major population fluctuations occur naturally as a result of Paralytic Shellfish Poisoning (Part 3.6). Assessment of adult:juvenile ratios in the months following breeding is one approach that is currently being used to assess the "health" of the population. These ratios are most easily assessed at known roost sites. This monitoring is being carried out in conjunction with cohort colour ringing of chicks at offshore islands. All island chicks disperse to the mainland (Part 5.2) and this allows a measure of the importance of islands to the population's productivity. Annual counts of breeding birds at offshore islands should also be made. Preliminary investigations suggest that islands are of major importance (Part 5.2).

It is recommended that the following measures be given consideration in a management plan for the conservation of the African Black Oystercatcher:

1. That the conservation status of offshore islands be improved by affording them and their intertidal zones full Nature Reserve status; that there be no further introduction of mammalian predators, and that existing predators be removed.

2. That consideration be given to proclaiming new Coastal Nature Reserves, including their intertidal zones, at the six other mainland areas designated in Table 12, and that the proclamation of a coastal Nature Reserve in Algoa Bay be given high priority as this is also a breeding locality for the rare Damara Tern (Randall & McLachlan, 1982).

3. That the Cape of Good Hope Nature Reserve and other coastal Nature Reserves be extended to include the intertidal zone.

4. That off-road vehicles be excluded from the areas designated in Table 12 and their use on the whole southern African coast be controlled.

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Part 2. MORPHOMETRICS

Part 2.1. Morphometrics and sexing of the African Black Oystercatcher *Haematopus moquini*.

Ostrich 52 (1981):244-247

ABSTRACT

One hundred and nine African Black Oystercatchers (Haematopus moquini) were caught, measured, and sexed by cloacal examination during the 1979/1980 breeding season. Six standard taxonomic variables were measured - females were larger than males in all dimensions considered. The most dimorphic characters were exposed culmen length and mass. The data were subjected to stepwise discriminant analysis and a linear function was derived which allowed birds of unknown sex to be sexed. The function is $D = -0.391X_1 - 0.016X_2 + 0.218X_3 + 0.714X_4 + 15.946$ where X_1 = exposed culmen length (mm), X_2 = body mass (g), X_3 = length of tarsometatarsus (mm) and X_4 = culmen depth at the gonys. Values of D from the above equation less than zero indicate a female and those greater than zero indicate a male. The greater the divergence of D from zero, the higher the probability of correctly sexing a unknown individual: Once $D > \pm 1.2$, $p > 0.99$.

INTRODUCTION

The classification of the African Black Oystercatcher Haematopus moquini and its phenetic relationships to other species of oystercatchers are uncertain: Peters (1934) and Larson (1957) chose to classify it as a subspecies of the European Oystercatcher H. ostralegus, while Heppleston (1973) and Clancey (1980) accorded it specific status. It has been suggested that the African Black Oystercatcher is a phenetically intermediate species, males being nearer to the Old World group of males and females to the New World group (Baker, 1977). The "New World" included the Australasian species except for the South Island Pied Oystercatcher H. o. finschi which is thought to be a Palaearctic element in the New Zealand fauna (Baker, 1977).

A problem inherent in these studies has been the lack of data, both morphological and ecological, concerning the African Black Oystercatcher. Some details of mass and basic morphometrics are available for unsexed birds (Summers & Cooper, 1977; Prater *et al*., 1977). The species has a small population and the collection of enough specimens to provide satisfactory morphological data is precluded by its conservation status (Summers & Cooper, 1977).

In view of this, the aims of this study are to present details of morphological variation in African Black Oystercatchers using standard taxonomic measurements, to describe differences between the sexes and provide a mathematical technique for sexing individuals from standard field measurements in the manner of Baker (1974a) and Heppleston & Kerridge (1970). Brief criteria for the separation of sexes in the field are presented.

METHODS

A total of 109 birds (55 males, 54 females) was trapped during the 1979/1980 breeding season at Marcus (33 03S, 17 58E) and Malgas Islands (33 03S, 17 55E) in the southwestern Cape, South Africa. Incubating birds were caught at the nest using a wire mesh treadle trap. The trap is a circular cage, 0.60 m in diameter and 0.55 m high, open at the bottom: a drop door is triggered by the bird stepping on the treadle. At the time of trapping, the eggs were substituted with hard boiled coloured chicken eggs to prevent breakage since trapped birds panic when approached. Birds normally were trapped four to ten days after clutch completion and were sexed by examination of the cloaca for signs of distension that are still evident in the female at this stage. Whenever possible, birds were trapped within this limited time period relative to clutch completion, as mass variation can occur during incubation (Mercer, 1968). Observations also were made of colour-ringed birds copulating and no discrepancies were found between the two techniques. An obvious limitation of this technique is that criteria for sexing can be developed only for mature breeding birds.

The following measurements were made: exposed culmen length to the nearest 0.1 mm: the length of the tarsometatarsus, measured from the depression in the angle of the intertarsal joint to the base of the complete scale before the toes diverge, to the nearest 0.1 mm: body mass to the nearest 1 g: wing length (flattened chord) to the nearest 1 mm, and culmen depth at the skull and gonys to the nearest 0.1 mm (Anon, 1976).

Stepwise discriminant analysis (BMDP-77) was used to separate the populations of males and females (Brown, 1977). Discriminant analysis is concerned with the problem of classifying an object of unknown origin (sex) into one or more distinct groups (male or female) or populations on the basis of observations made on it (Fatti _et_ _al_., 1981). In this instance measurements made on birds of known sex were analysed to produce a formula enabling birds of unknown sex to be sexed with a certain probability of correct classification.

RESULTS

The means, standard deviations and ranges of the six taxonomic measurements recorded are detailed in Table 13 for males and females separately. The four characters most important in determining sex are exposed culmen length (X_1), body mass (X_2),

TABLE 13. MORPHOMETRICS OF THE AFRICAN BLACK OYSTERCATCHER AS DETERMINED FROM BREEDING BIRDS

Sex	Exposed culmen length (mm)	Culmen depth at base (mm)	Culmen depth at gonys (mm)	Wing length (mm)	Tarsus (mm)	Mass (g)
Male						
Mean	63.0	17.0	12.8	275.5	56.0	665.5
S.D.[+]	2.8	1.0	0.5	5.2	2.1	35.2
Range	57.7-69.5	15.0-18.8	11.8-13.8	265-286	50.6-60.8	582-757
Female						
Mean	71.7	17.7	12.7	279.2	57.7	722.3
S.D.	2.2	1.2	0.5	5.0	2.0	34.1
Range	67.4-76.9	15.5-19.9	11.6-13.8	265-289	52.0-62.0	646-800

[+] Standard deviation

tarsus length (X_3) and culmen depth at the gonys (X_4). The linear function for separating sexes, obtained from discriminant analysis is: $D = -0.391X_1 - 0.016X_2 + 0.218X_3 + 0.714X_4 + 15.946$. The probability of correct sexing using this expression is not 100 %. Fig. 7 shows the distribution of D-values for male and female African Black Oystercatchers: values of D less than zero from the above equation indicate a female, while values greater than zero indicate a male. The birds of known sex were "re-sexed" using this expression with 98.2 % accuracy, with 99 % confidence limits of 91.8 % to 99.9 % (Diem & Lentner, 1975, p. 99). However, values of D between +1.2 and -1.2 fall within a "zone of uncertainty" (Fig. 8) and such birds cannot be sexed with 100 % certainty using this method.

Separation of male and female African Black Oystercatchers in the field is not easy, though paired birds can often be sexed from observation of bill morphology. The male has a short, stout bill, with the upper mandible appearing straight and an impression of an upward bend in the lower mandible at the gonys. The female's bill is long, pointed, and often appears to "droop" towards the tip. These field and mathematical criteria should be used only on adult birds: Baker (1974a) found that the bill dimensions of South Island Pied Oystercatchers changed in the first three years of life.

DISCUSSION

Mean mass of male and female African Black Oystercatchers combined was 694 g. This is similar to the mean of 680 ± 45 g for 27 unsexed breeding adults trapped at Marcus Island in 1976/77 (Summers & Cooper, 1977). As with all oystercatcher species for

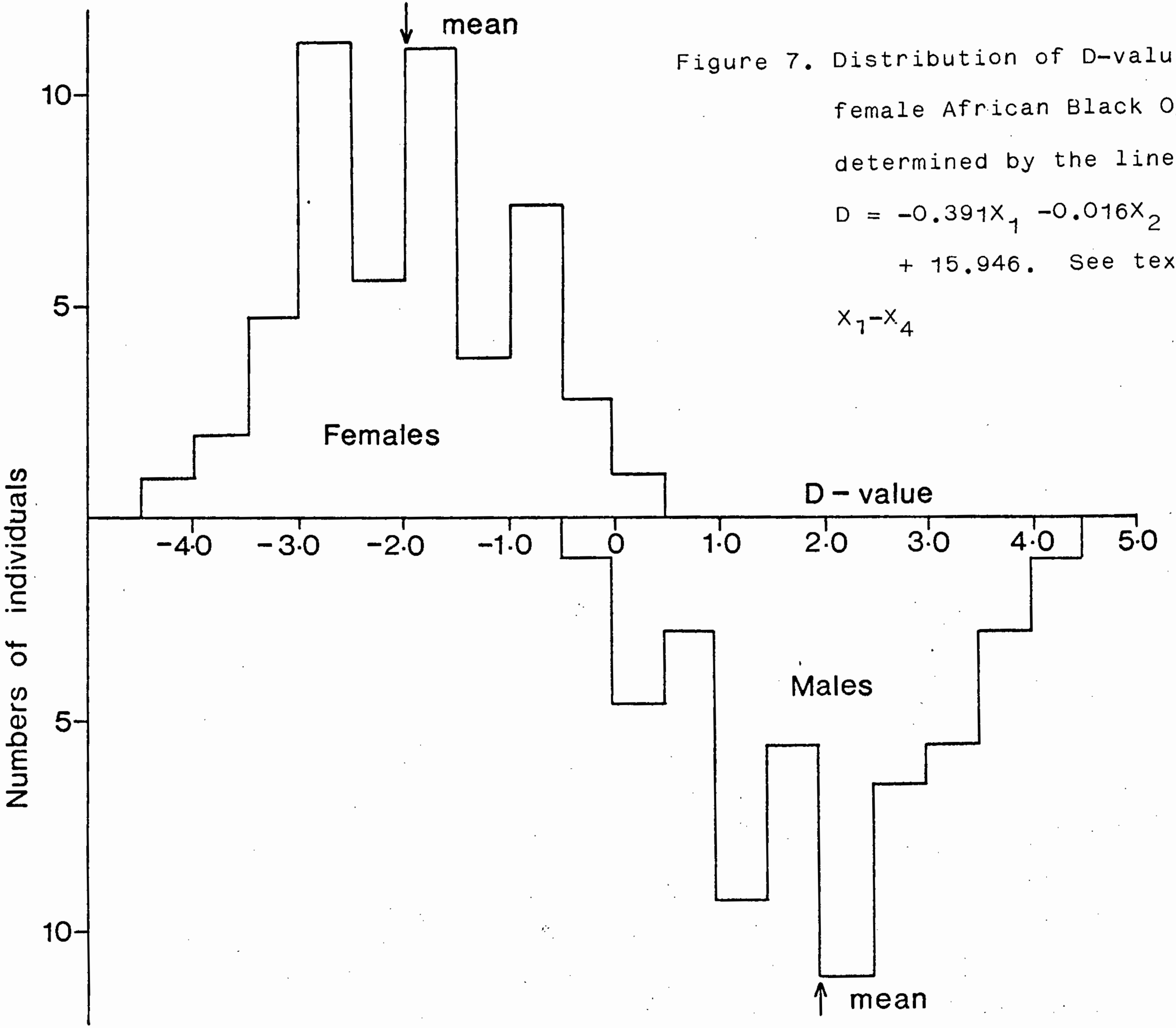
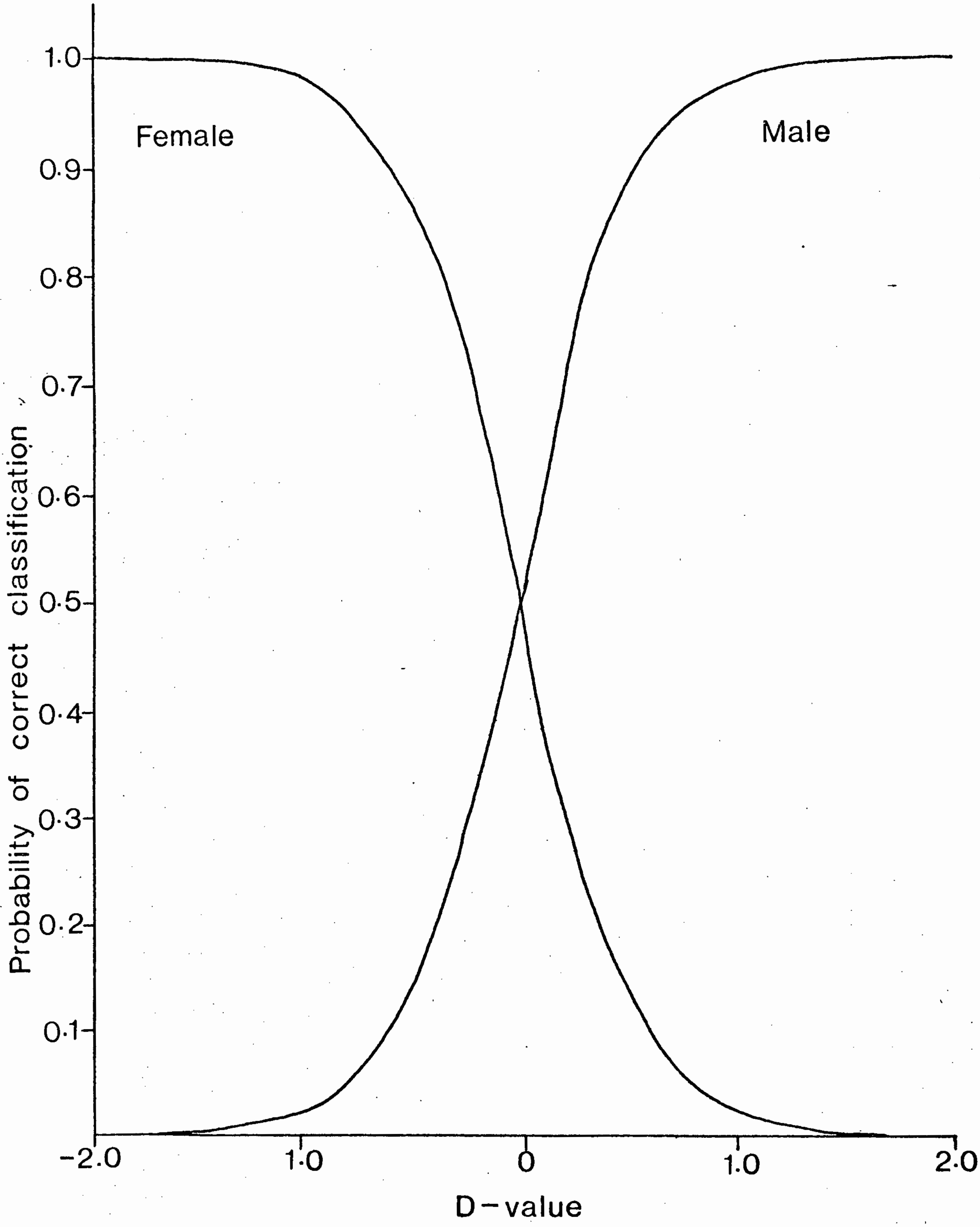


Figure 7. Distribution of D-values for male and female African Black Oystercatchers as determined by the linear expression: $D = -0.391X_1 - 0.016X_2 + 0.218X_3 + 0.714X_4 + 15.946$. See text for parameters of X_1-X_4

Figure 8. The probability of correct classification of an African Black Oystercatcher as male or female for differing values of D



which data are available, culmen length is the character exhibiting greatest sexual dimorphism in African Black Oystercatchers (Baker, 1974a; Prater *et al*., 1977; McKean, 1978).

Table 14 compares mean exposed culmen lengths of six black species of oystercatcher and of five pied forms. Mean culmen lengths of African Black Oystercatchers are markedly shorter than those of all other species. Body mass is comparable to that of other black species; the mean mass of males and females combined (694 g) matches that of the Variable Oystercatcher *H. unicolor* (692 g) (Baker, 1974b). Pied species are smaller overall: *H. o. occidentalis* weighs approximately 500 g and *H. o. finschi* 568 g (Heppleston, 1971; Baker, 1974b).

The linear function and discriminating values presented here were developed for breeding birds feeding in a rocky area. There are two major constraints that should be taken into consideration when applying this function. It may not apply so closely to birds from a sandy area where the extent of bill abrasion and subsequent alteration of bill length may vary depending on the food source (White & Gittins, 1965; Heppleston, 1970). To recapture territorial individuals during the non-breeding season is difficult, and until mass during incubation can be compared with mass at other times of the year, workers using this function to sex non-breeding birds should probably allow a greater margin of error in interpreting their results with regard to the probabilities of misclassification shown in Fig. 8 (see Mercer, 1968).

ACKNOWLEDGEMENTS

TABLE 14. A COMPARISON OF THE CULMEN MEASUREMENTS OF AFRICAN BLACK OYSTERCATCHERS WITH OTHER OYSTERCATCHERS

	Mean exposed culmen length (mm)		
Species / subspecies	Male	Female	Source
Black forms			
H. moquini	63.0	71.7	This study
H. bachmani	64.8	75.6	Ridgway (1919)
H. ater		77.4	Jehl (1978)
H. fuliginosus ophthalmicus	67.9	78.2	McKean (1978)
H. f. fuliginosus	73.0	80.8	McKean (1978)
H. unicolor	81.7	90.6	Baker (1974a)
	84.4	95.2	Baker (1974b)
Pied forms			
H. chathamensis	67.8	76.8	Baker (1974a)
H. leucopodus		78.2	Jehl (1978)
H. ostralegus occidentalis	71.4	79.8	Prater *et al.* (1977)
H. palliatus palliatus	79.7	88.0	Prater *et al.* (1977)
H. o. finschi	82.2	91.5	Baker (1974a)

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Part 3. FEEDING ECOLOGY

Part 3.1. Introduction

Previous studies of oystercatcher feeding ecology have concentrated largely on the European Oystercatcher Haematopus ostralegus (e.g. Heppleston, 1971; Hulscher, 1982), and to a lesser extent on the American Black Oystercatcher H. bachmani (e.g. Hartwick, 1976; Morrell et al., 1979) and the New Zealand oystercatchers (Baker, 1974). Information on the feeding of European Oystercatchers has been supplemented by observations of captive birds (Drinnan, 1958; Heppleston, 1971; Hulscher, 1974, 1982; Koene, 1978).

Considering the European and American Black Oystercatchers as the most studied species, the ecology of these species differs from that of the African Black Oystercatcher H. moquini in several respects. The African Black Oystercatcher is (in the areas studied here) territorial throughout the year, though there is some local movement of adults during the breeding season (Part 1.2). Both the European and American Black Oystercatchers, however, are territorial in the classical sense only during the breeding season (see Vines, 1980). At other times of the year they forage in flocks, often in estuarine habitats (e.g. Horwood & Goss-Custard, 1977; Hartwick & Blaycock, 1979) and, in the case of European Oystercatchers, feed inland in fields (Heppleston, 1971).

Some studies have adopted a classical approach and attempted to identify changes in foraging strategy of the birds in relation to prey density and depletion (O'Connor & Brown, 1977; Zwarts & Drent, 1981), and others have concentrated on the potential problem of the European Oystercatcher as an economic pest of cockle fisheries (Drinnan, 1957; Davidson, 1967, 1968; Hancock, 1971; Horwood & Goss-Custard, 1977). Attempts have been made to examine foraging strategies of oystercatchers in more complex (higher prey diversity) environments in the light of optimal foraging theory (Hartwick, 1976; Groves, 1981), but it is normally possible to ascribe profitability values to a limited suite of prey species (Hartwick, 1976), which presents problems in interpreting the results.

European Oystercatchers are known, from observations of captive birds, to feed at night (Heppleston, 1971; Hulscher, 1974), and this behaviour has been observed, though not quantified, in the field (Hulscher, 1982): it has been questioned whether American Black Oystercatchers feed at night at all (Hartwick & Blaycock, 1979).

Although the impact of oystercatcher predation on invertebrate prey populations in sandy and muddy substrata has been investigated (*op. cit.*), the extent and consequences of prey depletion on rocky shores is not known (but see Hartwick, 1981). Rocky shores in South Africa frequently support rich, diverse and highly conspicuous invertebrate communities and prey often appear to be superabundant in relation to the low densities of birds as compared with estuarine feeding flocks. On the rocky shores of southern Africa, principal invertebrate prey species, mussels and limpets, generally grow to larger sizes than in the northern hemisphere and thus may present different problems to oystercatchers in capture and handling, necessitating the evolution of specialized techniques.

A favourite approach to the study of feeding ecology has been to attempt to explain foraging behaviour in the light of optimal foraging theory and existing models (e.g. Hartwick, 1976). Such models normally have been developed under controlled or laboratory conditions (Holling, 1965; Horsley _et al._, 1979) and may not apply to predators hunting in complex environments (Schluter, 1981). Many models have evolved into such complex mathematical presentations that they are effectively untestable in the field (e.g. Royama, 1971; Manly, 1973; Estabrook & Dunham, 1976; Norberg, 1977; Bobisud & Voxman, 1979).

"Many important papers . . . . are so overloaded with turgid mathematical formalism that they are unintelligible even to the authors of other important papers" (Horn, 1978).

"An ecologist rightly reacts against reducing his animals to the algebraic abstractions of x, y and z. Algebra has a seductive beauty of its own . . . . but an algebraic conclusion is not an end-point: the conclusion must then be transformed back to animals living in a real world. The conclusion expressed in terms of the animals themselves is invariably dishevelled compared with the algebraic conclusions, but the animals rather than the mathematics are the subject of study and the conclusion must be biological, not mathematical" (Caughley, 1977).

This study of feeding ecology sets out to answer three main questions:

1. What are the techniques used by African Black Oystercatchers for locating, capturing and handling prey, and how do these compare with techniques used by other species of oystercatchers?

2. What is the diet of the African Black Oystercatcher (on rocky shores) and, more specifically, what are the sources and extent of variation in the diet in a species which retains the

same territory throughout the year?

3. What are the effects of oystercatcher predation on prey populations (limpets) and, more importantly, if oystercatchers significantly affect prey populations, what are the consequences for a). intertidal community structure, and b). other predators of intertidal invertebrates?

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ABSTRACT

Feeding techniques of the African Black Oystercatcher on several intertidal invertebrate species are described. Emphasis is placed on the predation of mussels and limpets since these are the most important dietary items on rocky shores, the preferred habitat of the African Black Oystercatcher. Considerable differences in handling techniques exist between the African Black Oystercatcher and the European Oystercatcher Haematopus ostralegus for both mussels and limpets. The European Oystercatcher normally opens mussels by hammering whereas the African Black Oystercatcher does not, and the direction of attack at limpets is opposite in the two species. Reasons for these differences are suggested. Foraging strategies for sandy shore bivalves appear to reflect relative abundance of the prey, and there is behavioural though not morphological evidence for sinistralism in the handling technique of African Black Oystercatchers, a phenomenon observed in at least three other species of oystercatchers.

INTRODUCTION

The African Black Oystercatcher Haematopus moquini breeds along the southern African coast from Seal Island (South West Africa/Namibia) to Mazeppa Bay (Transkei), rarely occurring outside this range (Summers & Cooper, 1977; Cooper et al., 1980, Part 1.2). It is the only representative of the family Haematopodidae which breeds in Africa. The adult population is largely sedentary, and the highest densities of birds are found on rocky shores and islands (Summers & Cooper, 1977). On sandy shores in the southeastern Cape Province the African Black Oystercatcher feeds almost exclusively on two species of sand mussel, *Donax serra* and *D. sordidus* (McLachlan *et al.*, 1980). In rocky areas, many birds defend small feeding territories throughout the year and the spectrum of invertebrate species available to a particular pair is therefore a function of territory size, exposure and topography.

This study aims to describe the techniques used by African Black Oystercatchers in locating and handling a range of invertebrates and, where data exist, to compare the findings with studies of other species of oystercatchers.

METHODS

Direct observations of feeding behaviour were made at Marcus Island (33 03S, 17 58E) southwestern Cape, South Africa, between July and September 1979, and in St. Francis Bay (33 59S, 25 17E) eastern Cape, South Africa, during August 1980.

Marcus Island is small (11 ha) and granitic, with a coastline of 1.6 km. It supports a resident population of approximately 120 African Black Oystercatchers (Part 1.2). Coastal exposure is moderate to severe, with frequent storms during the winter. St. Francis Bay is an exposed sandy beach backed by dunes.

These observations were supplemented with additional data from other islands in the southwestern Cape and off the coast of South West Africa/Namibia and from one mainland locality in the eastern Cape Province. At these sites, collections of emptied mollusc shells were made at chick feeding piles (middens) between January and April in 1980 and 1981.

RESULTS

Rocky Shores

African Black Oystercatchers prey on a wide spectrum of invertebrates on rocky shores. The principal species can be divided into three main classes: pelecypods, gastropods and polychaetes. Important species within these classes are pelecypods such as the black mussel Choromytilus meridionalis, the brown mussel Perna perna and the ribbed mussel Aulacomya ater; gastropods such as the limpets Patella granularis, P. argenvillei, P. cochlear, P. longicosta, P. granatina and Cellana capensis; the whelks Burnupena catarrhacta and Nucella spp. and winkles Oxystele spp; and polychaetes such as the mussel-worm Pseudonereis variegata (Part 3.3). Smaller polychaetes are taken, but field identification of such small prey normally is not feasible. Isopods, including the large Paridotea spp., and probably amphipods, are also taken, but do not constitute a significant fraction of the diet, and feeding techniques on these prey are not described.

Pelecypods

Black Mussel

African Black Oystercatchers actively search for gaping black mussels at the edge of the tide and in pools and crevices. When a gaping mussel is found, the bird aligns itself with the longitudinal axis of the mussel and stabs through the posterior sector (Fig. 9). This action usually severs the posterior adductor muscle which connects the two valves: one of two courses of action is then followed. The mussel may be cleaned in situ or removed from the substrate and cleaned of flesh while wedged in a

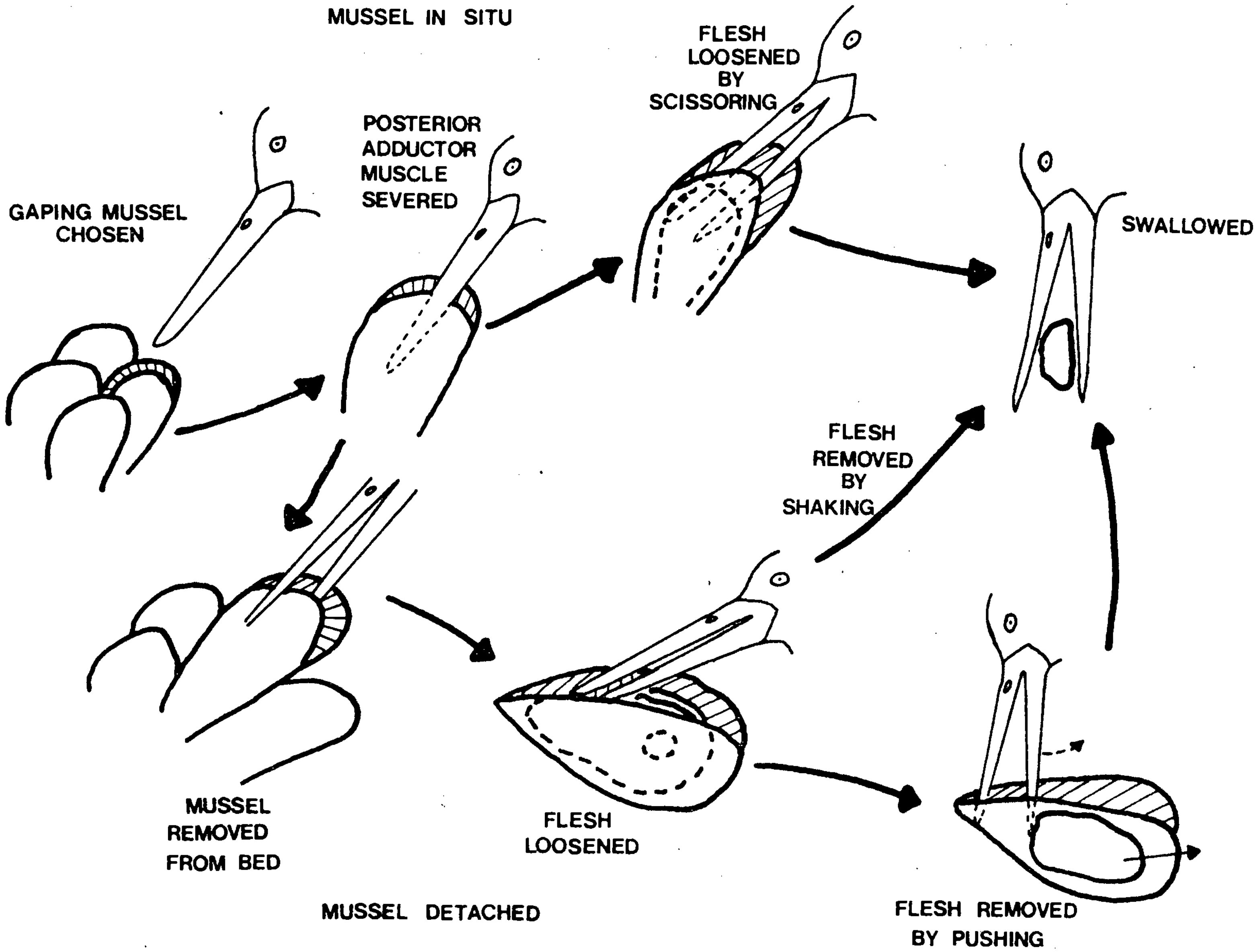

Figure 9

Diagrammatic representation of mussel handling techniques of African Black Oystercatchers suitable site. If the flesh is removed <u>in situ</u> the mussel is opened with a sideways movement of the bill acting as a lever to force the valves apart: this sometimes causes the mussel to become detached. Once the mussel is opened the flesh is scissored away and swallowed in one to five pieces depending on its size.

Mussels are detached when they are in an unsuitable position to be cleaned <u>in situ</u>, such as deeply submerged in water, on a very steep slope or in an area being repeatedly swamped by waves. The handling time (time elapsed from onset of attack by the bird until prey item abandoned) was recorded for mussels detached from the substrate and those cleaned <u>in situ</u>. Data were obtained from four individually colour-ringed birds feeding on adjacent territories. For black mussels, the mean handling time ± S.D. for mussels cleaned <u>in situ</u> was 24.0 ± 5.9 s (n=8) and for detached mussels was 63.7 ± 28.3 s (n=11). The corresponding values for ribbed mussels were: <u>in situ</u> 26.8 ±8.6 s (n=12) and detached 71.6 ±20.2 s(n = 11). These differences are significant both for black mussels ($t=2.81$, d.f.=17, $p<0.02$) and ribbed mussels ($t=5.31$, d.f.=20, $p<0.001$); detachment therefore significantly increases mean handling time. Before detachment, the posterior adductor muscle is severed by stabbing. The mussel is then removed by gripping one valve and pulling at the same time as twisting from side to side. Detached mussels frequently are taken to the same site for cleaning. Once at the handling site the mussel is positioned ventral side uppermost and the bill tip is inserted through the periostracum where the byssus threads protrude ventrally and the valves are not fully closed (Fig. 9). Some scissoring is needed before the bill is turned through 90 degrees and opened to force the valves apart. In some cases, when the handling site is wedge-shaped, the mussel is immobilized to the extent where it can be cleaned as though <u>in situ</u>. Once the flesh is loose within the shell, it is either gripped and the shell shaken off or it is pushed out gently. In the latter technique the closed bill is inserted through the now widely gaping ventral valve margins anteriorly, and, using the anterior apex of the shell as a buffer for the upper mandible, the bill is opened, forcing the flesh out through the posterior sector (Fig. 9).

It is not unusual for shells that initially have been cleaned <u>in</u>

situ to be detached from the substrate after the bulk of the flesh has been removed. This permits the valves to be prized further apart than the dense packing of the mussel beds allows, and hence the shell can be cleaned more efficiently.

During severe storm conditions, when the intertidal zone remains submerged throughout the tidal cycle, mussels may be torn from the skears (beds) by the swell and deposited above the high water mark. The valves of these mussels are closed and African Black Oystercatchers use a hammering technique to open them. The bill is forced through the periostracum and moved posteriorly until the adductor muscle is severed. Birds occasionally push at the valve margins of closed mussels on exposed beds, but unless access is gained immediately these attacks are not followed through to completion.

Over 1 000 black mussel shells cleaned by African Black Oystercatchers under calm conditions were examined for signs of damage: less than 1 % were chipped or fractured. Black mussels consumed were in the size range 20 to 110 mm.

Ribbed mussel

The ribbed mussel is abundant at Marcus Island, growing in dense beds which support a high faunal diversity in the interstitial spaces (Hockey & Branch, ms.). Densities of shells greater than 15 mm in length range from approximately 4 000 to 14 000 per m^2. The ribbed mussel occurs from midtide, below the Patella granularis (upper balanoid) zone, to the low water mark. As with black mussels, only gaping shells are attacked. The flesh normally is swallowed in one or two pieces, the ribbed mussel being a smaller species than the black mussel.

Gastropods

Limpets

At least fifteen species of limpet, Patella, Helcion and Cellana spp. are taken by African Black Oystercatchers at the sites studied. Only four of these (Patella granularis, P. argenvillei, P. cochlear and P. granatina) are taken regularly in the western Cape. Patella granularis is the most abundant species of limpet on exposed rocks in the upper balanoid zone, P. granatina occurs from midtide down, whilst P. argenvillei and P. cochlear occur immediately above and within the kelp zone. Patella granularis is exposed by the tide and theoretically is available for longer than the other species and is important in the diet, comprising between 24 % and 90 % of all prey items in chick middens at islands off the west coast. (Part 3.3).

Larger limpets normally are consumed only when they are first exposed by the tide or are regularly splashed by water when the shell is not drawn tightly over the foot (pers. obs.). Patella granularis, which is primarily a nocturnally foraging species (Branch, 1971), forms a greater proportion of the diet at night (Part 3.3).

Small limpets (less than 25 mm in length) are attacked in one of two ways. Either the lower mandible is inserted under the shell mantle with the upper mandible gripping the apex and the shell is levered away from the rock, or a sharp blow is directed at the margin of the shell with the bill closed. This blow is often sufficient to dislodge the limpet. Failing this, the shell is gripped in the bill and prized off. Large limpets (over 25 mm) are dealt an initial blow and then pushed to dislodge the foot.

If pushing is unsuccessful, the bill is laid parallel to the ground, inserted under the shell and used as a lever. Once detached, limpets are cleaned of flesh with a circular scissoring movement. The bird stabs at the adductor muscle of the limpet with its bill slightly opened. Once the muscle is pierced, the bill is opened further and the outer edges of the mandibles serve to tear the muscle away from the shell.

Occasionally both shell and flesh are swallowed when either the limpet is very small or the initial blow damages the shell to such an extent that the flesh cannot easily be removed. On one occasion an oystercatcher was seen to gain access to a large P. granatina by hammering through the shell near the apex. Shells collected at chick middens provide further evidence of the African Black Oystercatcher's strategy for attacking limpets. During the attack, shells may be chipped or fractured at the point of attack thus providing a measure of the distribution of attacks. In view of the high tenacity of the limpet foot, the technique and direction of attack are probably crucial to the bird's success rate. The proportion of damaged shells of individual prosobranch species (Patella and Cellana) is inversely and logarithmically related to their tenacity (% damaged = 64.85 - 30.41 ln tenacity (kg cm^{-2}), r = 0.84; $p<0.05$) (Fig. 10 Table 15). This suggests that the more tenacious species must be removed more rapidly when the shell is partly raised since once the latter is lowered the probability of success decreases. Alternatively, the thicker shells of the lowtide species, P. argenvillei and P. cochlear, are more resistant to chipping.

The distribution of attacks in six sectors of the shell margin (Fig. 11) was analysed for eight species of limpet. In all

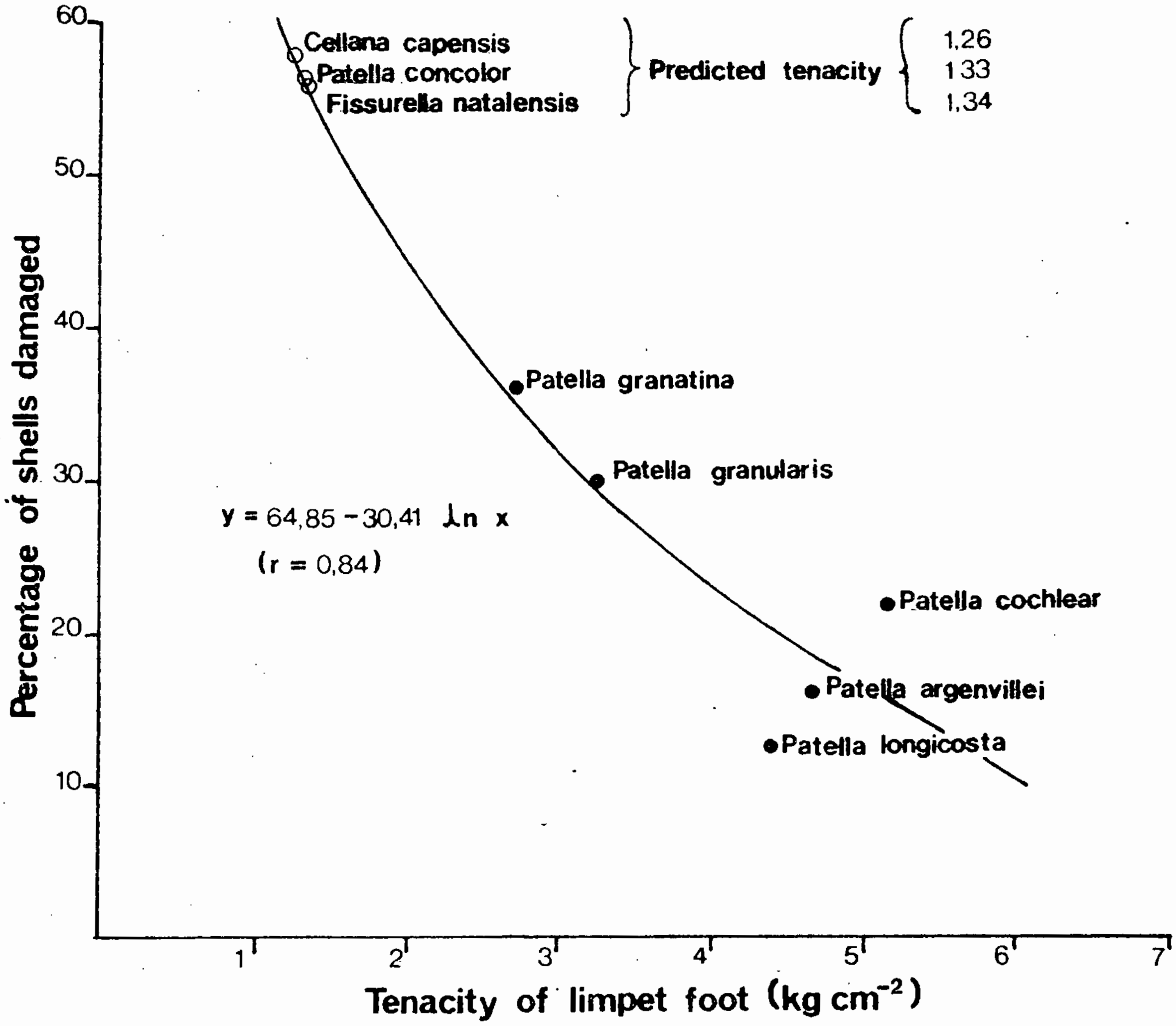

Figure 10

The relationship between the percentage of limpet shells damaged by African Black Oystercatchers during successful attacks and the tenacity of the limpet foot

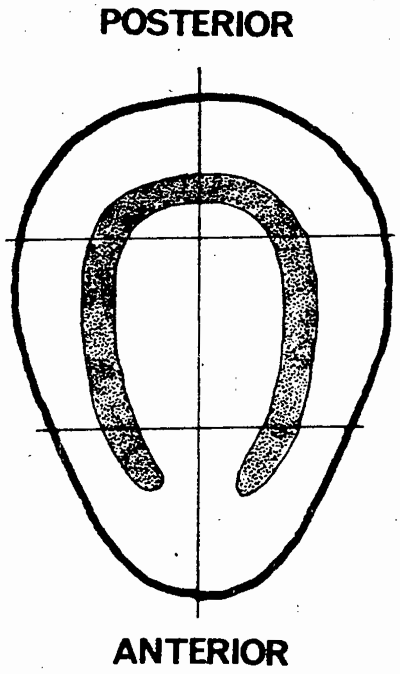

Figure 11

A view of the underside of a limpet shell showing the six sectors into which the shell margin is divided for analysis of the direction of attack, and the position of attachment of the adductor muscle. (after Feare 1971) prosobranch limpet species the attack strategy is similar: attacks are concentrated at the posterior margin of the shell (Table 15). There is between species variability in the consistency of "correct" posterior/anterior attack decisions: the more frequent posterior attack is assumed to be the correct decision.

To test whether this is a function of shell form (i.e. are correct decisions made less frequently with shells of uniform shape?), the percentage of correct attacks was compared with a Shell Uniformity Index (SUI) (Fig. 12). The SUI was calculated as Width of shell 10 mm from anterior apex/Width of shell 10 mm from posterior apex. Thus a species in which the posterior apex is the mirror image of the anterior apex would have a SUI of 1 (Table 15). Ten shells of each species were measured; in all cases the standard deviation was less than 5 % of the mean. The measurement of SUI was later modified to make values less variable between individuals of differing size (Part 3.5). The percentage of correct decisions is directly related to shell uniformity (% correct decisions = 108.11 - 64.24 SUI, $r = 0.96$; $p<0.01$).

Whelks and winkles

Whelks and winkles are not as important in the diet as mussels or limpets (Part 3.3) and tend to be preyed on by individual "specialist" birds (pers. obs.). These shells are easily removed from the substrate, which is normally a mussel bed, either by delivering a single blow with the bill to the base of the shell or by being picked up in the bill with no apparent effort. The latter technique is used when the animal is damp and active. The opercular opening is stabbed immediately the animal is overturned and the animal is then carried, with the bill wedged inside, to a suitable handling site: the mollusc foot is presumably held in

TABLE 15

DISTRIBUTION OF AFRICAN BLACK OYSTERCATCHER *HAEMATOPUS MOQUINI* ATTACKS ON EIGHT LIMPET SPECIES, INCLUDING THE PERCENTAGE DAMAGED, THE TENACITY OF THE FOOT AND THE SHELL UNIFORMITY INDEX (SUI). CHI-SQUARED VALUES AND SIGNIFICANCE LEVELS ARE GIVEN TO COMPARE ATTACK FREQUENCY BETWEEN DIFFERENT ZONES OF THE SHELL

Species	Distribution of attacks (see Fig. 3)	Percentage damaged	Tenacity[x] (kg cm^{-2})	SUI	Differences in attack frequency Posterior vs Anterior	 Posterior vs Middle	 Anterior vs Middle	 Right vs Left
Patella cochlear	39 31 (P) 5 9 13 14 (A)	21,9	5,18	0,70	X^2 19,06 $p < 0,001$	X^2 37,33 $p < 0,001$	X^2 4,12 $p < 0,05$	X^2 0,08 ns
Cellana capensis	19 25 13 13 12 5	57,8	(1,26)	0,87	X^2 11,96 $p < 0,001$	X^2 4,62 $p < 0,05$	X^2 1,88 ns	X^2 0,04 ns
Patella granatina	29 31 5 15 10 19	36,1	2,71	0,86	X^2 10,80 $p < 0,005$	X^2 20,00 $p < 0,001$	X^2 1,66 ns	X^2 4,04 $p < 0,05$
P. longicosta	6 4 0 0 0 0	12,4	4,40	0,86	X^2 10,00 $p < 0,01$	X^2 10,00 $p < 0,01$		X^2 0,40 ns
P. granularis	120 120 31 28 91 97	29,9	3,25	0,86	X^2 6,32 $p < 0,02$	X^2 106,45 $p < 0,001$	X^2 67,37 $p < 0,001$	X^2 0,02 ns
P. concolor	2 5 2 3 1 0	56,3	(1,33)	0,84	X^2 4,50 $p < 0,05$	X^2 0,33 ns		X^2 0,69 ns
P. argenvillei	53 39 10 14 36 30	15,9	4,67	0,91	X^2 4,28 $p < 0,05$	X^2 39,86 $p < 0,001$	X^2 19,60 $X < 0,001$	X^2 1,41 ns
Fissurella natalensis	4 2 2 2 5 3	56,0	(1,34)	0,89	X^2 0,29 ns	X^2 0,40 ns	X^2 1,33 ns	X^2 0,89 ns

[x] Values in parentheses indicate calculated tenacity (see Fig. 2); other values are from Branch & Marsh (1978).

(P) = Posterior; (A) = Anterior

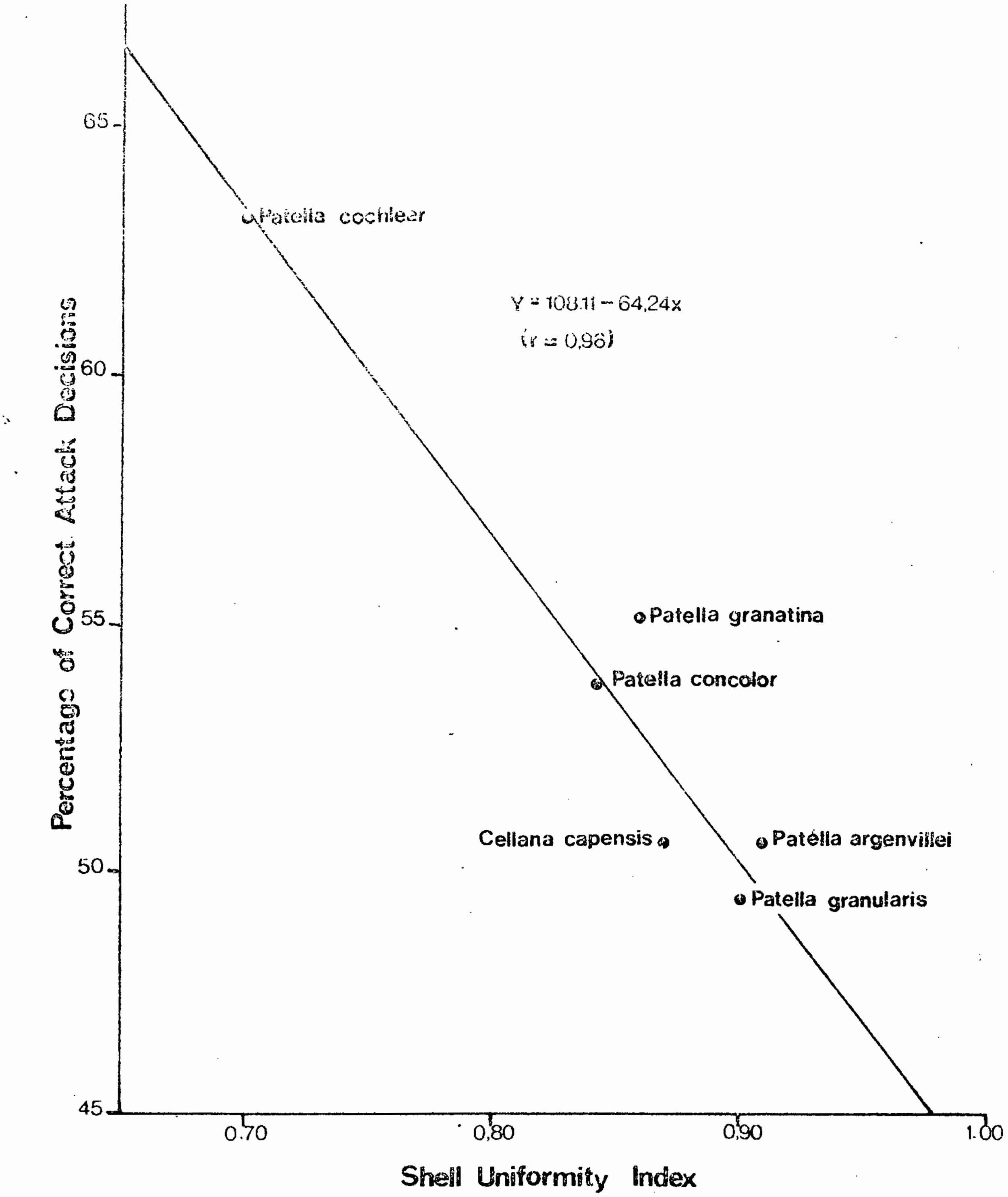

Figure 12

The relationship between the percentage of correct attack decisions made by African Black Oystercatchers and the Shell Uniformity Index (SUI) for six species of limpet. (See text for the calculation of SUI) the bill to prevent further retraction. The shell is sometimes broken during the cleaning process, especially in the case of the small winkles Oxystele spp. which do not have a robust shell. Flesh is loosened by rapid probing and scissoring and then is gripped while the shell is shaken free. Removal of flesh frequently is incomplete and on occasions shells are abandoned before any flesh is extracted.

Polychaetes

Unlike other prey items described, polychaetes, which occur primarily within the mussel beds, are not located by direct sight but by tactile stimuli. A considerable diversity of polychaete species is available, commonest species being syllids, Pseudonereis variegata, Marphysa depressa, Scoloplos johnstoni, and terebellids (pers. obs.). Worms are located by probing deeply into the mussel beds and the longer-billed female African Black Oystercatchers are more important predators of worms than are males (Part 3.3). When a worm is located it is drawn out slowly from among the mussels to avoid breakage, pulling may be continuous or accompanied by gentle tugs. Searching for worms occurs exclusively at the edge of the tide.

Sandy Shores

The diet of African Black Oystercatchers on sandy shores has not been studied in depth. Two prey species, the sand mussels Donax serra and D. sordidus are recorded in the literature (McLachlan et al., 1980). The bivalve Macoma littoralis is preyed on at Jeffreys Bay (34 05S, 24 55E) (specimens supplied by C.J. Vernon), and other estuarine species probably are eaten elsewhere.

Donax serra

These shells apparently are located by direct sight (single probe only), birds probably using the protruding siphons as a visual clue. The animal is stabbed through the lunular margin, at or close to the point (persistent gape) where the siphons protrude. The flesh is scissored out in a similar manner to that used on black mussels. Of 51 specimens examined, 39 (76.5 %) were undamaged. Of the remaining 12, eight showed damage to the left valve at the lunular margin, three had damaged right valves, and in one specimen, both valves were damaged.

Donax sordidus

The much smaller Donax sordidus is located by "stitching" through the soft sand at the edge of the tide near low water. "Stitching" is a series of rapid probes in the substrate with the bill partly open: the bill is not withdrawn fully between each probe. Occasionally the single probe (direct sight) technique is used. Eighty-four depredated animals were examined and all showed some damage to the shell. In 86 % of the cases the right valve was undamaged but the left valve was broken leaving only a small fragment at the umbo. In a further 5 % the left valve was chipped. The right valve only was broken in 7 % of cases. Direct observation of the exact methods by which these shells are opened is not feasible since the shell is usually partly buried in the sand during handling.

Macoma littoralis

Three of the 13 shells examined were damaged, all at the lunular margin.

COMPARISON OF THE FEEDING TECHNIQUES OF THE AFRICAN BLACK OYSTERCATCHER WITH OTHER SPECIES OF OYSTERCATCHERS

Mussels

The African Black Oystercatcher attacks only gaping mussels except under storm conditions when stranded, closed mussels are hammered open. Cleaned shells are almost invariably undamaged. The American Black Oystercatcher H. bachmani also attacks only gaping mussels (Mytilus edulis and M. californianus), but normally fractures one valve during the opening process (Webster, 1941). The Variable Oystercatcher H. unicolor of New Zealand and the Chatham Island Oystercatcher H. chathamensis prey on both gaping and closed mussels (Baker, 1974). Studies at 13 sites in Great Britain on the European Oystercatcher H. ostralegus found the hammering technique used on closed mussels to be the dominant method of attack at 10 sites, resulting in damage to more than 70 % of the shells (Heppleston, 1971a).

There are a number of possible reasons why African Black Oystercatchers should prey only on gaping mussels. The mussels eaten in southern Africa are large (20-110 mm), whereas mussels Mytilus edulis preyed on in Great Britain range from 20 to 70 mm (Heppleston, 1968). The resistance of the British M. edulis to hammering increases dramatically once they exceed 50 mm in length (Norton-Griffiths, 1967). The tidal range in southern Africa is small compared with that of Great Britain, being only 1.5 m at springs and 0.5 m at neaps at Marcus Island. This fact, coupled with the position of black mussels low on the intertidal gradient, means that when mussels are exposed they will be damp and gaping for much of the time. Black mussel-dominated communities tend to comprise individuals of fairly uniform size at high density; up to 3 600 per m^2 at Marcus Island (pers. obs.). This reduces travelling and recognition time of the foraging bird, thereby minimizing the interval between successive prey captures and raising the rate of net energy gain. African Black Oystercatchers feed for less than 50 % of the available time, except during storms, (Part 4.2), and are not subject to the physiological stresses experienced by European Oystercatchers during the boreal winter (Heppleston, 1971b). It is presumably energetically unnecessary to attempt predation of closed mussels by hammering. In addition, high invertebrate biomass and diversity allow other species to be eaten.

The Variable Oystercatcher and the Chatham Island Oystercatcher occasionally tear small mussels _Xenostrobus pulex_ from the substrate and swallow them whole: a third handling technique (Baker, 1974). I have not observed this behaviour in African Black Oystercatchers, though it is used by Kelp Gulls _Larus dominicanus_ at Marcus Island (pers. obs.).

Black mussels occur in dense beds leading to a vertical attitude in individuals, exposing the vulnerable posterior margins. Baker (1974) suggested that oystercatchers preferentially remove mussels from the substrate for cleaning and that larger mussels are not removed because birds are unable to overcome the force of the byssal attachment. Observations at Marcus Island suggest that mussels are only removed from the substrate when they cannot be dealt with _in situ_ since removal greatly increases the handling time. When mussels, and other molluscs, are removed from the substrate they are frequently taken to the same site for cleaning;

similar behaviour has been observed in the European Oystercatcher (Davidson, 1967; Heppleston, 1971a).

Limpets

The techniques used by African Black Oystercatchers in detaching limpets are broadly comparable to those used by European and Variable Oystercatchers (Feare, 1971; Baker, 1974). However, the prising technique, with the upper mandible gripping the shell apex and the lower mandible inserted under the shell margin of small limpets has not previously been described. Both the African Black and American Black Oystercatchers eat whole small limpets (pers. obs., Webster, 1941).

The distribution of attacks by the European Oystercatcher on the limpet Patella aspera has been analysed (Feare, 1971) and some interesting differences exist when compared with the African Black Oystercatcher. The majority (80 %) of European Oystercatcher attacks are directed at the anterior margin of the shell, whereas the African Black Oystercatcher directs between 50 % and 65 % of attacks at the posterior sector. Feare (1971) considered that "The adductor muscle of a limpet is horseshoe shaped, with the open end of the horseshoe at the anterior so that this end probably has the weakest hold on the substrate. If so, Oystercatcher attacks delivered here are more likely to be successful than attacks elsewhere on the margin." However, limpets are attached to the substrate by adhesion (Branch & Marsh, 1978) and although it is possible that the shell is less strongly attached to the foot anteriorly, the foot is uniform across its area, and adhesion of the foot itself to the substrate is likely to be no different. Since it is removal of the foot from the substrate and not the shell from the foot that is critical initially, it seems likely some other factor is in operation. An alternative hypothesis to account for the differing strategy of the African Black Oystercatcher is that posterior attack delays detection of the predator by the limpet, whose sense organs are situated anteriorly, thereby raising the likelihood of detachment with the initial blow. The consistency of the African Black Oystercatchers' attack strategy between species, although it is not as consistent within species as is the European Oystercatcher (Feare, 1971), implies there may be an important behavioural or morphological difference between the African limpets examined in this study and the European P. aspera that has led to the evolution of different attack strategies by the respective oystercatcher predators.

Limpets taken by African Black Oystercatchers are larger than those recorded by Feare (1971) for the European Oystercatcher (Table 24, Part 3.3). Since absolute tenacity is a function of foot area (Branch & Marsh, 1978), the forces to be overcome are greater for African limpets and the element of surprise is probably of paramount importance. This may be especially true in the case of P. argenvillei which can draw the shell over the foot extremely rapidly (G. M. Branch, pers. comm.).

Whelks and winkles

Both the European Oystercatcher and the South Island Pied Oystercatcher H. o. finschi attempt breakage of the shell to reach the flesh (Dewar, 1910; Baker, 1974). The European Oystercatcher may also peck at the opercular opening immediately on overturning, in the manner of the African Black Oystercatcher, and remove the flesh without damaging the shell. The latter technique in Europe was found to be approximately three times more successful than breaking the shell (Feare, 1971).

Polychaetes

When feeding on earthworms, the European Oystercatcher has a much higher success rate than would be expected by random probing (Heppleston, 1971a). The signs eliciting the probing response are unknown. Numerous sensory nerve endings in the bill tip presumably aid prey identification when contact is made (Heppleston , 1971a). Unfortunately no comparative data on techniques used when handling marine polychaetes exist, but it is likely that similar factors operate when birds probe into mussel beds for polychaetes and when birds probe in fields for earthworms.

Sandy shore bivalves

The two location techniques described for African Black Oystercatchers, namely the single probe (Donax serra) and multiple probing or "stitching" (D. sordidus) have been described for other species of oystercatchers (Drinnan, 1958; Brown & O'Connor, 1974; Hulscher, 1976). Hulscher (1976) found that European Oystercatchers feeding on the cockle Cardium edule normally used the single probe by day and stitching by night. Stitching was only used by day when cockle density was low (13 to 40 per m^2). This observation compares with the situation in St. Francis Bay where Donax serra occur at densities of up to 282 per m^2 while the abundance of D. sordidus is only c. 24 per m^2 (McLachlan, 1977). Drinnan (1957) found that stitching was a response to soft sand and single probes were used in firm sand. Donax sordidus are taken only at the water's edge where the sand is thixotropic.

Entrance to the shell through the persistent gape at the lunular margin is normal. In small shells such as Cardium edule (Drinnan, 1957) and D. sordidus, the gape is not large enough to allow entrance of the bill without breakage of the shell. In larger species such as D. serra, and oceanic bivalves in New Zealand, the shell is broken less frequently (Baker, 1974).

Sinistralism

The question of sinistralism has been raised in studies of three other species of oystercatchers (Dewar, 1908; Webster, 1941; Baker, 1974). When birds rotate in order to lever apart valves with the bill, the direction of rotation in other species normally has been to the left. Not enough observations were made of African Black Oystercatchers in the sandy shore environment to test this. However, in both Donax species, the left valve was damaged more frequently: this is consistent with a sinistral rotation as the upper edge of the closed bill, which is narrower than the lower edge, would press against the left valve, exerting greatest pressure on this surface. Baker (1974) found that although the majority of South Island Pied Oystercatchers had straight bills, the majority of those in which a bend was evident, bent to the left. The bend is probably a modification of the rhamphothecae rather than of the skull as was suggested by Stresemann (1929) (Baker, 1974). In a sample of 128 adult African Black Oystercatchers, 74 % had straight bills, 20 % bent to the left and 6 % bent to the right (pers. obs.). Although there appears to be some behavioural, if not morphological evidence for sinistralism in techniques of oystercatchers for attacking bivalves, this is not reflected in the distribution of attacks on limpets by African Black Oystercatchers (Table 15).

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Part 3.3. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation.

S. Afr. J. Zool. (in press)

ABSTRACT

Diet of the African Black Oystercatcher Haemaotpus moquini was investigated throughout the species' range and emphasis was placed on understanding variations in diet related to time, place and sex of the bird. Correspondence analysis was chosen as the technique most appropriate for describing regional variation and it highlighted the dangers of generalizing about diet from limited data. African Black Oystercatchers prey mainly on mussels and limpets on the rocky shores of southern Africa. Principal prey species on the west coast are black mussels Choromytilus meridionalis and the limpets Patella granularis and P. argenvillei. The mussel Perna perna predominates in the diet on the south and southeast coasts. To account for 75 % of predicted prey species richness at islands, using collection of chick middens as the sampling technique, between 15 % and 27 % of the oystercatcher population (pairs) needs to be sampled. Less food is taken by night than by day, and at night the nocturnally active P. 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 intersexual competition for food by removing prey in differing relative proportions, males taking a greater proportion of limpets and whelks, and females a greater proportion of polychaetes and small unshelled items. Diet separation is a function of bill dimorphism and habitat complexity. Small prey items generally are not selected, and prey size selection is consistent within prey species and between localities.

INTRODUCTION

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 (Part 1.2). The species' techniques of feeding on certain rocky shore invertebrates have been described (Part 3.2) but its diet on rocky shores has been described only at 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 (Part 1.2) where the intertidal zone is characterized by tropical and subtropical invertebrates (Stephenson, 1948).

Few quantitative assessments of oystercatcher diet have been made in areas where more than one species of prey is involved. 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 *et al.*, 1979). Diet of African Black Oystercatchers on a sandy shore in Algoa Bay has been described from two stomach samples (McLachlan *et al.*, 1980)

This study has five principal objectives: to quantify diet of African Black Oystercatchers on rocky shores; to describe variations in the diet within and between geographical regions and specific localities; to investigate whether any temporal variations in diet exist; to determine whether there are within-pair (i.e. intersexual) differences in diet, and to consider prey size selection and its predictability between localities. Assessment is made of the value of correspondence analysis in this type of diet study.

In addition to describing sources of variation in African Black Oystercatcher diet, this paper aims to identify problems and pitfalls of generalization and resulting errors that frequently arise in diet studies, which have often been treated in a somewhat cavalier and generalized manner.

METHODS

When African Black Oystercatchers feed chicks, piles of emptied mollusc shells (middens) 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 (Fig. 13). No collections were made in Transkei, the extreme easterly limit of the breeding range (Part 1.2). 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 rarely were found at middens. To check the validity of analysing variations in diet based solely on the mollusc component, direct observations of feeding were made at Marcus Island (33 03S, 17 58E), southwestern 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* in the lower intertidal and by the limpet *Patella granularis* in the upper

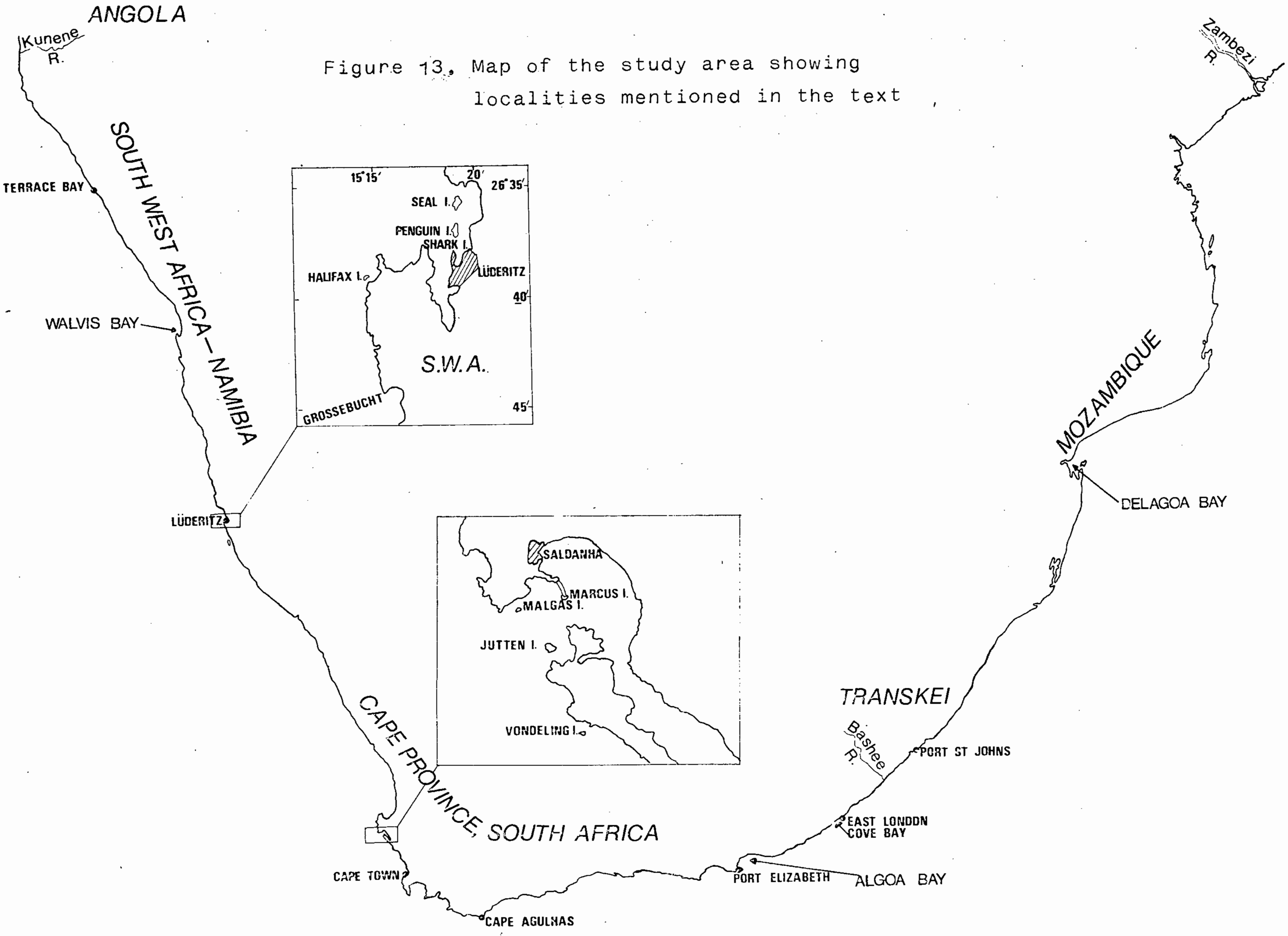


Figure 13. Map of the study area showing localities mentioned in the text

intertidal. Pair 2 defended a territory dominated by black mussels Choromytilus meridionalis in the lower intertidal and by P. granularis in the upper intertidal. Adults of both pairs were individually colour ringed and had been sexed at capture by cloacal examination (Part 1.2). Diet was recorded for both members of a pair during the same observation periods. Observations were made from a hide and prey were identified at the moment of capture using a 25x 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 diet. 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 results have 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 prey populations is meaningless in terms of demonstrating selection (Part 3.4). Size preferences of mussels during the breeding season (Perna perna fed to chicks on the southeast coast) and during the nonbreeding season (C. meridionalis preyed on by adults on the west coast) were assessed.

A technique analagous to the species-area curve, substituting "number of pairs of birds" for "area" was used to predict the probable number of mollusc species occurring in the diet at four islands if the entire oystercatcher population was sampled. To improve the fit of the data, data pairs were cumulated randomly three times.

A novel approach to the analysis of diet was adopted, namely correspondence analysis. Correspondence analysis (Benzecri, 1973), also known as reciprocal averaging (Hill, 1973, 1974) and dual scaling (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 a more thorough discussion of correspondence analysis see Greenacre (1978) or Greenacre and Underhill (1982).

The graphical displays produced by correspondence analysis may be thought of as a "photograph" of the data (a projection into two dimensions of a "cloud" of data points in multidimensional space) taken at the angle which minimizes misrepresentation of the data. Correspondence analysis simultaneously displays both the variables and object points; consequently there are two clouds of data points; one representing the objects (middens) and the other the variables (attributes) (prey species), respectively the rows and columns of the data matrix. The two clouds are in a state of balance with one another, an equilibrium described mathematically by the transition formulae (Appendix 1). 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 which are plotted close to the origin 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: 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. This allows analysis of more subtle variations within the majority of the data.

Graphical displays produced by the correspondence analysis are supplemented by a series of tables which determine the distortion in the "photograph" as a whole and which further break down the distortion of each point. These tables show how accurately the correspondence analysis algorithm is able to project the cloud of data points into two dimensions (Appendix 1).

RESULTS

Geographical Variation in Diet

The mollusc component of African Black Oystercatcher diet throughout its range comprised mainly mussels and limpets (Table 16). At sites in Namibia, where mussels are scarce or absent (pers. obs.), 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).

Table 16. Frequency occurrence (%) of 31 mollusc species in African Black Oystercatcher middens.

LOCALITY	PREY SPECIES															
	Choromytilus meridionalis	Perna perna	Aulacomya ater	Donax serra	Venerupis corrugatus	Haliotis spadicea	Fissurella mutabilis	F. natalensis	Helcion pectunculus	Cellana capensis	Patella cochlear	P. compressa	P. granularis	P.argenvillei	P. barbara	P. miniata
NAMIBIA																
Seal Is.	6.0	0.3	9.4										31.2	51.0		0.7
Shark Is.			1.7										89.7			
Halifax Is.													58.0	40.1		0.4
Grossebucht													9.1	88.3		
Possession Is.	0.7		5.0				T		T			0.1	45.2	47.5	0.1	0.3
SW CAPE																
Jutten Is.	11.4	0.2	54.6	T‡							0.3	T	25.9	3.4	T	T
Malgas Is.	34.0	2.7	19.6		0.1				T		0.3		35.7	5.8		T
Saldanha	56.5		37.6	5.9												
Vondeling Is.	37.9	1.4	14.3	0.4					T		11.0		23.5	9.8		T
S & SE COAST																
Robberg		35.0									55.2		3.6	4.4	0.9	
St. Croix Is.*		90.4				T	0.1				1.0		7.2	T	0.9	0.1
Cove Rock		70.9		1.0				1.8		4.7	4.2		1.4	5.1	T	
% Sites where species recorded	50.0	58.3	58.3	33.3	8.3	8.3	16.7	8.3	25.0	8.3	50.0	16.7	91.7	83.3	41.7	66.7

* data from Randall and Randall (1982)

‡ T = trace (<0.05%)

Table 16. Continued.

LOCALITY	P. concolor	P. longicosta	P. granatina	P. oculus	Siphonaria aspera	S. capensis	Turbo sarmaticus	Oxystele sinensis	O. variegata	Burnupena catarrhacta	B. lagenaria	Nucella cingulata	N. squamosa	Thais capensis	N. dubia	Sample size	Number of species
NAMIBIA																	
Seal Is.			1.3									0.1				695	8
Shark Is.			6.9							1.7						58	4
Halifax Is.			1.1							0.4						262	5
Grossebucht			1.3						1.3							143	4
Possession Is.			0.7							0.3						5 394	11
SW CAPE																	
Jutten Is.			0.3							T		0.2	T			18 901	15
Malgas Is.			0.7						0.5	0.2		0.1				6 597	13
Saldanha																69	3
Vondeling Is.			0.9						0.6	0.1		T				3 850	14
S & SE COAST																	
Robberg						0.4									0.4	223	5
St. Croix Is.*		T		0.1							T				0.1	3 102	13
Cove Rock	0.2	6.2		4.3	T		T	0.2						0.2		1 403	15
% Sites where species recorded	8.3	16.7	66.7	41.7	8.3	16.7	8.3	8.3	25.0	50.0	8.3	33.3	8.3	8.3	16.7	40 697	31

In the southwestern Cape, the mussels *Choromytilus meridionalis* and *Aulacomya ater* formed a large proportion of the diet along with the limpet *P. granularis*. *Patella argenvillei*, *P. cochlear* and *P. granatina* regularly were recorded (Table 16). Prey species richness in the southwestern Cape was greater than in Namibia with 17 species recorded, and up to 15 species at one locality.

Diet on the south and southeast coasts was dominated (up to 90.4 %) by brown mussels *Perna perna*. At Robberg, (34 06S, 23 24E) *Patella cochlear* formed 55.2 % of the diet by numbers: this species was preyed on regularly at all south coast sites. *Patella granularis* and *P. barbara* also were recorded on the south coast, making it the region with the greatest prey species richness: a maximum of 15 species was recorded at one site. Sand mussels *Donax serra* were recorded at some sites, these were 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 17).

The first two factors (Appendix 2) of the correspondence analysis are shown for all middens in Figure 14. "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.

The first four factors accounted for 93 % of the inertia (Appendix 2, Table 18): an additional 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 were treated as supplementary points and as such did not influence the overall analysis: prey species which are

Table 17. Recorded prey species of the African Black Oystercatcher, (1 = important prey species, 2 = regular, 3 = uncommon, 4 = rare, ^{x} = 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. (3)^{x}

Class AMPHINEURA (chitons)
  Acanthochiton garnoti (3)

Class PELECYPODA (bivalves)
  Choromytilus meridionalis (1)
  Perna perna (1)
  Aulacomya ater (1)
  Venerupis corrugatus (4)
  Donax serra (1)^{x}
  D. sordidus (1)^{x}
  Macoma spp. (3)^{x}

Class GASTROPODA (gastropods)
  Haliotis spadicea (4)
  Fissurella natalensis (2)
  F. mutabilis (4)
  Crepidula porcellana (4)
  Helcion pectunculus (4)
  H. pruinosus (4)
  Cellana capensis (2)
  Patella cochlear (1)
  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)

Figure 14. A correspondence analysis plot of 96 African Black Oystercatcher middens showing the relationship of individual middens to component prey species. (See Appendix 2 for interpretation rules.)

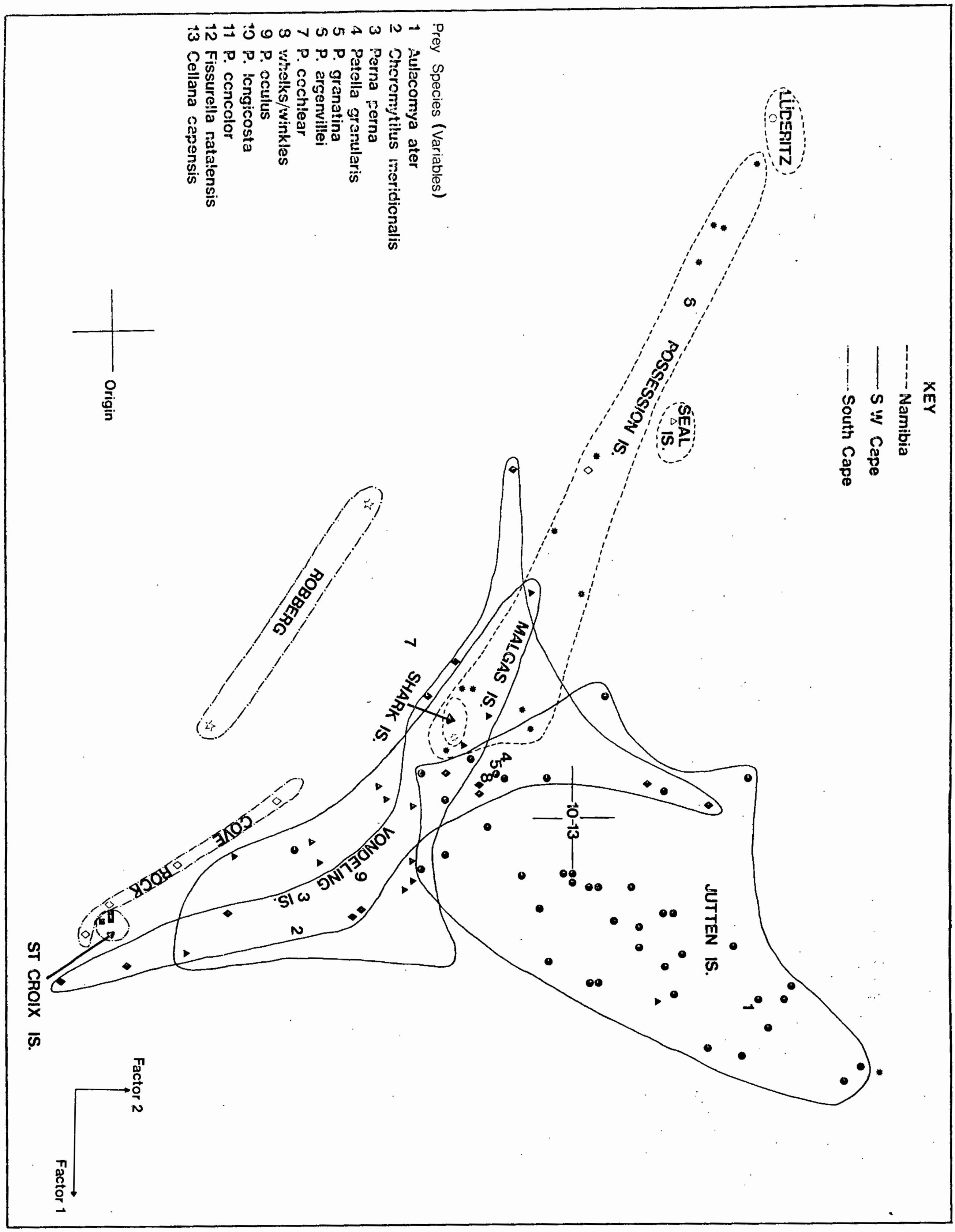


Table 18. The correspondence analysis of the prey species of African Black Oystercatchers showing the co-ordinates and the relative and absolute contributions to inertia of each of the prey species on the first four factors. See appendix 2 for details of interpretation.

Prey species				Factor 1			Factor 2		
	Mass	Quality	Inertia	Coord-inate	Relative contrib-ution	Absolute contrib-ution	Coord-inate	Relative contrib-ution	Absolute contrib-ution
Aulacomya ater	0.336	1.000	0.194	0.617	0.526	0.263	0.573	0.454	0.378
Choromytilus meridionalis	0.180	0.995	0.173	0.347	0.100	0.045	-0.871	0.633	0.469
Perna perna	0.009	0.309	0.021	0.253	0.023	0.001	-0.841	0.251	0.023
Patella granularis	0.323	0.998	0.119	-0.189	0.078	0.024	-0.208	0.094	0.048
P. granatina	0.006	0.158	0.014	-0.154	0.008	0.000	-0.236	0.018	0.001
P. argenvillei	0.127	1.000	0.297	-1.589	0.863	0.659	0.392	0.053	0.067
P. cochlear	0.015	0.999	0.138	-0.535	0.025	0.009	-0.487	0.021	0.012
Whelks/winkles	0.005	0.013	0.036	-0.110	0.001	0.000	-0.250	0.006	0.001
P. oculus	0.000	0.011	0.008	0.192	0.001	0.000	-0.647	0.009	0.000

Table 18. contd.

Prey species	Factor 3			Factor 4		
	Coordinate	Relative contribution	Absolute contribution	Coordinate	Relative contribution	Absolute contribution
Aulacomya ater	0.108	0.016	0.018	0.049	0.003	0.005
Choromytilus meridionalis	0.559	0.261	0.265	-0.031	0.001	0.001
Perna perna	0.315	0.035	0.004	0.022	0.000	0.000
Patella granularis	-0.591	0.760	0.529	-0.174	0.066	0.058
P. granatina	-0.651	0.140	0.012	0.076	0.002	0.000
P. argenvillei	0.494	0.084	0.145	-0.036	0.000	0.001
P. cochlear	-0.608	0.032	0.026	3.259	0.922	0.935
Whelks/winkles	0.181	0.003	0.001	0.129	0.002	0.000
P. oculus	-0.185	0.001	0.000	0.175	0.001	0.000

unique to these sites appear at the origin in Fig. 14).

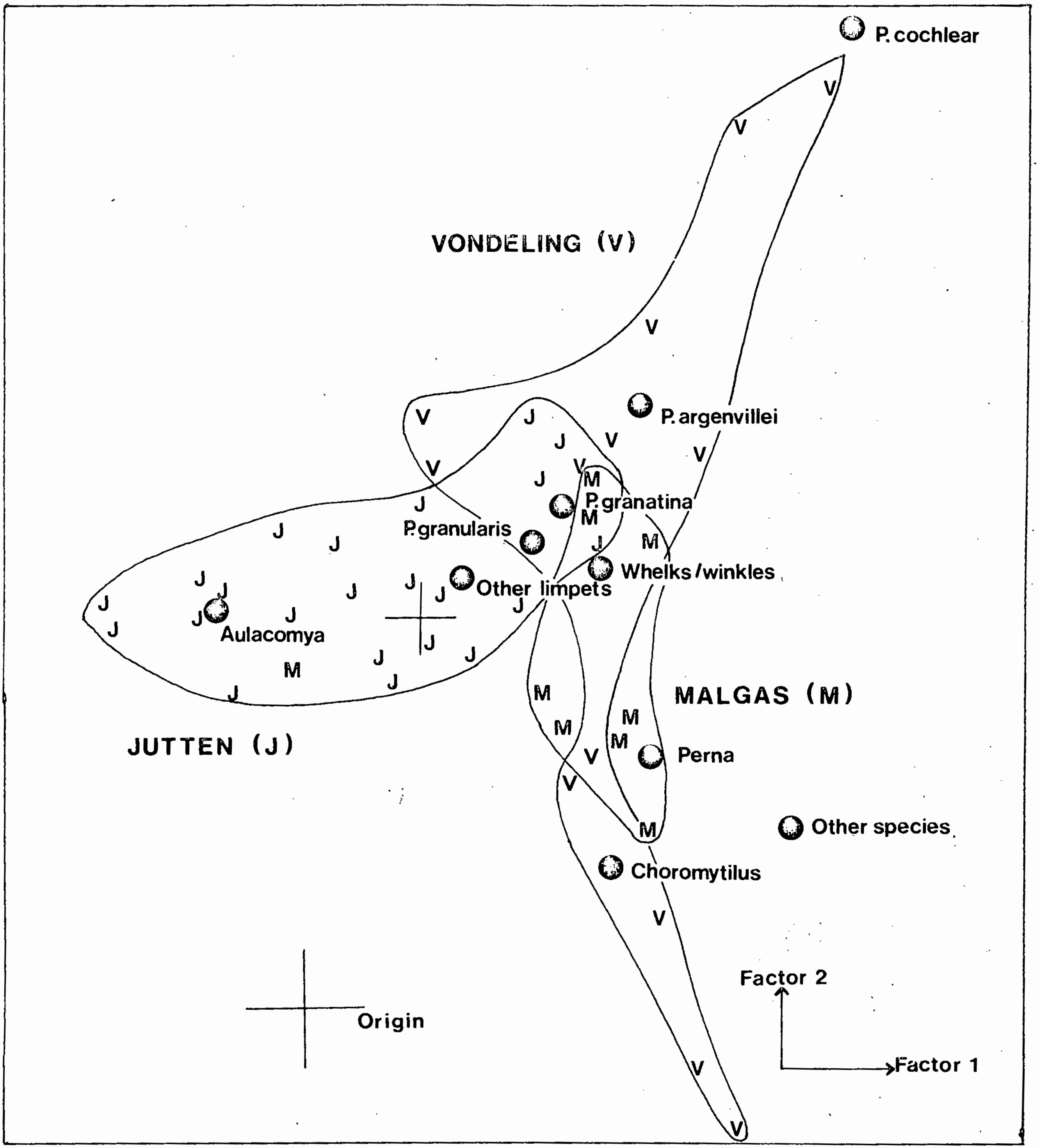
Factor 1 distinguished those middens with a high proportion of P. argenvillei, primarily Namibian middens, from those with a high proportion of A. ater (southwestern Cape). This distinction accounted for 92 % of the inertia in the first factor (Table 18), and for 36 % of the total inertia. Factor 2 separated those middens with a high proportion of A. ater from those with high proportions of C. meridionalis and P. 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 P. 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 southwestern Cape Islands (Jutten, Malgas and Vondeling) were considered separately (1980 data only) (Fig. 15), 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 of the data from the other two islands. Birds from Vondeling Island exhibited the greatest within island variability in diet in the southwestern Cape.

In summary, P. argenvillei was highly characteristic of Namibia, and A. ater was highly characteristic of Jutten Island. Patella

Figure 15. A comparison of African Black Oystercatcher midden composition at three islands in the southwestern Cape



granularis, *P. granatina* and whelks and winkles emerged close to the origin: the proportions of these species in the diet were 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 significant geographic variation in diet on the west coast.

At Jutten Island, chosen because most middens were sampled there, there was a positive correlation between the number of shells (N') and prey species richness (SR) in an individual midden (Fig. 16). $SR = 0.68 \ln N' + 2.15$ ($r = 0.57$; $p<0.001$). Prey species richness (SR) was closely related to the number of middens sampled (N) at individual islands:

Malgas Is. (1980 + 1981) $SR = 2.99 \ln N + 6.43$ ($r = 0.84$)
Vondeling (1980 + 1981) $SR = 2.58 \ln N + 7.07$ ($r = 0.82$)
Possession (1981) $SR = 2.15 \ln N + 5.49$ ($r = 0.73$)
Jutten (1980) $SR = 2.28 \ln N + 5.45$ ($r = 0.90$)
Jutten (1981) $SR = 2.70 \ln N + 5.40$ ($r = 0.90$)

The species richness for all the sites combined was a function of the number of middens sampled (N). $SR = 2.27 \ln N - 6.26$ ($r = 0.92$; $p<0.001$). Similarly, when individual curves were projected to the point at which every pair of birds on the island would have been sampled (assuming every pair had a chick), the predicted number of mollusc species in the diet fell between 16 and 18 species in all instances regardless of island size or oystercatcher population (Fig. 17). Oystercatcher populations were taken from Part 1.2. In order to account for 75 % of the predicted prey species richness, between 15 % and 27 % of an island population needed to be sampled, and to account for 90 %,

Figure 16. The relationship between the number of prey species per midden and the number of prey items per midden at Jutten Island

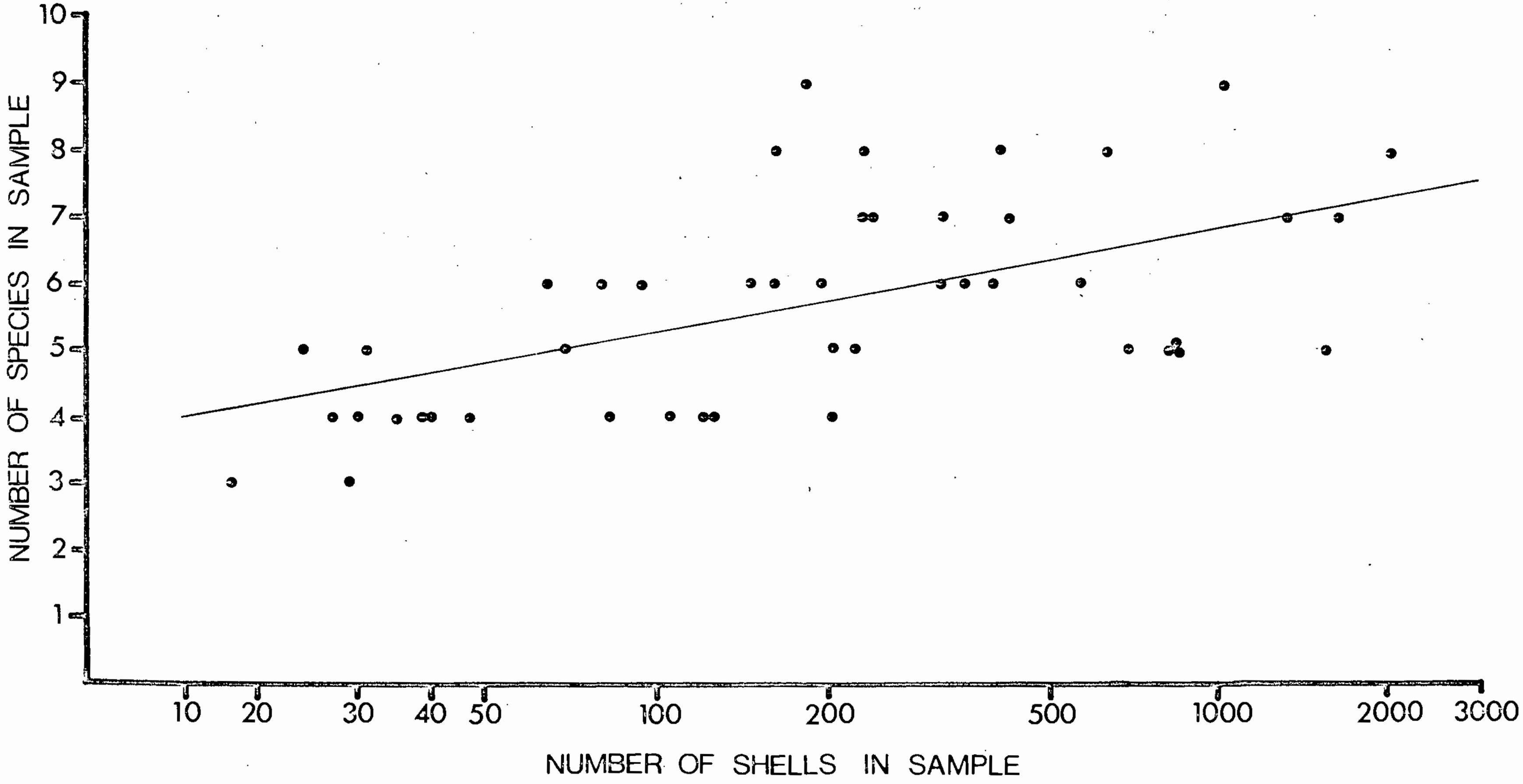
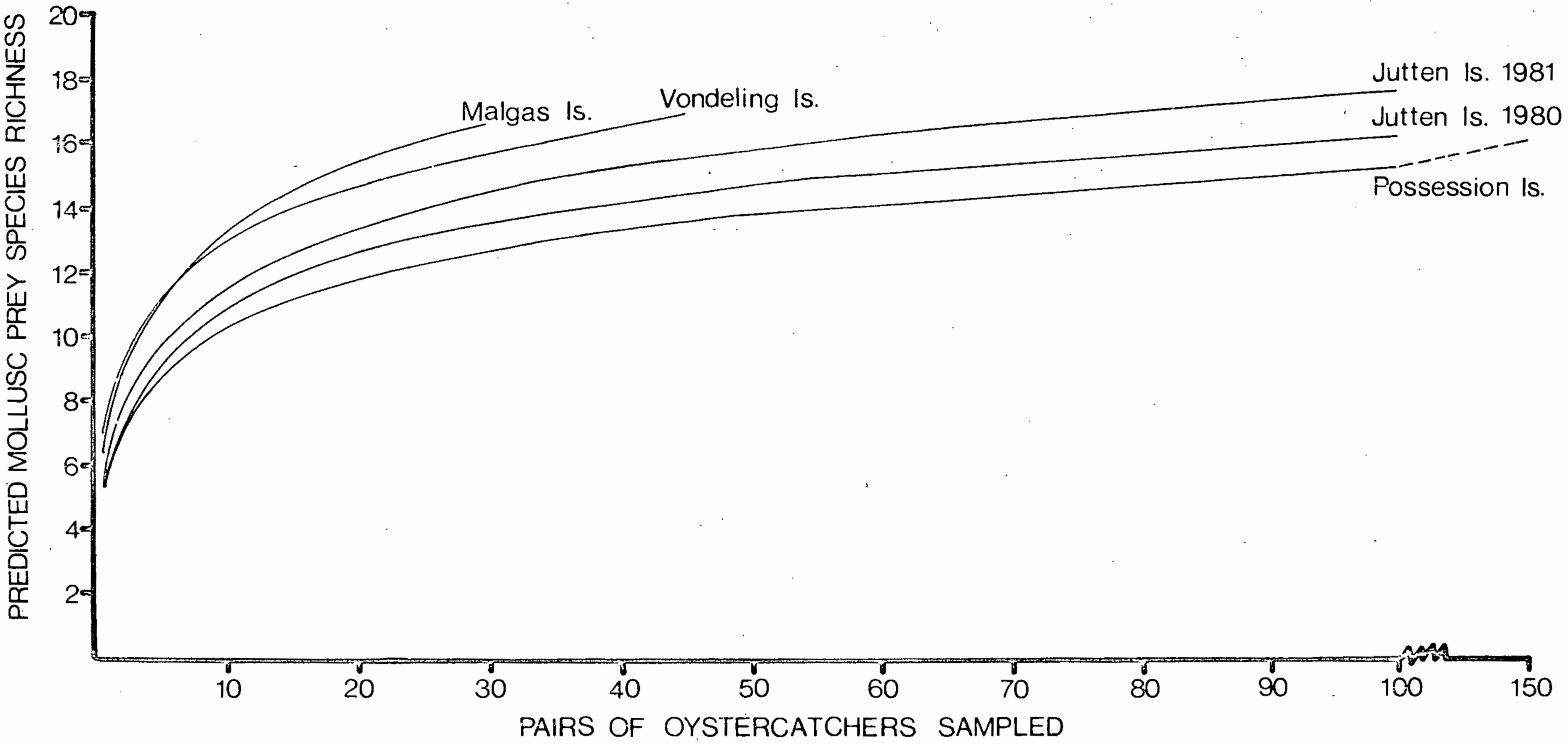


Figure 17. The relationship of prey species richness to sampling intensity for African Black Oystercatcher middens at four west coast islands



between 47 % and 60 % (Table 19).

Temporal Variation in Diet

Comparing diet at Jutten Island between two years, 1980 and 1981, correspondence analysis indicated some interesting differences (Fig. 18). In 1980, _A. ater_ and _P. cochlear_ influenced overall diet composition, whilst in 1981, _C. meridionalis_, _P. argenvillei_ and _P. perna_ were important differentiating species. The overall proportions (%) of these species recorded at middens in 1980 and 1981 were: _P. argenvillei_ 3.4, 3.6; _A. ater_ 54.6, 41.3; _P. cochlear_ 0.3, 0.7; _C. meridionalis_ 11.43, 20.07 and _P. perna_ 0.20, 1.47, respectively.

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 20). 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 (X^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 36.1 % 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 21, 22). At Jutten Island (Table 21) there was a higher frequency of mussels and correspondingly lower frequency of limpets in middens of older chicks (X^2 = 362.3; d.f. = 6; $p<0.001$). This pattern was repeated at Malgas Island (Table 22) where sequential collections were made at one midden (X^2 = 114.7; d.f. = 10; $p<0.001$).

Table 19. Sample sizes (number of pairs) expressed as a percentage of island oystercatcher populations, necessary to account for 50 %, 75 % and 90 % of the predicted mollusc prey species in the diet at four localities

Island	Oystercatcher population (No. pairs)	Predicted prey species richness	Sample sizes needed to account for fractions of predicted prey species richness					
			50 %		75 %		90 %	
			N	%	N	%	N	%
Malagas	30	16.6	2	7	8	27	18	60
Vondeling	45	16.9	2	4	9	20	24	53
Possession	150	16.3	4	3	23	15	71	47
Jutten (1980)	100	16.0	4	4	18	18	50	50
(1981)	100	17.8	4	4	20	20	52	52

Figure 18. A correspondence analysis plot comparing the diet of African Black Oystercatchers at Jutten Island in 1980 and 1981

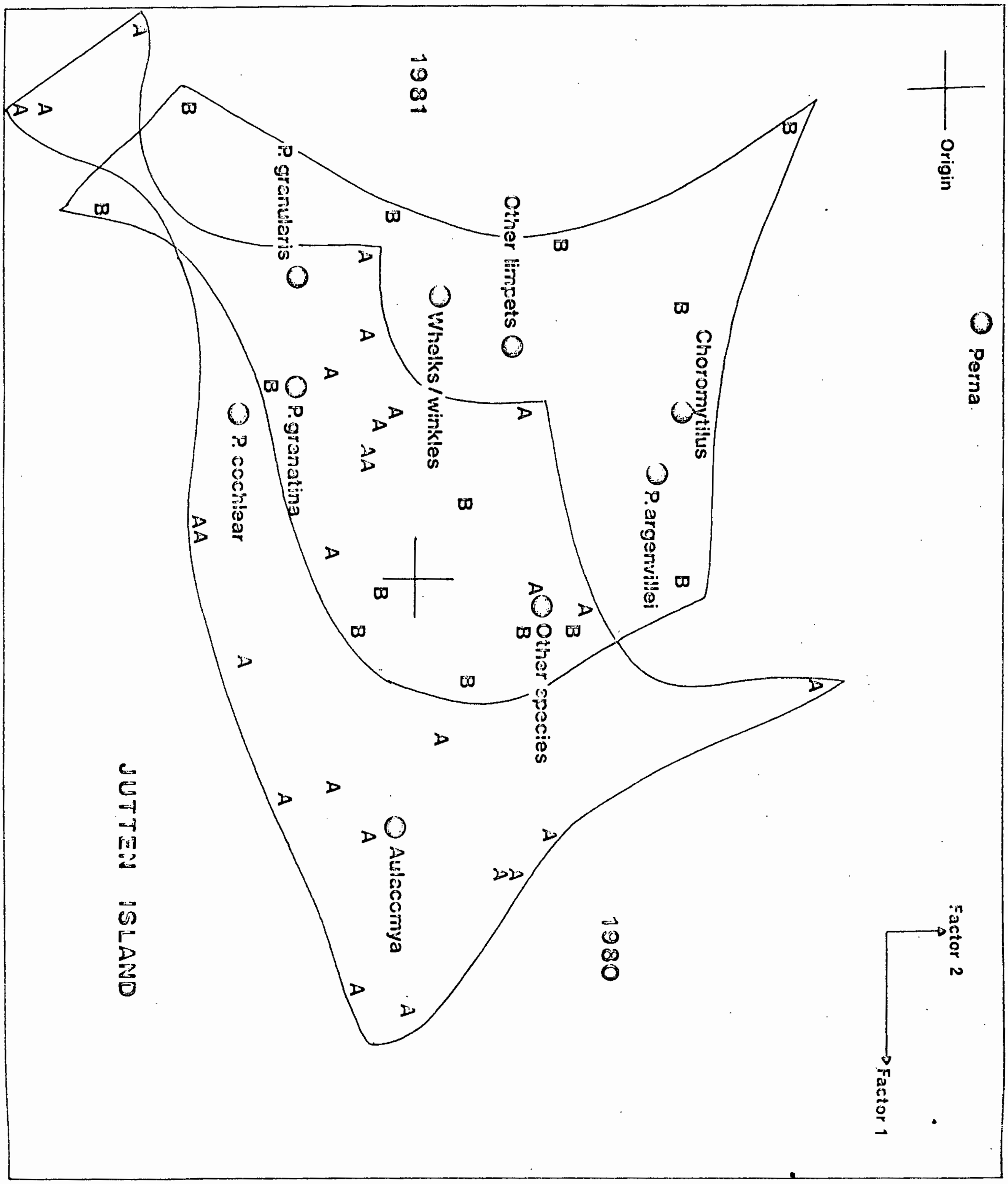


Table 20. Numbers and relative proportions (%) (in parentheses) of prey species in feeding piles at Jutten Island by day and night.

	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 21. 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

Table 22. 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	33.5	1.7	31.1	6.4	0.9	1474

Sex-related Differences in Diet

A total of 620 prey items was recorded for Pair 1 (male 328, female 292) (Table 23). The differences in diet between male and female were highly significant ($X^2 = 303.73$; 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, and polychaetes and small unshelled items favoured by the female. The female also removed a smaller proportion of A. ater than the male ($X^2 = 12.98$; d.f. = 1; $p<0.001$).

Pair 2 preyed on a smaller suite of species, reflecting the lower invertebrate diversity in beds of C. meridionalis (Hockey & Branch, ms.), but there was still a significant difference in diet ($X^2 = 35.19$; 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 numbers and the pair in the C. meridionalis dominated area took 95.9 % molluscs.

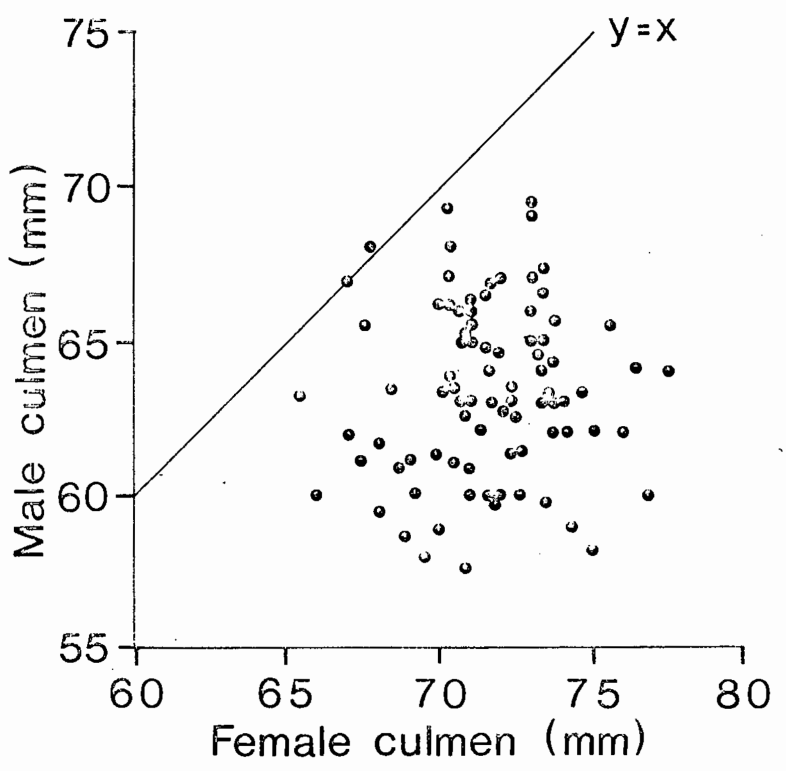
Bill shape in African Black Oystercatchers is sexually dimorphic, with females having longer and more pointed bills on average, but with some sexual overlap (Part 2.1). Within pairs however, the bill of the female is almost invariably longer than that of the male (Fig. 19).

Prey Size Selection

Table 23. Percentage frequency analysis of diet by sex in two pairs of African Black Oystercatchers. (See text for descriptions of foraging areas.)

Pair 1 Prey species	Male %	Female %	Sample N
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	197
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

Figure 19. The relationship between male and female exposed culmen lengths of 85 pairs of African Black Oystercatchers from rocky environments in the southwestern Cape



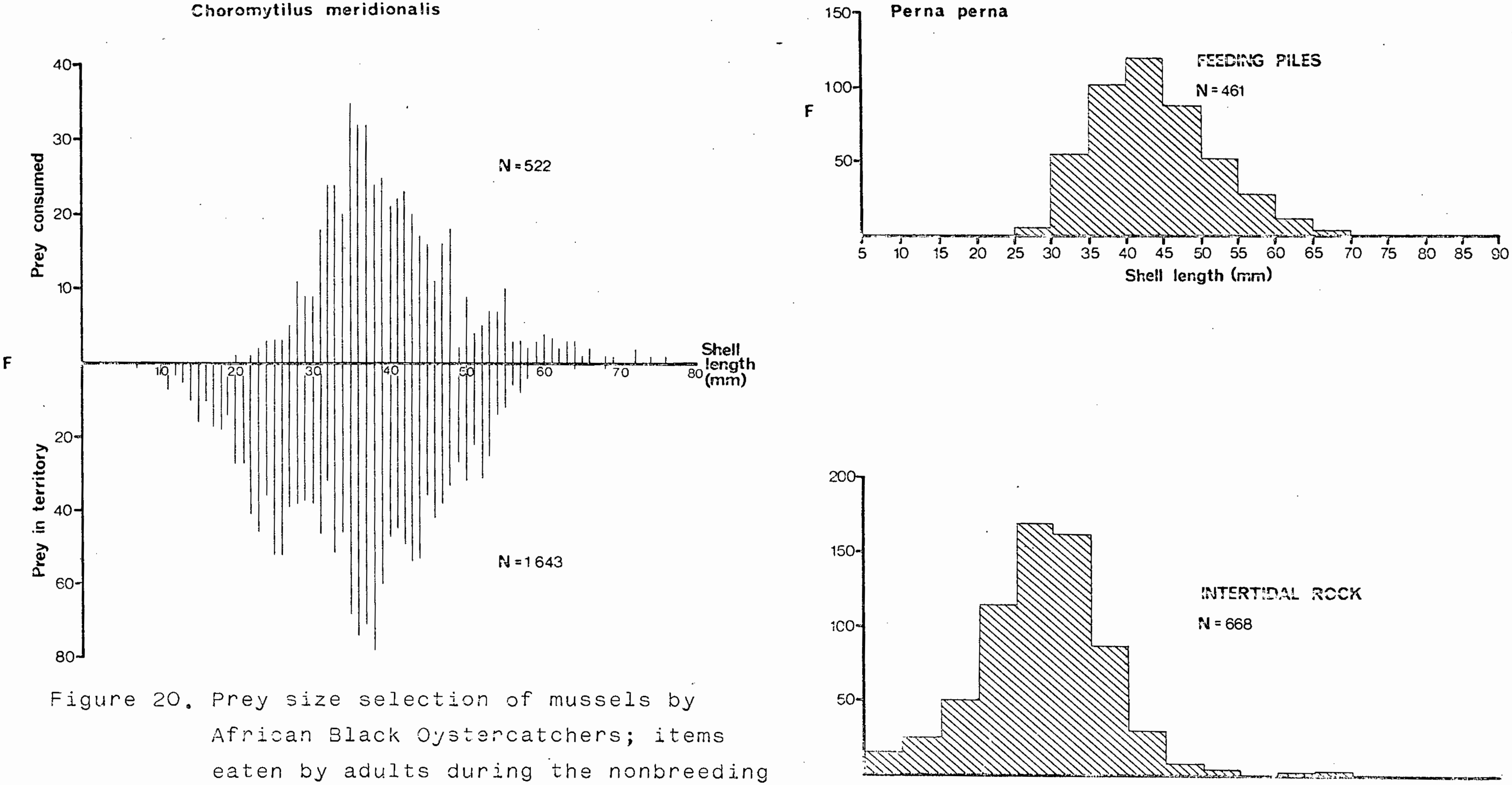
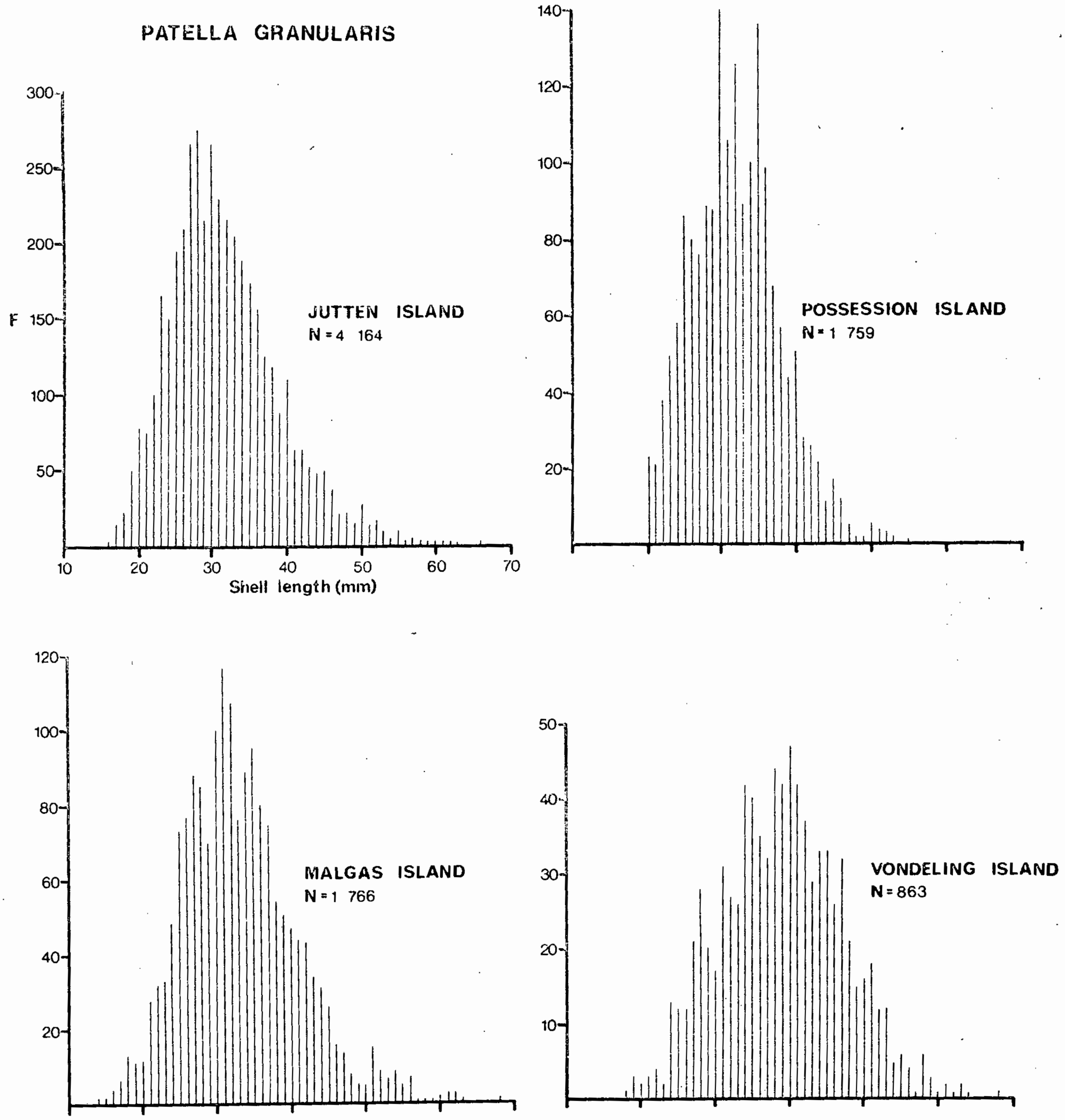


Figure 20. Prey size selection of mussels by African Black Oystercatchers; items eaten by adults during the nonbreeding season (C. meridionalis), and items fed to the chicks (P. perna)

Figure 21. Patella granularis: size selection by African Black Oystercatchers at four west coast islands



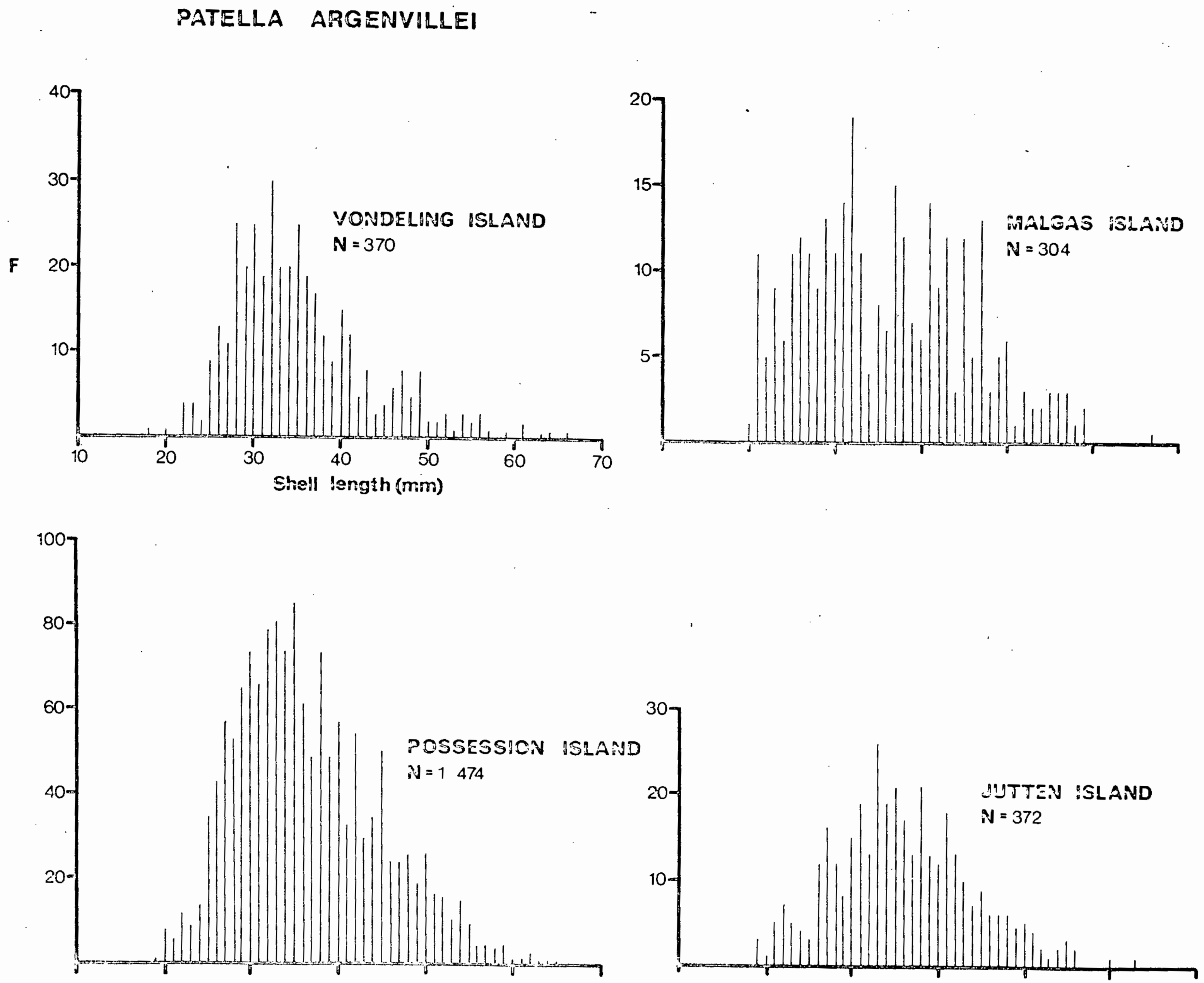
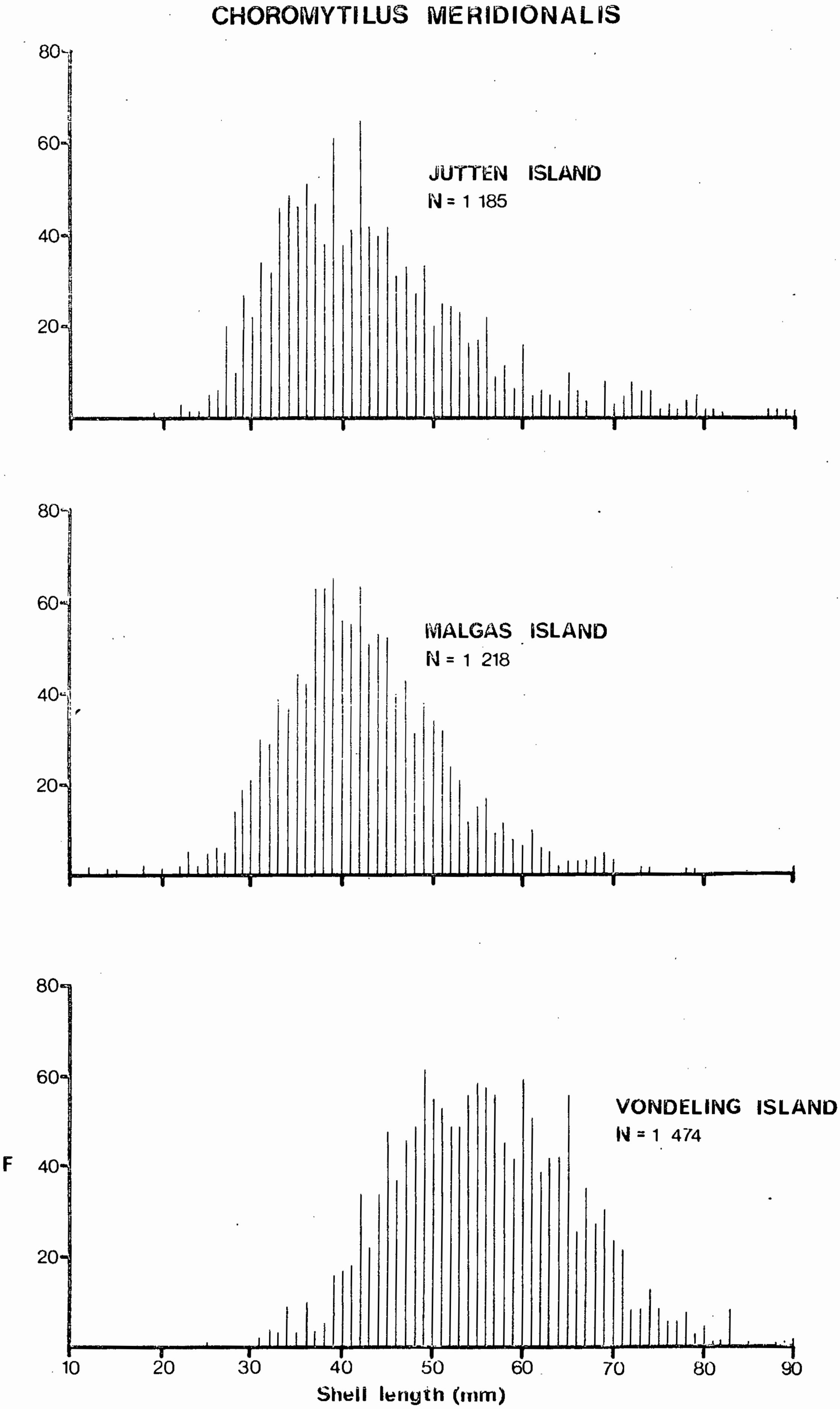


Figure 22. Patella argenvillei: size selection by African Black Oystercatchers at four west coast islands

Figure 23. Choromytilus meridionalis: size selection by African Black Oystercatchers at three islands in the southwestern Cape



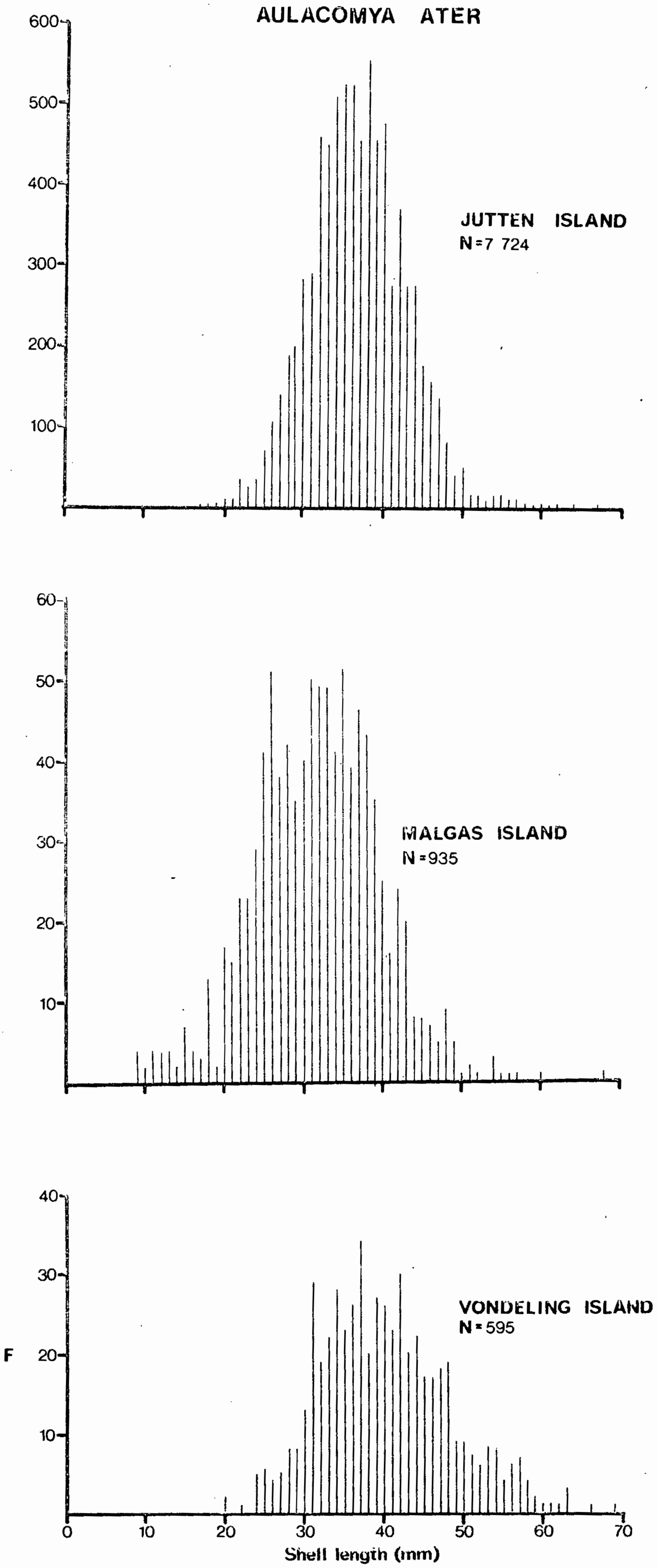


Figure 24. Aulacomya ater: size selection by African Black Oystercatchers at three islands in the southwestern Cape

African Black Oystercatchers avoid selecting small mussels both when feeding chicks ($X^2 = 592.6$; d.f.= 25; $p<0.001$) and during the nonbreeding season ($X^2 = 180.6$; d.f.= 29; $p<0.001$) (Fig. 20). The size classes of limpets P. granularis and P. argenvillei preyed on was consistent between localities (Figs. 21, 22). Most P. granularis eaten were between 25 mm and 40 mm in length.

During 1980, larger C. meridionalis were selected at Vondeling Island than at nearby Malgas and Jutten Islands (Fig. 23), but this trend was not evident in predation of the other abundant mussel, A. ater (Fig. 24).

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 mussels (29.4 %), limpets (44.3 %) 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 H. unicolor 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).

Studies of European Oystercatchers H. ostralegus in Britain, feeding in estuarine habitats, demonstrate a preference for mussels, cockles and nereid worms. Other gastropods (Littorina spp.), decapods, isopods, amphipods and other polychaetes are also eaten (Heppleston, 1971; Dare & Mercer, 1973).

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 prosobranch limpets and away from siphonarians (Randall & Randall, 1982). Data presented in this study therefore may be considered to reflect the relative abundance of prey species on a geographical basis. *Choromytilus meridionalis* and *A. ater* are clearly the dominant rocky shore bivalves on the west coast and *P. perna* is dominant in the south and east. *Patella granularis* and *P. argenvillei* become increasingly dominant in the west and north; *P. miniata* and *P. granatina* are evenly but relatively sparsely distributed along the west and south coasts.

The siphonarians (false limpets) *Siphonaria capensis* and *S. aspera* occur commonly throughout the study area (pers. obs.), though *S. aspera* is absent from Namibia (Day, 1974). However, they were consumed only at south coast sites, and then so infrequently as to be insignificant in the diet. Siphonarians adhere weakly to the rock and are easily detached, 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 (pers. obs.). No other intertidal predators are known to eat siphonarians (Cherry & Branch, ms.).

Although there is geographical variation in prey species taken by African Black Oystercatchers, the types of animals eaten are similar throughout the range. In the southwestern Cape, a greater degree of dietary overlap might have been expected at the three islands analysed (see Fig. 15). The islands lie within 12 km of one another, yet variability in the diet at Vondeling Island is clearly 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 easily located. 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 Variations 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 % (Fig. 18). 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* preys only on 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 (Part 4.2). 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 (Part 4.2). The increasing proportion of mussels brought to older chicks agrees with the findings of Hartwick (1976) for the American Black Oystercatcher.

Sex-related Variation in Diet

Sex-related differences in diet have not been reported in any other species of oystercatchers. All species of oystercatchers exhibit sexual dimorphism in bill dimensions, females having on average longer and more pointed bills than males (Part 2.1). The internal anatomy of the bill is the same in both sexes of *H. ostralegus* (Heppleston 1970), and 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 (Fig. 19) but it appears that this dimorphism performs an additional function in allowing efficient exploitation of resources within a territory by reducing intersexual competition. Although males and females take similar proportions of mussels, males, with their more robust, chizel-shaped bills favour limpets, and females select worms whose capture necessitates probing into mussel beds (Part 2.2). 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 take 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 birds per km. These densities do not allow acceptance of the hypothesis, but highest densities of birds were recorded at the two sites where A. ater is a dominant prey species, namely Marcus and Jutten Islands.

Prey Size Selection

Prey size selection is consistent within prey species and between localities. American Black Oystercatchers have been shown to select similar sized mussels from mussel beds with significantly different size distributions (Hartwick & Blaycock, 1979). During the nonbreeding season at Marcus Island, the modal size of C. meridionalis consumed 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 P. perna fed to chicks was considerably larger than the modal size of available mussels (Fig. 20). An analogous observation was made at Cleland Island where the 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 Oystercatchers select 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 24). 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).

Table 24. A comparison of the modal size classes of mussels and limpets depredated by three species of oystercatcher. (x = mean size)

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

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 longer term variation in diet. Males and females take prey species in differing proportions; chick diet is age dependent, and sizes of mussels eaten by adults during the nonbreeding season 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, territorial species, and probably other species, are important. 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 the technique has highlighted very clearly the dangers of generalizing about diet in a territorial species. It has also identified those prey species which form predictable and unpredictable proportions of the diet throughout the study area and may therefore be suitable for a geographical study of the impact of predation on populations of a particular prey species.

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Appendix 1. The algorithm for correspondence analysis

1. We are given an nxm data matrix $X = (x_{ij})$ with all x_{ij} positive. We assume $n \geqslant m$ (if not, transpose x to x^t). Thus in general we have m variables observed on n objects. (In the particular application described in this paper we have 13 variables (prey species) observed on 96 objects (oystercatcher middens)).

2. Compute a matrix P such that $P_{ij} = x_{ij} / \sum_{ij} x_{ij}$ thus the elements of P sum to one.

3. Compute $r = P1$, where 1 is an n-vector of ones. The n-vector r contains the row sums of P.

4. Compute $c = P^t 1$. The m-vector c contains the column sums of P.

5. Compute $Q = P - rc^t$. This describes the deviations of P from its "centre".

6. Compute $S = D_c^{-0.5} Q^T D_r^{-1} Q D_r^{-0.5}$. D_r and D_c are diagonal matrices with diagonal elements equal to the vectors r and c respectively.

7. Find the eigenstructure of S: $S = V D_\mu V^T$ where $V^T V = I$. $D_\mu = \mathrm{diag}\ (\mu r - \mu m)$ and $\mu_1 \mu_2 \geqslant \mu m$.

8. Compute $G = D_c^{-0.5} V D_\mu^{-0.5}$ and $F = D_r^{-1} Q D_c^{-0.5} V$. The rows of F and G contain coordinates for objects and variables respectively. The first two elements in each row can be used to provide plots in two dimensions.

9. It can also be shown that $G = D_c^{-1} P^t F D_\mu^{-1}$ and $F = D_r^{-1} P_{cr}$

D_{μ}^{-1} . These are the transition formulae and are important in the interpretation of correspondence analysis and the plotting of supplementary points.

10. The sum of the eigenvalues (i.e. $I = \sum_{i=1}^{m} \mu_i$) is defined to be the inertia of the matrix.

11. The proportion of the inertia which can be explained by the first P dimensions is: $\lambda = \sum_{i=1}^{P} \mu_i / \sum_{i=1}^{m} \mu_i$.

12. The inertia can be further decomposed. It can be shown that $d_{ik} = r_i f_{ik}^2$. This is the contribution of the ith object to the inertia of the kth dimension. The contribution of the jth variable to the inertia of the kth dimension is $c_j g_{jk}^2$. $A_{ik} = f_{ik}^2 / \sum_{i=1}^{m} f_{ik}^2$ is the relative contribution of the kth dimension to the inertia of the ith object, and $b_{jk} = g_{jk}^2 / \sum_{i=1} g_{jk}^2$ is the relative contribution of the kth dimension to the inertia of the jth variable.

For details of mathematical derivations of the quantities, and supplementary points, see Greenacre (1978).

Appendix 2. Correspondence analysis: interpretation rules for graphical displays

These rules are written in the context of the present application. To generalize them read "objects" for middens and "variables" for prey species.

1. The point occupied by any midden in the display represents the position of this midden in relation to all the middens and all the prey species.

2. Similarly, the point for any variable represents the balancing point for this prey species.

3. If points for two middens are close together, this means that the composition of prey species in these middens is similar. Conversely, if two points are far apart, their prey species composition is very different.

4. If points for two prey species are close, then these prey species tend to be co-present or co-absent in the middens. If points for prey species are far apart it follows that one of the prey species will tend to be absent when the other is present.

5. Proximity of points belonging to different clouds (i.e. proximity of middens to prey species) may not be interpreted directly in terms of distances.

6. The relationship between points belonging to different clouds is described by the transition formulae (Appendix 1). The final position of a midden is the point where the attraction of all the prey species is in equilibrium. This means that middens will be in the same general direction from the origin

as the prey species which determine them; e.g. the point for a midden with a high proportion of Aulacomya ater will be in the same general direction from the origin as the point for the variable Aulacomya ater.

Interpretation rules for tables

A pair of tables, one for the row points, one for the column points, present a detailed breakdown of the precision with which the points are represented in the graphical displays. Table 18 is the table for the column points (i.e. the variables) and each column of this table is discussed below. The first three columns of the table present general information on the points; there are then three columns of information for each of the factors interpreted (four factors are considered here).

Column 1. The mass of a column indicates the proportion of the total table accounted for by that column. Thus 33.6 % of all prey items were Aulacomya ater. This is the weighting attached to the variable in the correspondence analysis.

Column 2. The quality of a variable indicates how well the factors interpreted represent the data for that variable. Thus, all (100 %) information on A. ater is represented, but only 30.9 % of the information on Perna perna. The quality is in fact the sum of the values in the "relative contribution" columns for that variable; i.e. for A. ater, 1.000 = 0.526 + 0.454 + 0.016 + 0.003, and for P. perna, 0.309 = 0.023 + 0.251 + 0.035 + 0.000.

Column 3. Inertia is a concept borrowed from applied mathematics, defined as mass x distance^2. Inertia here is defined as the mass of the point (column 1) multiplied by the square of the "distance" of the point from the origin. (The distance is a weighted Euclidean distance in the multidimensional space in which the graphical display "photographs" are taken). Inertia is expressed as a proportion of the total inertia (Appendix 1). Thus A. ater accounts for 19.4 % of the total inertia, while Patella argenvillei accounts for 29.7 %, even though it has a much smaller mass. This means that the latter is farther from the origin, and therefore plays a more important rôle in determining the positioning of the factors. An important part of the interpretation of the correspondence analysis tables is to locate those variables which account for a large proportion of the total inertia.

Columns 4, 7, 10 and 13, the coordinates of the variables for plotting the graphical displays. The largest and smallest values in each column usually are of particular interest as the factor may generally be interpreted as a contrast between those with large positive (>0.5) and large negative (<-0.5) values.

Columns 5, 8, 11 and 14, the relative contributions. Each point makes a contribution to the total inertia. This is further subdivided into the contribution of the point on each factor. The relative contribution indicates the percentage of a point's contribution to the total inertia that is accounted for by each factor. Thus 52.6 % of the inertia of A. ater is accounted for by the first factor, and a further 45.4 % by the second factor.

Columns 6, 9, 12 and 15, the absolute contributions. Each factor makes a contribution to the total inertia. This is further subdivided into the contribution of each point to the inertia of the factor. The absolute contribution indicates the proportion of the point's contribution to the inertia of the factor. Thus, factor 1 accounted for 36 % of the total inertia: 26.3 % of this was due to *A. ater*, and 4.5 % due to *C. meridionalis* etc.

To summarize, in interpreting the factors, attention is focussed on those variables (here species) which make large contributions to the inertia.

Part 3.4. Oystercatchers and limpets: impact and implications. A preliminary assessment.

Ardea (in press)

INTRODUCTION

The African Black Oystercatcher Haematopus moquini is endemic to the coasts of southern Africa. Its densities at rocky offshore seabird islands may be as high as 75 birds per km of coast, whereas densities on the mainland are rarely as high as five birds per km (Part 1.2).

The rocky shores of southern Africa support a high diversity of limpets (Branch, 1971) and these are important prey items for oystercatchers (Part 3.3). In the mid- and upper intertidal on the west coast of southern Africa, the limpet Patella granularis is dominant (Branch 1971) and this is the most important limpet species in the diet of African Black Oystercatchers (Part 3.3).

Edwards et al. (1982) recently have stressed the potential importance of mobile predators in modifying intertidal community structure. The idea that avian predators may influence the structure of limpet populations is not new (Giesel, 1970; Hartwick, 1981), but the implications of such predation in terms of intertidal community dynamics have not been investigated. In the southwestern Cape, South Africa, there are some very obvious differences in community structure of the upper intertidal at different sites. At offshore islands there are large beds of macroalgae, primarily Ulva, Enteromorpha and Porphyra, growing in and above the upper balanoid zone. On mainland shores, however, these algal beds are absent or much reduced in size, and are replaced by populations of Patella granularis and Littorina africana knysnaensis. In view of the great differences in predation pressure on P. granularis in the upper balanoid zone between islands and mainland, it seemed possible that this considerable (and consistent) difference in community structure may be related, at least in part, to the presence of oystercatchers.

This paper sets out to examine this hypothesis and to consider the mechanism by which island limpet populations are maintained in the presence of heavy predation.

STUDY AREA AND METHODS

Data were collected at two exposed, offshore islands in the southwestern Cape; Jutten Island (33 05S, 17 57E) and Malgas Island (33 03S, 17 55E), and at one equally exposed locality on the mainland, at Cape Columbine (32 49S, 17 50E). At each locality, distinction was made between sheltered sites and those exposed to strong wave action - this distinction was relative rather than absolute. Densities of P. granularis were determined using transects 1 m wide and extending down the shore from the upper to the lower limit of the species' occurrence. The size structures of the limpet populations at each locality were investigated separately in sites that were respectively accessible, and inaccessible, to oystercatchers. Inaccessibility generally was defined as a function of the slope of the rock, but was, of necessity, ultimately determined in the field, as some limpets on vertical rock faces are accessible to oystercatchers if there is a nearby ledge where the bird can stand. Size structures were sampled at a number of sites within each category of exposed/sheltered and accessible/inaccessible. Sampling was done systematically within a grid of quadrats, each of area 0.063 m^2, until each sample contained at least 50 animals.

The effect of limpet density on macroalgal growth was assessed using quadrats of 0.125 m^2. Usng these quadrats, transects were run from the lower to the upper limit of occurrence of *P. granularis* on the shore. within each quadrat, the numbers of *P. granularis* and of the smaller false limpet *Siphonaria capensis* were recorded, as was the percentage cover of macroalgae. In addition, as a check of the extent to which limpets alone were responsible for limiting macroalgal growth, limpet exclusion plots were set up in the upper balanoid zone. High copper-content anti-fouling paint was used to exclude limpets from areas of 0.25.m^2, all limpets inside the plots being removed beforehand. Maximum size of *P. granularis* at Cape Columbine and Jutten Island was taken as the mean of the five largest animals located.

RESULTS

Limpet densities

Mean limpet density per m of shore ranged from 134 on the sheltered side of Jutten Island to 650 on the exposed coast at Cape Columbine (Table 25). At all localities, densities were higher in exposed situations, and, similarly, were consistently higher in the lower half of the upper balanoid zone (Table 25). Densities per square m were fairly consistent in the upper half of the upper balanoid zone where most macroalgal growth occurred (Table 25), except for the exposed shore at Jutten Island which had a marginally lower density than the exposed shore at Cape Columbine ($t=2.21$, $p<0.05$). Using Bonferroni's t statistic, this difference was not significant ($p > 0.05$). Comparing limpet densities between sites that were accessible and inaccessible to oystercatchers, far more dramatic differences were found (Table 26). At islands, regardless of the degree of

TABLE 25. DENSITIES (MEAN AND STANDARD DEVIATION) OF PATELLA GRANULARIS PER M OF SHORE, AND PER M^2 OF SHORE IN THE UPPER AND LOWER HALVES OF THE UPPER BALANOID ZONE, AT TWO ISLANDS AND ONE MAINLAND LOCALITY IN THE SOUTHWESTERN CAPE, SOUTH AFRICA. SAMPLE SIZES IN PARENTHESES

Locality and site	Density of *Patella granularis* per m of shore	per m^2 of shore upper 50 %	lower 50 %
Jutten Island			
exposed shore	336 ± 189 (6)	13 ± 8	74 ± 23
sheltered shore	134 ± 50 (6)	23 ± 9	60 ± 17
Malgas Island			
exposed shore	547 ± 206 (9)	36 ± 36	147 ± 90
sheltered shore	360 ± 233 (4)	22 ± 5	96 ± 44
Cape Columbine			
exposed shore	650 ± 305 (7)	34 ± 29	189 ± 75
sheltered shore	410 ± 150 (5)	20 ± 12	140 ± 33

TABLE 26. DENSITIES (MEAN AND STANDARD DEVIATION) OF *PATELLA GRANULARIS* PER M^2 RELATED TO EXPOSURE AND ACCESSIBILITY TO AFRICAN BLACK OYSTERCATCHERS AT TWO ISLANDS AND ONE MAINLAND LOCALITY IN THE SOUTHWESTERN CAPE, SOUTH AFRICA

Locality	Exposed shore		Sheltered shore	
	Accessible	Inaccessible	Accessible	Inaccessible
Jutten Island	77 ± 30	224 ± 170	96 ± 83	185 ± 117
Malgas Island	68 ± 32	344 ± 221	87 ± 87	124 ± 74
Cape Columbine	196 ± 119	174 ± 106	130 ± 38	209 ± 126

exposure, densities of limpets in accessible sites were always much lower than in corresponding inaccessible areas. The only statistically significant within-site and exposure difference in density was on the exposed shore at Malgas Island ($t=3.51$, $p<0.01$); but if the independent tests are combined (Winer, 1971, pp 49-50), accessible sites had much lower densities of limpets than inaccessible sites at islands ($X^2 =33.08$, 8 d.f., $p<0.001$). In contrast, at the mainland site, the differences in density related to accessibility were not significant ($X^2=5.66$ d.f.=4, $p>0.05$).

Limpet density vs macroalgal cover

Macroalgal cover and the density of P. granularis were inversely related (Fig. 25). Macroalgal cover decreased most rapidly as the density of P. granularis increased from 0 to 30 limpets per m^2. Density of the smaller pulmonate limpet Siphonaria capensis also was inversely correlated with algal cover, but to a lesser extent (Fig. 25). Interestingly, at a given density of P. granularis, algal cover often was greater in the presence of between 10 and 30 S. capensis per m^2 than in their absence (Fig. 25). This is probably an artifact of two operative factors. Firstly, the size of the sampling quadrat was smaller than the foraging range of P. granularis, and secondly, sampling was done during the day, when P. granularis, being primarily nocturnal foragers (Branch 1971), return to their "home scars". Siphonaria capensis has a smaller foraging range than P. granularis and it is probable that, in areas where S. capensis density is relatively high, P. granularis recorded as being present in the quadrat during the day were actually feeding outside the quadrat area at night, and therefore their local effect on macroalgae was underestimated.

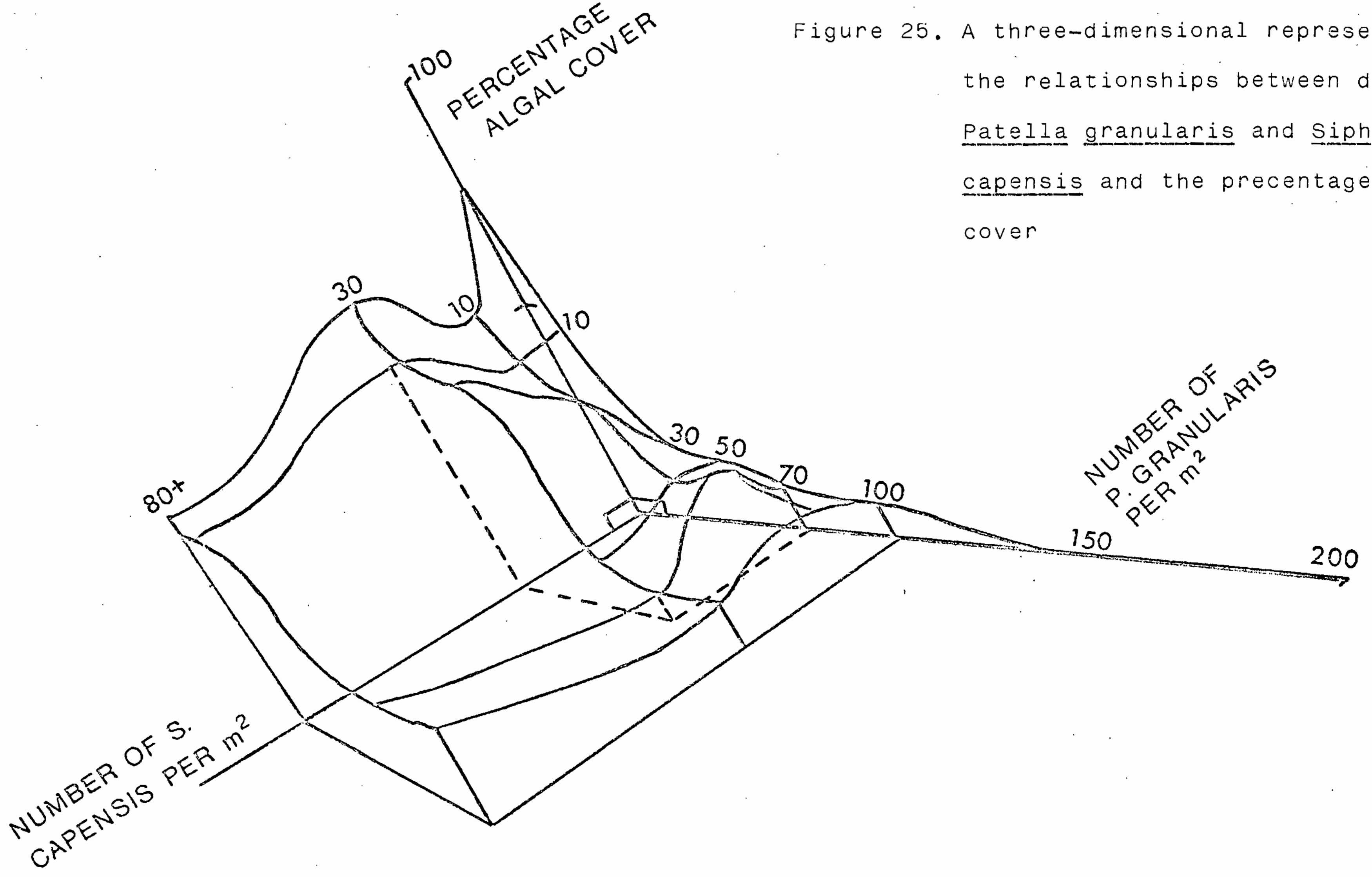


Figure 25. A three-dimensional representation of the relationships between densities of _Patella granularis_ and _Siphonaria capensis_ and the precentage of macroalgal cover

In the experimental plots where limpets were artificially excluded, macroalgal growth was rapid, and beds of Enteromorpha, Ulva and Porphyra became established within two weeks. In control areas on the surrounding rock face where limpets continued to graze, the surface remained bare and macroalgal growth was totally suppressed.

These two sets of observations support the hypothesis that limpets are the prime controllers of macroalgal growth through their grazing action on the algal sporelings.

Limpet population size structures

The size structures of those sections of the island limpet populations respectively accessible and inaccessible to oystercatchers were very different (Fig. 26). At accessible sites there was clear depletion of those size categories preferentially preyed on by oystercatchers. On the mainland, however, the size structures of limpets in accessible and inaccessible sites were identical (Fig 27). At islands, an appreciable proportion of the limpets had grown to the point where they were effectively free from oystercatcher predation by virtue of their size. No limpets at Cape Columbine fell into this category.

Production and reproduction in island and mainland limpet populations

In populations of P. granularis, maximum size is a reliable indicator of growth rate (Branch, 1974b). The estimated relationships of size (maximum length in mm) to annual increment at Jutten Island and Cape Columbine are shown in Figure 28. These relationships were derived from the maximum recorded size of P. granularis at these sites, coupled with the mean slope relating annual increment to initial length for seven different

Figure 26. The size structures of Patella granularis populations in four habitats at Jutten Island. The dotted line represents the size classes consumed by African Black Oystercatchers (data from Part 3.3)

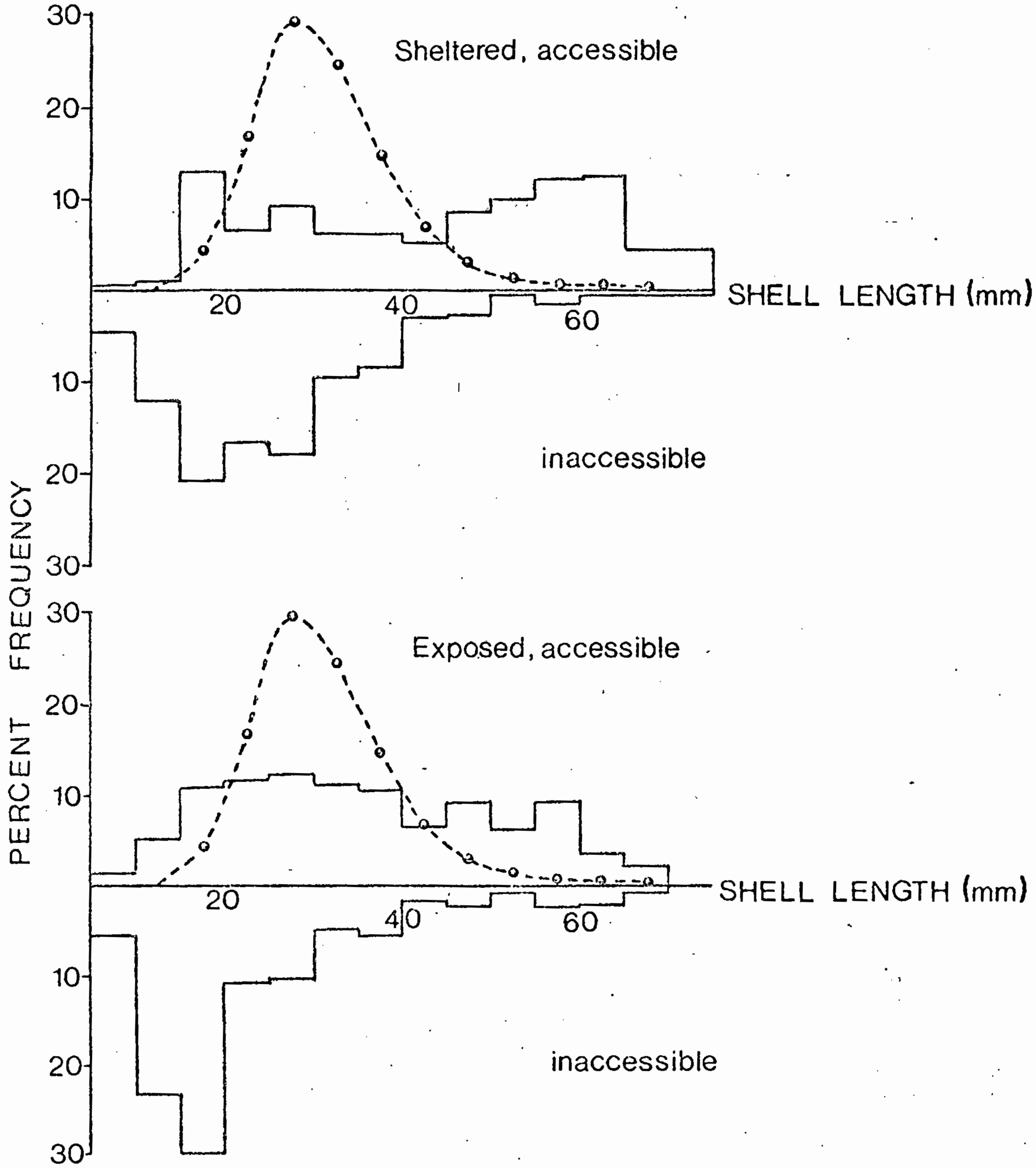
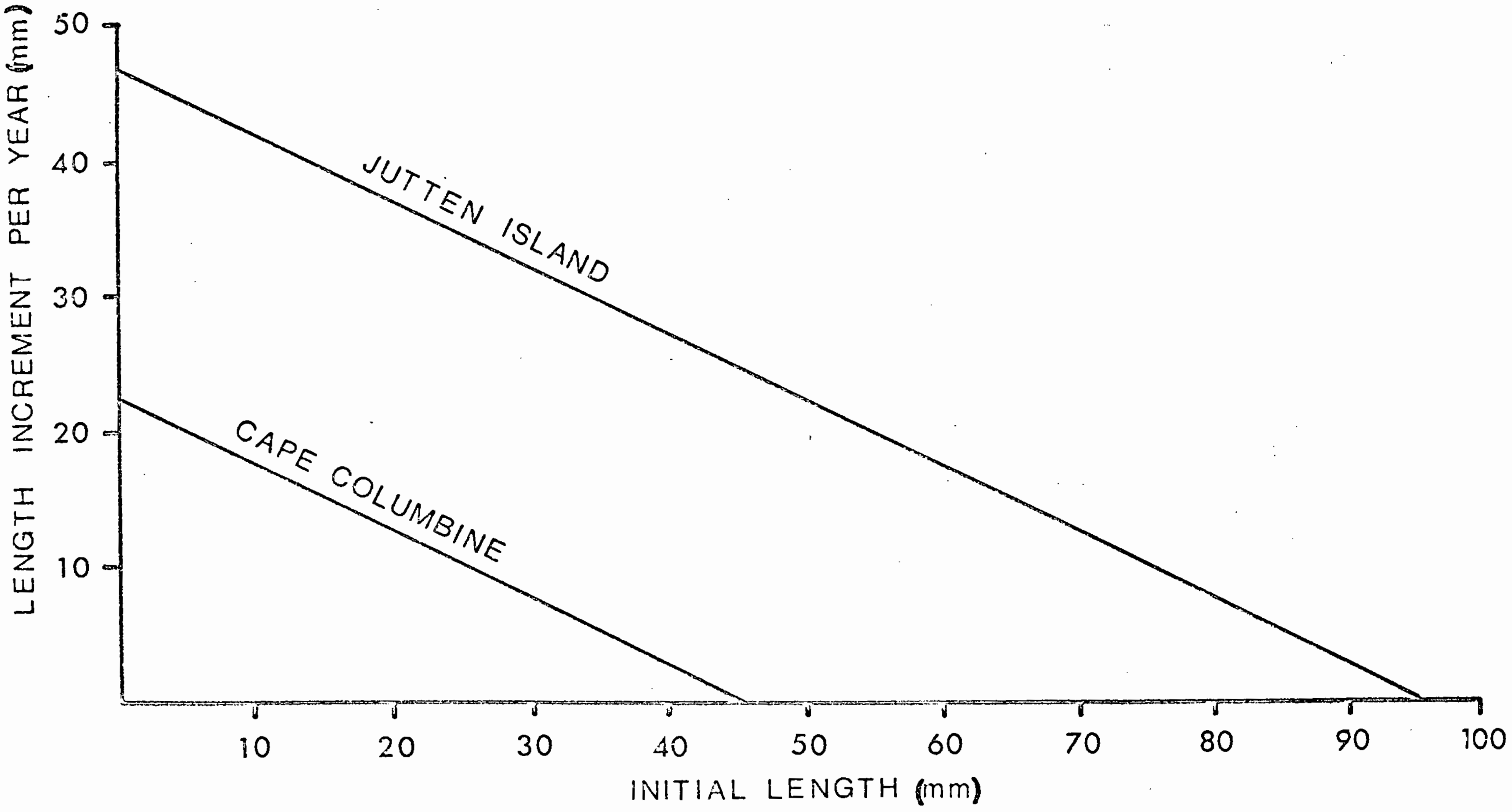


Figure 28. Growth rates of _Patella granularis_ at Jutten Island and Cape Columbine



habitats in the southwestern Cape (Branch, 1974b). Length of _P. granularis_ (L, in mm) is closely related to somatic weight (S) (wet g): $L = 1.86 \times 10^{-5} S^{3.19}$ ($r = 0.98$, $p<0.001$). Using this regression the somatic mass of limpets could be calculated from size composition and density of the population. The somatic biomass of _P. granularis_ at Jutten Island ranged from 198 g per m^2 in exposed inaccessible sites, to 388 g per m^2 in sheltered accessible sites (Table 27). The range at Cape Columbine, where size distributions were consistent between sites (Fig. 26), was between 51 g and 92 g per m^2. Somatic production due to growth (Pg) was much greater at Jutten Island than at Cape Columbine, with maximum somatic production : biomass ratios of 6.95, compared with a maximum of 3.40 at Cape Columbine.

To obtain an estimate of gamete production, regressions of gonad weight on somatic weight were calculated (from data in Branch, 1974b) for pre- and post-spawning _P. granularis_ (not all gametic material is released at spawning) (Fig. 29). The resulting regression of female gamete release (Gf) on somatic weight (S) was $Gf = 0.67S - 0.44$. Female limpets comprise approximately 41 % of the population (Branch, 1974b). Female gamete release per m^2 ranged between 48 g and 96 g at Jutten Island and between 4 g and 9 g at Cape Columbine (Table 28). The proportion of female gamete release accounted for by limpets larger than those preyed on by oystercatchers at Jutten Island ranged from 43 % (sheltered, inaccessible) to 86 % (sheltered, accessible), with an overall mean of 66 % ± 18 % S.D. On the mainland no limpets grew large enough to be free from potential predation.

DISCUSSION

TABLE 27. SOMATIC BIOMASS (WET G PER M^2), SOMATIC PRODUCTION (WET G PER M^2 PER YEAR) AND SOMATIC PRODUCTION: BIOMASS RATIOS FOR POPULATIONS OF <u>PATELLA GRANULARIS</u> IN FOUR HABITATS AT JUTTEN ISLAND AND CAPE COLUMBINE

Habitat	Jutten Island			Cape Columbine		
	Biomass (wet g per m^2)	Production (wet g per m^2)	P/B	Biomass (wet g per m^2)	Production (wet g per m^2)	P/B
Sheltered, accessible	387.9	743.6	1.92	51.6	163.4	3.16
Sheltered, inaccessible	257.6	1779.2	6.90	81.1	280.9	3.23
Exposed, accessible	282.3	880.9	3.12	90.6	249.3	2.75
Exposed, inaccessible	198.0	1375.1	6.95	62.5	212.8	3.40

Figure 29. Regressions of female gonad weight (wet g) for *Patella granularis* before and after gamete release (data from Branch 1974b)

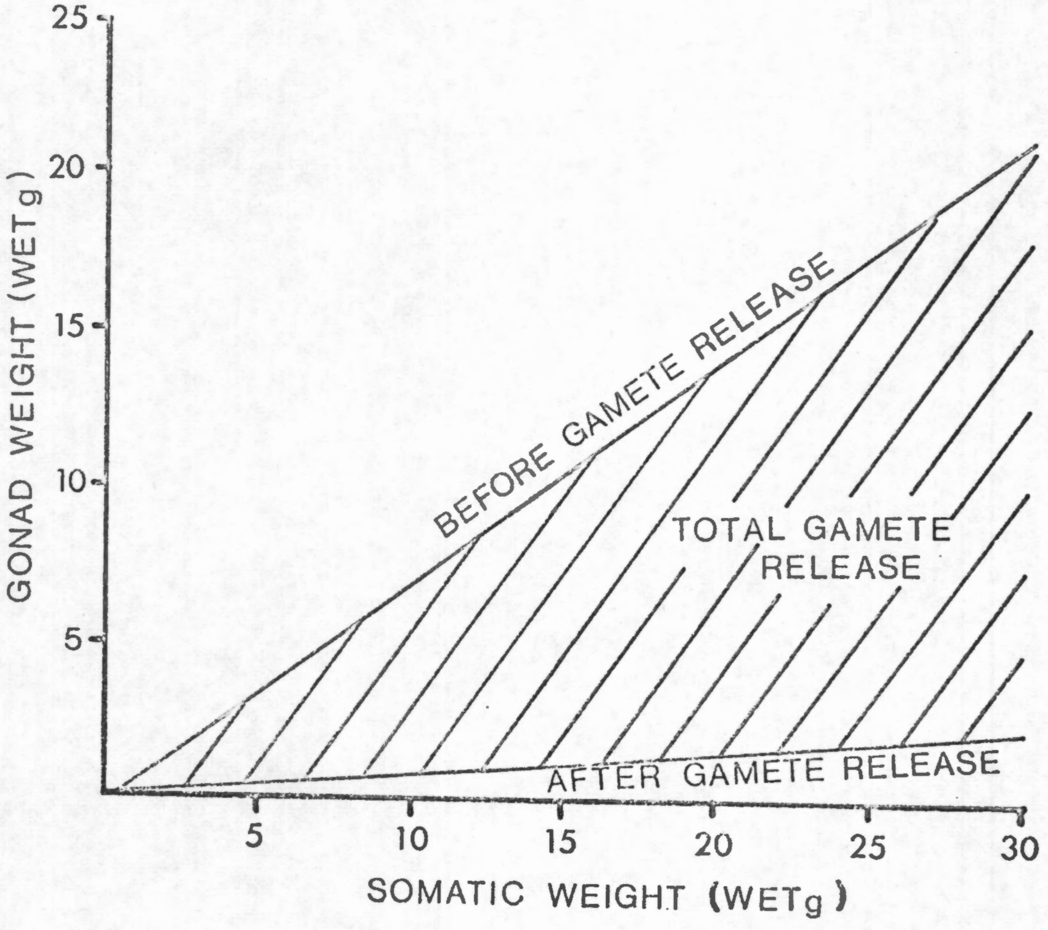


TABLE 28. ANNUAL FEMALE GAMETE RELEASE BY *PATELLA GRANULARIS* (WET G PER M^2) IN FOUR HABITATS AT JUTTEN ISLAND AND CAPE COLUMBINE

Habitat	Jutten Island	Cape Columbine
Sheltered, accessible	95.6	3.8
Sheltered, inaccessible	48.4	6.1
Exposed, accessible	64.8	8.8
Exposed, inaccessible	39.8	4.7

There is much more macroalgal growth in the upper intertidal zone at offshore seabird islands than on the nearby mainland in the southwestern Cape, South Africa, and it appears that algal growth is largely limited by the grazing action of the limpet Patella granularis. At Jutten Island, this species provides 29 % of the energy requirements of the African Black Oystercatcher (calculated from data in Part 3.3) and, based on a knowledge of the oystercatcher population of c. 100 pairs (Part 1.2), the energy requirements of oystercatchers (Part 4.4) and the size classes of limpets consumed by oystercatchers (Part 3.3) this corresponds to an annual removal by birds of approximately 2.8 x 10^6 limpets, from a coastline of c. 2.5 km. Despite this heavy predation pressure, overall limpet densities (per m of shore) are not as radically different between islands and the mainland as might be expected if a similar population mechanism was operating. On a more local scale however, oystercatchers radically influence the density and size structures of limpets accessible to predation at islands. Such size-selective predation results in an unusually high proportion of large limpets in the population. On the mainland, in contrast, limpets do not grow as large or as fast as at islands, presumably due to slower algal growth rates (P. Britz, unpubl. data), and never grow so large as to be unavailable to oystercatchers. It has been demonstrated that seabird colonies can locally enhance the nutrient status of adjacent water masses (Golovkin, 1963, 1967, in press; Golovkin & Garkavaya, 1975; Golovkin & Gurevich, 1973; Golovkin & Pozdnyakova, 1966; Golovkin & Zelickman, 1965; Zelickman & Golovkin, 1972; P. Britz, unpubl. data) and it seems likely that guano runoff and duano dust deposition enhances algal growth rates at the islands studied here. The virtual absence of macroalgae at Cape Columbine implies that the growth rate and population biomass of P. granularis here are limited by food supply, and the existing population controls algal growth at the sporeling stage. This is definitely not the case in the upper region of the P. granularis zone at islands, and the limpet population here probably is limited by predation.

The mechanism for limpet population maintenance at islands is dependent on the relatively high proportion of large limpets in the population. These "predator-free" limpets account for a large proportion of the total gamete release, which is itself much greater than on the mainland. This high gamete release is guaranteed regardless of predation pressure by birds on the population as a whole. Limpet larvae are planktonic and marine during the first few days of life, and thus not all island-spawned larvae will contribute to recruitment at any one island locality. However, some recruitment at islands may result from larvae that have been spawned elsewhere. A study by Hartwick (1981) on the effect of predation by the American Black Oystercatcher H. bachmani on the limpet Collisella digitalis suggests that immunity to predation is achieved either by being in an inaccessible site or by "hiding" among algae in the lower intertidal, but not by size. In this situation, population maintenance of limpets (which never grow large enough to escape predators by virtue of size alone) may be linked to the seasonality of predation.

The observations of limpets at islands in the western Cape, where they are subjected to heavy natural predation, have implications for intertidal management in areas, such as Transkei, where limpet populations are heavily exploited by man for food. Human consumption of P. concolor and Cellana capensis in Transkei has led to major reductions in the density of limpet populations and the maximum size of individuals (Branch, 1975). The reduction in size, and consequently gonad output, and the resulting need to collect even more animals for food, leads to a vicious circle and ever decreasing limpet populations. Casual observations along the Transkei coast suggest that, when limpet populations are severely reduced in this manner, ground cover of barnacles increases. This leads to a depauperate shore, not only in terms of invertebrate and bird diversity, but also in terms of the viability of the shore as an economic resource.

One noteworthy effect of the extensive macroalgal growth at islands in the southwestern Cape is to improve the quality of the foraging environment for smaller wading birds. Macroalgal beds support large populations of small crustaceans and gastropods (Hockey & Branch ms.) which provide food for birds such as Turnstones _Arenaria interpres_ and Curlew Sandpipers _Calidris ferruginea_. Densities of Turnstones and Curlew Sandpipers (birds per km of coast) at islands respectively are approximately four times and two times the densities on mainland rocky shores (unpubl. data). Thus, rather than competition determining the structure of the intertidal wader community, predation of limpets by oystercatchers actually facilitates the feeding of smaller wading birds.

It would be naïve to assume that algal growth rate and predation _per se_ are the only factors influencing limpet density and population size structure. Desiccation is an important factor in controlling limpet distribution and behaviour (Branch, 1971), and the question of differential growth rates in different local situations has not been considered. Extensive macroalgal growth does not occur on vertical rock faces (pers. obs.) and this may be related to faster throughflow of nutrients and/or lower insolation. In Australia, low on the shore, algal growth is too fast for limpets (Cellana) to control the sporelings, consequently macroalgae develop. Furthermore, the limpets starve to death in the presence of macroalgal beds since they rely on sporelings for food (Underwood, 1980; Underwood & Jernakoff, 1981). The implications of high shore macroalgae for limpet populations in the south western Cape need to be investigated further.

Whilst it is undeniable that predation by oystercatchers has a major effect on populations of P. granularis in areas where the predation pressure is high, investigations are now underway to try and elucidate the relative impact of other biotic and abiotic influences and processes on community structure in the upper intertidal.

SUMMARY

At rocky seabird islands in the southwestern Cape, South Africa, the upper intertidal zone often is characterized by large beds of macroalgae which are conspicuously absent at nearby mainland localities. These beds are believed to be, at least in part, a product of heavy predation by African Black Oystercatchers Haematopus moquini on the upper shore limpet Patella granularis. Densities of limpets in sites accessible to oystercatchers are reduced to the point where the limpets no longer control algal growth by grazing algal sporelings. Both limpet and algal growth rates are faster at islands than on the mainland, and the establishment of high shore macroalgal beds, with their associated invertebrate fauna, facilitates the feeding of smaller wading

birds. By virtue of their faster growth rate and larger size, an appreciable proportion of the limpets at islands are too large for oystercatchers to prey on. Since gamete output in limpets is proportional to size, it is these large limpets (which account for up to 86 % of the total gamete release) that provide the key to population maintenance in the presence of high predation pressure. Recruitment to the limpet population is thus guaranteed, regardless of predation pressure on smaller size classes. These observations have important implications for the conservation-management of intertidal invertebrate resources.

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Part 3.5. Do oystercatchers influence limpet shell shape?

Veliger 26:139-141

INTRODUCTION

Variations in predation pressure on gastropod populations by fish and invertebrates can lead to regional adaptations in shell morphology (Ebling _et al_., 1964; Vermeij, 1978; Palmer, 1979), but very little is known about predation by birds in relation to gastropod shell form (Vermeij, 1978).

African Black Oystercatchers _Haematopus moquini_ preferentially attack limpets _Patella_ and _Cellana_ spp. at the posterior margins, and make "correct" attack decisions most consistently on limpet species whose posterior and anterior sectors are clearly distinguishable, such as _Patella cochlear_ (Part 3.2). The dominant limpet in the diet of the African Black Oystercatcher is _P_. _granularis_, an essentially elliptical species of the mid- and upper intertidal of southern Africa (Part 3.3). The proportions of attacks delivered by African Black Oystercatchers at the posterior, mid- and anterior shell margins of _P_. _granularis_ are respectively 49.3 %, 12.1 % and 38.6 % (n = 487) (Part 3.2).

If African Black Oystercatchers are most successful when attacking limpets posteriorly, it would be advantageous, when dealing with an elliptical species, to attack those individuals which are more pear-shaped, and hence have most recognizable posterior ends.

If oystercatchers adopt this strategy, two testable hypotheses emerge concerning shell shape between and within populations of _P_. _granularis_. Firstly, limpets in regions where there are no oystercatchers will be more pear-shaped than limpets in areas where oystercatchers occur, where pear-shaped limpets will have been removed preferentially. Secondly, within regions where oystercatchers occur, limpets in inaccessible sites (vertical rock faces) will be more pear-shaped than accessible limpets but, assuming genetic control of shell shape, more elliptical than limpets in areas where there are no oystercatchers.

METHODS

Random samples of P. granularis were collected at five localities in South Africa and southern Namibia within the range of H. moquini. Three groups of limpets were distinguished: eaten by oystercatchers (shells collected from chick "middens" (Part 3.3)); living on rocks accessible to oystercatchers; and, living on rocks inaccessible to oystercatchers (vertical faces). Additionally, collections were made at seven localities in northern Namibia where African Black Oystercatchers occur only as rare vagrants (Part 1.2). Each sample contained 30 individuals of varying sizes: all samples were taken from high energy shores.

A Shell Uniformity Index (SUI) was calculated for each limpet. The SUI was the ratio of the width of the shell one third of the was from the anterior apex to the width one third of the way from the posterior apex. Thus, individuals with SUIs close to unity were more elliptical than those with smaller SUIs. Shell width was measured with vernier calipers to the nearest 0.5 mm. Data (SUIs) were normalised using an arc sin transformation ($Y' = \sin^{-1}(\sqrt{Y})$) (R. Sokal, in litt.). For each sample the mean ± S.D. was calculated, and means were compared using a t-test.

RESULTS

Shell Uniformity Indexes ranged from 0.86 ± 0.04 to 0.95 ± 0.03 (Table 29). T-tests indicated the following differences between populations of limpets in different regions and sites.

Table 29. Mean Shell Uniformity Indexes (SUIs) ± S.D. for 17 samples of *Patella granularis* from southern Africa

Type of limpet population	Sampling location	Mean ± S.D.
Depredated by oystercatchers	Malgas Is. (33°03'S, 17°55'E)	0.91 ± 0.03
	Possession Is. (27°01'S, 15°12'E)	0.92 ± 0.06
	Jutten Is. (33°05'S, 17°57'E)	0.92 ± 0.04
	Overall mean	0.92 ± 0.05
Accessible to oystercatchers	Malgas Is.	0.95 ± 0.03
	Owen Is. (29°16'S, 16°52'E)	0.94 ± 0.04
	Jutten Is.	0.93 ± 0.03
	Cape Columbine (32°50'S, 17°50'E)	0.94 ± 0.04
	Overall mean	0.94 ± 0.04
Inaccessible to oystercatchers	Malgas Is.	0.92 ± 0.04
	Jutten Is.	0.91 ± 0.04
	Cape Columbine	0.93 ± 0.06
	Overall mean	0.92 ± 0.04
Predator-free	Swakop River (22°41'S, 14°31'E)	0.86 ± 0.08
	Mile 105 (21°25'S, 13°50'E)	0.87 ± 0.04
	Terrace Bay (20°00'S, 13°00'E)	0.93 ± 0.03
	Mowe Bay (19°20'S, 12°43'E)	0.90 ± 0.05
	Rocky Point (19°01'S, 12°29'E)	0.92 ± 0.04
	Angra Fria (18°20'S, 11°58'E)	0.86 ± 0.09
	Kunene River (17°20'S, 11°50'E)	0.88 ± 0.07
	Overall mean	0.89 ± 0.06

a. The mean SUI for all limpets in populations free from oystercatcher predation (0.89 ± 0.06, n = 210) was significantly lower (t = 6.89; $p<0.001$) than for limpets from populations subjected to oystercatcher predation (0.93 ± 0.04, n = 300).

b. Limpets inaccessible to oystercatchers had a significantly lower SUI than accessible limpets at Malgas Island (t = 3.16; $p<0.01$) and Jutten Island (t = 2.27; $p<0.05$), both islands with high densities of oystercatchers, respectively 60 and 63 birds per km of shore. Inaccessible limpets were not significantly different in shape from accessible limpets at Cape Columbine (t = 1.07, $p<0.1$), an area with lower oystercatcher density (two birds per km), although the trend was in the expected direction. Overall, inaccessible limpets had a significantly lower SUI than accessible limpets (t = 2.93; $p<0.01$).

c. Limpets eaten by oystercatchers had a significantly lower SUI than accessible limpets at Malgas Island (t = 4.64; $p<0.001$), but at Jutten Island the difference was not significant (t = 0.25; $p>0.1$) although the trend was in the expected direction. Overall, limpets taken by oystercatchers had a lower SUI than all accessible limpets (t = 3.49; $p<0.001$).

d. Inaccessible limpets in populations subjected to predation by oystercatchers overall had a higher SUI than limpets in populations free from oystercatcher predation (t = 2.32; $p<0.05$).

DISCUSSION

The hypothesis that limpets in populations free from oystercatcher predation will be more pear-shaped than those in populations experiencing predation, was upheld. Similarly, the hypothesis that accessible limpets will be more elliptical than inaccessible limpets was supported in areas where the densities of oystercatchers were high. At a site with a low density of oystercatchers (Cape Columbine), the trend was the same but not significant.

The mean SUI for inaccessible limpets and for limpets consumed by oystercatchers was the same, but the former was significantly higher (i.e. shells more elliptical) than the mean SUI of limpets in populations free from oystercatcher predation. This further supports the second hypothesis and implies that shell shape is genetically determined and that predation by oystercatchers influences the limpet gene pool. If this were not the case, limpets in accessible and predator-free populations would have similar SUIs.

The possibility of a latitudinal influence on shell shape was considered, but Table 29 clearly illustrates that there is no trend in shape with decreasing latitude.

<u>Patella granularis</u> has no other important vertebrate predators. Very small individuals are occasionally taken from mussel beds by Turnstones <u>Arenaria interpres</u>; and the Giant Clingfish <u>Chorisochismus dentex</u> preys on limpets, but <u>P</u>. <u>granularis</u> is a negligible component of the diets of both species (Stobbs, 1980, Branch, 1981; pers. obs.). The influence of invertebrate predators on the shell shape of <u>P</u>. <u>granularis</u> is not known, but the findings of this study suggest that the selective influence by oystercatchers alone on the genotypes of <u>P</u>. <u>granularis</u> is

sufficient to be detectable in phenotypes.

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Part 3.6. Paralytic Shellfish Poisoning - a controlling factor in African Black Oystercatcher populations?

Ostrich 51 (1980): 188-190

Outbreaks of paralytic shellfish poisoning (PSP) have been reported on a number of occasions this century in South Africa (Grindley & Sapeika, 1969; Horstman, 1981). During early May 1978, an outbreak of PSP occurred between Lambert's Bay and Bloubergstrand, southwestern Cape (Popkiss et al., 1979; Horstman, 1981). PSP is caused by a neurotoxin synthesized by dinoflagellates, which often occur as 'red tides'. The toxin is accumulated in the flesh of filter-feeding bivalves and acts by obstructing the transmission of neuro-muscular impulses (Shilo, 1967). The organism involved in the May 1978 occurrence has been identified as Gonyaulax catanella (Popkiss et al., 1979; Horstman, 1981). This note reports on the mortality of African Black Oystercatchers Haematopus moquini from PSP in May 1978 and discusses the rôle of poisoning in the species' population.

Red tide was noticed near Marcus Island, Saldanha Bay on 3-5 May 1978 (G.H. Nicholls, pers. comm.), the first reported case of human poisoning was on 10 May (Popkiss et al., 1979). Freshly dead oystercatchers were first found on Marcus Island on 22 May (G.H. Nicholls, pers. comm.). Censuses were undertaken during June and July 1978 to count live and dead oystercatchers at a number of localities for which previous censuses existed (Summers & Cooper, 1977; unpubl. data) (Table 30). Populations were approximately halved following the outbreak. Dead oystercatchers showing no signs of predation are very rarely found (pers. obs.) and the number of corpses discovered (Table 30) reflects an unusually high mortality.

Repeat censuses were undertaken in June and July 1979 to ascertain the long-term effect of the poisoning episode (Table 30). Counts were made in the same months of the year in 1978 and 1979 to avoid

TABLE 30. CHANGES IN POPULATION SIZE AND NUMBERS OF AFRICAN BLACK OYSTERCATCHERS FOUND DEAD DUE TO PARALYTIC SHELLFISH POISONING AT FIVE LOCALITIES AFFECTED BY RED TIDE IN MAY 1978

Locality	Numbers present prior to red tide	Numbers present after red tide, June - July 1978	Numbers present June - July 1979	Numbers found dead May - July 1978
Marcus Island	114 (Aug 1977)	60	88	9
Malgas Island	40 (Jul 1977)	27	55	?
Jutten Island	175 (Jan 1977)[x]	57	112	7[+]
Dassen Island	223 (Jul 1971)[x]	131	202	2
Klein Island	72 (Aug 1976)	18	39 (Sept)	?
Total	624	293	488	18 (minimum)
% reduction	-	53 %	22 %	-

[x] data from Summers & Cooper (1977)

[+] S. Smit, pers. comm.

error from seasonal fluctuations in numbers that occur on islands (Part 1.2). Results show a partial recovery in 1979.

Four freshly dead oystercatchers collected on 22 and 23 May 1978 were dissected; pathological lesions and bleeding of the stomach and intestine were noticed. The symptoms are indicative of PSP (Coulson _et_ _al_., 1968). The stomachs were empty. Three of these birds had been ringed and weighed previously. Table 31 shows that a mean mass loss of 36 % had occurred. The corpses were emaciated and had no fat deposits. It is considered that the birds starved to death. Samples of pectoral muscle, liver and heart were combined from each corpse and analyzed for the presence of neurotoxin using the technique described by Prakash _et_ _al_. (1971). Results were negative for all birds (D.A. Horstman, pers. comm.). similar tests on marine birds killed by PSP in England were also negative (Armstrong _et_ _al_., 1978). They concluded that a better technique for identifying the presence of neurotoxin in birds is required.

Black mussels _Choromytilus_ _meridionalis_ collected in the vicinity of Marcus Island in May 1978 contained high levels of the neurotoxin causing PSP (Popkiss _et_ _al_., 1979; Horstman, 1981). African Black Oystercatchers at Marcus Island eat both live attached and stranded mussels (Part 3.2), rendering them susceptible to poisoning.

Large numbers of washed-up sand mussels _Donax_ _serra_, presumably killed by red tide (de Villiers, 1975; Popkiss _et_ _al_., 1979; Horstman, 1981) were noticed on the sandy shore north of Ysterfontein during June and July 1978. Six dead oystercatchers were found on 25 km of shoreline at the time. Subsequent monthly surveys yielded no further corpses (G. Avery, pers. comm.). The

TABLE 31. LOSS OF MASS IN AFRICAN BLACK OYSTERCATCHERS KILLED BY PARALYTIC SHELLFISH POISONING, MAY 1978

Individual bird	Mass when ringed (g)	Mass when found dead (g)	Mass loss (g)	% mass loss
A	685	457	228	33
B	760	446	314	41
C	680	458	222	33
Mean	708	454	254	36

African Black Oystercatcher is known to feed on sand mussels (McLachlan *et al*., 1980). Numbers of dead Kelp Gulls *Larus dominicanus* and Hartlaub's Gulls *L. hartlaubii* also were found on the Ysterfontein shore, presumably having succumbed to PSP.

PSP of marine birds has been reported on several occasions (McKernan & Scheffer, 1942; Coulson *et al*., 1968; Bicknell & Walsh, 1975; Armstrong *et al*., 1978) but has not been recorded previously in South Africa. Shags *Phalacrocorax aristotelia* lost 16.% of their mass from PSP, approximately half the percentage lost through starvation (Coulson *et al*., 1968). Other species of birds killed by the same incident did not show significant mass losses.

PSP causes loss of motor coordination, followed by paralysis (Coulson *et al*., 1968) and it is likely that the oystercatchers were unable to feed effectively when first poisoned and died from starvation.

The African Black Oystercatcher has a low rate of recruitment to the adult population (Summers & Cooper, 1977, Part 5.2) and like the European Oystercatcher *H. ostralegus* (Rydzewski, 1978) is probably long-lived. Recovery after a PSP outbreak is therefore likely to be slow. The partial recovery during 1979 (Table 30) is thought to be due to immigration of adult birds into the survey localities and not due to a real increase in population size. It is not known what effect previous outbreaks of PSP in South Africa have had on oystercatchers. A rapid succession of outbreaks may have serious implications for a species already in need of conservation (Summers & Cooper, 1977, Part 1.2).

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Part 3.7. Summary

African Black Oystercatchers employ a wide range of prey-specific feeding techniques, each of which is adapted to the particular morphology of the prey species. The small tidal range in southern Africa, combined with the fact that mussels extend their distribution infratidally, allows African Black Oystercatchers to attack gaping individuals at the water's edge, thus eliminating the need for energy costly hammering techniques employed by the European Oystercatcher. One consequence of their heavy dependence on filter-feeding molluscs as a food source is that African Black Oystercatcher populations are highly susceptible to outbreaks of Paralytic Shelfish Poisoning. Motor coordination is inhibited through the action of neurotoxins and birds are unable to execute their highly evolved feeding techniques, and consequently starve to death. Such outbreaks may cause considerable mortality in the population.

Different techniques are used to detach limpets from rocks depending on the size of the limpet. Large limpets are attacked posteriorly, presumably in order to delay detection by the limpet, and it is the limpet shell shape (narrower anteriorly) that provides the cue to oystercatchers as to the correct direction of attack. In the case of the oval shaped upper shore limpet Patella granularis, selection by oystercatchers for less uniformly shaped individuals (i.e. those with more readily identifiable anterior and posterior sections) appears to have influenced the limpet gene pool in areas where predation pressure is high.

Although the majority of African Black Oystercatchers are territorial, and defend the same territories throughout the year, there are variations in diet due to a number of factors. There is spatial variation on both a geographical and local scale; there is temporal variation on a daily basis, with a preponderance of nocturnally active prey in the diet at night, and there is also sex-related variation which is due to the differing bill morphologies of males and females. Indeed, prey size selection was the only aspect of diet studied that was consistent within and between localities, and hence pairs. This study clearly highlights the potential dangers of generalizing about diet in a territorial species.

The heavy predation pressure exerted by African Black Oystercatchers on the limpet _P_. _granularis_ at islands has a major effect on the limpet populations. At islands, densities of limpets are dramatically reduced in areas where they are accessible to oystercatchers, and there is marked depletion of favoured size classes. Limpet populations at islands are able to maintain themselves under such heavy predation pressure by virtue of their faster growth rate, and the fact that there is a "pool" of individuals which have grown too large to be preyed on and thus guarantee recruitment to the population regardless of predation on smaller individuals. One effect of the reduced densities of _P_. _granularis_ in the upper intertidal is the formation of beds of macroalgae, since the density of limpets is no longer high enough to control algal growth at the sporeling stage, which happens on the mainland. These algal beds support rich invertebrate faunas (primarily small crustaceans) which provide food for smaller waders. Thus, feeding facilitation, resulting from oystercatcher predation on limpets is, to some extent, responsible for shaping the intertidal avifaunal communities of rocky offshore islands.

Part 4. ACTIVITY AND ENERGETICS

Part 4.1. Introduction

Studies of the activity and energy budgets of wading birds (and birds in general) frequently have been bugged by one major question - what do they do at night? In the case of oystercatchers, extrapolations have been made from observations of captive birds to the wild situation (Heppleston, 1971; Hulscher, 1982), but no quantitative check of their validity has yet been made in the field. In most cases, nocturnal activity either is conveniently ignored, or an "estimate" is applied to it to join the host of other "estimates" that are prevalent in energetics studies (Puttick, 1979; Maxson & Oring, 1980).

Determining the activity budgets of birds poses considerable problems in cases where individuals cannot safely be identified. Instantaneous scans (Altmann, 1974) are useful for estimating activities of flocking birds, but do not supply the critical information as to whether the same birds are present throughout the observation period. This can lead to unidentifiable over- or under-estimates of different activities.

The aim of constructing an activity budget is often to produce an energy budget, relying on the application of correction factors to standard metabolic rates, in turn normally derived from standard equations (e.g. Schartz & Zimmerman, 1971; Maxson & Oring, 1980; Mugaas & King, 1981). There are numerous problems inherent in this technique, principally the choice of correction factors. Another frequently adpoted approach to estimating energy expenditure has been through food intake or oxygen consumption of captive birds (e.g. Kahl, 1964; West, 1968; Kendeigh, 1973). In this study, energy budgets were derived from a combination of food intake of captive birds and activity budgets of wild birds.

The most accurate technique devised to date (and the most expensive) for measuring the energy costs of free existence is use of turnover rates of radioactive isotopes D_2O and H_2O^{18} : the latter technique has been used successfully in a study of breeding House Martins Delichon rubica (Hails & Bryant, 1979). For a review of available techniques, see Gessaman (1973).

The African Black Oystercatcher, being largely territorial and often roosting on, or close to the feeding territory, lends itself to a study of activity rhythms. Since birds only form flocks when roosting, individually colour-ringed birds can be followed during the day and their activities recorded; at night it is not possible to identify individual birds.

Not only are the energy requirements for free existence of adults of interest, but also the energetic requirements for chick growth, as this is the time when maximum demands are placed on the adults. Oystercatcher chicks are subprecocial, being fed by the parents until after fledging. Almost no detailed analyses exist of the growth rates of wading birds (Charadrii), due in part to the difficulties in locating the young at regular intervals. Growth rate in the African Black Oystercatcher has been described from only one chick (Rand, 1950). The energetic requirements for growth have not been reported for any Charadrii. Since techniques of estimating meal size or oxygen consumption, applicable in some seabirds (Koelink, 1972; Dunn, 1975; Ricklefs et al., 1980) are not applicable to precocial or subprecocial Charadrii, energy requirements for growth can only be estimated using captive chicks growing at a rate comparable to wild chicks.

This study of activity and energetics sets out to answer the following questions:

1. What are the diurnal and nocturnal activity rhythms of African Black Oystercatchers and what are their causative factors?

2. Since the African Black Oystercatcher is strongly territorial, what are the advantages of roosting communally?

3. What are the energy requirements for growth and for free existence in the African Black Oystercatcher?

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Part 4.2. Behaviour patterns of nonbreeding African Black Oystercatchers *Haematopus moquini* at offshore islands.

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ABSTRACT

The activity of African Black Oystercatchers Haematopus moquini at Marcus Island is determined by tidal and swell conditions. Foraging activity can be described by the logarithmic function $F = 26.64 - 43.16 \ln T$, where F = percentage of the population foraging and T = predicted tidal height in metres ($r = 0.79$; $p<0.001$). The corresponding equation describing resting (roosting or sitting birds) is $R = 63.59 + 47.12 \ln T$ ($r = 0.81$; $p<0.001$).

During any one tidal cycle the relationship of foraging activity to tidal height within a defined habitat was linear. Foraging activity followed a cyclic pattern even under conditions when food theoretically was available throughout the tidal cycle. There was a slight tendency for foraging activity to be greater during a falling tide than during a rising tide by day and vice versa by night.

By day, birds remaining in one area foraged for 27.5 % to 46.4 % of the time when food was available. During storm conditions this component exceeded 50 % and additional energy expended in foraging was counterbalanced by a decrease in time spent preening and bathing. Foraging time in individual birds was consistent between tidal regimes (storms excluded) and amounted to approximately 220 minutes per day (feeding on beds of ribbed mussels) as compared to approximately 530 minutes per day spent feeding by European Oystercatchers H. ostralegus. The duration of individual feeding bouts did not vary between tidal regimes or swell conditions. Nocturnal foraging activity was 0.59 times diurnal foraging activity. At night birds ceased feeding while the tide was still relatively low and gathered into communal roosts away from the feeding area. During the 24 hour cycle birds fed for

approximately 24 % of the time.

The mean diurnal commitment to territory was 53.7 % with a range of 92.6 % to 14.8 %. Mean commitment over 24 hours was 38.1 %. Birds with a territorial commitment of 60 % or more were able to satisfy their feeding requirements on the territory. There was a greater tendency for birds to roost communally by night than by day. Birds at night roosts were more closely packed and less vocal than by day. This is adaptive as an anti-predator strategy.

The African Black Oystercatcher is able to satisfy its energy requirements during the nonbreeding season in less time than the European Oystercatcher, spending only 40 % as much time foraging by day. Seasonal fluctuations in energy demand are less in the African Black Oystercatcher than in the European Oystercatcher.

INTRODUCTION

Several species of shorebirds (Charadrii), including the African Black Oystercatcher Haematopus moquini, defend feeding territories during the nonbreeding season: the extent of territorial commitment (proportion of total time spent on the territory) is variable (Myers et al., 1979; pers. obs.). Daily patterns of territorial occupancy are largely determined by cyclic environmental conditions, such as tidal height. Territorial birds usually gather into communal roosts at night and travel to other feeding areas when foraging on the territory is temporarily impractical (Myers et al., 1979).

The African Black Oystercatcher has a small population and this fact, coupled with the bird's territorial nature and varying degrees of territorial commitment, poses several problems in attempting an analysis of activity partitioning. Large aggregations of foraging and resting birds do not occur within a readily defined and observable area and this precludes effective use of the Feeding Activity Index adopted for the European Oystercatcher H. ostralegus (Heppleston, 1971). The activity partitioning of an individual cannot therefore be accurately deduced from observations of the entire population.

This paper considers the types of information that can be obtained by considering activity of a territorial shorebird, the African Black Oystercatcher, at three levels: an entire island population, a sub-population of that island, and at the level of the individual. The paper aims to consider the following topics: how activity is affected by tidal level and variations in tidal regime and swell conditions; the adaptiveness of variations in diurnal and nocturnal behaviour patterns; variations in territorial commitment and, behaviour sequences and associations. The paper is intended to provide the data base for a more extensive analysis of energetics of the African Black Oystercatcher (Part 4.4).

THE STUDY AREA

Marcus Island (33 03S, 17 58E), southwestern Cape, South Africa, is small (11 ha) and granitic. The coastline of 1.6 km is predominantly rocky, and coastal exposure ranges from moderate to severe. The island supported a population of approximately 55 pairs of African Black Oystercatchers during 1979-1980 with small numbers of nonbreeding birds present (Part 5.2). The sub-population observed in this study occupied an area of gently sloping, moderately exposed shore with an easterly aspect. Beds of ribbed mussel Aulacomya ater dominated the lower shore, and the limpet Patella granularis dominated the upper balanoid zone. Marcus Island was connected to the mainland by a causeway in February 1976. The spending beach of the causeway floods following heavy swells and African Black Oystercatchers roost at the edge of a pool which results from the flooding. Mean tidal levels at Marcus Island are:

	Spring	Neap
Mean high water	1.76 m	1.26 m
Mean low water	0.26 m	0.76 m

The mean tidal level is 1.01 m. These levels are computed from at least a year's prediction and are adjusted for long period variations to give values which are the average over the whole of the cycle (South African Navy, 1980).

METHODS

Observations were made during the nonbreeding seasons of 1979 and 1980 at Marcus Island, using the instantaneous scan technique (Altmann, 1974). This was used at two levels: the island population as a whole and a discrete sub-population of territorial birds.

The island population

During my scans I traversed the whole shoreline of Marcus Island. My presence was therefore a possible source of disturbance, hence only four easily identifiable behaviour types were recognised: foraging, roosting, sitting and preening (including bathing). An "other" category was used to lump behaviour such as walking, flying and copulating. Analysis of this component was not taken further since flying and walking behaviour, as recorded in instantaneous scans may have been related to foraging or alarm/display, but could not accurately be ascribed to either. A total of 129 scans was made under varying tidal and swell conditions over several months in 1979 prior to breeding and at all times of day and tide. The interval between scans was random, with a duration of approximately 40 minutes. Data were analysed with regard to the predicted tidal height in m as determined from hourly tide tables (South African Navy, 1980).

The subpopulation

The subpopulation was chosen for its observability and the presence of several individually colour-marked birds within a defined area. Birds were not disturbed by the presence of the observer and the additional category of alarmed or displaying birds was included with the categories listed above. The interval between scans was five minutes, with a duration of approximately one minute.

Nocturnal activity and roosting behaviour

The subpopulation was observed continuously for 72 h (three days and three nights between 28 April 1980 and 1 May 1980. Observations at night were made using a KOT 1 image intensifying binocular with a magnification of 4.7. Behavioural categories were recorded as above, but bathing and walking were included as discrete categories and alarm and vocal display behaviour were separated. During this period counts were made by day and night at a nearby communal roost. "Night" was taken to be the period when observation was not possible without the use of an image intensifier: at the time of observation this was equal to 12 h. Behavioural observations were made at five-minute intervals at a communal roost during the day. Brief qualitative observations of roosting behaviour also were made at night.

Behaviour sequences and associations

Individual behaviour sequences were too complex to describe categorically, therefore a system of probability was used. Observations of individually identifiable birds with strong territorial commitment were analysed with respect to sequence frequency i.e. the frequency with which behaviour type A was immediately followed by type A, B, C or D etc. The degree of association of different types of behaviour was calculated from the frequencies of direct associations. A value of less than one indicates negative association, and more than one, positive association.

RESULTS

Diurnal activity and the tidal cycle

The African Black Oystercatcher feeds exclusively on intertidal invertebrates and can therefore forage only when the intertidal zone is exposed by the tide or when invertebrates are washed ashore during storm conditions. The relationship between the percentage of the island population foraging (F) and the predicted tidal height (T, in m) is described by the logarithmic function $F = 26.64 - 43.16 \ln T$, ($r = 0.79$; $p<0.001$). The corresponding expression for resting birds (R) is $R = 63.59 + 47.12 \ln T$, ($r = 0.81$; $p<0.001$). From these two functions the frequency distribution of other behaviour patterns such as preening or displaying can be determined (Fig. 30). The relationship of foraging activity to the time of low water is symmetrical, peaking just before low water (Fig. 31), based on a total of 10 881 bird observations made between June and November, 1979.

Although these data provide a general picture of the behaviour of

Figure 30. Gross activity partitioning by African Black Oystercatchers at Marcus Island in relation to the predicted tidal height (T)

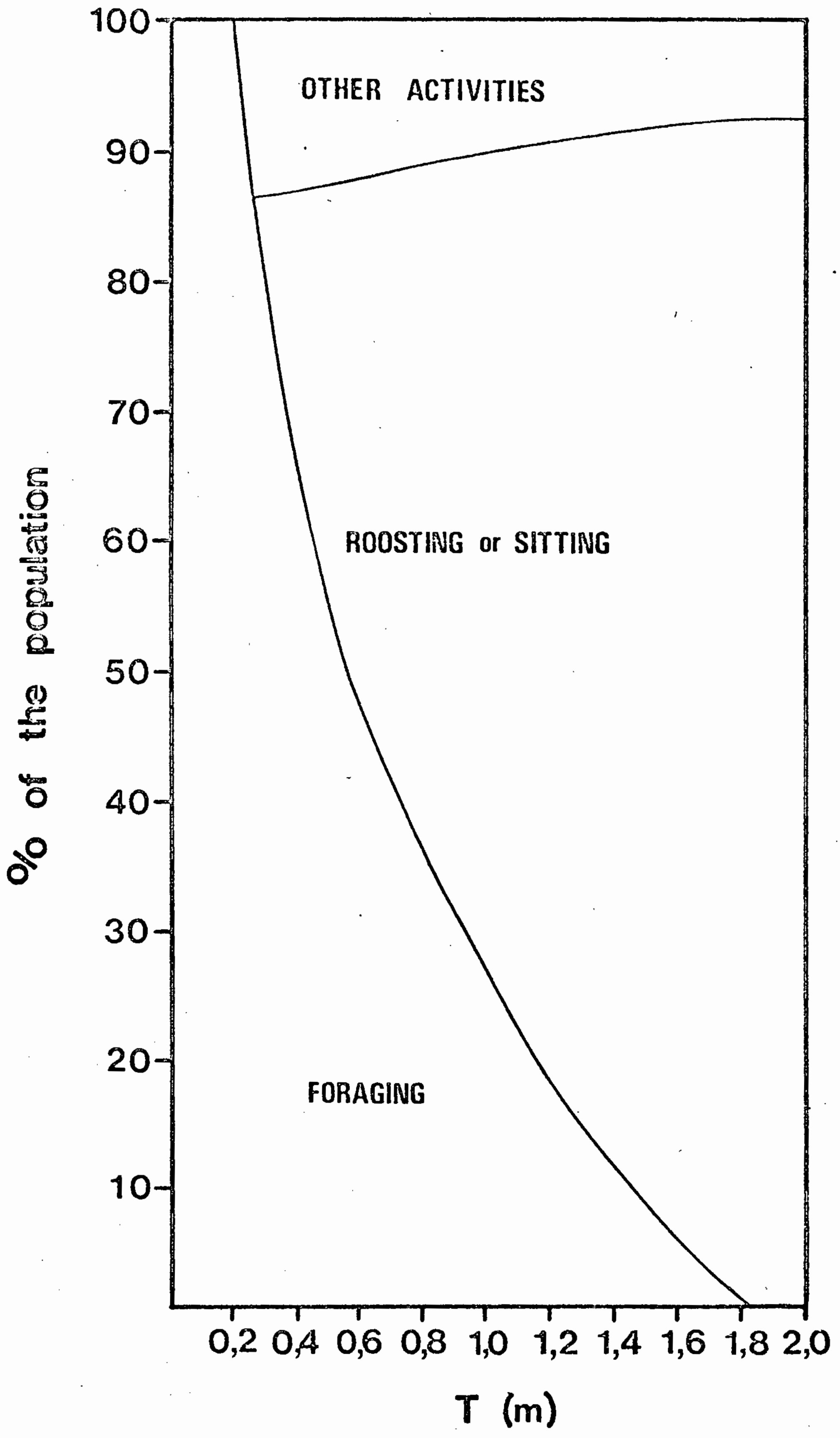
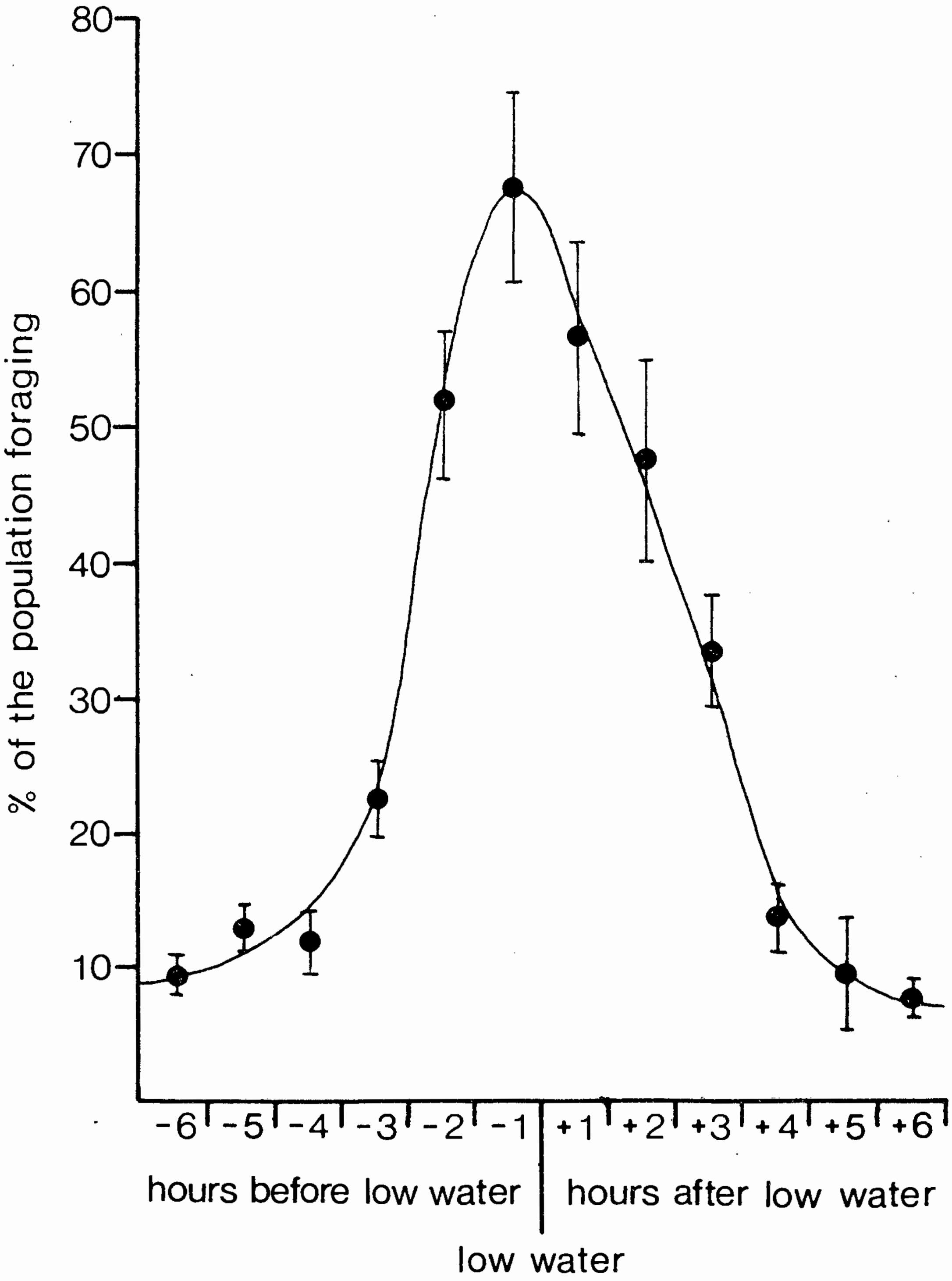


Figure 31. Foraging activity (means ±SE) of African Black Oystercatchers at Marcus Island in relation to the time of low water



the population under the full range of tidal heights experienced, they do not explain how behaviour may vary under different tidal regimes. To obtain this it is necessary to consider behaviour at the level of a sub-population that can be kept under continuous observation, and at the level of the individual.

Foraging activity of the sub-population was linearly related to tidal height regardless of tidal regime (Fig. 32). Components of the linear regression ($F = mT + C$) are detailed in Table 32 for seven full tidal cycles during calm conditions and during one storm. Birds invariably followed a cyclic foraging pattern even when food theoretically was available throughout the tidal cycle. As tidal range decreased (neap tides) the intensity of foraging activity increased more rapidly at comparable tidal levels than during intermediate or spring tides. During the continuous 72 h observation period there was a slight tendency for foraging activity to be greater on a falling than a rising tide by day, and *vice versa* at night.

Activity partitioning was compared between periods when foraging was possible and not possible (Table 33). Under calm conditions over the range of tidal extremes, birds in the area during the foraging period foraged on average for 33.3 % to 41.9 % of the available time (range 27.0% to 46.4%). During storm conditions, when birds were foraging on stranded invertebrates, this increased to 54% (Table 33). During the high tide part of the cycle birds spent the majority of the time resting. Territorial conflicts (alarm/display) were more frequent when more birds were present i.e. on spring and neap tides. (Tables 32,33).

A major problem in analysing group scan data of this nature is that the number of individuals in the study area was not constant, nor did it fluctuate randomly: fluctuations in the number of individuals present were controlled by tidal level (Fig. 33). It

Figure 32. The relationship between foraging activity of African Black Oystercatchers and predicted tidal height (T) over eight full tidal cycles. 1 = calm spring; 2 - 4 = calm intermediate, 5 - 7 = calm neap; 8 = storm

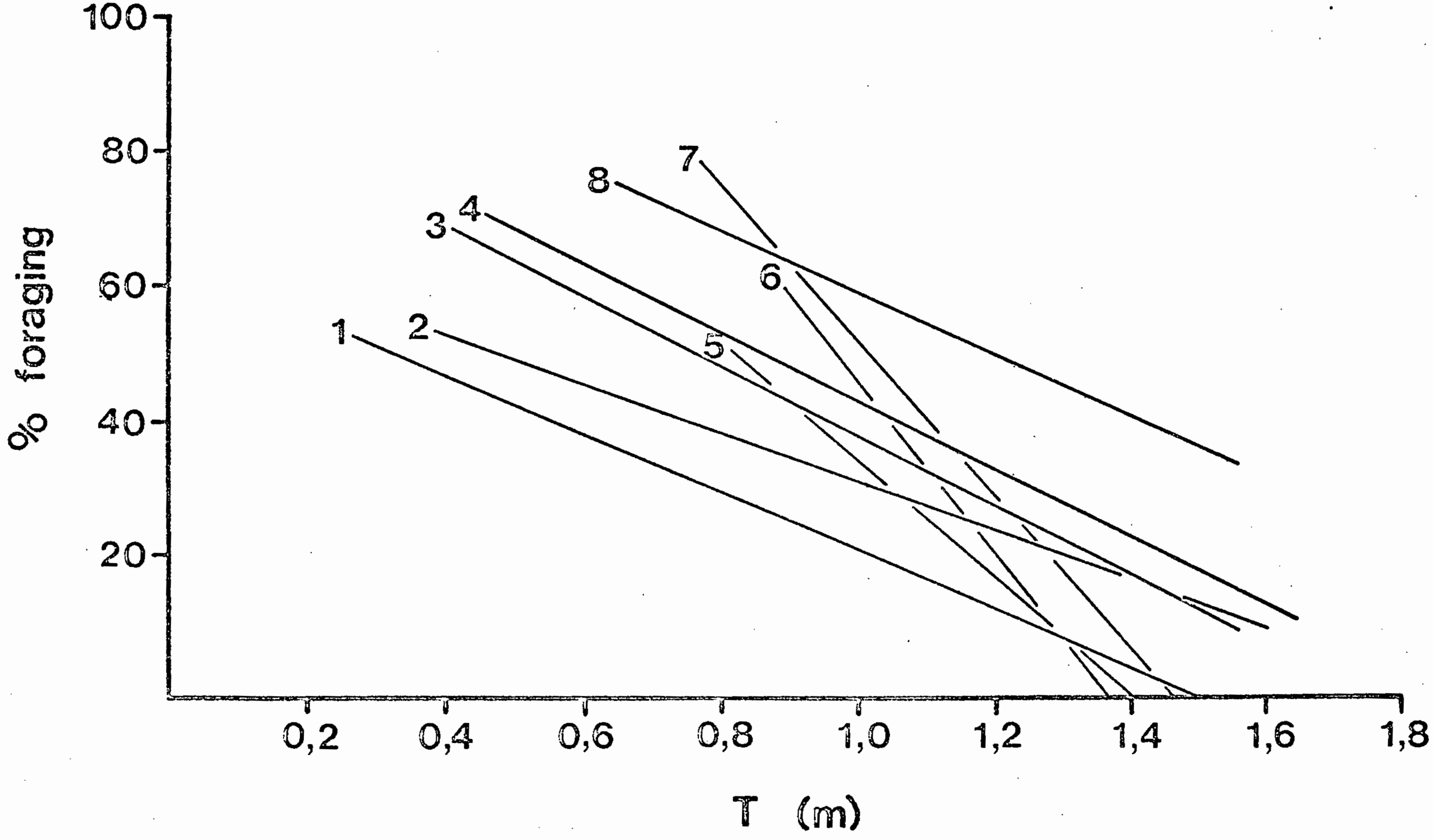


TABLE 32. MEAN NUMBERS OF NONBREEDING AFRICAN BLACK OYSTERCATCHERS PRESENT ON THE STUDY AREA DURING PERIODS WHEN FORAGING WAS POSSIBLE DURING EIGHT FULL TIDAL CYCLES, AND COMPONENTS OF THE LINEAR REGRESSIONS RELATING FORAGING ACTIVITY (F) TO THE PREDICTED TIDAL HEIGHT (T). IN ALL INSTANCES $P<0.001$

Day	Tidal conditions	Mean number of birds	Regression $F = mT + C^*$		
			m	c	r
1.	Calm spring	11.2	-43.24	64.48	0.83
2.	Calm intermediate	7.5	-34.85	67.90	0.77
3.	" "	8.1	-51.52	89.19	0.95
4.	" "	6.9	-50.32	93.53	0.84
5.	Calm neap	10.5	-85.54	119.76	0.81
6.	" "	12.1	-127.93	174.83	0.88
7.	" "	7.3	-113.51	165.96	0.92
8.	Storm	6.5	-45.73	104.30	0.68

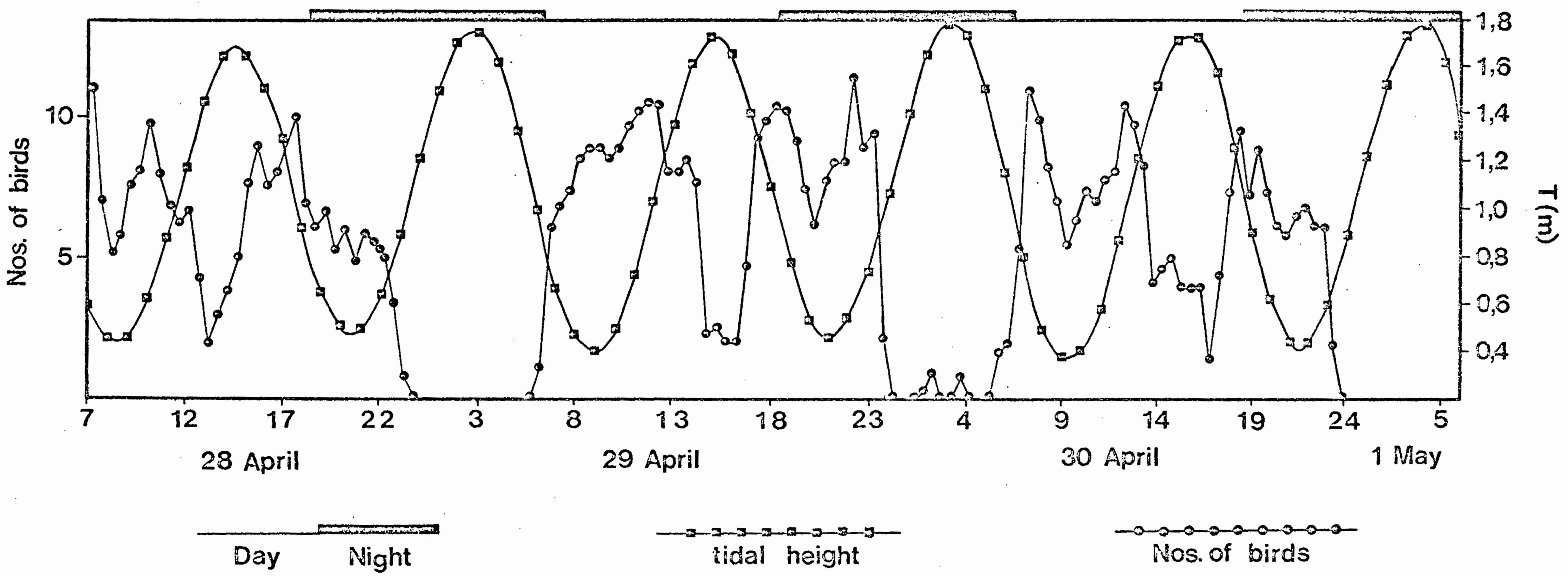
* F = % birds foraging

T = predicted tidal height in metres

TABLE 33. RELATIONSHIP OF ACTIVITY PARTITIONING BY NONBREEDING AFRICAN BLACK OYSTERCATCHERS DURING THE DAY, EXPRESSED AS A PERCENTAGE, TO TIDAL REGIME DURING PERIODS WHEN INTERTIDAL FORAGING WAS THEORETICALLY POSSIBLE OR IMPOSSIBLE

Tidal regime	Foraging	Roosting	Sitting	Preening/ bathing	Alarm/ display	Other
			Foraging possible			
Spring	33.3	21.6	14.3	15.9	13.6	1.3
Intermediate	41.9	18.4	7.8	20.4	3.5	7.9
Neap	34.1	26.9	9.4	19.0	9.9	0.8
Storm	54.4	31.9	2.7	3.2	5.8	2.0
			Foraging impossible			
Spring	0.5	48.6	35.1	13.8	1.2	0.8
Intermediate	0.5	48.7	30.2	17.3	0.9	2.5

Figure 33. Mean numbers of African Black Oystercatchers present per half hour period within five adjacent territories over a three day period, Marcus Island, 1980.



was possible to obtain an overall activity budget for individually identifiable birds with a high territorial commitment. The diurnal activity budget of both members of such a pair is summarized in Table 34. Foraging activity was the most consistent component of activity throughout the range of tidal regimes. Overall, the greatest difference between the sexes was the time spent resting. The origin of this variation is probably differences in the time spent away from the territory. Incorporating the nocturnal/diurnal feeding activity ratio of 0.59 calculated in this study, the male of one pair fed, on average, for 24.9 % of the 24 hours, the corresponding value for the female was 23.1 %.

The duration of individual foraging bouts also was recorded for these two birds to determine whether this varied under differing tidal regimes (Table 35). No significant differences exist between the varying conditions ($X^2 = 10.41$; $p>0.05$). The pattern is one of behavioural regularity despite considerable variations in environmental conditions.

Diurnal compared with nocturnal activity

There were considerable variations in the patterns of occupancy of the subpopulation area between day and night that were primarily tidally controlled. By day, numbers decreased during the high part of the tidal cycle, although some birds were always present. At night however, the area was completely deserted once the tidal level rose to between 0.9 and 1.0 m (Fig. 33). By day, approximately 40 % of birds were still foraging at this stage (Fig. 34). The ratio of day to night utilization of the area was 2.4. Six high tide counts were made at a nearby communal roost

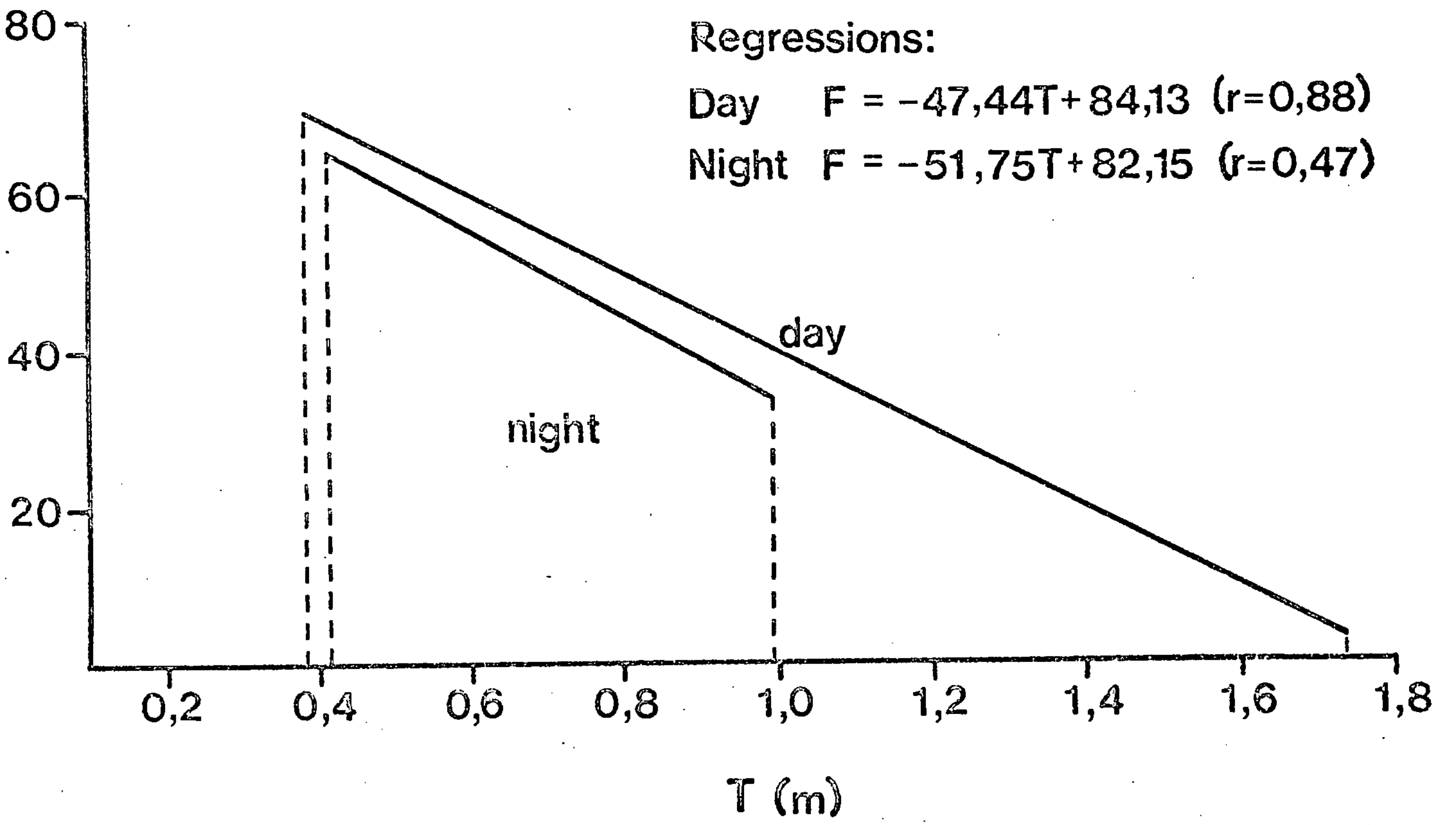
TABLE 34. THE PERCENTAGE OF DAYLIGHT HOURS SPENT IN DIFFERENT ACTIVITIES BY A PAIR OF AFRICAN BLACK OYSTERCATCHERS AT MARCUS ISLAND UNDER DIFFERENT TIDAL REGIMES

Tidal regime	Foraging		Roosting/ sitting		Preening/ bathing		Alarm/ display		Other	
	M	F	M	F	M	F	M	F	M	F
Spring tide	31.9	31.9	36.8	44.4	17.4	11.8	9.7	10.4	4.2	1.5
Intermediate	29.2	28.5	36.1	36.8	23.6	25.0	1.4	2.1	9.7	7.6
"	30.6	25.0	35.4	41.7	17.4	22.2	2.8	2.8	13.8	8.3
"	29.9	27.8	21.5	36.1	18.0	17.4	4.9	2.8	25.6	16.0
Neap tide	32.6	27.1	23.6	29.9	20.2	22.2	15.3	17.4	8.3	3.5
"	31.9	26.4	46.6	50.7	13.9	15.3	7.6	0.9	0.0	0.7
"	33.3	36.6	37.5	39.6	17.4	14.6	10.4	6.9	1.4	2.1
Mean	31.3	29.1	34.0	39.9	18.3	18.4	7.4	7.0	9.0	5.6
Standard deviation	1.5	4.0	8.8	6.7	3.0	4.9	4.9	5.5	8.8	5.4

TABLE 35. DURATION OF INDIVIDUAL FORAGING BOUTS OF NONBREEDING AFRICAN BLACK OYSTERCATCHERS UNDER DIFFERENT TIDAL REGIMES, EXPRESSED AS A PERCENTAGE

Duration of foraging bout (minutes)	Tidal condition				Overall
	Spring	Intermediate	Neap	Storm	
less than 5	24.0	32.9	30.7	34.1	31.3
6-10	16.0	26.6	29.7	34.1	28.0
11-15	16.0	20.2	11.9	14.7	15.5
16-20	16.0	8.9	11.9	7.3	10.6
over 20	28.0	11.4	15.8	9.8	14.6
Number of observations	25	79	101	41	246

Figure 34. The relationship between diurnal and nocturnal foraging activity (related to tidal height) of a territorial subpopulation of African Black Oystercatchers at Marcus Island



during the same period: daytime counts were of 51, 13 and 20 birds and the corresponding counts at night were of 65, 119 and 51 respectively. This suggests that there was greater tendency to form communal roosts at night.

Although foraging activity at night was slightly less than by day at corresponding tidal levels, 10 % more of the time spent on the area at night was utilized for foraging than by day (Table 36). The difference between overall diurnal and nocturnal activity partitioning on the territory was highly significant ($X^2 = 18.38$; $p<0.001$).

The relationship between the percentage of birds foraging and predicted tidal height is shown for both day and night (Fig. 34). By day, feeding occurred over the tidal range 0.38 - 1.74 m while at night birds fed only between o.41 m and 0.99 m. Within these limits the rate of tidal rise and fall is very close to linear (Fig. 33) therefore the tidal scale may be considered as a time scale. The ratio of the areas under the two regression lines is the ratio of diurnal to nocturnal foraging activity. This ratio is 1.7, alternatively birds feed 0.59 times as much as by night as by day. The foraging activity ratio relates only to the amount of time spent foraging and does not take into account any variations in foraging efficiency that may exist between day and night.

The moon was close to full during the three nights of observation: on the first and second nights the sky was clear and the feeding area was partly illuminated. On the third night the sky was overcast but the extent of foraging activity remained almost identical to that of the previous night (Table 36).

Territorial commitment

TABLE 36. A COMPARISON OF DIURNAL AND NOCTURNAL ACTIVITY PARTITIONING BY AFRICAN BLACK OYSTERCATCHERS IN AN AREA OCCUPIED BY TERRITORIAL BIRDS. ACTIVITY IS EXPRESSED AS A PERCENTAGE OF TIME SPENT IN THE AREA DURING THREE CONSECUTIVE DAYS AND NIGHTS

Day	Foraging	Roosting	Sitting	Preening	Bathing	Alarm	Vocal display	Walking	Other
1.	44.8	12.9	13.8	17.4	0.5	2.6	1.1	6.0	0.9
2.	40.0	25.8	4.5	20.7	0.6	0.9	1.9	5.1	0.5
3.	33.7	21.5	10.8	20.0	1.0	2.5	0.9	8.3	1.3
Mean	39.6	20.3	9.5	19.4	0.7	2.0	1.4	6.4	0.8
Night									
1.	65.6	13.6	0.0	7.9	0.3	1.7	2.6	6.6	1.7
2.	44.9	25.8	0.4	18.6	0.2	5.2	0.2	3.8	0.9
3.	43.4	28.0	0.3	19.3	0.0	2.4	0.3	5.0	1.3
Mean	49.5	23.5	0.2	16.2	0.2	3.5	0.8	4.9	1.2

Territorial commitment, expressed as a percentage of the daylight period spent on the territory, varied from 92.6 % to 14.8 %, with an overall mean of 53.7 % (10 birds) (Table 37). There was little variation between members of a pair, but considerable variation between pairs. Including the night, when occupancy of the area was 41.7 % of daytime occupancy, the overall territorial commitment in 24 h was 31.8 %. There was a tendency for time spent foraging to decrease progressively once territorial commitment exceeded 60 % (Fig. 35). This could be interpreted as meaning that a 60 % territorial commitment is the threshold for satisfying feeding requirements on the territory. Data do not exist to verify this hypothesis. Data are for daytime only and the sample is of 30 "bird days".

Communal roosting behaviour

There was a greater tendency for birds to roost communally by night than by day. Activity partitioning at the roost was compared with activity partitioning on the territory (Table 38). The difference in behaviour at the communal roost and on the feeding area when the intertidal zone was inundated was significant (X^2 = 64.9. $p<0.001$). There was more aggressive behaviour at the communal roost (X^2 = 12.96; $p<0.001$) and more preening and bathing activity (X^2 = 34.77; $p<0.001$).

Behavioural sequences and associations

In all instances, except that of aggressive behaviour, the behaviour at time X+5 minutes was mostlikely to be the same as the behaviour at time X. Alarm or display behaviour was most likely to be followed by foraging (Table 39). The predictability of aggressive behaviour was less than other categories since it

TABLE 37. THE EXTENT OF COMMITMENT OF FIVE PAIRS OF AFRICAN BLACK OYSTERCATCHERS TO THEIR TERRITORIES AS DETERMINED OVER THREE SUCCESSIVE 12 HOUR DAYTIME PERIODS OF OBSERVATION

Pair number	Sex	% of time on the territory			Overall commitment (%)
		Day 1	Day 2	Day 3	
1.	M	81.3	95.1	100.0	92.1
	F	93.1	90.3	94.4	92.6
2.	M	71.5	66.0	85.4	75.5
	F	74.3	68.1	86.8	76.4
3.	M	49.3	81.9	46.5	59.2
	F	47.2	79.2	59.0	61.8
4.	M	29.2	27.8	19.4	25.5
	F	16.7	25.0	17.4	19.7
5.	M	2.1	27.8	14.6	14.8
	F	6.3	27.1	26.0	19.8

Figure 35. The relationship between territorial commitment and time spent foraging on the territory for five pairs of African Black Oystercatchers at Marcus Island. The curve is fitted by eye

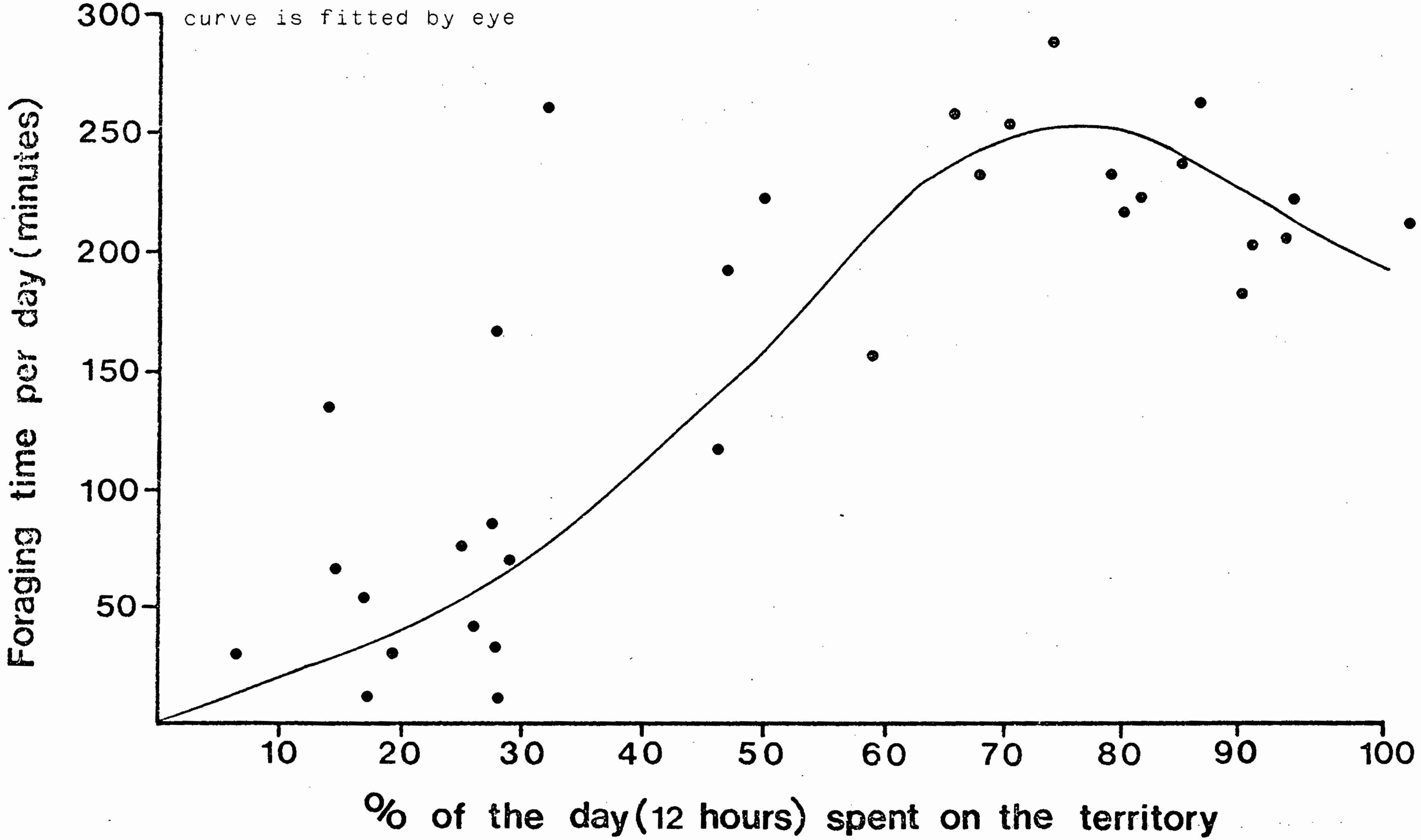


TABLE 38. A COMPARISON OF THE DIURNAL ACTIVITY PARTITIONING OF AFRICAN BLACK OYSTERCATCHERS IN THREE DIFFERENT SITUATIONS: i. BIRDS ON THE TERRITORY WHEN THE INTERTIDAL ZONE IS EXPOSED; ii. BIRDS ON THE TERRITORY WHEN THE INTERTIDAL ZONE IS FLOODED; iii. BIRDS AT A COMMUNAL ROOST AWAY FROM THE TERRITORY

Situation	% time				Sample size
	Foraging	Roosting/ sitting	Preening/ bathing	Alarm/ display	
i	37.0	34.4	19.9	8.7	7 944
ii	0.5	83.2	15.2	1.1	607
iii	0.0	66.2	29.4	4.4	1 543

TABLE 39. AN ANALYSIS OF THE PROBABILITY OF A PARTICULAR FORM OF BEHAVIOUR OF AFRICAN BLACK OYSTERCATCHERS AT TIME X BEING FOLLOWED BY THE SAME OR A DIFFERENT FORM AT TIME X + 5 MINUTES. STANDARD DEVIATIONS IN PARENTHESES.

Behaviour at time X + 5 minutes	Behaviour at time X			
	Foraging	Roosting/ sitting	Preening/ bathing	Alarm/ display
Foraging	0.666 (0.058)	0.071 (0.333)	0.191 (0.074)	0.490 (0.116)
Roosting/ sitting	0.073 (0.037)	0.753 (0.118)	0.317 (0.093)	0.235 (0.151)
Preening/ bathing	0.144 (0.074)	0.135 (0.048)	0.448 (0.091)	0.065 (0.072)
Alarm/ display	0.117 (0.054)	0.041 (0.059)	0.044 (0.043)	0.210 (0.143)

was extrinsically determined by the number of birds present in the area during the day. Data are computed from 1 844 sequential observations of behaviour. Aggressive behaviour was strongly associated with foraging (the lower part of the tidal cycle), and preening and bathing activity was associated with resting (the higher part of the cycle) (Table 40).

DISCUSSION

No detailed quantitative analysis of activity partitioning by any species of oystercatcher exists beyond analysis of the foraging component (e.g. Heppleston, 1971), discussion is therefore centred on this aspect.

Activity and the tidal cycle

All species of oystercatchers studied to date exhibit a bimodal pattern of feeding activity-which peaks before and after low water (Tinbergen & Norton-Griffiths, 1964; Baker, 1974a; Hartwick, 1978). In the case of the American Black Oystercatcher H. bachmani low tide appears to be a period of low food availability, especially in the summer when most of the intertidal zone dries out at low tide and molluscs are available only in pools (Hartwick, 1978). Foraging activity of the African Black Oystercatcher does not diminish during the slack water period (Fig. 31). The reason for continued foraging activity is probably the narrow tidal range: only a small swell is required for much of the intertidal zone to be dampened regularly, especially during neap tides when the tidal range is only 0.5 m. Additionally, food is always available at the tide's edge since many of the mollusc species consumed extend their distribution infratidally (pers.

TABLE 40. ASSOCIATED BEHAVIOURAL PATTERNS OF AFRICAN BLACK OYSTERCATCHERS AND THE CORRESPONDING ASSOCIATION INDEXES

Positive association	Neutral association	Negative association
Foraging & Alarm/ display	Foraging & Preening /bathing	Foraging & Roosting/ sitting
1.674	0.944	0.672
Roosting/ sitting & Preening/ bathing	Roosting/ sitting & Alarm/ display	Preening/ bathing & Alarm/ display
1.466	0.823	0.294

obs.).

When the relationship of foraging activity to tidal height was compared for the whole population and the sub-population, overall foraging activity in the former was less (Figs. 30, 32). The reason for this is a bias created in favour of resting birds higher up the shore during scans of the whole island: The physical nature of the shoreline is such that some foraging birds either escaped observation or were disturbed and therefore were excluded from the sample.

During storm conditions when birds relied almost exclusively on invertebrates torn from the substratum and washed ashore, there was a decrease in foraging efficiency resulting in an increase in time spent foraging (Table 33). The resting component of activity remained unchanged ($X^2 = 0.92$; $p>0.1$) when compared to calm conditions, but the preening and bathing component, an energetically costly behaviour, was significantly reduced ($X^2 = 121.08$; $p<0.001$). This presumably acts as a form of energy conservation counterbalancing the decrease in foraging efficiency. Only during storm conditions did the proportion of time spent foraging exceed 50 % (Table 33). However, this figure cannot be directly related to the proportion of time spent foraging by an individual.

During the boreal winter, the European Oystercatcher <u>H</u>. <u>ostralegus</u> spends an average of 93.1 % of available time foraging by day (Heppleston, 1971). The mean figure for the sub-population of African Black Oystercatchers observed was 37.3 %. The figures for the two birds with a very high territorial commitment were 31.3 % and 29.1% for male and female respectively. All figures relate to daytime only, and in the case of the African Black Oystercatcher, remained constant independent of the tidal regime. Over the 24 h period, these two birds foraged for an average of 346 minutes: the corresponding figure for the European Oystercatcher, using data from Heppleston (1971) and assuming nocturnal and diurnal feeding rates are equal for the latter species, is 837 minutes in 24 h. This implies that the European Oystercatcher takes 2.4 times as long as the African Black Oystercatcher to satisfy its daily energy demands. The European Oystercatcher weighs approximately 500 g during the boreal winter (Heppleston, 1971): data are not available for the masses of African Black Oystercatchers during the austral winter. During the austral summer, African Black Oystercatchers have a mean mass of 694 g (Part 2.1) as compared with a mean mass for incubating European Oystercatchers of 518 g (Harris, 1967). From this mass difference, the implication is that the African Black Oystercatcher can forage more efficiently than the European Oystercatcher, probably due to high intertidal invertebrate biomass and diversity found at the islands where they occur.

Nocturnal behaviour and the adaptiveness of communal roosting

The ratio of nocturnal to diurnal foraging activity in the African Black Oystercatcher was 0.59. Three estimates of this ratio have been made for the European Oystercatcher: 0.50 (Drinnan, 1958), 0.58 (Heppleston, 1971) and 0.86 (Hulscher, 1974). All three ratios were based on studies of captive birds. Heppleston's estimate of 0.58 agrees very closely with the ratio of 0.59 obtained from this study. No field data are available for comparison.

The greater tendency to form communal roosts at night is probably an anti-predator strategy. Most shore birds, including those holding territories, respond to predators by flocking and communal roosting of territorial shorebirds by night is common (Myers *et al.*, 1979). Little is known regarding predation pressure on fully grown African Black Oystercatchers under natural conditions. At Marcus Island there is a single record of predation by a Peregrine Falcon *Falco peregrinus* (J.C. Sinclair, pers. comm.) and strong circumstantial evidence of appreciable predation (Cooper, Hockey & Brooke, in press; Part 4.3) by two nocturnal species of mammal, the Small Spotted Genet *Genetta genetta* and the Cape Fox *Vulpes chama*. Both species are known predators of birds (Haltenorth & Diller, 1980). In each instance, a spate of oystercatcher deaths ceased when the mammal was trapped and removed (Cooper, Hockey & Brooke, in press). At Dassen Island (33 25S, 18 06E) the Feral House Cat *Felis catus* is a nocturnal predator of adult African Black Oystercatchers (Cooper, 1977). It is likely that the major threat to African Black Oystercatchers is from mammalian predators and occurs at night.

Territorial birds leave the feeding area at night while the tide is still low enough to permit foraging (Fig. 34). Foraging efficiency may be lower by night than by day and a point arises at mid-tide when the benefits of continued foraging are no longer balanced with the birds' need to rest and the potential risk of predation: therefore it would be more adaptive for birds to form a communal roost where they can rest. Individual roosting birds would need to remain very much more alert at night and by virtue of "safety in numbers" birds may roost more efficiently in a flock. Alternatively, as the tide rises, birds are pushed closer to the vegetation line where cover for nocturnal predators is greater and therefore risk to the individual may be increased. African Black

Oystercatchers are by nature very alert and the probability of succumbing to a nocturnal predator low on the intertidal zone is small. No quantitative data exist to describe behaviour at a night roost, although the level of vocalization appeared to be less than by day and birds were more tightly spaced in the flock. Both behaviours may be regarded as adaptive anti-predator strategies.

Daytime communal roosts form on islands where there are no terrestrial predators (Part 4.3), presumably nocturnal roosts also form in these places. This behaviour probably has its adaptive origins on the mainland. Some birds from Vondeling Island (33 09S, 17 59E), which has no mammalian predators (Cooper, Hockey & Brooke, in press), leave the island at high tide and form a roost at a sandy spit on the adjacent mainland 1 km away (Part 4.3). This behaviour seems maladaptive and suggests that birds living on islands have at some time been exposed to predation threat on the mainland: ringing data show that the majority of juveniles disperse from islands to the mainland within the first five months of life. [illegible] The question of communal roosting and its adaptive function in African Black Oystercatchers is considered in more detail in Part 4.3.

Behavioural associations and predictability

Aggressive interaction is primarily associated with foraging during the lower part of the tidal cycle. Birds that remain in their territories at high tide tolerate the presence of close territorial birds (as the tide rises, the territorial birds are pushed closer to one another).

Seasonal fluctuation in energy demand

This paper has not considered the seasonality of energy partitioning. The activity partitioning of any bird ultimately is determined by the time taken to satisfy its daily and seasonal energy demands. During the seasonal cycle, certain physiological functions such as moult, reproduction and the pre-migratory deposition of fat demand energy surplus to normal maintenance requirements (Murton & Westwood, 1971). When compared with the European Oystercatcher, seasonal fluctuations in energy demand of the African Black Oystercatcher theoretically are small for the following reasons.

The African Black Oystercatcher is non-migratory, though some local movement occurs (Part 1.2), whereas part of the European Oystercatcher population migrates from its breeding grounds in the Western Palaearctic as far south as the coasts of Ghana and Tanzania, the Arabian Sea, southeast China and Japan (Moreau, 1972), occasionally reaching South Africa (McLachlan & Liversidge, 1978; Appendix 1.1). The African Black Oystercatcher does not experience the climatic extremes of the boreal winter and the associated metabolic stress (Heppleston, 1971; Marcstrom & Masher, 1979). The primary moult period of the European Oystercatcher is six months (Dare & Mercer, 1974), whereas that of the African Black Oystercatcher extends for at least eight months (Summers & Cooper, 1977). The normal three-egg clutch of the European Oystercatcher accounts for 26 % of female body mass (Summers & Cooper, 1977) and is therefore a greater energetic investment than the two-egg clutch of the African Black Oystercatcher which accounts for approximately 15.4 % of female body mass (Parts 2.1, 5.2). Reproduction, and the subsequent care of the chicks, is likely to be the primary seasonal energy demand of the African Black Oystercatcher. The ability of the species to replace clutches rapidly after loss (Part 5.2) suggests that when a short term energy demand arises the birds are able to satisfy it quickly.

In conclusion, major seasonal energy demands probably do not exist, except for a slight increase at egg laying and subsequent incubation and care of the young. The large amount of unutilized foraging time, even during the winter months, renders it unlikely that the birds ever suffer metabolic stress. One exception to this may be during extended periods of heavy swell in areas where large infratidal mussel beds do not exist. During one such storm in 1976, the numbers of African Black Oystercatchers at Marcus Island more than quadrupled, to approximately 600 birds, which fed on stranded mussels (J.C. Sinclair, pers. comm.): these birds may have been experiencing a temporary food shortage elsewhere.

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Part 4.3. Communal roosting by African Black Oystercatchers and its probable adaptive significance.

Ornis Scand (submitted)

INTRODUCTION

A communal roost may be defined as a place for resting or sleeping where many animals converge which have been feeding solitarily or in flocks which are not of constant composition (Ward & Zahavi, 1973). Communal roosting by birds is a well-recognized phenomenon, but only in the last 20 years have hypotheses been put forward to explain its adaptive function. There are at least four main schools of thought regarding this, not necessarily mutually exclusive:

1. It assists in population regulation through epideictic displays (Wynne Edwards, 1962).
2. It confers physiological advantages on participating individuals (Bremner, 1965; Francis, 1976).
3. It is a form of anti-predator behaviour (Lack, 1966).
4. It serves as an information centre permitting efficient exploitation of patchily distributed prey (Ward & Zahavi, 1973; Krebs, 1974).

The African Black Oystercatcher _Haematopus_ _moquini_ is a communally roosting bird with a different social organization to any considered previously: it is a resident, territorial wader which joins communal roosts at high tide during the nonbreeding season but does not breed communally (Parts 4.2, 5.2). This paper examines characteristics of its roosting behaviour and interprets the possible adaptive significance of communal roosting by this species in the light of theories 2-4 above. Theory 1 involves the acceptance of an important rôle for group selection which is a generally discredited theory (Dawkins, 1976; Krebs & Davies, 1978), and is not considered further here.

STUDY AREA AND METHODS

The study area lay along the coast of southern Africa between Pelican Point (22 53S, 14 27E), South West Africa/Namibia and Dwesa (32 18S, 28 50E), Transkei, a region containing more than 99 % of the world population of the African Black Oystercatcher (Part 1.2). During 1980-81 one or more counts were made at diurnal high tides at each of 35 roost sites within this area. More regular counts, up to 10 in total, were made at those roosts between St Helena Bay and Cape Town. Certain physical characteristics of roost sites were recorded: exposure relative to the adjacent coast (<, = or >), the substratum, slope (ranked on a scale of 0 (flat) to 3 (steeply sloping)), the distance from the Mean High Water Mark at Spring Tides (MHWMS), and the presence of nearby offshore rocks.

A total census of African Black Oystercatchers along 74.5 km of shore north of Mauritz Bay was made during January 1981 by the Western Cape Wader Study Group. A comparison of this census with counts at the nine roosts located in this area allowed an estimate to be made of the proportion of the mainland population that joins diurnal roosts.

More detailed observations of both diurnal and nocturnal activity were carried out at a roost in Saldanha Bay (33 03S, 17 58E) using the Instantaneous Group Scan Technique (Altmann, 1974) at five minute intervals. These were compared with activity of individuals from the same population which remained on their feeding territories at high tide. Night observations were made using a KOT 1 Image Intensifying binocular. Further frequent counts were made at another roost in Saldanha Bay, at Hoedjies Point, that formed during the 1979/1980 breeding season and comprised mainly nonbreeders and failed breeders.

Finally, use was made of a natural experiment at Marcus Island, Saldanha Bay. In 1976, this island, previously predator-free, was joined to the mainland by a large causeway as part of harbour developments. This allowed access to terrestrial mainland predators which could not be fully controlled by trapping. The seasonality of their predation on African Black Oystercatchers was recorded between June 1979 and March 1982.

RESULTS

Roost site

Roost sites, to which there was very high fidelity, had a number of common physical features (Table 41). They tended to be sited on either small promontories (west coast) or at river mouths (southeast coast). On the west coast roosts normally were adjacent to the high water mark whereas southeast coast roosts were sometimes several hundred metres from the sea's edge. Near Cape Town, where the coast is heavily disturbed, roosts were recorded at two coastal wetlands, Rietvlei and Strandfontein Sewage Works. Roosts on promontories usually were sited so that exposure to prevailing weather was less than on the adjacent coast. The substratum of roost sites varied, but sandy and shell-covered sections of predominantly rocky areas were frequently used. Seventy-six percent of west coast roosts were sited adjacent to offshore rocks to which birds flew regularly if disturbed. Southeast coast roosts tended to be in flat areas with extensive all round visibility.

African Black Oystercatchers normally formed monospecific roosts,

TABLE 41

Details of roost sites and roost sizes for 35 African Black Oystercatcher roosts around the southern African coast

Location	Grid ref.	Relative exposure	Substratum	Slope (0-3)	Offshore rocks?	No. of counts	Min. count	Max. count	Mean count	Month of max. count	Distance to MHWMS (m)
Pelican Point, SWA	22 53'S,14 27'E		sand	1	no	2^{+}	40	44	42	01	0
Penguin Is., SWA	26 37'S,15 09'E	=	rock	2	yes	1^{+}			24	(03)	1
Grossebucht, SWA	26 44'S,15 06'E		rock & shell	1	yes	1^{+}			25	(03)	0
St. Helena Bay	32 46'S,18 02'E	=	rock	1	yes	3	0	17	6	07	0
Shell Bay Point	32 42'S,17 58'E		sand & shell	1	yes	10	5	41	19	07	0
Britannia Bay	32 42'S,17 58'E	=	sand	1	no	7	0	11	2	07	0
Grootpaternoster -punt(x)	32 44'S,17 53'E	=	sand	1	yes	10	2	43	16	06	0
Steenbrasbaai (x)	32 44'S,17 53'E		sand	1	yes	10	0	48	13	09	0
Paternoster	32 46'S,17 54'E		shell	1	yes	3	3	13	9	08	0
Cape Columbine	32 50'S,17 50'E		sand & shell	1	yes	8	0	22	5	07	0
Duminy Point	32 54'S,17 52'E	=	sand & shell	1	yes	7	2	16	9	08	0
Hospital Point	32 58'S,17 53'E		sand	2	yes	8	2	20	9	06	0
Mauritz Bay	32 59'S,17 53'E		stones	0	yes	8	0	28	13	06	0
North Bay	33 02'S,17 56'E		rock	1	no	1			10	(07)	0
Klein Island beach	33 08'S,18 00'E		sand	1	yes	5	36	103	69	04	0-15
Schaap Island	33 21'S,18 09'E	=	rock	2	yes	6	8	24	17	04,06	10
Rietvlei	33 50'S,18 30'E		grass	0	no	1			13	(01)	400
Kommetjie	34 08'S,18 19'E	=	rock	0	yes	2	8	11	10	05	10
De Mond	34 14'S,18 22'E		sand	0	no	1			17	(08)	5
St. James	34 07'S,18 27'E		rock	1	yes	8	8	13	10	09	0-5
Strandfontein A	34 06'S,18 31'E		sand	2	no	3	16	19	18	04	150
Strandfontein B	" "	=	sand	0	no	2	10	14	12	09	10
Strandfontein C	" "		hard grit	0	no	1			8	(04)	100
Cape Agulhas	34 50'S,20 01'E		sand	2	yes	1			19	(06)	2
Struispunt	34 41'S,20 14'E	?	rock	1	?	1			22	(07)	?
Koppie Alleens	34 29'S,20 31'E	?	?	?	?	1			12	(07)	?
Holkom Meester se baai	34 23'S,21 48'E	?	rock	?	?	1			7	(07)	?
Kleinbrak River	34 05'S,22 09'E		sand	0	no	1			5	(09)	100
Goukamma	34 03'S,22 52'E		sand	1	no	1			5	(09)	0
Kabeljous River	34 00'S,24 56'E		sand	0	no	1			8	(09)	100
Gamtoos Lagoon A	33 58'S,25 04'E		sand	0	no	2	14	16	15	(09)	500
Gamtoos Lagoon B	" "		sand	1	no	1			7	(09)	500
Van Stadens River	33 58'S,25 13'E		sand	0	no	3	5	13	10	(09)	60
Maitland River	33 59'S,25 18'E		sand	1	no	2	6	13	10	(09)	10-60
Dweza, Transkei	32 18'S,28 50'E	=	rock	0	no	5	8	17	14	(09)	0

( ) = counts made only during one month. + = summer counts only available. (x) = interchangeable roosts but occasionally roosted with cormorants, gulls, terns and other waders.

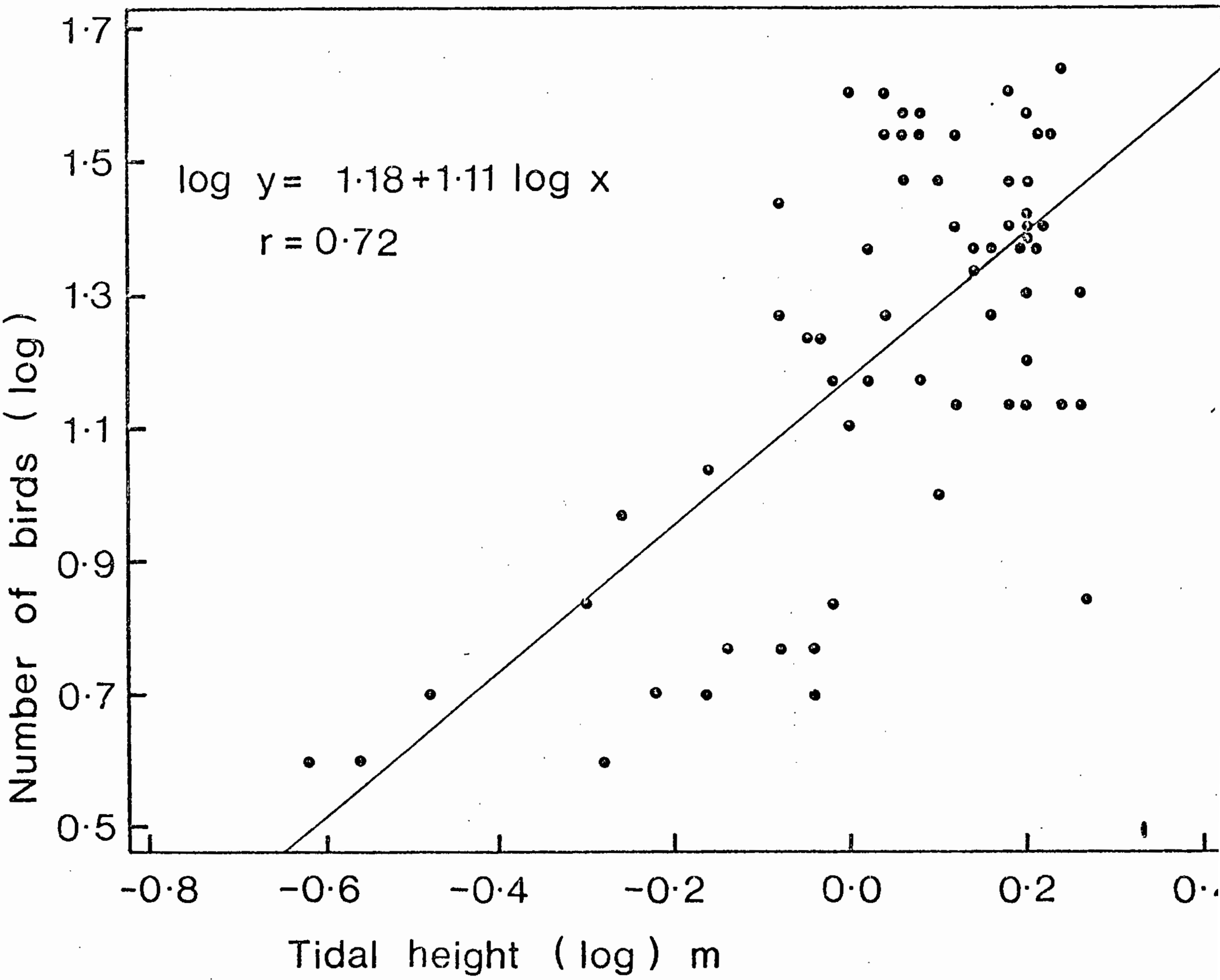
Roost size

Diurnal roosts generally were small and variable in size. Of 16 roosts counted on more than three occasions, only one, at Klein Island beach, regularly contained more than 50 birds, and the mean number at all roosts was 15 ± 15 (S.D.) birds (Table 41). Numbers at individual roosts fluctuated greatly, and in most cases, maximum numbers were recorded between June and August, i.e. the middle of the nonbreeding season. At five out of nine roosts censused regularly, maximum counts coincided with heavy swell conditions. The four most regularly occupied winter roost sites were all unused during early February 1982, the middle of the breeding season (Part 5.2). No individually colour ringed birds were recorded at more than one roost site.

In comparison with the population census of 261 birds for the 74.5 km of shore north of Mauritz Bay, maximum counts at the nine roosts found in this area totalled 242 birds (93 %) and mean counts 105 birds (40 %). Assuming strong roost fidelity this indicates that most birds use communal roosts at least occasionally.

In addition to gross seasonal variation, roost size also varied considerably in relation to both tidal height and time of day. The increase in numbers of birds present with increasing tidal height is well demonstrated by the frequent counts made at the Hoedjies Point roost (Fig. 36). Observations at another Saldanha Bay roost showed that a greater proportion of the population joined communal roosts by night than during the day. This roost,

Figure 36. The relationship of the number of African Black Oystercatchers at a roost at Hoedjies Point, Saldanha Bay, to the predicted tidal height



situated on the causeway leading to Marcus Island, contained 51, 13, and 20 birds at high tide on three consecutive days, and 65, 119 and 51 birds on the corresponding nights (Part 4.2).

The presence of birds at island roosts appeared to be less predictable than at mainland roosts, with the exception of a roost at Dassen Island where introduced Feral House Cats *Felis catus* are present (Cooper, 1977). Occasionally, island birds join mainland roosts and *vice versa*. Some birds from Vondeling Island fly to the mainland Klein Island beach roost, while in South West Africa/ Namibia, some of the birds roosting on Pomona (27 11S, 15 15E) and Halifax (26 37S, 15 04E) Islands, originate on the mainland. Vondeling Island is 1 km from the mainland, and Pomona and Halifax Islands are both less than 500 m from the mainland.

Behaviour at the roost

Subjective observations indicated both that mainland roosts generally were more tightly packed than island roosts, and that birds roosted closer together in nocturnal than in diurnal roosts. In addition, birds roosted for longer at night, leaving their territories at a lower tidal level than during the day, and were less vocal (Part 4.2). Birds roosting communally at high tide spent more time involved in agonistic displays than birds which remained on their feeding territories (Part 4.2). Agonistic displays at roosts normally are triggered by birds arriving at a roost or by disturbing the roost (pers. obs.). They normally take the form of piping displays (Heppleston, 1970), often preceded by pseudo-sleeping (Williamson, 1950). The pseudo-sleeping posture is often adopted by both members of a pair when one returns from outside the territory and appears to be a precautionary measure adopted during a brief "recognition period". When a roost has reached maximum size (i.e. no more birds are arriving) the level of aggression diminishes (pers. obs.).

Predation

Reactions of roosting African Black Oystercatchers to natural predators have not been observed, but light aircraft flying close to a roost or overflying islands where oystercatchers are abundant, invariably elicited a highly vocal aerial flocking response. There is strong circumstantial evidence that the principal predators of African Black Oystercatchers are nocturnal, terrestrial mammals such as the Cape Fox Vulpes chama and the Small Spotted Genet Genetta genetta (Cooper, Hockey & Brooke, in press). The abundant diurnal Cape Grey Mongoose Herpestes pulverulentus may be an important predator of eggs on the mainland, and is capable of killing birds the size of oystercatchers (Haltenorth & Diller, 1980). A pair of African Black Oystercatchers was seen to react to the presence of a Cape Grey Mongoose in their territory by running towards the animal with wings slightly raised, head down and bill pointing forward.

At Marcus Island, carcasses of 28 African Black Oystercatchers killed by mammalian predators (approximately 23 % of the resident population) were found over a period of 33 months (Table 42). Seventeen of these were killed between December and March, the peak of the breeding season (Part 5.2). This increased predation pressure during the breeding season was significant ($X^2 = 9.46$; $p<0.01$). Only one carcass, found in June, was recovered at a roost site on the island (an area where there are also several pairs of territorial residents). All other carcasses were found on or near the territories of the

TABLE 42

Monthly mortality of African Black Oystercatchers at Marcus Island, southwestern Cape, South Africa between June 1979 and March 1982

	BREEDING SEASON					NON-BREEDING SEASON						
Month	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct
No. of carcasses	1	0	6	6	5	2	0	2	0	2	0	4

birds concerned. In the breeding season at high tide, the non-incubating member of a pair normally roosted close to the incubating adult.

DISCUSSION

At least two physical features common to roosts tend to reduce risk from predators. Firstly, a site at the water's edge on a promontory minimizes both access routes for terrestrial predators and vegetation cover available to them. Secondly, offshore rocks minimize the distance birds have to fly to escape terrestrial predators; oystercatchers do not roost on these rocks habitually, probably because they are often washed over by swells or, if large, are used as roosts by cormorants.

Strong roost fidelity of individuals suggest that they utilize the nearest available roost to their territories and are therefore regularly in contact with the same individuals. Roosts are small when compared with many other wader species (Hale, 1980), and the area from which roosting birds are drawn is restricted as indicated by the close spacing of roosts (one per 8.3 km on 74.5 km of coast in the southwestern Cape). Roosts theoretically should function most efficiently as information centres when their members are drawn from a large number of feeding stations (Ward & Zahavi, 1973). There is only slim evidence, even under conditions of food shortage, that roosts of 1 000+ corvids act as functional information centres (Loman & Tamm, 1980). The facts that African Black Oystercatchers feed largely territorially, with only limited feeding performed elsewhere (Part 4.2) and form only small roosts drawn from restricted areas render it unlikely that their roosts could be of importance as information centres.

Gross seasonal variation in diurnal roost size can be explained simply: during the breeding season most birds are committed to eggs or chicks throughout the day. Shorter-term variations in patterns of diurnal roost occupancy are at least partly explained by tidal amplitude variations, though there appears to be a threshold tidal height above which the correlation with numbers at the roost is less strong (Fig. 36). Nevertheless, fluctuations in numbers at the roosts were recorded at high spring tides, indicating that even under these conditions not all of the population joins a roost. Subjective observations indicated that high counts at roosts often coincided with heavy swell, which also affected the extent of territory flooding. This suggests that diurnal roosting may be a function of territory flooding, with the benefits of joining a daytime roost being balanced against the benefits of continued foraging on a partially flooded territory and the need to defend a diminishing territory. This contrasts with the behaviour of nonbreeding European Oystercatchers _H. ostralegus_ where counts made at diurnal roosts and during the feeding period agree closely (Goss-Custard, 1981).

By night the pattern is different and a higher proportion of the population joins roosts and birds roost for longer, consistently leaving their feeding territories at mid-tide. Nocturnal roosts are tightly packed and normally silent and birds roosting at night are far less approachable than during the day (Part 4.2): tight packing may conserve heat and silence may be a result of birds sleeping or serve to reduce roost advertisement to predators. The earlier departure to roosts at night may also be explained in terms of predation risk. Foraging efficiency may be lower at night and a point arises at mid-tide when the benefits of continued foraging are no longer balanced with the birds' need to rest and the risk of predation, which presumably increases as birds are pushed by the tide closer to the vegetation line.

Perhaps the strongest evidence supporting the importance of roosts in reducing predation is provided by the demonstration that predation was highest at Marcus Island during the breeding season when mean roost size effectively is reduced to two and incubating birds must remain with their nests high up on the shore. Nests of African Black Oystercatchers normally are distributed linearly along the shore (Part 5.3) and, depending on the direction of approach of a predator, a maximum of one pair of adjacent conspecifics can give warning of the danger (see Horn, 1968). Assuming mammalian predators pounce rather than chase, this combination of decreased vigilance and increased vegetation cover is probably crucial to their success. Mainland birds in South West Africa/Namibia which fly to predator-free offshore islands to roost avoid regular disturbance by Blackbacked Jackals *Canis mesomelas* which are abundant and active throughout the day in undisturbed areas (Haltenorth & Diller, 1980). The behaviour of the Vondeling Island birds remains an enigma.

To sum up, roosting in African Black Oystercatchers apparently confers adaptive advantage by reducing the level of predation, and may confer physiological advantage at night through close packing and heat conservation. There is no evidence that these roosts could act as efficient information centres: indeed, it is difficult to see how roosts can act as information centres for any species which is territorial throughout the year and does not feed communally. In order to establish feeding areas, individuals of such species must either displace resident birds from established territories or occupy vacant areas - in neither instance is information transmission at the roost relevant. The theory is also inapplicable to species which feed in large groups during the day but disband to roost in smaller groups at night such as Hadeda Ibis *Bostrychia hagedash* and Helmeted Guineafowl *Numida meleagris* (Skead, 1951, 1962).

Whether this interpretation of roosting behaviour can be extended to waders as a whole is doubtful as there are several facets of the African Black Oystercatcher's roosting behaviour that are atypical of waders, e.g. small roost size and lack of roost advertisement (Hale, 1980). However, species of similar social organisation, such as the Whitefronted Plover *Charadrius marginatus* probably have evolved communal roosting for similar reasons as the African Black Oystercatcher (Summers & Hockey, 1980).

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Part 4.4. Growth and energetics of the African Black Oystercatcher *Haematopus moquini*.

Ardea (in press)

INTRODUCTION

Oystercatchers (Haematopodidae) are subprecocial birds (Skutch, 1976): chicks leave the nest soon after hatching and are fed by the adults until after fledging. Behavioural aspects of the organization and development of parental feeding in the European Oystercatcher *Haematopus ostralegus* have been studied intensively, but almost nothing is known of the energetics of growth in oystercatchers or of the energy requirements for free living (Lind, 1961; Norton-Griffiths, 1969). This study aims to quantify both the growth rate of the African Black Oystercatcher *Haematopus moquini* and the energy requirements for growth and maintenance. Additionally it aims to quantify energy return to the system in the form of guano, and to calculate energy requirements of free living adults based on a knowledge of maintenance requirements and activty rhythms (Part 4.2).

METHODS

Growth rates of wild chicks (exposed culmen and tarsus to the nearest 0.1 mm, wing (flattened chord) to the nearest 1 mm and mass to the nearest 1 g) were recorded at Marcus Island (33 03S, 17 58E) and the adjacent mainland during the 1979-1980 breeding season. When possible, measurements were made at daily intervals, but the problems in locating chicks among granite boulders meant that not every chick was caught daily. During the study period one chick was kept in captivity at Marcus Island: it was less than 24 h old when captured on 20 February 1980, and its growth rate was monitored as for wild chicks. During the first seven days this chick was kept in an artificially heated environment; subsequently the chick was kept outside (uncaged) during the day and in a well ventilated room at night. Details of temperatures during the study period at nearby Cape Columbine (32 49S, 17 50E) are given in Table 43. The chick was fed _ad lib_. with natural food, and water was always available for drinking and bathing. During the first seven days it was fed on the intertidal polychaete _Pseudonereis variegata_ and black mussels _Choromytilus meridionalis_: subsequently, the limpet _Patella granularis_ comprised over 98 % of the diet. Limpets were chosen because the flesh can be removed easily and efficiently from the shell by hand. Fresh food was collected daily and only live animals were fed to the bird. Every 24 h emptied shells were collected and measured (maximum length to the nearest 1 mm). Regressions of dry mass on length, and hence energy content, were calculated for _C. meridionalis_ and _P. granularis_. Energy values of worms were obtained by measuring wet weight before consumption, and converting to energy using a wet/dry weight ratio and the energy value of dry flesh.

Energy requirements for maintenance (ME) were obtained from the Marcus Island bird. Maintenance Energy was defined as Gross Energy Intake at a low level of activity. Energy intake was measured over a 48 day period at constant mass, during June and July.

In the 1981-1982 breeding season an additional four chicks were kept in captivity in Cape Town. They were fed exclusively on _P. granularis_ which had been stored frozed. None of these four chicks grew normally up to fledging and, although energy intake was monitored continuously, only energy intake during normal growth periods was used in calculations or plotted in figures.

The daily energy requirement of a free living bird was estimated

Table 43. Temperature (°C) recorded at Cape Columbine during the study period. (Data from monthly weather records, South African Weather Bureau, Department of Transport).

Month (1980)	Maximum recorded	Minimum recorded	Mean daily maximum	Mean daily minimum
February	29.5	10.4	21.4	13.2
March	27.6	10.4	21.0	13.5
April	25.0	10.2	19.3	13.0
May	24.0	8.3	17.5	10.7
June	26.6	4.8	16.8	10.2
July	25.0	5.2	18.2	10.1

from measured ME and a knowledge of diurnal and nocturnal activity rhythms (Part 4.2) with an additional component for flight. The allocation of correction factors applied to ME for various activities is problematical. Several calculations have been made for different species of birds using extensive subdivisions of activity, and consequently a plethora of conversion factors has emerged (e.g. Maxson & Oring, 1980; Mugaas & King, 1981). Mugaas & King (1981) conclude that flight is the major energetic consideration and conversion factors for other activities fall within a relatively narrow band. The errors inherent in estimating conversion factors render the value of fine separation doubtful (e.g. Schartz & Zimmerman, 1971; Mugaas & King, 1981). The following conversion factors were chosen for this study based on my own knowledge of the birds' behaviour (e.g. prey handling is a relatively high energy cost activity - Part 3.2) and using the conversion factors of Maxson & Oring (1980) and Mugaas & King (1981) as a guideline: resting (0.8 x ME), walking (1.0 x ME), foraging, including handling prey, (1.5 x ME), preening/bathing (1.5 x ME), agonistic behaviour (2.0 x ME) and flight (6.0 x ME). Measurements of activity were made at a time when day and night were of equal length (Part 4.2) and, for the sake of simplicity, this condition was assumed to apply throughout the nonbreeding season. The calculation of energy requirements for egg production was based on two assumptions: energy content of the eggs was 5.48 kJ per g fresh weight (Maxson & Oring, 1980) and the efficiency of egg production was 70 % (King, 1973). For the sake of conservatism, energy requirements for incubation were considered equal to DEE for nonbreeding birds as recent work has questioned whether incubation is an energy costly or energy saving behaviour (Walsberg & King, 1978). The energy cost of parental care was taken as DEE + 0.4 x DEE (Drent & Daan, 1980).

Assimilation efficiency ((energy in - energy out)/energy in) (%) was measured four times during the growth of the Marcus Island captive chick (7, 13, 18 and 24 days) and four times for a fledged subadult (Cape Town bird) at constant mass. For a 24 h period the birds were enclosed in a wire mesh cage suspended over a sheet of foil of known mass. Food and water were available _ad lib_. throughout the 24 h and all guano produced was collected, dried to constant mass, weighed and its energy content determined by bomb calorimetry.

RESULTS

Growth

The growth of wild chicks is shown in Figures 37 and 38. Birds fledged (first flew) at 35-40 days, when mass was approximately 450 g, 65 % of mean adult mass (Part 2.1). Tarsus growth was completed at approximately 45 days, but both culmen and wing were still actively growing at this stage, being approximately 70 % of mean adult dimensions (Fig. 38) (Part 2.1). Culmen growth was completed at _c_. 120 days, and wing growth at _c_. 75 days (captive bird). Maximum growth rate (absolute mass increment) of 15.6 g per day was achieved between 15 and 31 days, and growth rate slowed slightly immediately prior to fledging. All chicks lost weight in the first 48 h after hatching.

Of the five captive chicks, only one, the Marcus Island bird, maintained a growth rate representative of wild chicks up to and beyond fledging (Figs. 37, 39). All five captive chicks grew marginally slower than wild chicks after 15 days, but the general

Figure 37. Growth (mass) of wild African Black Oystercatchers (solid line) compared with growth of a captive chick (dotted line). Vertical bars indicate ranges and sample sizes

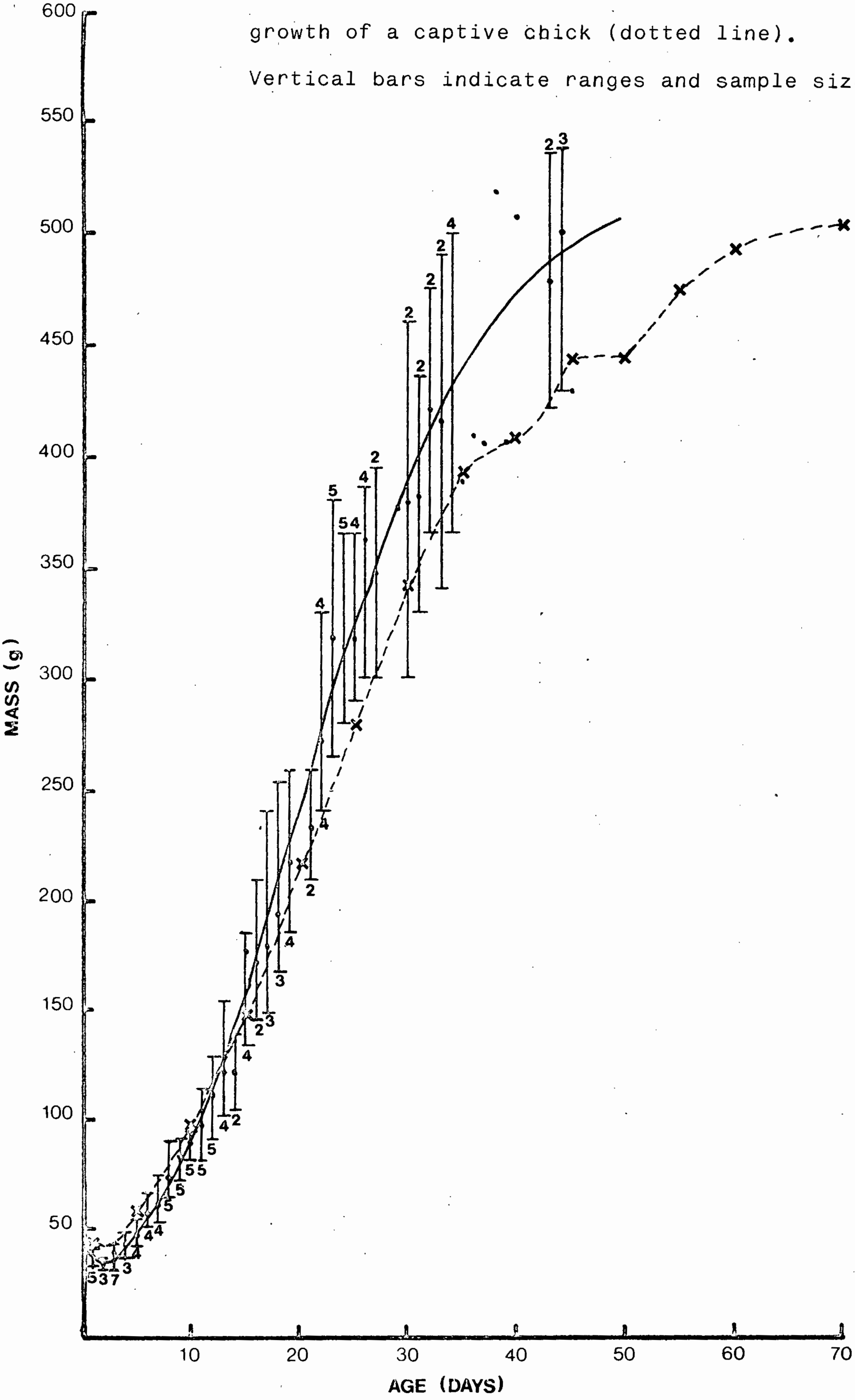
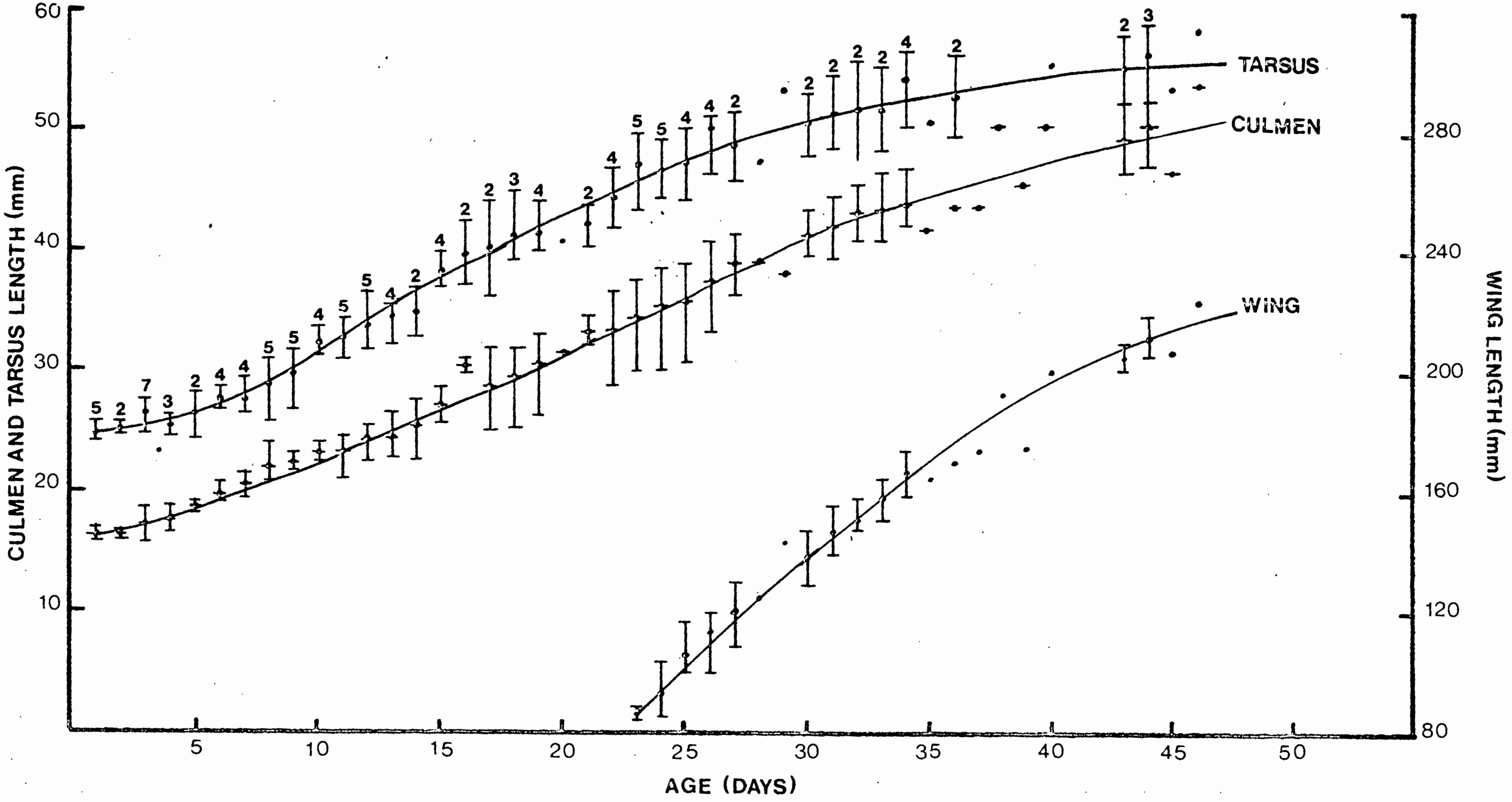


Figure 38. Culmen, tarsus and wing growth of wild African Black Oystercatcher chicks



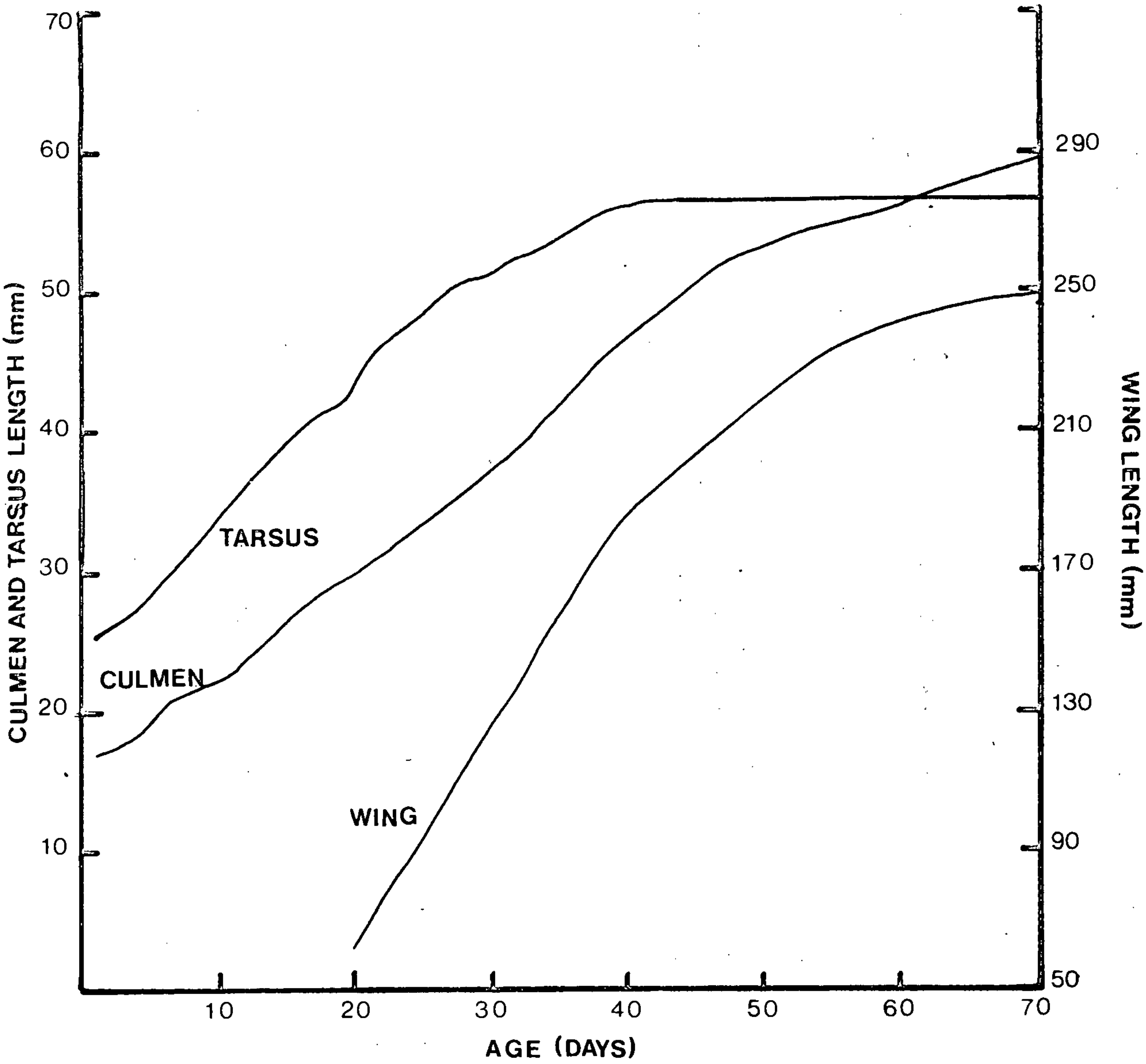


Figure 39. Culmen, tarsus and wing growth of a captive African Black Oystercatcher chick plotted as three day moving averages

form of the growth curve was consistent in both wild and captive birds and conformed closely to the von Bertalanffy growth equation (Ricklefs, 1967).

Energetics

Table 44 details energy intake during growth of captive chicks: daily energy intake is related to age in Fig. 40. Daily energy intake peaked at, or immediately prior to, fledging: up to 30 days, increase in daily energy intake was linear (Fig. 40). Estimated total energy requirement in the first 90 days was 32 333 kJ (Table 44).

The Basal Metabolic Rate (BMR) of an adult African Black Oystercatcher, calculated from Lasiewski & Dawson's (1967) equation is 254.5 kJ per day. A captive bird, retaining constant mass of 565 g over 48 days, has a mean daily energy intake (ME) of 437.1 kJ. Mean adult mass is 694 g (Part 2.1). Assuming the ratio of ME:BMR is constant over the weight range 565-649 g, and ME is therefore proportional to $W^{0.723}$ (Lasiewski & Dawson, 1967), the ME of a mean adult would be 437.1 x $694^{0.723}$ $/565^{0.723}$ = 507.2 kJ per day, twice BMR. Using activity budgets, DEE of a nonbreeding adult was calculated at 629.0 kJ (Table 45).

Assimilation efficiency of a growing chick ranged from 68 % to 76 % with a mean of 72 % (Table 46). The mean assimilation efficiency of a fledged subadult was 73 % (Table 46).

From estimates of DEE and assimilation efficiency it was possible to produce a rough annual energy budget for a pair of African Black Oystercatchers laying two eggs and rearing one chick which remained in the parental territory for 90 days (Table 47). Gross

Table 44. Energy intake during growth of African Black Oystercatcher chicks.

Age	Captive chicks: energy intake (kJ)							
(days)	A	B	C	D	E	Mean	SD	Cumulative
0-10		900	643		825	789	132	789
11-20	2996	2217	1858	2650	2516	2447	432	3236
21-30	3481	4316*	3909	3837	3336	3776	385	7012
31-40	4128		6157	3414*		4566	1423	11578
41-50	4025							15603
51-60	4197							19800
61-70	4226*							24026
71-80	4288*							28314
81-90	4019							32333

* extrapolated from less than 10 data points

Figure 40. Daily energy intake (kJ) of five captive African Black Oystercatcher chicks: each individual is represented by a different symbol

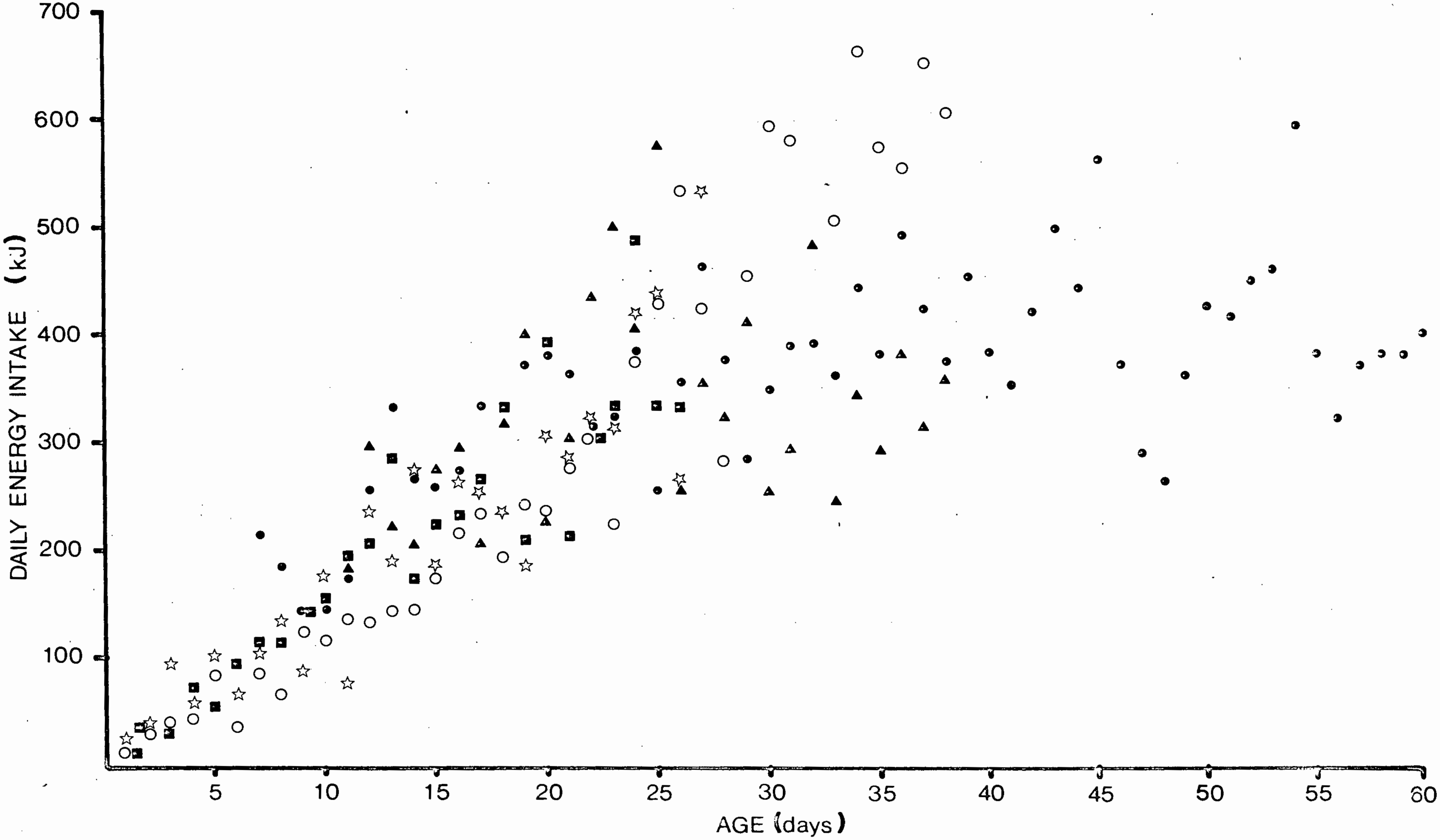


Table 45. Activity partitioning (% of 24 h) and estimated energy requirements as a function of Maintenance Energy for nonbreeding African Black Oystercatchers.

Activity		Day	Night	Total
Resting	%	14.2	27.5	41.7
0.8 x ME	kJ	57.6	111.6	169.2
Walking	%	3.6	1.9	5.5
1.0 x ME	kJ	18.3	9.6	27.9
Foraging	%	19.8	14.4	34.2
1.5 x ME	kJ	150.6	109.6	260.2
Preening/bathing	%	10.0	4.7	14.7
1.5 x ME	kJ	76.1	35.8	111.9
Agonistic behaviour	%	1.7	1.2	2.9
2.0 x ME	kJ	17.2	12.2	29.4
Flying	%	0.7	0.3	1.0
6.0 x ME	kJ	21.3	9.1	30.4
Totals	%	50.0	50.0	100.0
	kJ	341.1	287.9	629.0

Table 46. Energy intake and output, metabolized energy and assimilation efficiency of a hand-reared African Black Oystercatcher chick and a hand-reared subadult bird.

Age (days)		Energy intake (kJ)	Dry mass of guano (g)	Guano energy (kJ per g dry mass)	Energy (kJ) excreted	Metabolized energy (kJ)	Assimilation efficiency (%)
Chick	7	212.1	5.4	9.5	51.3	160.8	75.8
	13	334.6	9.1	10.3	93.7	240.9	72.0
	18	329.8	10.6	10.1	107.1	222.7	67.5
	21	386.5	9.4	11.1	104.3	282.2	73.0
					Mean assimilation efficiency 72.1 ± 3.5%		
Sub-adult	160	490.9	13.2	11.2	147.8	343.1	69.9
	161	501.2	13.0	11.1	144.3	356.9	71.2
	162	690.8	13.1	11.9	155.9	534.8	77.4
	163	671.6	17.1	10.9	186.4	485.2	72.2
					Mean assimilation efficiency 72.7 ± 3.3%		

Table 47. An approximate annual energy budget for a pair of African Black Oystercatchers laying two eggs and rearing one chick which remains on the territory for 90 days. All values in kJ.

Activity	No. days	Adults			Chicks		Total	
		Intake per bird per day (Table 45)	Total intake	Return (guano)[+] (Table 46)	Intake	Return	Intake	Return
Nonbreeding	243	629	305 694	83 454			305 694	83 454
Egg production (female only)			874	239			874	239
Incubation	32	629	40 256	10 990			40 256	10 990
Chick rearing	90	881	158 580	43 292	32 333	9021	190 913	52 313
Total	365		505 404	137 975	32 333	9021	537 733	146 996

[+] Assimilation efficiency of adults was assumed equal to that measured for a subadult bird (Table 46).

energy removal under these conditions was estimated as 537 733 kJ, net energy removal was therefore 390 737 kJ.

DISCUSSION

Growth

Rand (1950) followed the growth of a single African Black Oystercatcher chick at Sinclairs Island, Namibia (27 40S, 15 31E) up to 70 days old and his results clearly show decreasing growth rate with age. At nine weeks of age the chick was 83 % of adult mass and 28 % heavier than the mean fledging mass of chicks from the southwestern Cape.

The daily mass increment (15.6 g) recorded during the period of maximal growth in this study is a much smaller increment than the 25.6 g per day predicted by the Drent & Daan (1980) equation for altricial and subprecocial seabirds. The modal clutch of H. moquini is two, but normally only one or fewer chicks are reared per pair per year (Part 5.2). Species with reduced broods generally have lower growth rates than those with normal broods (Drent & Daan, 1980): this may partly explain the slow growth rate observed.

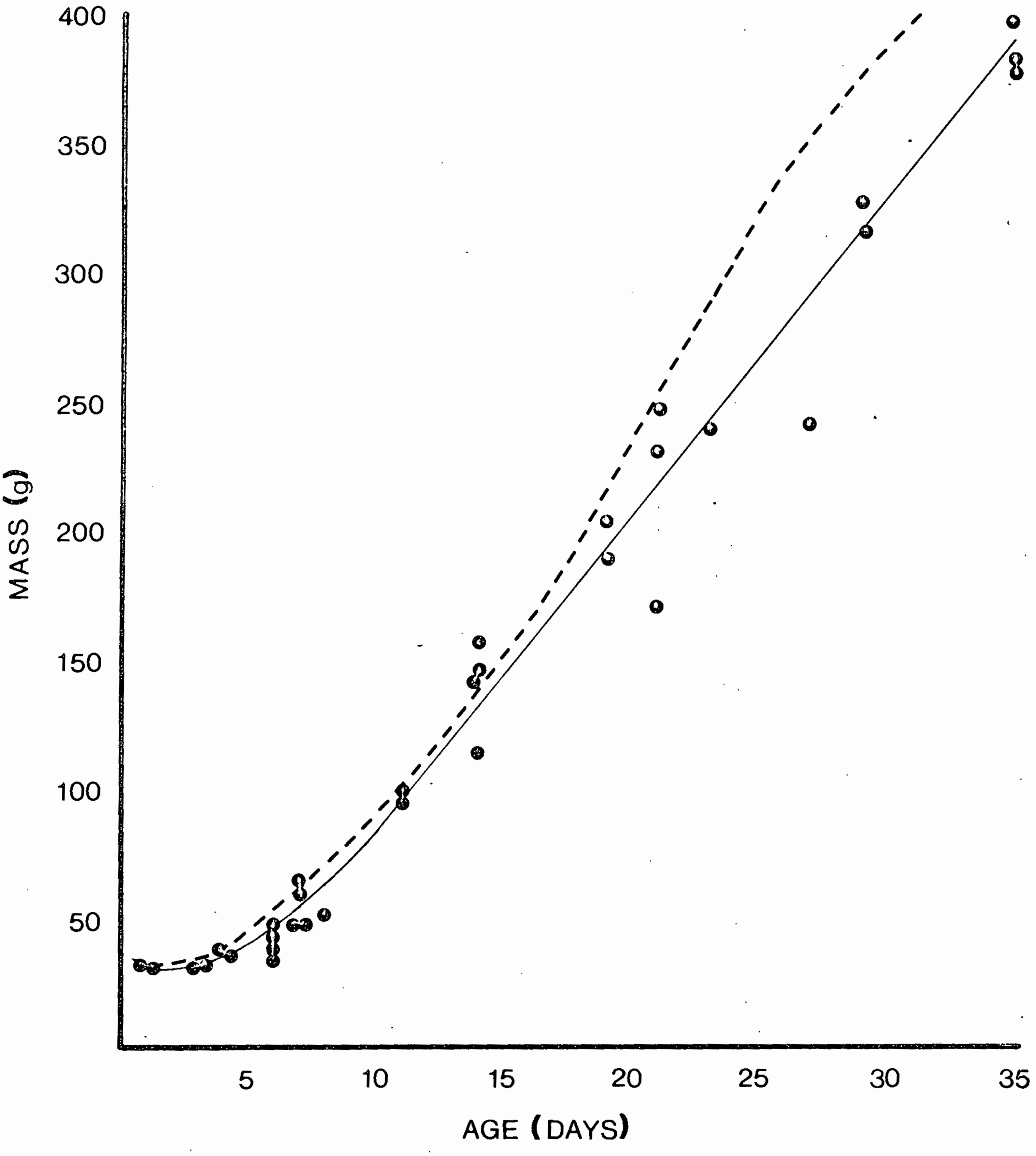
The relatively rapid growth of the tarsus is advantageous in a subprecocial species as it increases pre-fledging mobility and hence speed of escape from predators. Usually African Black Oystercatchers escape from potential predators (humans) by hiding, but they also swim well, travelling up to 60 m from the shore: occasionally chicks dive underwater to escape predators (pers. obs.).

Growth rates of other oystercatcher species are largely unrecorded. Growth rates of *H. moquini* and the American Black Oystercatcher *H. bachmani* are very similar (Fig. 41), though *H. moquini* has a faster growth rate during the second half of the pre-fledging period.

Growth related to social behaviour

African Black Oystercatchers fledge at 65 % of mean adult mass, when wing length is 70 % of adult wing length. A similar early fledging strategy has been reported in Common Snipe *Gallinago gallinago*, also a territorial subprecocial wader. Common Snipe do not attain adult mass until *c*. 52 days, but fledge at *c*. 21 days when mass is 70 % of adult mass and wing length 73 % of adult dimensions (Tuck, 1972). Amongst subprecocial Charadriiformes there appears to be a difference in fledging strategy between territorial Charadrii and colonial Larii. Black-legged Kittiwakes *Rissa tridactilis* fledge at *c*. 42 days: mass at 29 days is 98 % of adult mass, whereafter mass decreases until fledging, and wing length is close to adult wing length at fledging (Maunder & Threlfall, 1972). California Gulls *Larus californicus* fledge at 98.5 % of adult mass (Smith & Diem, 1972). Territorial species appear to fledge small and early, and colonial species large and late (see Burger (1980) for further details of fledging periods in larids). The adaptiveness of early fledging in territorial species is presumably predator-related. Whereas colonial species breed on inaccessible cliffs or crèche as an anti-predator strategy, territorial ground-nesting species must rely largely on the ability of the individual to escape predators and hence benefit from early fledging.

Figure 41. A comparison of growth rates (mass) of African Black Oystercatcher chicks (dotted line) with American Black Oystercatcher chicks (solid line). (Data for American Black Oystercatchers from Webster (1941))



Energetics

Energy requirements for growth in subprecocial waders, oystercatchers, pratincoles and snipes, have not been reported previously. Limited data available for Charadriiformes support the hypothesis that early fledging is important in territorial species. Energy demand of African Black Oystercatchers peaks close to fledging: the only larid for which energy requirements for growth have been published, the Glaucous-winged Gull *Larus glaucescens*, shows a peak in energy demand at 25 days, *c*. 19 days before fledging (Vermeer, 1963; Drent & Daan, 1980).

The DEE of adult African Black Oystercatchers was estimated at 629 kJ (nonbreeding). This is very close to the estimate of 642 kJ obtained from Walsberg's (1980) equation. Measurements of energy intake by captive *H. ostralegus* are high compared with those of *H. moquini* (Table 48). A possible explanation is that all *H. ostralegus* used in the studies tabulated were fed either *Cerastoderma* or *Mytilus*, both bivalves. Oystercatchers do not clean bivalves 100 % efficiently (pers. obs.) and this would lead to an overestimate of food intake if the latter was calculated from shell lengths. Smaller species (*H. ostralegus* is approximately 72 % of the mass of *H. moquini*) have relatively higher metabolic rates and sensitivity to cold (Kendeigh, 1970). The effect of temperature on existence metabolism (0.8 x ME) in *H. ostralegus* was estimated, in another study, at 89.7 - 0.97T (Kcal per day) (Kendeigh *et al*., 1977): the study bird weighed 385 g. At a mean temperature of 13.8°C, as experienced by the Marcus Island study bird during June and July (Table 43), the estimated ME of a 385 g bird is 399.4 kJ per day. Correcting for the weight difference (ME proportional to $W^{0.723}$), this equation predicts ME

Table 48. A comparison between *H. ostralegus* and *H. moquini* of a). measured ME (data for *H. ostralegus* in Hulscher (1982)), b). estimated DEE from data in Heppleston (1971) and Hulscher (1982) based on the assumptions that energy requirements of free living birds are (i) 2x those of captive birds (Heppleston 1971) and (ii) 1.3x those of captive birds (Hulscher 1982) (*H. ostralegus*). DEE of *H. moquini* estimated from ME and activity budget, c). DEE calculated from Walsberg's (1980) equation. Energy values have been standardized as kJ per g bird mass per day.

Month	Measured ME	Estimated DEE		Calculated DEE
		(i)	(ii)	
H. ostralegus				
March	1.63		2.12	1.02
(13°C)	1.48	2.96	1.92	1.10
June-August	1.39		1.80	1.06
October	1.76	3.18	2.29	1.01
December	2.21	3.45	2.87	1.06
H. moquini				
June-July (13.8°C)	0.73	0.91		0.93

for a mean African Black Oystercatcher weighing 694 g at 399.4 x $694^{0.723}/385^{0.723}$ = 611.5 kJ per day: this is 20.6 % more than the value obtained in this study. Substituting data from Heppleston's (1971) bird in the equations of Kendeigh _et al_. (1977) and correcting for the weight difference, predicted ME at 13°C for a 420 g bird is 430.3 kJ per day: the measured ME for this bird was 621.8 kJ, some 44.5 % greater. Values for DEE of _H. ostralegus_ based on the assumptions of, and data presented by Heppleston (1971) and Hulscher (1982) range from 1.80 to 3.45 kJ per g body mass per day, as compared with the Walsberg (1980) estimate of 1.01-1.10 kJ per g per day (Table 48). Further experimentation with other species of subprecocial waders is needed before the large discrepancy in energy requirements between _H. moquini_ and _H. ostralegus_ can be resolved fully.

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SUMMARY

African Black Oystercatchers fledge at 35-40 days, being significantly smaller than adults in all dimensions except tarsal length. Maximum growth rate (15.6 g per day) occurs between 15 and 31 days and is less than predicted by Drent & Daan (1980) for

subprecocial seabirds. Within the Charadriiformes, it appears that a colonial or territorial breeding strategy influences age and size at fledging: territorial birds fledge small and early whereas colonial breeders normally fledge large and late. Early fledging is probably adaptive as an anti-predator strategy in a territorial species.

Daily energy intake of African Black Oystercatcher chicks peaked at or immediately prior to fledging.

Daily existence energy of nonbreeding adult African Black Oystercatchers was calculated at 629 kJ, 2.47 x BMR: this is close to the value predicted by Walsberg (1980). The gross annual energy removal by one pair of birds laying two eggs and rearing one chick was estimated at 537 733 kJ. the mean assimilation efficiency of a growing chick was 72 %, and of a fledged subadult was 73 %.

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Part 4.5. Summary

African Black Oystercatchers follow a tidally controlled foraging regime, with a single peak in foraging activity at low tide. Even when food is theoretically available throughout the tidal cycle, as at extreme neap tides, foraging activity is cyclic. Except under storm conditions, less than 50 % of available time is spent foraging, and absolute foraging time is less than half that of the smaller European Oystercatcher during the winter. During the day, the extent of territorial commitment varies between pairs but is fairly consistent within pairs. Birds with a territorial commitment of 60 % or more appear to satisfy their feeding requirements on the territory. Nocturnal foraging activity (nonbreeding) is 59 % of diurnal foraging activity: birds leaving the feeding areas at night when the tide is still relatively low and forming communal roosts. Communal roosting by African Black Oystercatchers is thought to have evolved primarily as an anti-predator strategy. This behaviour is more pronounced at night when the threat from mammalian predators is greatest; and, during the breeding season, when birds cannot form roosts due to commitment to the nest site, mortality due to predation is maximal.

African Black Oystercatcher chicks grow rapidly up to fledging, and fledge at 35-40 days, some time before adult dimensions are attained. Energy demand peaks at, or close to fledging. Early fledging is advantageous in a noncolonial, ground-nesting species when the ability of the individual to escape potential predators is of paramount importance since social behaviour such as crèching or flocking is not possible.

The daily existence energy of nonbreeding adults was calculated at 2.5 x Basal Metabolic Rate, a value close to that predicted by standard equations, and the mean adult assimilation efficiency was 73 %.

Part 5. BREEDING BIOLOGY

Part 5.1. Introduction

The breeding biology of the European Oystercatcher Haematopus ostralegus has been well studied in many parts of its range (e.g. Buxton, 1939; Keighley & Buxton, 1948; Harris, 1967, 1969, 1970; Schnakenwinkel, 1970; Hausmann & Hausmann, 1972, 1973; Heppleston, 1972; Glutz von Blotzheim et al., 1975; Bianki, 1977; Swennen & de Bruijn, 1980). Some studies have been made on the breeding of the American Black Oystercatcher H. bachmani (Webster, 1941; Hartwick, 1974), and a little is known of the breeding behaviour of the American Pied Oystercatcher H. palliatus (Baker & Cadman, 1980).

Nest site and nesting behaviour of African Black Oystercatchers H. moquini have been described (from sandy beaches) (Hall, 1959), and some further observations on breeding (seasonality, clutch size, and egg dimensions) were made by Summers & Cooper (1977). Oystercatchers have several elaborate and highly vocal displays associated with breeding and several workers have attempted to describe and interpret these (e.g. H. ostralegus, Huxley & Montague, 1925; Edwards et al., 1948; Williamson, 1943, 1950a,b, 1952; Heppleston, 1970; H. leucopodus, Miller & Baker, 1980; H. palliatus, Kilham, 1980; Miller & Baker, 1980; H. unicolor, Watt, 1955; H. ater, Miller & Baker, 1980).

Oystercatchers are almost invariably ground-nesting birds, though exceptions have been recorded (Smith, 1981), and they are territorial when breeding. Highest breeding densities normally occur at islands (Harris, 1967; Hartwick, 1974; Swennen & de Bruijn, 1980). Islands are also favoured breeding localities for gulls, which may eat eggs and chicks of oystercatchers (Harris, 1967).

Being territorial, nests and chicks are well spaced, and oystercatchers cannot rely on social behaviour such as crèching or flocking for protection from predators. During the egg and chick stages (at least prior to fledging), crypticity of nests and chicks is important in ensuring freedom from predation.

The aims of this study of breeding biology are:

1. To supplement and complement existing data on basic aspects of breeding biology such as seasonality, egg dimensions and nest spacing;

2. To consider the sources and extent of egg and chick loss and their conservation implications;

3. To analyse the extent, timing and range of juvenile dispersal with emphasis on dispersal from islands with high breeding densities, and to consider the importance of such sites for recruitment to the population;

4. To examine nest site selection with special reference to the ways in which site selection and the crypticity of the eggs themselves may enhance nest survival.

Displays associated with breeding are not considered in this thesis, but a manuscript is in preparation for publication elsewhere (Baker & Hockey, in prep.).

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Part 5.2. Aspects of the breeding biology of the African Black Oystercatcher *Haematopus moquini*.

Ostrich 54 (1983):26-35

SUMMARY

Fifty-five pairs of African Black Oystercatchers Haematopus moquini bred at Marcus Island in 1979-1980. Sixteen pairs laid replacement clutches: the mean interval between loss of the first clutch and laying of a replacement clutch was 22.2 days. Mean inter-nest distance was 19.4 m. The modal clutch size was two, with a mean of 1.74. Mean dimensions of 105 eggs were 60.7 x 40.1 mm and mean fresh egg mass was 55.8 g. There were differences in egg masses and dimensions between eggs in one- and two-egg clutches. Rate of egg loss was high, due mainly to predation by Kelp Gulls Larus dominicanus promoted by human disturbance. Fledging success was lower at a disturbed site than at undisturbed sites, with highest chick mortality occurring in the first week of life. Mortality of first-year birds of eight days and older was estimated at 48 % and 69 % in two successive seasons. All juvenile birds dispersed from their natal sites, and were resighted up to 168 km away. Dispersed juveniles were concentrated at the edge of an area of high oystercatcher density.

INTRODUCTION

The African Black Oystercatcher Haematopus moquini breeds along the coast and at the offshore islands of Namibia and South Africa (Part 1.2). Various studies have been made of the species' breeding ecology: Hall (1959) examined nest sites and behaviour associated with breeding; Summers & Cooper (1977) presented data on clutch size and egg masses, breeding populations, breeding seasonality and adult dispersal; Part 5.3 discusses factors governing nest site selection and nest spacing, the positions of feeding territories and the adaptiveness of egg coloration.

This report concentrates on the following aspects of the African Black Oystercatcher's breeding biology: seasonality, nest spacing, clutch size, egg dimensions, clutch loss and replacement, breeding success, juvenile mortality, dispersal and population age structure.

STUDY AREA AND METHODS

Much of the study was carried out at Marcus Island (33 03S, 17 58E), Saldanha Bay, in the southwestern Cape, South Africa. Chicks were ringed at nearby Jutten (33 05S, 17 58E), Malgas (33 03S, 17 55E) and Vondeling (33 10S, 17 59E) Islands. A cohort colour code and an island code were used during 1979-1980 and 1980-1981. Additional data were collected on the causeway leading to Marcus Island and at adjacent mainland sites. Intensive trapping and colour ringing of incubating birds was carried out (see Part 2.1 for trapping technique). Nests were monitored daily during 1979-1980, and first and second-laid eggs were marked, weighed and measured when fresh. Nests were located before egg laying and any found after clutch completion were ignored for the purpose of measurements or clutch size determination. Inter-nest distances were measured to the nearest 0.1 m, and for calculating nest spacing only original (i.e. not replacement) nests were used. The distances between original and replacement nests were computed separately.

Owing to unnatural disturbance at Marcus Island during the study period, an indirect measure of reproductive output was obtained at other islands using the ratios of ringed:unringed chicks.

Juvenile dispersal and population age structure were assessed by regular visits to high-tide roosts between St Helena Bay (32 42S, 17 58E) and Vondeling Island. All birds at these roosts were aged and checked for rings. Details of criteria used in ageing birds are presented on pages 370 and 371. Published requests for details of sightings of ringed birds resulted in some reports from outside the main study area.

RESULTS

Breeding Season

In 1979, only one clutch was initiated before the second week of December (Fig. 42). In 1980 the first nest was found on 18 November, and in 1981, a nest with 2 eggs was located on 5 November (R. Wilson, pers. comm.). At Jutten Island in 1982, at least one pair of birds laid eggs in mid-October. The peak egg laying period in 1979/1980 was mid-December to mid-January and the beginning of February was the peak period for laying of replacement clutches. A total of 55 pairs of oystercatchers nested and 16 of these are believed to have laid replacement clutches. Most pairs which relaid did so once and the interval between loss of the first clutch and commencement of the replacement clutch was 22.2 ± 8.3 days. One pair laid three clutches, the first (two eggs) on 16 December (lost on 13 January), the second (one egg) laid on 4 February (lost on 10 February) and the third (two eggs) laid on 25 February and lost on 7 March. The total fresh mass of the five eggs was 276.5 g. Since the female weighed 690 g, it laid eggs totalling 40.1 % of its body mass in 72 days.

Nest spacing

The mean inter-nest distance for 54 original nests was 19.4 m ± 14.0 m, with 68 % of nests being less than 20 m apart (Fig.43). This figure relates to all original nests: not all original nests were active at the same time.

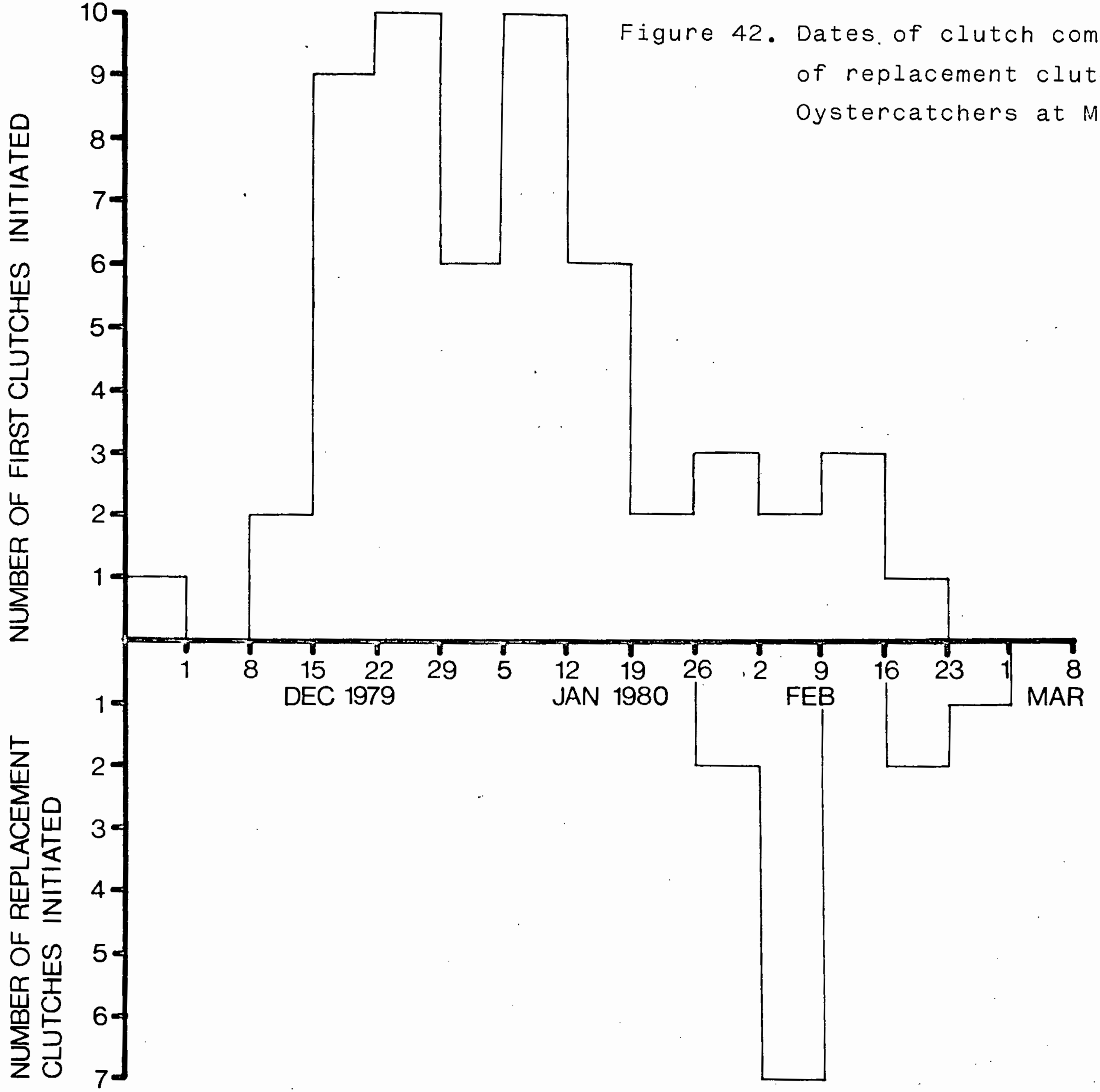


Figure 42. Dates of clutch commencement and laying of replacement clutches by African Black Oystercatchers at Marcus Island, 1979-1980

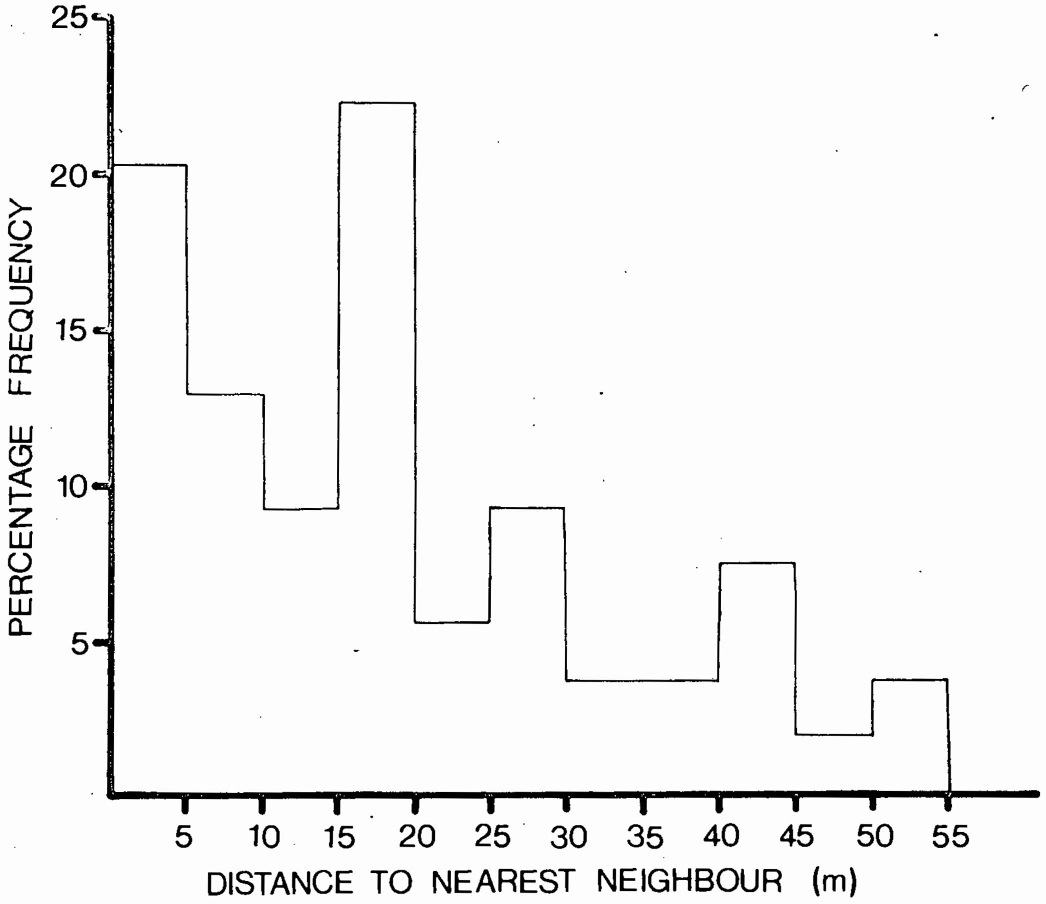


Figure 43. Nest spacing of African Black Oystercatchers at Marcus Island, 1979-1980. (All replacement clutches ignored.)

The mean distance between a replacement nest and the original nest of the same pair was 11.6 m ± 6.6 m. Replacement nests were significantly closer to the originals than originals were to other originals ($t=3.08$; $p<0.005$). The closest original nests were 1.5 m apart. Only one replacement clutch was laid in an original nest, all others were laid between 2.5 m and 22.5 m away. The mean nest dimensions were (85 nests): internal diameter 208 ± 24 mm and depth 40 ± 9 mm.

Clutch size and egg dimensions

All original clutches contained either 1 or 2 eggs and the mean clutch size (46 clutches) was 1.74. In 2-egg clutches, eggs were laid at an interval of 2 days. Egg dimensions were 55.8 - 65.2 x 37.9 - 43.7 mm (mean 60.7 x 40.1 mm) (105 eggs) and the range in fresh mass was 45.0 - 65.0 g (mean 55.8 g) (105 eggs). A full analysis of egg dimensions is given in Table 49. There were no significant differences in mass or dimensions between eggs in modal 2-egg clutches either in initial or replacement clutches. In single-egg clutches however, the initial egg was lighter than the first-laid egg in a 2-egg clutch ($t = 2.18$; $p<0.05$) (also longer ($t = 2.84$; $p<0.01$) and narrower ($t = 2.78$; $p<0.01$)) and was longer than the second-laid egg in a 2-egg clutch ($t = 2.63$; $p<0.05$). Replacement single eggs were heavier ($t = 2.63$; $p<0.02$) and wider ($t = 2.59$; $p<0.02$) than second-laid eggs in 2-egg clutches. They were also wider than second eggs in replacement 2-egg clutches ($t = 2.18$; $p<0.05$). Initial single eggs were heavier ($t = 2.80$; $p<0.02$) but narrower ($t = 3.46$; $p<0.01$) than relaid single eggs. Using the Bonferroni t statistic, none of these differences was significant.

There was no significant difference between the ratios of 1-egg to

Table 49. MASS AND DIMENSIONS OF EGGS OF AFRICAN BLACK OYSTERCATCHERS

EGG TYPE		Mean	Standard deviation	Range
One egg clutches				
First clutch (n=11)				
	length (mm)	62.06	1.53	59.7 - 65.2
	width (mm)	40.27	0.99	37.9 - 41.3
	mass (g)	54.00	3.63	48.5 - 59.0
Replacement clutch (n=8)				
	length	60.68	1.33	58.2 - 61.9
	width	41.91	1.06	40.9 - 43.7
	mass	58.81	3.79	52.5 - 65.0
Two egg clutches				
First clutch (n=35)				
Egg 1:	length	60.46	1.66	57.0 - 63.8
	width	41.26	1.04	39.3 - 42.8
	mass	56.44	3.12	49.5 - 63.0
Egg 2:	length	60.76	1.71	55.8 - 63.7
	width	40.91	0.97	38.0 - 42.7
	mass	55.33	3.28	45.0 - 62.5
Replacement clutch (n=8)				
Egg 1:	length	60.35	2.27	57.3 - 62.7
	width	40.86	1.56	38.0 - 42.3
	mass	56.06	5.61	46.5 - 61.5
Egg 2:	length	60.20	2.58	56.1 - 63.5
	width	40.54	1.43	38.4 - 42.5
	mass	54.88	5.39	46.5 - 60.0

2-egg clutches in initial and replacement clutches ($X^2 = 0.06$; $p>0.05$) (Table 50), nor was a bird which initially laid 2 eggs any more or less likely to relay a 2-egg clutch than a bird which initially laid a single egg ($X^2 = 0.15$; $p>0.15$) (Yates' Correction Factor applied) (Table 51).

When clutch mass (first clutch, modal clutches only) was compared with female mass there was a tenuous relationship suggesting increasing clutch mass with increasing female mass (Fig. 44). Clutch mass (g) = 0.05 x female mass (g) + 78.67 ($r = 0.26$; $t = 1.77$; $0.05<p<0.1$).

Incubation period was 27-39 days per egg (mean 32.1 days): first-laid eggs 30-39 days (mean 34.0 days), and second-laid eggs 27-34 days (mean 30.5 days). Incubation was discontinuous prior to clutch completion, and first- and second-laid eggs normally hatched within 24 h of one another.

Clutch loss and chick mortality

Clutch losses at Marcus Island were high. Eighty-six nests were located in the study area: predation of eggs occurred at 62 nests (76 %). The principal and probably the only diurnal predator was the Kelp Gull Larus dominicanus which preyed on eggs of several species, notably penguins and cormorants, when they were unattended (pers. obs.). During the study a number of African Black Oystercatchers were killed at night. This spate of deaths ceased after four Cape Foxes Vulpes chama were killed in the study area. This species preys on ground-nesting birds and their eggs (Haltenorth & Diller, 1980) and may have been responsible for some nocturnal predation of oystercatcher eggs, but there is no proof of this.

Heavy egg predation did not start at the island until

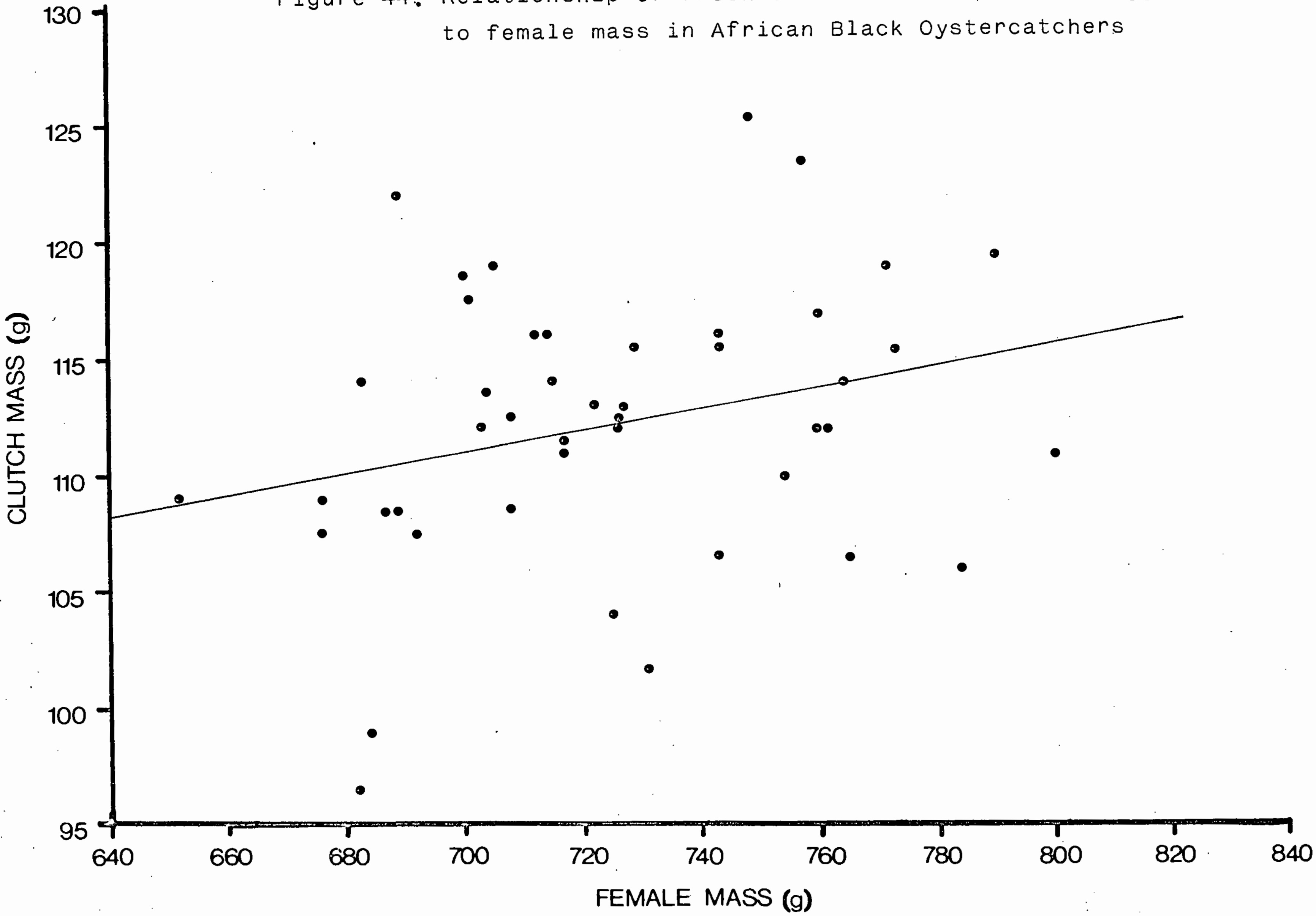
Table 50. THE FREQUENCY OF ONE EGG AND TWO EGG CLUTCHES IN FIRST LAID AND REPLACEMENT CLUTCHES OF AFRICAN BLACK OYSTERCATCHERS

	NUMBER OF CLUTCHES RECORDED		
Clutch size	First clutches	Replacement clutches	Total
One egg	12	3	15
Two eggs	52	17	69
Total	64	20	84

Table 51. THE RELATIONSHIP OF REPLACEMENT CLUTCH SIZE TO FIRST CLUTCH SIZE IN AFRICAN BLACK OYSTERCATCHERS

	FIRST CLUTCH SIZE		
	One egg	Two eggs	Total
REPLACEMENT CLUTCH SIZE			
One egg	1	7	8
Two eggs	2	10	12
Total	3	17	20

Figure 44. Relationship of fresh clutch mass (modal two egg clutches only) to female mass in African Black Oystercatchers



approximately 50 eggs were present (Fig. 45). Predation then continued at a constant rate until the end of the egg-laying period, paralleling the rate of egg production. The mortality rate of chicks also was high: only one chick was reared from 15 eggs that hatched at Marcus Island (Fig. 45). Including the adjacent causeway 21 eggs hatched (four chicks died during hatching) (Table 52). Of these 21 chicks, 16 died before fledging, 14 of the 16 (66.7 % of the total) dying within seven days of hatching. Two of the remaining seven chicks died before fledging, therefore mortality between seven days and fledging was 28.6 %. Only one clutch was lost during heavy swells during the 1979-1980 breeding season but a severe storm immediately before the 1980-1981 breeding season washed over 12 (16 %) of the previous season's nests. In instances where chicks disappeared from the feeding site predation was deemed to be the cause with two exceptions when the feeding area was inundated during storms. In the latter instances it was assumed that the chicks were drowned. Although chicks were checked daily it is not impossible that between visits, some very small chicks may have died in the nest and subsequently been scavenged. Thus, predation was believed to be the main cause of chick mortality (Table 52).

Breeding success, juvenile dispersal and population age structure

Twenty-nine African Black Oystercatcher chicks at least one week old (pre-fledging) were ringed at Jutten Island in 1979-1980. A complete count at Jutten Island on 19 April 1980 revealed two ringed and nine unringed juveniles (post-fledging), and on 20 April 1980 three ringed and seven unringed, giving an overall ringed:unringed ratio of 5:16 (i.e. 23.8 % ringed). This implies that 93 (92.8) chicks at Jutten Island reached at least one week old. The breeding population at Jutten Island was estimated at 98 pairs; therefore 0.95 young per pair reached seven days old. At Malgas Island, seven chicks were ringed, and the ringed:unringed ratio from two counts on 20 April 1980 was 2:5. This implies that 17.5 young reached seven days old (0.58 young per pair). On 22 May 1980 four first-year birds were counted at Jutten Island and two at Malgas Island: by 23 July 1980 no first-year birds remained at either island indicating total dispersal of juveniles by this time.

In the entire Saldanha Bay area (including Vondeling Island), 48 chicks were ringed in 1979-1980 and 35 in 1980-1981. The greatest

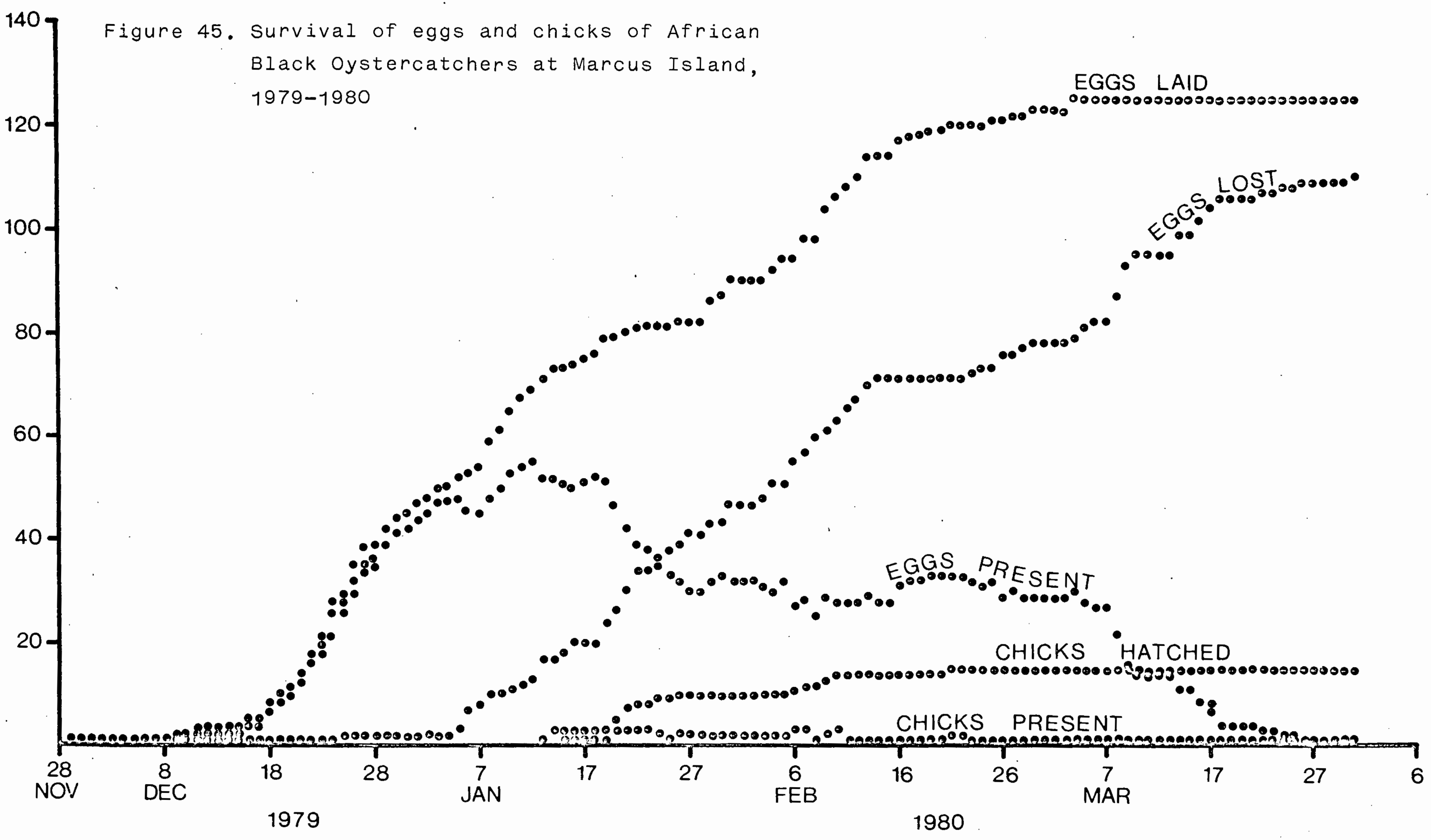


Figure 45. Survival of eggs and chicks of African Black Oystercatchers at Marcus Island, 1979–1980

Table 52. THE FATES OF 25 AFRICAN BLACK OYSTERCATCHER CHICKS IN THE STUDY AREA, 1979-1980

	Number of chicks
Died while hatching	4
Died in nest (<24 h old)	2
Unknown: presumed depredated	12
Probably washed away	2
Fledged	5

number of chicks in both years was ringed at Jutten Island and these birds provided the greatest number and range of resightings (Figs. 46, 47). Juvenile displacement in excess of 100 km from the natal site was recorded on four occasions. Maximum displacement was of a chick ringed near Van Stadens River Mouth (33 58S, 25 10E) in December 1973, and recovered at Glentana Beach (34 03S, 22 19E) in November 1974, a distance of 310 km (Table 53).

Chicks ringed at Saldanha Bay were regularly resighted between St Helena Bay and Ysterfontein (Figs. 46, 47). Age compositions of populations roosting in this area are summarized in Table 54. There was a steady increase in the proportion of first- and second-year birds at roosts from April to November (Fig. 48). The average proportions of first-year birds at roosts in 1980 and 1981 were 15.6 % and 8.7 % respectively. Incorporating proportions of ringed birds and the known adult population of the study area (Western Cape Wader Study Group, unpubl. data), it is possible to make an estimate of juvenile mortality between seven days and about eight months of age (Table 55). In 1980, an estimated 47.9 % of chicks/juveniles died or left the study area (at least four chicks are known to have dispersed beyond the main study area (Fig. 46)). The equivalent figure for 1981 was 68.6 %.

Ringed chicks comprised a greater proportion, on average, of the first-year mainland population than of the island populations when censused towards the end of the breeding season in April 1980.

DISCUSSION

Breeding season and population

Figure 46. Dispersal of juvenile African Black Oystercatchers from Jutten Island

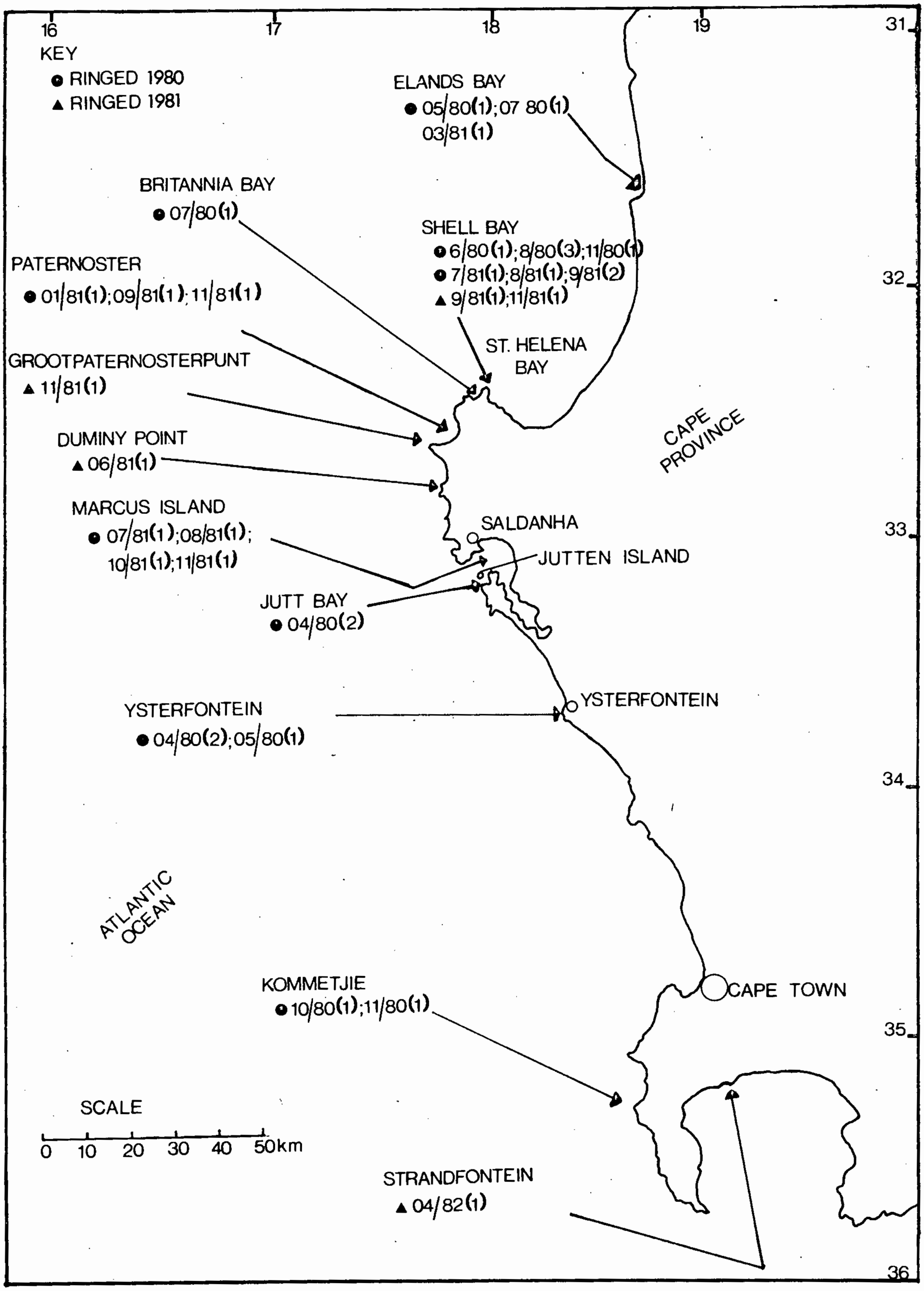


Figure 47. Dispersal of juvenile African Black Oystercatchers from Marcus, Malgas and Vondeling Islands

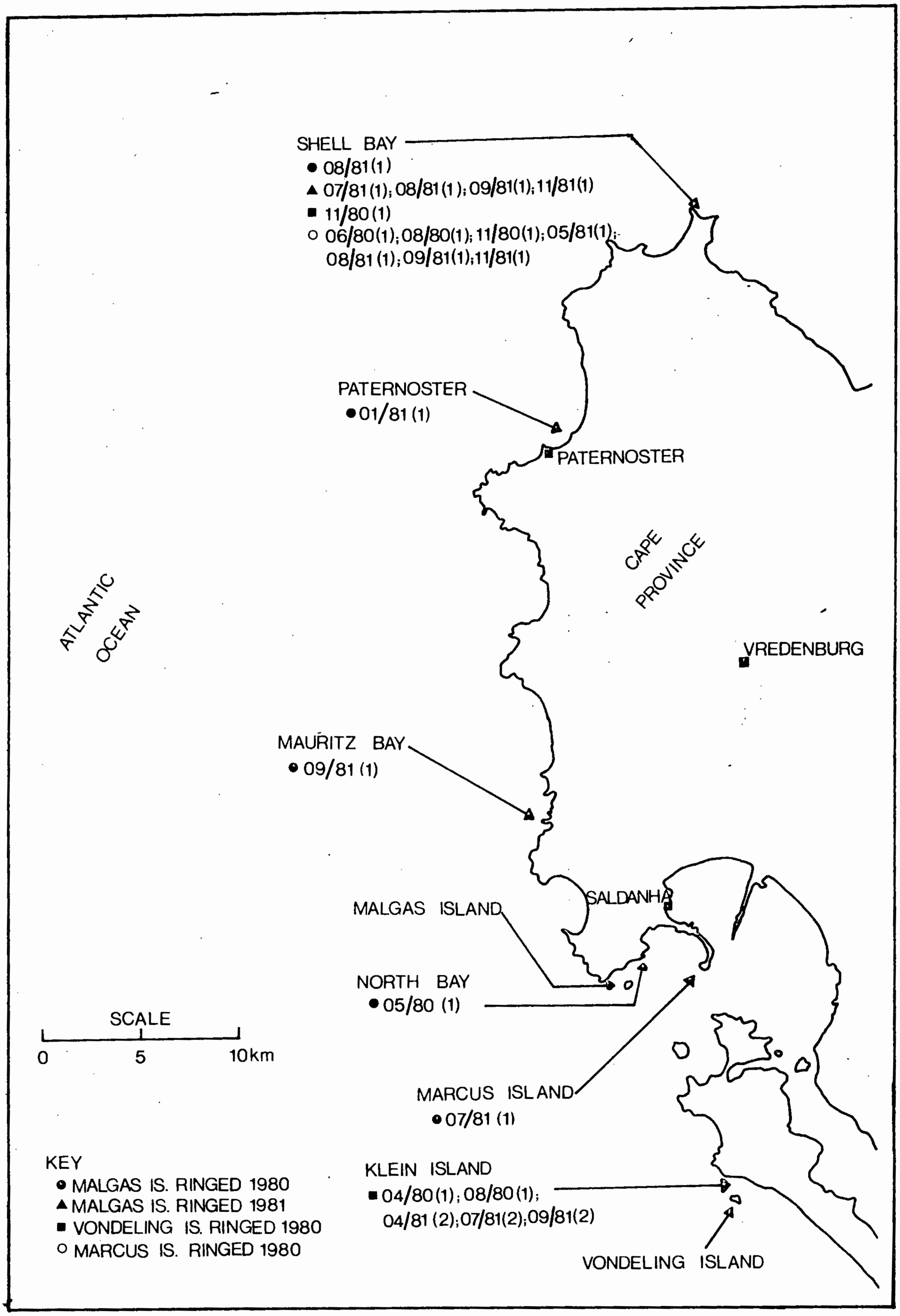


Table 53. RINGING AND RECOVERY/RESIGHTING DETAILS OF FOUR AFRICAN BLACK OYSTERCATCHER CHICKS WHICH DISPERSED MORE THAN 100 km FROM THEIR NATAL SITES

Ringing coordinates	Ringing date	Recovery/resighting coordinates	Recovery date	Distance (km)
33 58S, 25 10E	Dec 1973	34 03S, 22 19E	Nov 1974	310
33 05S, 17 57E	Mar 1981	34 05S, 18 31E	April 1982	168
33 05S, 17 57E	Mar 1980	34 08S, 18 19E	Oct - Nov 1980	150
33 05S, 17 57E	Mar 1980	32 19S, 18 19E	May 1980 - Mar 1981	123

Table 54. THE OVERALL AGE COMPOSITION (%) OF ROOSTS OF AFRICAN BLACK OYSTERCATCHERS BETWEEN ST. HELENA BAY AND VONDELING ISLAND, JUNE 1980 - NOVEMBER 1981

DATE	PERCENT ADULT	PERCENT SECOND YEAR	PERCENT FIRST YEAR	N
June 1980	97.1	0.0	2.9	128
July 1980	96.0	0.0	4.0	123
August 1980	86.9	1.3	11.8	63
November 1980	69.7	0.0	30.3	30
April 1981	97.3	2.0	0.7	150
May 1981	95.7	4.3	0.0	70
July 1981	93.5	3.9	2.6	184
August 1981	85.6	5.8	8.6	107
September 1981	82.7	5.6	11.7	150
November 1981	76.6	8.5	14.9	25

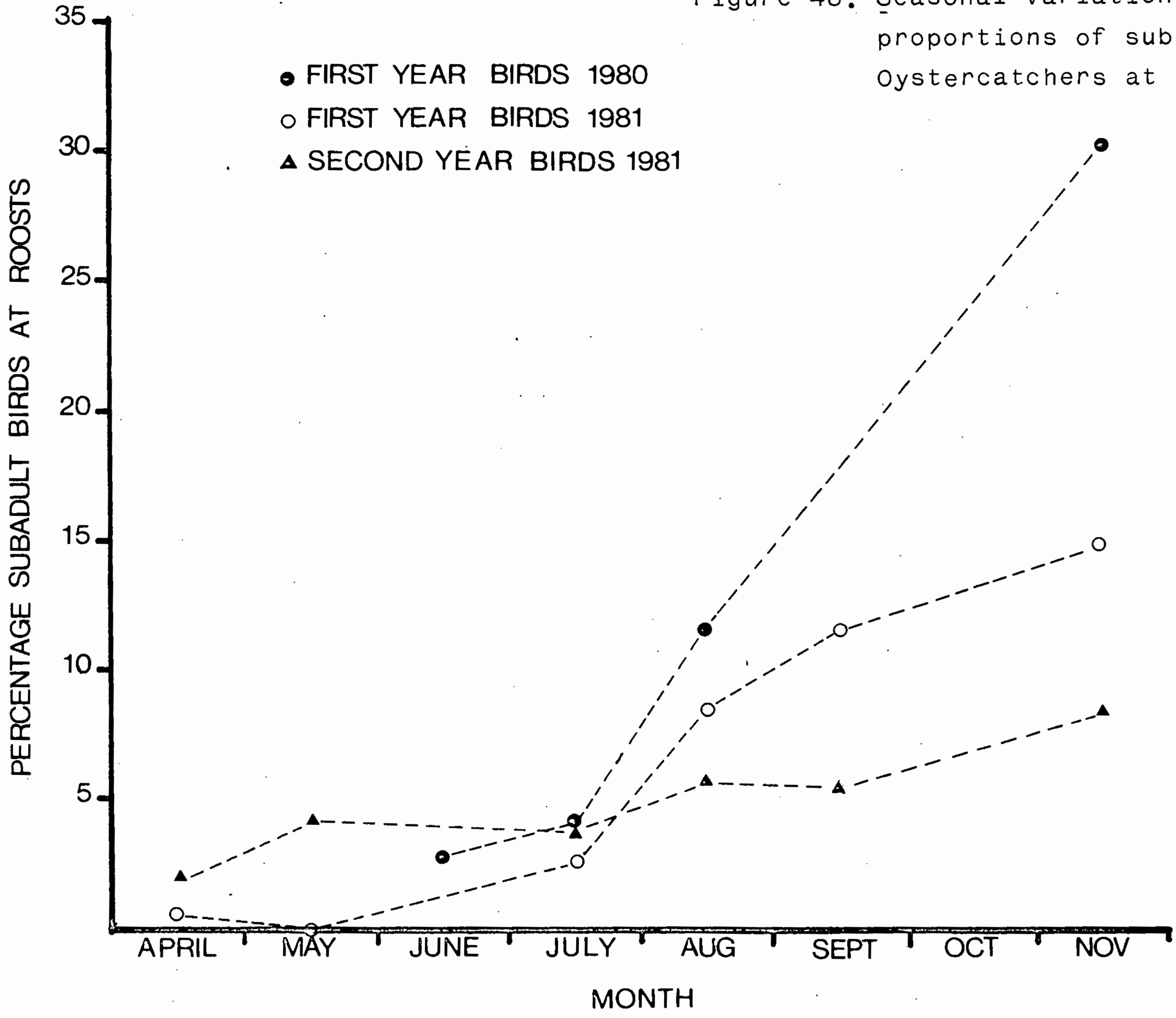


Figure 48. Seasonal variations in the proportions of subadult African Black Oystercatchers at high tide roosts

Table 55. STEPS IN THE CALCULATION OF THE PERCENTAGE OF FIRST YEAR AFRICAN BLACK OYSTERCATCHERS (>7 DAYS OLD) WHICH DIED OR DISPERSED OUT OF THE STUDY AREA IN 1980 AND 1981

	1980	1981
1. Number of chicks ringed	48	35
2. Percentage of first year birds in the mainland population	15.2	8.7
3. Proportion of ringed first year birds in the mainland population	31.6	25.0
4. Theoretical mainland population (all ages) assuming no pre-dispersal mortality of ringed birds	1000	1609
5. Actual mainland population	515	515
6. Calculated number of first year birds in the mainland population	78	45
7. Calculated number of ringed chicks surviving in the study area	25	11
8. Calculated number of ringed chicks which died or dispersed out of the study area	23	24
9. No. 8 expressed as a percentage of the numbers ringed	47.9	68.6

The peak egg-laying period at Marcus Island in 1979-1980 was similar to that recorded at Dassen Island (33 25S, 18 05E) in 1971-1972 (Summers & Cooper, 1977). It appears that the onset of egg-laying varies from year to year. This may partly be related to weather conditions: egg laying in 1980 commenced earlier than in 1979, but a period of unseasonally cold weather delayed egg laying in most pairs.

The breeding population of 55 pairs at Marcus Island in 1979-1980 was much larger than the 24 pairs estimated in 1972-1973, 1974-1975 and 1975-1976 (Summers & Cooper, 1977). The estimates of Summers & Cooper (1977) were based on relatively few visits to the island and reflect more accurately the number of pairs breeding at one time than the true overall breeding population. Summers & Cooper (1977) implied that 80-90 nonbreeding birds were present during the breeding season. Ten birds is a more accurate estimate.

Nest spacing and breeding density

The mean inter-nest distance of 19.4 m found in this study is less than the 28.7 m measured by Summers & Cooper (1977) for reasons mentioned above. The breeding density at Marcus Island (5.0 pairs per ha) is high. In other island breeding situations, the density of breeding American Black Oystercatchers _H. bachmani_ at Cleland Island, British Columbia, fluctuated between 3.5 and 4.8 pairs/ha (data from Hartwick, 1974) and at Skokholm Island, Wales, densities of European Oystercatchers _H. ostralegus_ ranged from 0.3 to 0.5 pairs/ha between 1939 and 1965 (data from Harris, 1967). At Vlieland, a large island of 1 353 ha, breeding densities of _H. ostralegus_ ranged between 0.2 and 3.0 pairs/ha in different areas of the island (Swennen & de Bruijn, 1980).

Clutch size and egg dimensions

The mean clutch size of 1.74 recorded at Marcus Island falls within the range of 1.62-1.88 calculated at four localities by Summers & Cooper (1977). Three-egg clutches have been recorded once at Dassen Island (Summers & Cooper, 1977) and once at Schaapen Island (33 06S, 18 01E) (J. Cooper, pers. comm.). No 3-egg clutches were observed during this study. Two female H. bachmani, both monogamously mated, have been reported as laying a total of 6 eggs in one nest (Webster, 1941) and bigamy has been reported in H. ostralegus resulting in 6 and 7 eggs in one nest (Barnes, 1950; Ticehurst, 1950). Neither of these phenomena has been reported or observed in H. moquini. The modal clutch of all oystercatchers is 2 or 3 eggs. The modal clutch of 3 is more characteristic of subspecies of H. ostralegus (Caldwell & Caldwell, 1931; Dircksen, 1932; Dement'ev & Gladkov, 1969; Glutz von Blotzheim et al., 1975) and the American Pied Oystercatcher H. palliatus (Baker & Cadman, 1980), than of black species, such as H. moquini, H. ater (Johnson & Goodall, 1965) and H. bachmani (Webster, 1941; Bent, 1962; Hartwick, 1974) (Table 56).

The eggs of H. moquini are large relative to those of other oystercatchers, dimensions being exceeded only by H. fuliginosus of Australia (Serventy & Whittell, 1962) and H. ater of South America (Johnson & Goodall, 1965). Little published information exists on fresh egg masses, but eggs of H. moquini average 20 % heavier than those of H. ostralegus (Glutz von Blotzheim et al., 1975) and are heavier than those of any of the New Zealand oystercatchers (Baker, 1974), including the similar sized H.

TABLE 56. A COMPARISON OF CLUTCH SIZES, EGG MASSES AND MEASUREMENTS AND INCUBATION PERIODS OF OYSTERCATCHERS

Species/ subspecies	Clutch size		Mean egg length (mm)	Mean egg width (mm)	Mean egg mass (g)	Incubation period (days)	Sources
	modal	range					
NEARCTIC/NEOTROPICAL REGION							
Haematopus bachmani	2	1-4	56.2	39.5		26-30	Webster 1941, Bent 1962, Hartwick 1974
H. palliatus palliatus	3	1-4	56.8	39.7			Baker & Cadman 1980
H. palliatus x *bachmani*		1-3	57.1	38.8			Bent 1962
H. p. galapagensis	2	1-2					Lévêque 1964, Harris 1974
H. p. pitanay	? 3	2-3	58.1	39.4			Johnson & Goodall 1965
H. leucopodus	2	1-2	57.5	40.2			Johnson & Goodall 1965
H. ater	2	1-2	61.5	41.8			Johnson & Goodall 1965
PALAEARCTIC REGION							
H. ostralegus ostralegus	3	1-4	56.3	39.9	46.5	25-34	Dircksen 1932, Dement'ev & Gladkov 1969, Glutz von Blotzheim *et al.* 1975
H. o. longipes	3	2-4					Dement'ev & Galdkov 1969
H. o. osculans	3	2-4	58.4	31.9			Caldwell & Caldwell 1931, Dement'ev & Gladkov 1969
ETHIOPIAN REGION							
H. moquini	2	1-3	60.7	41.0	55.8	27-39	This study
AUSTRALASIAN REGION							
H. longirostris	2	2-3	58.7	41.1			Serventy & Whittell 1962, Pizzey 1980
H. fuliginosus	2	2-3	64.4	42.8			Serventy & Whittell 1962
H. unicolor	3		58.8	40.9	49.4		Baker 1974, Falla *et al.* 1979
H. o. finschi		2-3	56.0	38.6	44.2	24-28	Baker 1974, Falla *et al.* 1979
H. chathamensis			56.9	40.5	46.0		Baker 1974

unicolor. However, H. unicolor has a modal clutch of three eggs (Falla et al., 1979).

Until comparative data are available for other species, it is difficult to interpret possible variations in mass and dimensions between different eggs in the laying sequence. Egg size, within and between 2-egg (initial and replacement) clutches appears consistent, with the first-laid egg in a clutch being, on average, slightly heavier. Initial 1-egg clutches, however, tend to be light, and replacement single eggs to be heavy, a reverse trend. The reasons for this are obscure.

The suggestion of a relationship between fresh modal clutch mass and female mass differs from the finding of Baker & Cadman (1980) for H. palliatus: they found no correlation between egg size and female size. However, Baker & Cadman (1980) used bill length rather than mass as an index of female size. The relationship between mass and bill length was examined for 92 female H. moquini trapped during the breeding season and there was no correlation between the measurements ($r = 0.1$; $p>0.1$).

Clutch survival

The high rate of egg predation at Marcus Island resulted in a very low hatching success (12 %) in 1979-1980. This was lower than the hatching success of H. bachmani at Cleland Island (25-46 %) where eggs are lost to gulls and storms, and much lower than the hatching success of H. ostralegus at Skokholm Island (44-82 %) (Hartwick, 1974; Harris, 1967). During 1979-1980, the hatching success, as evidenced by ringing totals, was much higher at Jutten and Malgas Islands where human disturbance is minimal, and at Vondeling Island which is undisturbed by man. Although every effort was made to cover exposed eggs at Marcus Island, the island is so small that inevitably large numbers of oystercatchers were disturbed when the island was visited, and unattended eggs were available to gulls. At islands with high densities of breeding seabirds, Kelp Gulls have learned to follow people and feed on the eggs, chicks and regurgitations of disturbed birds (Crawford _et al_., 1982). This feeding may be considered as opportunistic scavenging rather than active predation _per se_. If Kelp Gulls were important natural predators of African Black Oystercatcher eggs at undisturbed offshore islands, a negative relationship between Kelp Gull and African Black Oystercatcher numbers might be expected at individual islands. This is not the case: both Kelp Gull and African Black Oystercatcher breeding populations are positively correlated with island area. Number of Kelp gulls = 777.2 ln area (ha) - 1138.2 ($r = 0.64$; $p<0.01$). Number of African Black Oystercatchers = 41.6 ln area - 38.2 ($r = 0.71$; $p<0.01$). Figures for Kelp Gull populations are from Crawford _et al_. (1981) and for African Black Oystercatchers from Part 1.2. Both species show increasing populations with increasing island area and there is consequently a positive secondary correlation between Kelp Gull and African Black Oystercatcher numbers: Number of oystercatchers = 21.4 ln number of Kelp Gulls - 44.9 ($r = 0.48$; $p<0.05$). The inference from this, supported by observations of highest breeding success at undisturbed islands is that predation by Kelp Gulls is much greater at disturbed localities. Harris (1967) found that _H. ostralegus_ which nested within colonies of Lesser Blackbacked Gulls _Larus fuscus_ had a lower breeding success than those which nested outside gull colonies. The conservation management implications are self evident.

Chick survival and juvenile dispersal

Greatest chick mortality (66.7 %) occurred in the first seven days after hatching. Resightings of ringed chicks suggest that mortality after seven days is much less. In the study area, mortality between seven days old and fledging was only 28.6 %. Heppleston (1972) found that the first week after hatching was the most perilous period for chicks of H. ostralegus, with 61-62 % of chick mortality occuring during this period. Pre-fledging mortality of H. ostralegus chicks at Skokholm Island was 63 % in 1963 and 41 % in 1964 (Harris, 1967). Estimates of chick mortality in H. ostralegus elsewhere in western Europe range from 31 % to 80 % (Heppleston, 1971). Chick mortality of H. bachmani at Cleland Island ranged between 63 % and 72 % during the period 1970-1972 (Hartwick, 1974). The corresponding figure for H. moquini at Marcus Island in 1979-1980 was 76 %. Based on the evidence above, all these mortality figures are probably artificially high because of unnatural mortality induced by the observer.

There appears to be total dispersal of juvenile H. moquini away from the breeding islands by mid-July. Breeding densities of African Black Oystercatchers are very much greater at offshore islands than on the mainland coast and there is a movement of adults towards islands during the breeding season (Part 1.2). Some juveniles observed away from the breeding islands soon after the end of the breeding season were seen in the company of a pair of adults; in these instances it appeared that the entire family group had dispersed together. Observations suggest that there is strong competition for feeding territories during the nonbreeding season (Part 4.2) and juveniles are ousted earlier from parental territories at islands than on the mainland. Harris (1970) found that territory size, and by implication food supply, limited the breeding population of *H. ostralegus* at Skokholm Island.

Interpretation of the dispersal data must be handled carefully as search intensity over the entire possible range of dispersal, indeed over the entire range of observed dispersal, was not constant. Only one dispersing juvenile was individually colour coded, namely the chick that fledged at Marcus Island in 1980. This bird was present at the Shell Bay roost between at least June 1980 and November 1981 and was not seen elsewhere (Fig. 47), suggesting a lack of nomadism in dispersed juveniles. Only one chick was recorded as returning to its natal site during the study period. The normal age of first breeding in *H. ostralegus* is four years (Harris, 1967); the one returning *H. moquini* chick was two years old, but there is no evidence that it attempted to breed. (In early 1983, at least six island-ringed chicks were present at islands in Saldanha Bay. Both two- and three-year old birds were observed, but there is no evidence that any attempted to breed.)

Observations of ringed juveniles (Figs. 5, 6) and the age structures of roosts show that the distribution of juveniles within the study area was far from uniform. There was almost invariably a much greater proportion of juveniles at the most northerly roost visited, Shell Bay. North of Shell Bay, which is very close to Slipper Bay (see Part 1.2) the density of oystercatchers on the mainland during the breeding season is 0.9 birds per km of shore, but in the area south of Slipper Bay towards Saldanha, the density is 3.6 birds per km, one of the highest densities on the entire southern African mainland shore (Part 1.2). Data from the islands suggest that high adult density may be correlated with juvenile dispersal. A similar, lesser effect may be operating on the mainland forcing juveniles to the edges of favoured areas. The increasing proportion of juveniles at roosts from April to November reflects two trends - an increasing number of juveniles dispersing from the islands in the early part of the period, and a decreasing number of adults joining roosts towards the start of the breeding season.

The ratio of ringed:unringed first year birds on the mainland was greater than at the breeding islands. There are two explanations for this. Either there is a shuttle effect in operation whereby dispersing island-bred juveniles arriving in areas where mainland-bred juveniles are present displace the latter, which then disperse out of the study area, or the breeding success on the mainland in this region is very low. Much of the mainland coast within the study area is heavily disturbed by fishermen, holiday makers and offroad vehicles. The deleterious effect of human disturbance on the breeding success of African Black Oystercatchers was clearly demonstrated at Marcus Island and the latter explanation is favoured. This provides further support for the creation of a mainland nature reserve in this area as proposed in Part 1.2.

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Part 5.3. Adaptiveness of nest site selection and egg coloration in the African Black Oystercatcher *Haematopus moquini*.

Behav Ecol Sociobiol 11 (1982):
117-123

SUMMARY

1. African Black Oystercatchers Haematopus moquini select nest sites according to macrohabitat type, local substratum, the presence of plants and other objects at and close to the nest, and shelter. Nest sites in both structurally complex and simple habitats are highly cryptic.

2. Eggs are cryptic and there are consistent differences in the patterns of pigmentation between first and second laid eggs within a clutch, but between females of the same population overall clutch pattern is similar and only the intensity of pigmentation varies. Within-clutch differences in egg markings did not result in differential predation rates of first and second eggs, but increased nest complexity and hence the crypticity of the clutch.

3. Nests usually are sited adjacent to feeding territories. When such sites are not available, birds "leapfrog" over the territories of neighbouring pairs rather than attempt nesting in marginal habitats, and may nest several hundred metres away from their feeding territories. Eggs of "leapfrogging" birds had the highest survival and hatching rates in the study area.

INTRODUCTION

This study considers the spatial arrangement of nests of African Black Oystercatchers Haematopus moquini and tests the hypothesis that site selection is random. Within- and between-clutch variations in egg markings are analysed and the adaptive advantages of nest site selection and egg coloration are discussed.

The African Black Oystercatcher is a territorial, ground-nesting species that breeds along all major shore types, and rarely at coastal wetlands, mainly on the west and southwestern coasts of southern Africa. Highest breeding densities occur at offshore islands (Part 1.2) where much of this investigation was carried out.

STUDY AREA AND METHODS

The study was made at three predominantly rocky islands and at four mainland sites in the southwestern Cape, South Africa. The islands, Marcus, Malgas and Jutten, are in Saldanha Bay (33 04S, 17 57E) and cover 11, 9 and 46 ha respectively. The mainland sites were mixed rocky/sandy shores at Hospital Bay (32 57S, 17 53E) and Hoedjies Point (33 02S, 17 58E); a sandy shore at Silverstroomstrand (33 35S, 18 21E); and a man-made rocky habitat along a causeway joining Marcus Island to the mainland. The causeway incorporates large areas of partly vegetated coarse sand.

To investigate nest site selection, the distribution of major habitat types (macrohabitat) above the Mean High Water Mark at spring tides (MHWM) was mapped at Marcus Island. Habitats were separated according to substratum type to a depth of 70 mm (the maximum depth of a nest) and vegetation. The numbers of nests in different habitats were recorded and compared with a random distribution. Habitat within a 1 m radius of the nest (microhabitat) was assessed according to substratum at the nest site and the presence or absence of objects conceivably enhancing the crypticity of the nest and incubating adult. Such objects were plants, stones, driftwood and mussel shells. The frequency with which these objects occurred at the nest margin, between the nest margin and 0.5 m from the nest, and between 0.5 and 1 m of the nest were recorded. To test for significant variation, an identical procedure was followed at a control point 2 m away from the nest and parallel to the MHWM. The control point was positioned parallel to the MHWM rather than randomly directed to avoid crossing macrohabitat boundaries as these tended to run parallel to MHWM close to the shore, especially on the northwestern coast of the island (Fig. 49).

The distances of all nests from the nearest point on the shore were measured to the nearest m and for 47 individually colour-ringed pairs the distance from the nest to the nearest point on their feeding territories was measured. Nest aspect was considered as the compass octant most exposed to the elements and was determined by local topography.

Reactions to coloured plastic discs, 30 mm in diameter, placed in and close to the nest during incubation, were measured as an additional test of the bird's awareness. On 162 occasions, three discs (one red, one yellow and one blue) were placed in the nest, and a further three were placed around the nest 1 m from the nest margin. The positions of the six discs relative to the nest were recorded 1 h later.

The extent of nest lining (mainly shell and rock fragments) was recorded as: 0 (no lining covering nest depression), 1 (1-25 % cover), 2 (26-50 % cover), 3 (51-75 % cover) and 4 (76-100 % cover).

The following attributes of the eggs themselves were recorded for first and second laid eggs in each clutch: the presence of large, medium and small blotches (which combination was present); the abundance of scrolls ranked on a scale of 0-4, absent to abundant;

and the intensity of pigmentation also ranked 0-4, absent to heavy, in three zones of the egg (blunt apex, equatorial band and pointed apex). Within-egg variation in pigmentation was calculated as $V = (A-B)+(B-C)+(A-C)$ where A, B and C relate to the pigmentation scores in the three zones. The difference between individual zones always was recorded as a positive value. Overall pigmentation intensity of the egg was scored as A+B+C.

Between clutch differences in egg markings were analysed using the Kruskal-Wallis one way analysis of variance test for two egg clutches (the modal clutch). Within clutch variations in egg markings were analysed using the Mann-Whitney rank sum test. Four variables were incorporated in these analyses: the combination of small, medium and large blotches on each egg ranked S=1, S+M=2, M=3, S+L=4, M+L=5 and S+M+L=6; the intensity of scrolling, the overall pigmentation intensity and the within-egg pigmentation variability (V).

RESULTS

Habitat preference

Six major habitat types (A-F) were recognized at Marcus Island (Fig. 49); A: bare rock with guano accumulated in some cracks and depressions (40 %), B: a mixture of rock and guano/humus, and vegetation dominated by the low shrub <u>Atriplex</u> <u>patula</u> and to a lesser extent by the creeping succulent <u>Prenia</u> <u>pallens</u> (28 %), C: rock with large accumulations of shell fragments, particularly of black mussel <u>Choromytilus</u> <u>meridionalis</u>, and vegetation dominated by <u>Prenia</u> (18 %), D: a mixture of rock and sand dominated by <u>Atriplex</u> with some <u>Prenia</u> (2 %), E: banks of storm-washed mussel

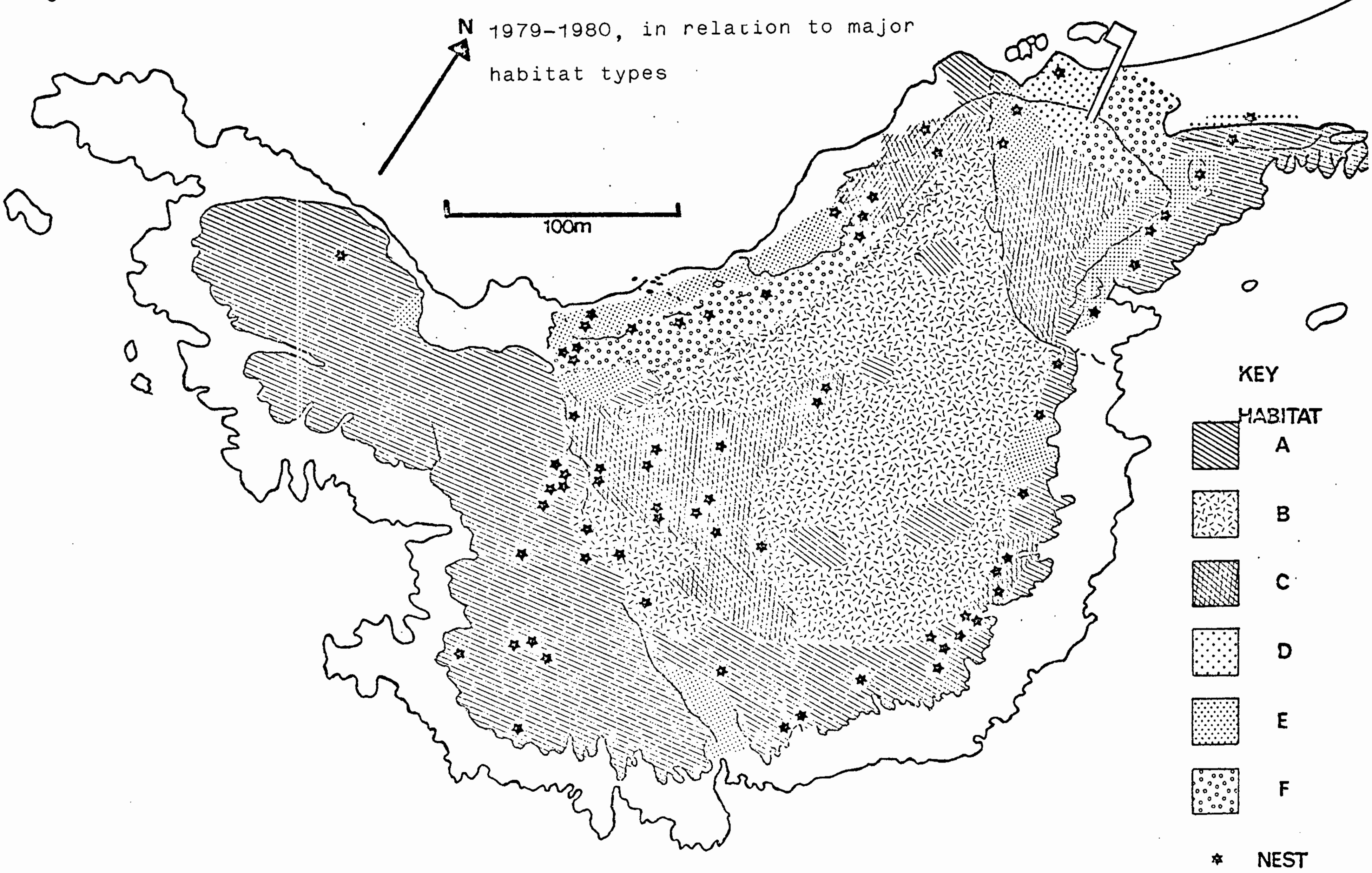


Figure 49. Distribution of African Black Oystercatcher nests at Marcus Island, 1979-1980, in relation to major habitat types

shells that remain above the MHWM (6 %) and F: sand, unvegetated or dominated by Atriplex (6 %).

Differences beween observed and randomly expected frequencies of nests in different habitats were highly significant ($X^2 = 35.81$; $p<0.001$), and birds showed a strong tendency to nest away from rock dominated habitats ($X^2 = 9.96$; $p<0.01$), preferring sandy and shell-strewn substrata.

At the nest, eight local substratum types were recognized at three islands (Table 57). At all three islands substrata d, e and f were preferred; birds tended not to nest on bare rock. Comparing E+F and G+H, $X^2=75.46$; $p<0.001$. In addition to showing selection for substratum type, birds showed a preference for nesting at, or close to, a substratum edge. Twenty-seven nests out of a total of 72 were located at, or close to, a substratum edge, as compared with only 10 control points that were so located: this difference is significant ($X^2=7.81$; $p<0.01$).

Objects at the nest

Birds showed a preference for nesting immediately adjacent to plants ($X^2=6.21$; $p<0.02$) and other three-dimensional objects ($X^2=31.72$; $p<0.001$) and for nesting within 0.5 m of the latter ($X^2=5.90$; $p<0.02$). In contrast there was no preference for nesting near two-dimensional objects such as mussel shells. Birds made up to eight nest scrapes before laying and site selection of unused scrapes followed a similar pattern but was not as clear cut, there being preference for three-dimensional objects only at the nest scrape itself, and not nearby.

Although these data suggest that birds do not select for two-dimensional objects at the nest, colour of such objects has

TABLE 57. Observed and expected frequencies of African Black Oystercatcher nests on eight substratum types at three islands

	Substratum	Marcus		Malgas		Jutten		Total	
		Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
a.	Sand	7	7					7	7
b.	Sand & shells	8	5			1		9	5
c.	Shells	8	9	2	2	2		12	11
d.	Shells & humus	13	6	1		1	1	15	7
e.	Humus & guano	10	5	6	6			16	11
f.	Guano & rock	11	2	6		3		20	2
g.	Rock	12	37	3	10	3	10	18	57
h.	Pebbles & stones	3	1			1		4	1
	TOTAL	72		18		11		101	

not been considered. Birds did react to the coloured discs placed in and near the nest. Of discs placed in the nest, 86 % were still in the nest after one hour. Birds reacted most strongly to yellow discs and in 6 % of replicates these were moved more than 1 m from the nest. Of the discs placed 1 m from the nest margin, 71 % had not been moved after 1 h, and 14 % were incorporated into the nest, with blue discs being incorporated most frequently ($X^2=8.67$; $p<0.05$). Yellow discs were again moved farthest away most frequently ($X^2=32.00$; $p<0.001$). Of the three colours used in trials, oystercatchers apparently preferred blue discs in and close to the nest and reacted most strongly against the presence of yellow discs.

Nest spacing, lining and aspect

The modal distance of nests from the adjacent shore at Marcus Island was 11-20 m and at the more exposed islands of Malgas and Jutten it was 21-30 m (Fig. 50). Both distributions are clearly skewed, the birds showing a preference for nesting close to the shore. At Marcus Island, 74.5 % of nests were less than 50 m from the feeding territory and 14.9 % were more than 110 m away (Fig. 51). Birds nesting in the middle of the island exhibited a "leapfrog" spacing effect whereby those with feeding territories farthest from available suitable breeding substrate "leapfrogged" over those defending territories closer to suitable substrate (Fig. 52).

The nest was usually a simple scrape in the ground formed by the bird leaning forward onto its breast and pushing backwards with its feet. Where the substrate was too hard for scraping, the rim of the nest was built up with shell fragments and rock chips. Nests at islands regularly were lined to varying extents, and the

Figure 50. The distribution of African Black Oystercatcher nests in relation to the Mean High Water Mark (MHWM) at three islands in the southwestern Cape

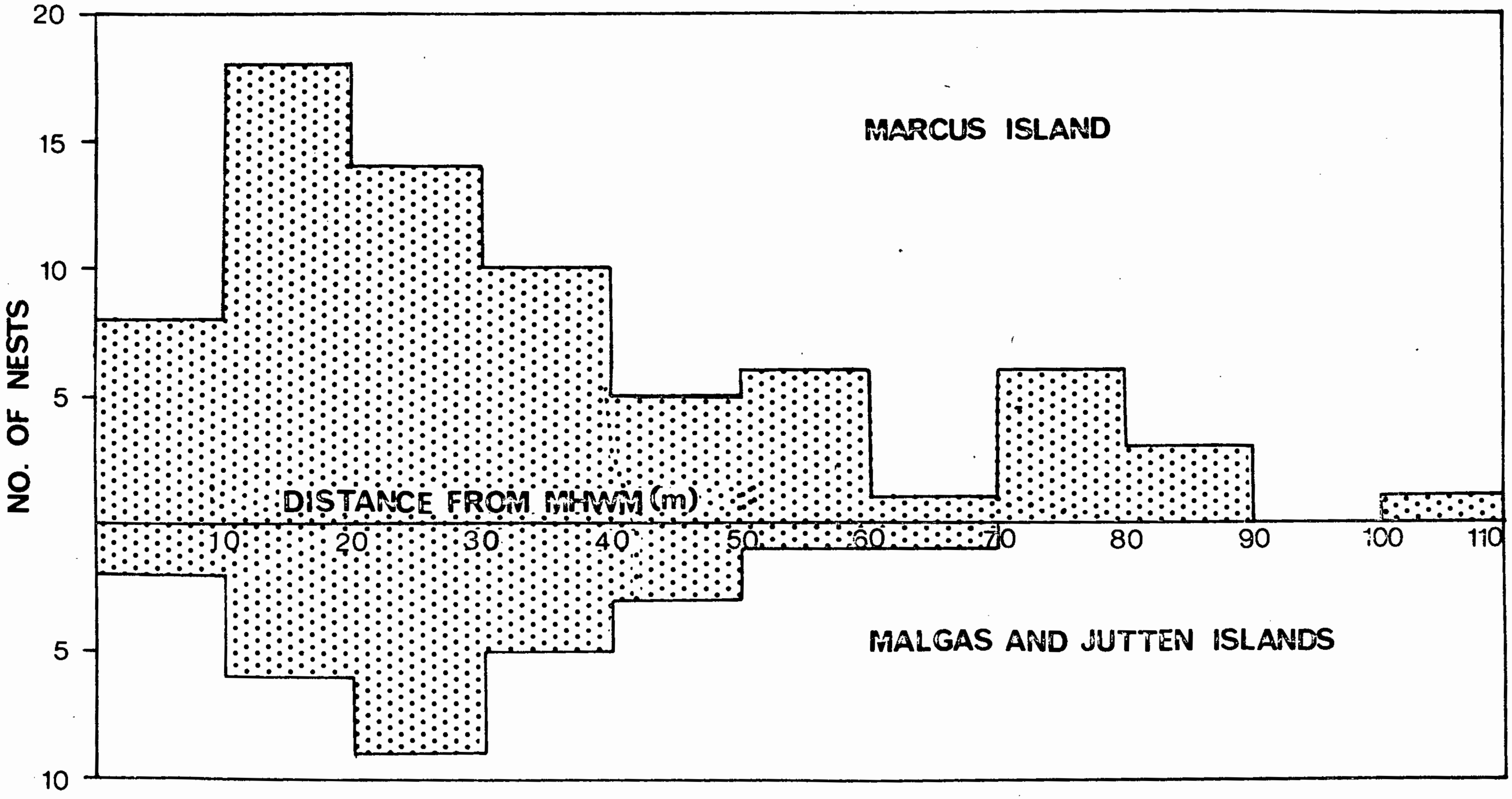
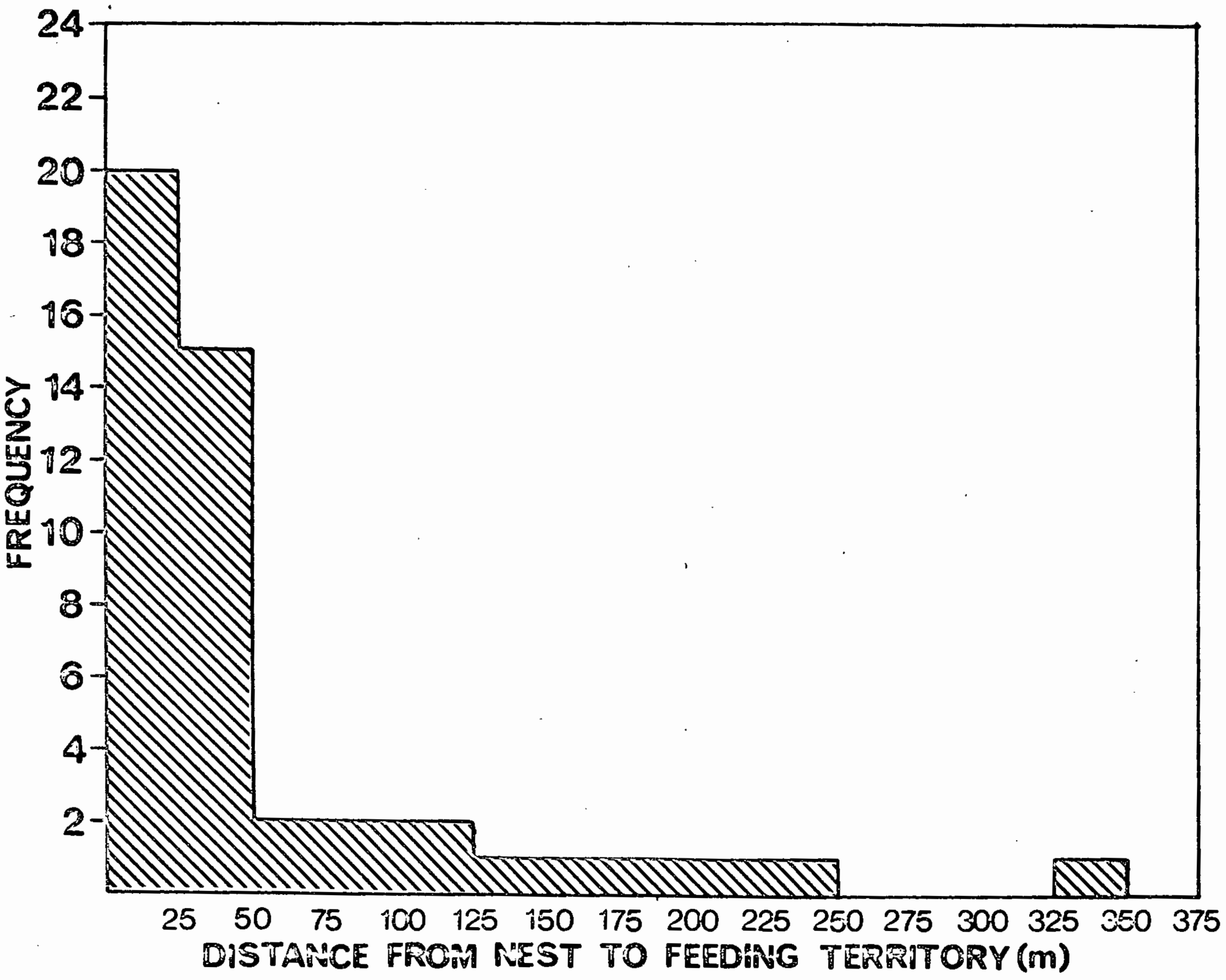


Figure 51. The distribution of African Black Oystercatcher nests at Marcus Island in relation to the distribution of feeding territories



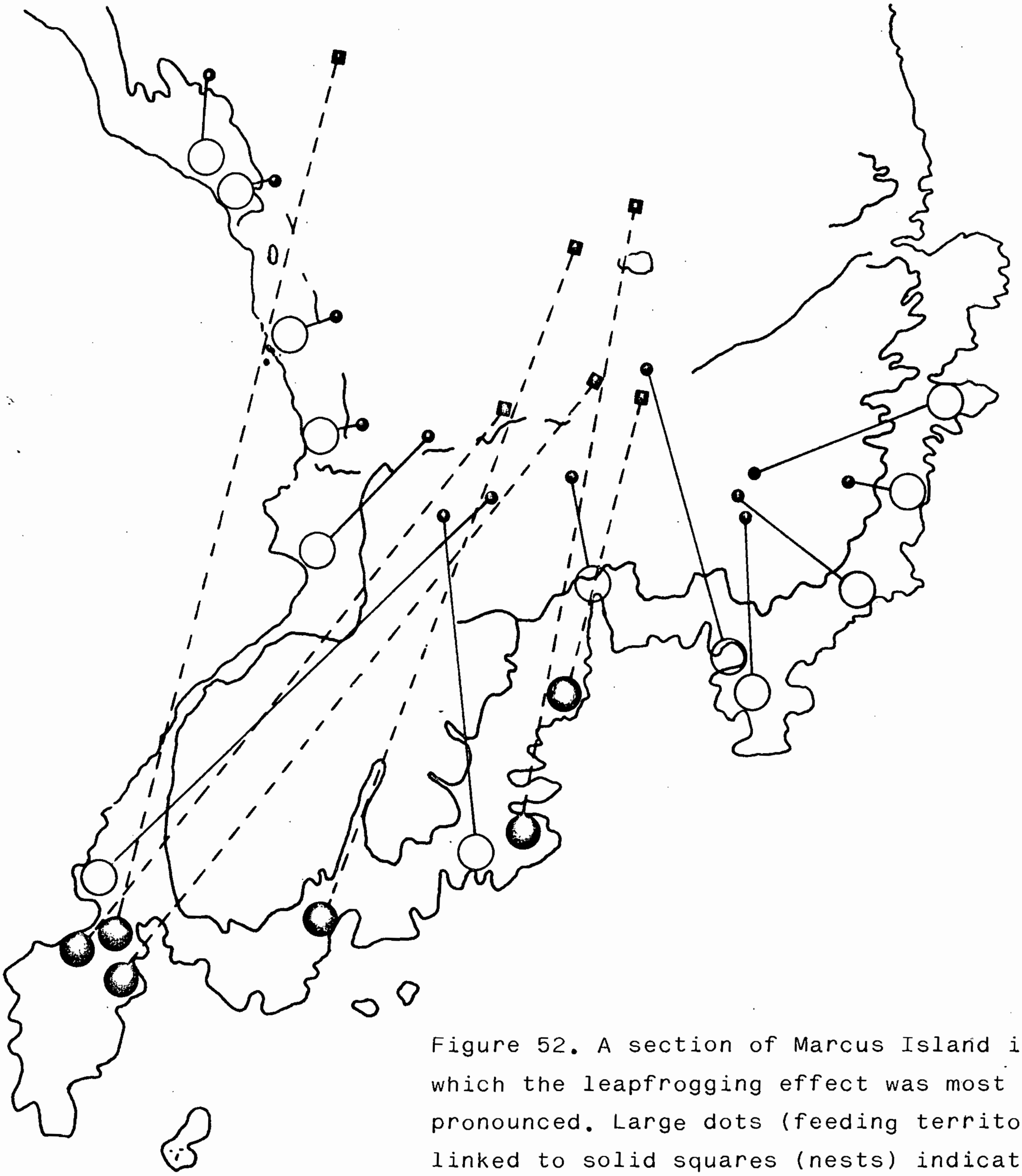


Figure 52. A section of Marcus Island in which the leapfrogging effect was most pronounced. Large dots (feeding territories) linked to solid squares (nests) indicate pairs that leapfrogged. Open circles linked to small dots indicate pairs that have not leapfrogged. Note: feeding territories are contiguous and have been stylised for simplicity

lining was added to during incubation.

The extent of nest lining was significantly higher on islands than at mainland sites (X^2=69.16; $p<0.001$). At the two mainland localities where Kelp Gulls Larus dominicanus breed, Hoedjies Point and the Marcus Island causeway, nests were lined more extensively than at other mainland sites (X^2=5.69, d.f.=1, $p<0.05$, n=17, Yates' correction applied).

The aspect of the majority (76.4 %) of the nests at Marcus Island fell in the 180° arc facing away from the prevailing wind, which is SSW during the breeding season: oystercatchers apparently prefer sheltered nest sites.

Egg coloration and predation

The base colour of African Black Oystercatcher eggs is pale beige washed with blue, green or brown and intermediates. Of 108 eggs examined, 0.6 % were washed with brown, 9.0 % blue/brown, 52.3 % blue, 25.4 % blue/green, 12.1 % green and 0.6 % green/brown. All eggs had blotches and scrolls of two or three shades of black and brown and there was no difference in blotch/scroll colours between first and second eggs.

A combination of small and medium sized blotches occurred most frequently on first laid eggs; second laid eggs most frequently had only small blotches (Table 58). Medium blotches occurred most consistently on first eggs (X^2=5.33; $p<0.05$). Comparing blotch size combinations, scrolling intensity, pigmentation intensity and pigmentation distribution between clutches (between females) showed that only the intensity of pigmentation varied (Kruskal-Wallis test statistic = 44.66; $p<0.05$; n=30 clutches). Within clutches, second eggs had significantly smaller blotches (Mann-Whitney test statistic = 734; $p<0.001$), significantly more

TABLE 58. Frequency of occurrence of blotches of varying size and size combinations of first and second eggs of African Black Oystercatchers.

S = small, M = medium, L = large blotches

Blotch sizes	Frequency of size combinations (%)			Frequency occurrence of blotch sizes (%)	
	Egg 1 (n=70)	Egg 2 (n=38)		Egg 1	Egg 2
S	13	50			
S+M	53	39			
M	17	0	S	79	97
S+L	0	3	M	87	47
M+L	4	0	L	17	8
S+M+L	13	8			
Difference	X^2=24.08, P 0.001				

scrolling (Mann-Whitney test statistic = 179; $p<0.001$) and a less uniform distribution of pigment (V) (Mann-Whitney test statistic = 286; $p<0.01$). The intensity of pigmentation did not differ between first and second eggs.

Although there were significant differences in the type and pattern of egg markings between first and second eggs, this did not result in differential predation rates. Eggs were lost from 35 two-egg clutches at Marcus Island during the 1979/1980 breeding season and in 21 instances, both eggs were lost simultaneously. Of the remaining 14 nests, seven lost the first egg first and seven the second. At 82 nests, including some monitored on the mainland, only one first laid egg was lost prior to clutch completion which normally occurred within 48 h.

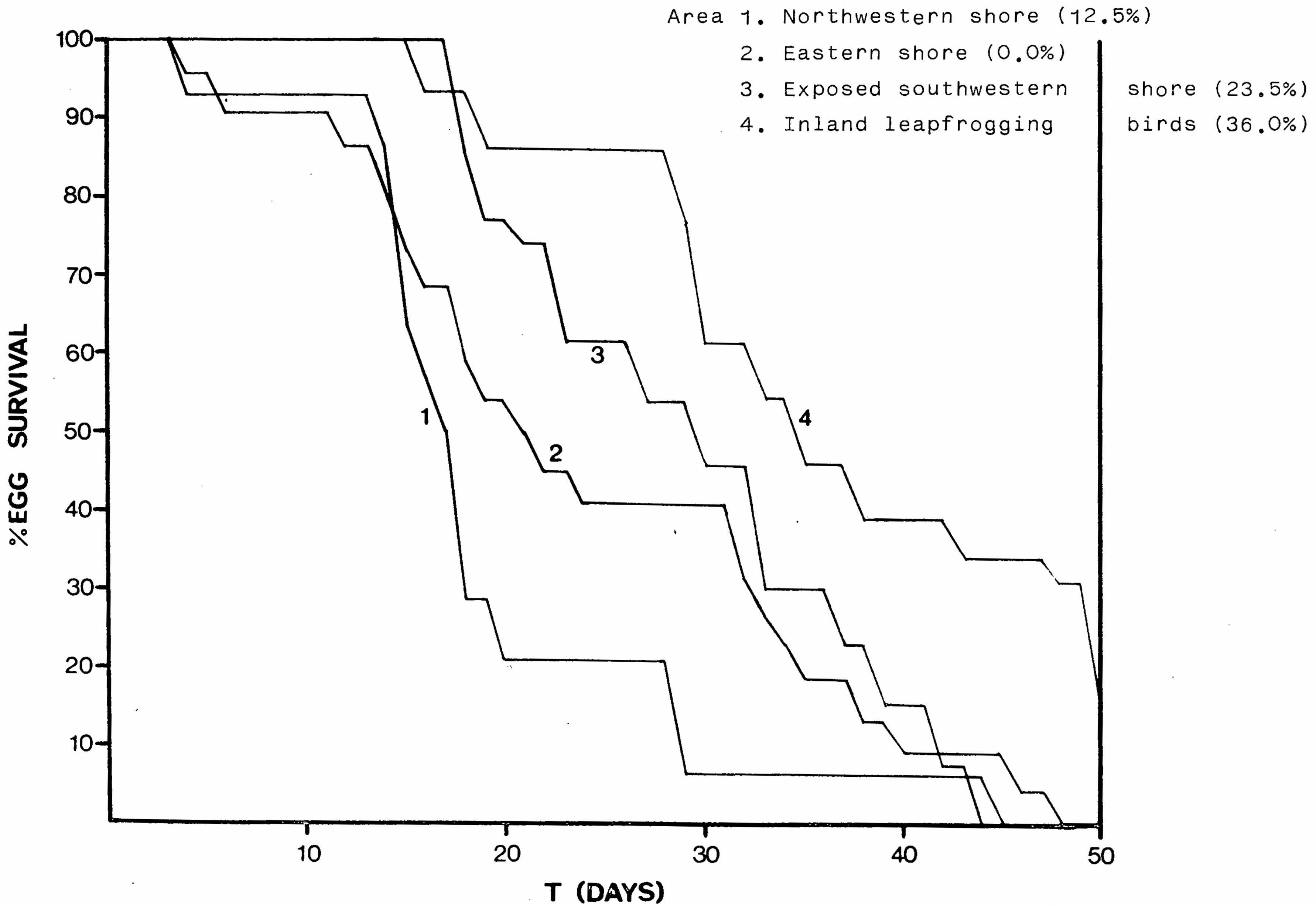
Of 85 monitored eggs that were lost, 16 were lost between one and 10 days of clutch completion, 27 between 11 and 20 days, 19 between 21 and 30 days and 23 were lost more than 30 days after clutch completion: these differences are not significant ($X^2=3.24$; $p>0.05$).

Comparing eggs lost with eggs hatched between leapfrogging and non-leapfrogging birds, the former achieved a significantly higher hatching success ($X^2=5.42$, d.f.=1, $p<0.05$) (Fig. 53).

DISCUSSION

African Black Oystercatchers select nest sites away from rock-dominated areas. However, rocky offshore islands with rich intertidal invertebrate communities support the highest breeding densities of oystercatchers (Summers & Cooper, 1977; Part 1.2).

Figure 53. Survival times (days) of depredated eggs in four areas of Marcus Island, 1979-1980. (Percentage of eggs hatching in parentheses)



Only eggs monitored throughout the incubation period are included in this figure.

The oystercatchers' different feeding and breeding habitat requirements suggest that the number of sites where both can be met is limited. However, rocky islands contain a wide spectrum of microhabitats within which the necessary substrata are available, though not evenly distributed. Selection for such areas is strong even though they may not be optimal in terms of energetic investment in parental care. Availability of nesting sites is limited by territorial spacing, island size, the presence of colonially breeding and roosting birds such as Jackass Penguins _Spheniscus_ _demersus_ and Cape Cormorants _Phalacrocorax_ _capensis_ and the extent of supralittoral flooding from summer storms. At Cleland Island, British Columbia, storms are a major source of American Black Oystercatcher _H_. _bachmani_ egg and chick loss (Hartwick, 1974). By normally nesting more than 10 m from the MHWM, African Black Oystercatchers ensure low nest loss at islands in the southwestern Cape. At Marcus Island, only one clutch and one chick were lost to flooding during the 1979/1980 breeding season, but a severe storm immediately prior to the 1980/1981 breeding season washed over 12 (16 %) of the previous season's nest sites.

African Black Oystercatchers prefer to nest near plants and other three-dimensional objects. Birds also attend to their two-dimensional and colour environment and will modify it at times. The significance of observed colour preference is not known: the incorporation of blue discs into the nest may be related to the fact that mussel shell fragments, the most frequently used type of nest lining, are blue. Selection for proximity to three-dimensional objects presents visual diversity (Croze, 1970) to predators such as Kelp Gulls flying overhead, as may the greater degree of nest lining at localities where Kelp

Gulls are common. Lack of lining at mainland sites, primarily sandy beaches, may be a function of conspicuousness and substrate qualities. In soft sand, shuffling at the start of an incubation bout can bury lining, including artificial lining.

American Pied Oystercatchers _H_. _palliatus_ and European Oystercatchers _H_. _ostralegus_ frequently lay their eggs in areas littered with shells and often line their nests with apparently conspicuous shells and fragments (Bent, 1921; Hausman & Hausman, 1972, cited in Montevecci, 1976). The significance of this apparently maladaptive behaviour is unknown but predation pressures may not have strongly selected against it (Montevecchi, 1976). African Black Oystercatchers do not make conspicuous nests. If nests were heavily lined on sandy beaches, aggregation of lining material into discrete clusters would render the nest conspicuous in a simple visual environment. Conspicuousness may enhance survival of oystercatcher nests if such conspicuousness was not contained within a visually hunting predator's search image strategy (Montevecchi, 1976). However, search image strategies are theoretically plastic (Hughes, 1979) and a predator could modify its strategy to cue on conspicuous nests with an immediate effect.

Patterns of egg markings of African Black Oystercatchers were consistent between females of a population although absolute pigment investment between clutches varied. Consistent differences in egg pattern within clutches occurred, suggesting selection for consistent clutch "appearance". It is not known whether more evenly pigmented first eggs, which are not incubated continuously prior to clutch completion, are more cryptic than second eggs. Differences did not cause differential predation.

Unlike sympatric Whitefronted Plovers Charadrius marginatus, African Black Oystercatchers do not cover their eggs when leaving the nest and the first laid egg is exposed regularly prior to clutch completion. In colonies of marsh nesting Laughing Gulls Larus atricilla where nest site selection is strongly influenced by flooding, egg coloration, based on experiments with artificial eggs, conferred no selective advantage when predators were allowed access to an experimental colony (Montvecchi, 1976, 1978; Burger & Schisler, 1980). Differential egg pigmentation has been reported in at least three larids but has not been shown to confer a selective advantage (Preston, 1957; Chamberlin, 1977). Since pigment investment by African Black Oystercatchers is consistent within clutches, pattern differences between first and second eggs are not a result of pigment being limited. Colour dimorphism may simply enhance clutch crypticity. Since two similar eggs in the same nest would present a larger "object" of uniform appearance than dimorphic eggs. African Black Oystercatchers select sites that present the least number of visual clues to potential predators irrespective of habitat.

The "leapfrog" effect of territorial spacing may have important energetic consequences for adults feeding chicks. That "leapfrogging" between feeding and breeding territories occurs suggests it is more adaptive to increase the energetic investment of parental care than to attempt nesting in marginal sites. The effects of "leapfrogging" will be reduced for those pairs which are able to move their chick(s) from the nest site to the edge of the feeding territory. A comparable spacing effect has been described in Whitefronted Plovers (Summers & Hockey, 1980). "Leapfrogging" pairs may have superior feeding territories compensating for the additional travel. Alternatively, "leapfrogging" birds may be relatively less fit individuals unable to secure neighbouring feeding and breeding territories.

Terrestrial predators had access to Marcus Island and several breeding adults were killed. Consequently, breeding success could not be used as a measure of fitness to test the above hypotheses, but the highest hatching rate was achieved by "leapfrogging" birds (36 % of eggs) even though they nested among breeding Kelp Gulls. Oystercatcher nests with lowest survival rates were linearly arranged (Fig. 49): this may reflect the predators' hunting strategies.

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Part 5.4. Summary

African Black Oystercatchers breed during the summer months, normally laying two, but sometimes one or three eggs. In the event of clutch loss, replacement clutches frequently are laid. The eggs are highly cryptic, and whilst the pattern of pigmentation varies consistently between first- and second-laid eggs, different females within a population lay clutches of similar appearance.

A number of factors influence the choice of nest site, including substratum and the proximity of potentially disruptive objects such as plants and stones. Nests are highly cryptic, both to terrestrial and avian predators, and are sheltered from the prevailing weather. Nests normally are sited adjacent to feeding territories, but in areas where no suitable nest sites exist, birds may nest several hundred metres from the feeding territory.

At the main study site (Marcus Island) the rate of egg and chick loss to predators was high. Two factors were considered responsible for this: the presence of mammalian predators on the island and enhanced predation by gulls as a consequence of human disturbance. Greatest chick mortality occurs in the first week of life, and mortality between eight days and c. eight months old was estimated at 49 % and 68 % in successive years.

All chicks born at islands disperse from their natal sites, and juvenile displacement of up to 310 km was recorded. Recruitment to the population from islands is probably vitally important in maintaining the population, further emphasizing the importance of islands as conservation areas.

SUMMARY AND CONCLUSIONS

1. The African Black Oystercatcher is endemic to the coast, islands and coastal wetlands of southern Africa, breeding from Seal Island, Namibia (26 36S; 15 10E) in the north, to Mazeppa Bay, Transkei (32 29S; 28 39E) in the east. Non-breeding birds have been recorded north to Lobito, Angola (12 35S; 13 25E) and east to Dawson's Rocks, Natal (28 38S; 32 18E). The southwestern Cape Province supports 53 % of the estimated world population of 4 800 birds. Small offshore rocky islands support 29 % of the population, and only 13 % of the population is located outside the political boundaries of South Africa.

2. Adult African Black Oystercatchers are largely sedentary: maximum recorded displacement of an adult from its breeding site is 15 km. There is a certain amount of seasonal shift in distribution. During the breeding season (summer) there is an increase in density of African Black Oystercatchers at offshore islands and sandy beaches, with a corresponding decrease in density on mainland rocky shores and at sheltered islands. On mixed shores, densities remain the same throughout the year, probably reflecting availability of rocky areas for feeding and sandy areas for breeding.

3. Female African Black Oystercatchers are larger than males, the most dimorphic characters being mass (females averaging 8.5 % heavier), and exposed culmen length (females 13.8 % longer). The ranges of all measurements overlap between the sexes. Within pairs, however, bill length is consistently dimorphic.

4. Mussels and limpets are important prey for African Black Oystercatchers, and the birds have evolved prey-specific feeding techniques to cope with differing prey morphologies. Mussels are attacked only when gaping (i.e. when the valves are partly separated), and the key to successful capture is the severing, by stabbing with the bill, of the posterior adductor muscle. Techniques used for capturing and handling limpets are size-dependent. Large limpets, which adhere strongly to the rocks, preferentially are attacked posteriorly. The cue to detection of anterior/posterior by oystercatchers is latitudinal asymmetry in the limpet's shell shape, and "correct" attack decisions are made most frequently on species exhibiting greatest asymmetry. It appears that selection for asymmetric individuals of the essentially oval-shaped upper shore limpet _Patella granularis_ has modified genetic structure of the limpet populations in areas where predation pressure is heavy.

5. Whilst mussels and limpets are important dietary items, foraging by African Black Oystercatchers is largely opportunistic, and scavenging of stranded invertebrates has been recorded. Although many pairs of oystercatchers at islands are territorial throughout the year, there are several sources of diet variation. Diet varies spatially: the diets of pairs on adjacent territories may vary more than diet of pairs at different islands, and there is geographical variation reflecting the distributions of prey species. Diet varies temporally: less feeding is done by night than by day, but, during the night, the nocturnally active limpet _P. granularis_ forms a much greater proportion of the diet than by day. Evidence was found of annual variation in diet of the same population, but this may have been an artifact of the sampling technique. There are within-pair sex-related differences in diet,

with females taking a greater proportion of polychaetes and small unshelled items, and males taking more limpets and whelks. Sexual dietary divergence is a function of differing bill morphologies, and consistent within-pair bill dimorphism is adaptive in allowing efficient resource exploitation within the territory. Larger mussels are fed to chicks than are preyed on normally by adults, and, as chicks age, an increasing proportion of mussels and correspondingly fewer limpets are included in the diet. The only aspect of diet studied that was consistent between localities was prey size selection, with oystercatchers consistently selecting away from smaller prey items.

6. At offshore islands, where oystercatcher densities are high, and predation pressure on invertebrates correspondingly high, African Black Oystercatchers have a significant effect on populations of _P. granularis_. African Black Oystercatchers reduce densities of _P. granularis_, in areas where they are accessible to predation, to a level where limpets no longer control algal growth at the sporeling stage. The resulting beds of macroalgae which develop on the upper shore support rich invertebrate (primarily crustacean) communities which provide food for smaller waders. Densities of such waders are higher at islands than on the mainland and their feeding is facilitated by oystercatcher predation on limpets. Limpets grow faster at islands than on the mainland, due to faster algal growth rates occasioned by high nutrient levels. An appreciable proportion of limpets at islands grow too large to be preyed on by African Black Oystercatchers, and it is the gamete output from these individuals that guarantees recruitment to the limpet population regardless of predation pressure on smaller individuals. Such observations of population mechanisms in situations where natural predation is heavy have

implications for the conservation management of intertidal resources in areas where uncontrolled exploitation by man for food and bait is heavy, such as in the eastern Cape Province and Transkei.

7. Activity rhythms of African Black Oystercatchers are tidally controlled, and there is a single peak in foraging activity at low tide. For the first time, quantitative field observations of nocturnal behaviour of oystercatchers were made, and the duration of nocturnal feeding was 59 % of daytime feeding duration. Territorial commitment in African Black Oystercatchers is variable, presumably reflecting resource availability. Pairs with a daytime commitment of 60 % or more are able to satisfy their feeding requirements on the territory. When the entire territory is flooded at high tide (spring tides), African Black Oystercatchers form communal roosts, but during neap tides many birds roost on their territories. Communal roosting behaviour is much more pronounced at night. Roosts tend to be sited either in areas where there is good all-round visibility, or where there are offshore rocks to which the birds can fly if disturbed. These observations, coupled with the fact that mortality due to predation is greatest during the breeding season, when roosts do not form because birds are committed to the nest sites, strongly suggest the communal roosting in this species has evolved primarily as an anti-predator strategy.

8. The daily energy expenditure of non-breeding African Black Oystercatchers was estimated (using food consumption of captive birds and activity budgets of wild individuals) at 629 kJ, approximately 2.5 x Basal Metabolic Rate. Annual energy requirement of a pair of birds rearing one chick was estimated as

5.4×10^5 kJ. Of this gross energy intake, some 1.5×10^5 kJ is returned to the system as guano. These estimates of energy requirements are much lower than those made for the smaller European Oystercatcher, and conform closely to predicted values from recently developed standard equations for the cost of free existence in birds. Energy requirements for chick growth were measured as 3.2×10^4 kJ during the first 90 days. Chicks grow rapidly up to fledging at 35-40 days, and energy demand peaks at or close to fledging. Chicks fledge long before adult dimensions are obtained. This is adaptive in a ground-nesting territorial species where the individual is unable to benefit from social anti-predator behaviour exhibited by colonial breeders.

9. African Black Oystercatchers lay a modal clutch of two eggs, and frequently relay if the initial clutch is lost. Nest site selection by birds is dependent on a number of factors which enhance survival of the clutch. The distance of the nest from the high water mark is determined by exposure of the site. In areas where flooding by storms is a threat, nests are sited farther inland. In areas where aerial predators, principally gulls, are common, nests are lined to varying extents with shell fragments, which are of similar colours to the eggs themselves. Birds select for the presence of potentially disruptive three-dimensional objects at and close to the nest, but experiments with coloured discs demostrated that birds are aware of the colour, as well as structural environment of the nest site. Loose substrata are preferred, and nests generally are sheltered from the prevailing weather. In areas where no suitable sites are available adjacent to the feeding territory, birds may nest several hundred metres away, "leapfrogging" over territories of other pairs. Eggs of "leapfrogging" birds had the highest survival rate. In addition

to selecting cryptic nest sites, the eggs themselves are highly cryptic. They are blotched and scrolled to varying extents, and, within clutches, there are consistent differences in the patterns of pigmentation between first- and second-laid eggs. This is thought to enhance crypticity of the clutch by not presenting a "super-object" (i.e. two identical objects) to predators. Differential pigmentation did not lead to differential predation rates of first and second eggs. Although there are differences in pigmentation pattern within clutches, pigmentation pattern does not vary between clutches, though there is some variation in the intensity of pigmentation between clutches. It appears therefore that evolution has selected for consistent clutch appearance.

10. Despite the very cryptic nature of oystercatcher clutches, the rate of egg loss at the main study site was high. This was largely an artifact of human disturbance. Due to human presence, clutches are left unattended for unnaturally long periods, and Kelp Gulls, which have learned to follow people and prey on exposed eggs and chicks, take an unnaturally high toll. Supporting evidence for this theory is the much higher productivity of oystercatchers at undisturbed islands (even though appreciable numbers of Kelp Gulls are present at these sites). The extent of egg loss at Marcus Island that could be ascribed to introduced mammalian predators is not known.

11. Chicks normally leave the nest within 24 h of hatching, and suffer highest mortality during the first week of life. Mortality between eight days and c. eight months was calculated at approximately 49 % and 69 % in successive years. In island populations, all juveniles disperse from their natal sites, some in the company of their parents. Juvenile displacement of up to

310 km has been recorded, but most dispersal is of more limited range. Observations of ringed juvenile birds on the mainland suggest that mainland productivity is low in relation to productivity at islands, due probably to presence of terrestrial predators and, more importantly, to the high levels of human disturbance along the coasts during the summer.

12. Although islands support only 29 % of the world population of African Black Oystercatchers, the birds are highly concentrated, and hence vulnerable, at these sites. Islands are a major source of recruitment to the population and warrant some type of special protection. Human disturbance to island breeding localities of African Black Oystercatchers during the summer seriously reduces productivity due to enhanced predation by gulls on eggs and chicks. Introduced mammalian predators are known to kill African Black Oystercatchers at three islands. This problem at Marcus Island has now been alleviated by construction of a predator-proof barrier across the causeway leading to the island.

In conclusion, islands are extremely important to the continued wellbeing of the southern African oystercatcher population. They are also important for several breeding seabird species. Although access to such islands is currently controlled, it is strongly recommended that consideration be given to declaring these islands as nature reserves, extending to the low water mark or even infratidally. Access to these islands should be strictly controlled during the breeding seasons of species susceptible to disturbance, such as terns and oystercatchers.

Haematopus moquini, a summary

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G.S. The Birds of Africa, Vol. 2.
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Haematopus moquini Bonaparte. African Black Oystercatcher. Huîtrier de Moquin.

Haematopus moquini Bonaparte. 1856. Comp. Rend. Acad. Sci. Paris 43, p. 1020; Africa; restricted type locality Cape of Good Hope, South Africa.

Range and status. Resident, breeding along southern African coast and offshore islands from Seal I., Namibia to Mazeppa Bay, Transkei, South Africa. Non-breeding, regular as far north as Hoanib Estuary, Namibia, and the Bashee River, Transkei. Rare in eastern Transkei and Natal; vagrant Angola (2 records). Records from Gabon and Mozambique require confirmation. Abundant to uncommon within range. Estimated world population 4 780, including 1 410 at offshore islands, 3 020 on mainland coast and 350 at coastal wetlands. Locally threatened by off-road vehicles and tourist disturbance to mainland breeding areas, heavy intertidal exploitation and the introduction of mammalian predators to offshore islands.

Description. ADULT M (breeding): plumage wholly glossy black. Bill orange-red; fleshy orbital ring orange and swollen; eye red; legs and feet fleshy pink. (Non-breeding): as above, but feathers worn and browner after end of breeding season. Sexes alike, but bill of F longer and more pointed than M. SIZE: wing, M (n=64) 265-286 (275), F (n=64) 265-289 (279); tail M (n=13) 104-112 (107.2), F (n=8) 101-111 (107.1); tarsus, M (n=64) 50.6-60.8 (56.1), F (n=64) 52.0-62.0 (57.8); culmen, M (n=64) 57.7-69.5 (63.2), F (n=64) 63.6-79.1 (71.6). WEIGHT (breeding): M (n=64) 582-735 (668), F (n=64) 646-835 (730).

IMMATURE: First year plumage wholly black. Proximal two-thirds of bill orange, distal third brownish; orbital ring burnt orange and much smaller than adults'; eye reddish brown; legs and feet greyish pink. Second year as adult but with small, duller orbital ring and marginally duller distal quarter of bill.

DOWNY YOUNG: Grey, with varying amounts of white on belly. Y-shaped black mark on back and dark stripes behind the eye and through the crown; dark stripe along flanks; dark areas are first parts of body to feather; legs grey, bill black. Highly cryptic in favoured granite areas.

Field Characters. A large dark wader; cannot be confused with any other African bird. The combination of plain black plumage, pink legs and long orange bill is unique in Africa. Immatures have dull orbital ring, greyish pink legs and distal third of bill brownish.

Voice. Normally a loud strident "Kleep", "Kleep-a" or "Kleep-eep". Similar but slower "Kleep-a" given during butterfly displays mainly in pre-breeding and breeding periods. During piping displays, given in territory defence, call much more rapid "Kleepee-Kleepee-Kleepee-Kleepee" varying in volume and speed, often preceded by and interspersed with rapid trilling. In defence of nest and young, call intermediate in speed between butterfly and piping displays, and very loud, also a penetrating "Pic .. pic .. pic ....". Very soft contact calls given between adults and small chicks. Captive immature birds often give soft chattering calls while resting.

General Habits. Intimately known. Highest densities, up to 70 birds per km of shore, occur at exposed rocky islands on the west coasts of Namibia and South Africa. On mainland, most abundant on mixed rocky/sandy shores although high mainland densities also occur on the extensive sandy beaches in the Port Elizabeth area (South Africa) where preferred prey, sand mussel (*Donax*) abundant.

Forage exclusively intertidally and foraging regime tidally controlled. Open mussels by jabbing at and severing the posterior adductor muscle of gaping individuals. Dislodge limpets normally by a sharp blow to posterior sector of shell and remove flesh by scissoring action. Approximately 38 % of foraging (time) at night. Peak foraging activity at low tide. Between 25 and 50 % of available time spent foraging by day under calm conditions, over 50 % during storms. Forage approximately 6 h per 24 h (non-breeding, rocky shores). Roost communally during non-breeding season, with larger proportion of the population roosting communally by night than by day. Mean % of daylight hours (non-breeding) in other activities : resting 37 %, preening/bathing 18 %, agonistic display 7 %.

Some seasonal movement occurs towards sandy beaches and exposed rocky islands during the breeding season with a corresponding decrease in numbers on mainland rocky shores. However, adult population largely sedentary, maximum proven displacement of adult from breeding site 15 km.

Food. Mainly gastropods (30 species recorded), especially mussels and limpets, notably *Choromytilus meridionalis*, *Perna perna*, *Aulacomya ater*, *Patella granularis* and *P. argenvillei*. Also whelks and winkles, notably *Burnupena* spp., *Oxystele* spp. and *Nucella* spp. Polychaetes eaten, mainly by females, especially *Pseudonereis variegata* (mussel worm), *Marphysa depressa* and syllids. On sandy shores, mussels, *Donax serra* and *D. sordidus*.

Breeding Habits. Well known. Monogamous; solitary nester in a scrape on the ground close to the shore. Most birds retain feeding territories throughout the year, mate fidelity is high and there are no elaborate courtship displays. Frequency of butterfly displays and switchback chases increases in the immediate pre-breeding period but their significance is not known.

NEST: A simple scrape in the ground lined to varying extents with shell fragments and stone chips. On hard substrata the edge of the nest built to form a cup. Lining is added during incubation. Birds show preference for nesting close to three-dimensional objects. Modal distance of nests from high water mark at islands is 10 - 30 m, maximum 110 m. Nests normally sited adjacent to feeding territories but where nest sites are unavailable birds may nest up to 350 m away from feeding territories. Mean internal nest diameter 210 mm, depth 40 mm (95 nests). On islands where breeding densities are high, nest sites may be as close as 1.5 m. Nest is constructed annually, old nests may be rebuilt where nest sites are limited.

EGGS: 1 or 2, rarely 3, laid at 2-day intervals; South Africa (southwestern Cape) mean (46 clutches) 1.74. Slightly pyriform, buffish, washed blue, green, or brown and intermediates. Spotted and scrolled with black and brown to varying extents. SIZE : (n=105, South Africa) 55.8-65.2 x 37.9-43.7 (60.7 x 41.0). WEIGHT: (n=105) 45.0-65.0 (55.8).

Laying dates : Oct - Apr, peak Dec - Feb. Breeds slightly later in Namibia than South Africa.

Incubation: 1st egg discontinuously incubated. Incubation by both sexes. Incubation period : 27-39 (32.1) days.

Newly hatched young weighs c. 40 g (72 % of fresh egg weight). Remains in nest approximately 24 h. Bill starts to change colour by 10 days old, proximal section becoming brown. By fledging (35-40 days) proximal two-thirds dull orange. Remiges and first back feathers appear c. 14 days, retrices by 18 days. Tarsus growth complete by 40 days. Culmen fully grown c. 120 days, wing at 75 days (captive bird). fledgling weighs c. 450 g. Growth rate: 100 g - 11 days, 200 g - 17 days, 300 g - 23 days, 400 g 32 days. Wing at fledging c. 200 mm, culmen c. 53 mm.

Small young closely attended by parents and hide under bushes, rocks and in cracks when alarm calls given; freeze in open when no cover available. Fed by both parents above or within intertidal zone depending on exposure and steepness of shore. Swim well and sometimes dive to escape potential predators. One adult often guards chick while other forages : prey items normally brought complete to chick, then flesh removed, hence formation of characteristic chick feeding piles.

At islands with high breeding densities all fledged chicks disperse to mainland by mid-July; some disperse in company of parents. Maximum proven dispersal 310 km. Young independent 2-6 months after fledging, all independent by Oct.

Productivity highest at offshore islands. Estimated 0.3-0.6 young/pair/year at undisturbed islands, much less on mainland. Almost certainly long lived, as are other oystercatchers. Highest adult mortality during breeding season, due to increased predation. Large mortalities may occur during outbreaks of paralytic shellfish poisoning.

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African Nature Foundation and the South African Defence Force.

Appendix 1. OTHER OYSTERCATCHERS IN AFRICA

Appendix 1.1. Occurrence of the European Oystercatcher Haematopus ostralegus in southern Africa.

Ardea 70 (1982):55-58

The European Oystercatcher Haematopus ostralegus breeds in the Palaearctic region and winters south to the coasts of Africa, the Arabian Sea, southeast China and Japan (Vaurie, 1965; Moreau, 1972; Dowsett, 1980). This paper details the seasonal and spatial distribution and age classes of European Oystercatchers in southern Africa and considers their origins.

The 30 original records, representing 37 individual European Oystercatchers, are listed in Table 59. The seasonal distribution of the records in southern Africa is given in Fig. 54. Individuals recorded regularly for more than one month have been recorded for each month of their stay. Nos. 15 and 16 (Table 59) may refer to the same individual. Significantly more bird months were recorded during the austral summer (September-March) than at other times ($X^2=6.78$; $p<0.01$). The December and January peak is highly significant ($X^2=16.53$; $p<0.001$), suggesting that European Oystercatchers arriving in southern Africa are migratory birds that have passed their normal wintering grounds and continued farther south.

European Oystercatchers in southern Africa cannot be approached as closely as African Black Oystercatchers (pers. obs.) and detailed plumage descriptions that enable birds to be aged accurately have rarely been made.

Two of the three birds seen at Sandwich Harbour on 17 March 1975 (No. 3) were described as attaining breeding plumage; all were absent on 21 April 1975 (Becker, 1977). It is likely that these birds were adults which had undergone northward migration by that time. Palaearctic waders leave Sandwich Harbour during April (Berry & Berry, 1975). Seven individuals stayed for more than one month; of these, six were first recorded in December. The seventh

TABLE 59 . RECORDS OF EUROPEAN OYSTERCATCHERS IN SOUTHERN AFRICA

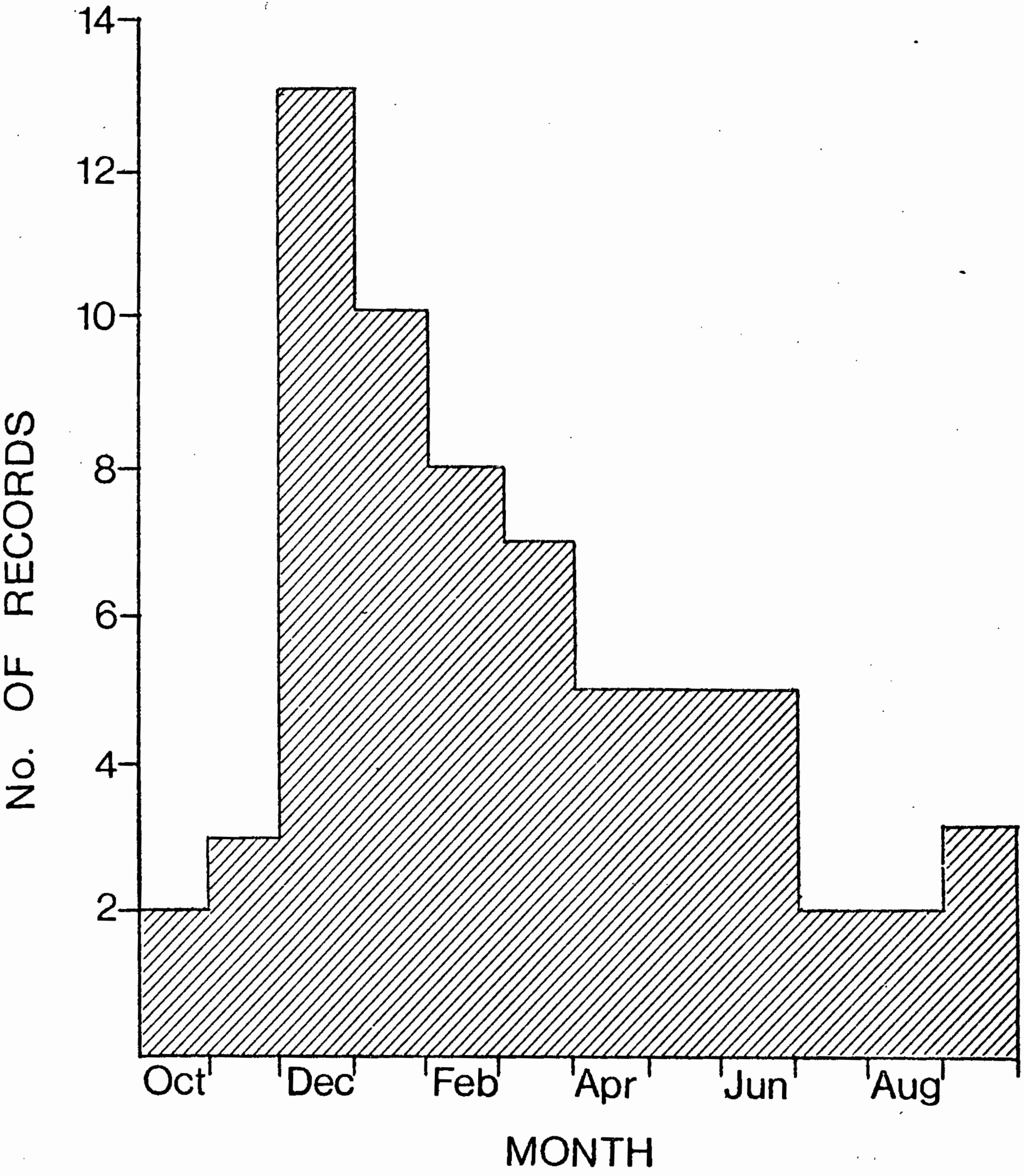
Record No.	Locality	Period of Observation	No.	Age	Association	Source
1.	Walvis Bay Lagoon	17 Jan 1978	1	-	+	Whitelaw *et al.* (1978)
2.	Sandwich Harbour	Jan 1960	1	-	+	Prozesky (1963)
3.	Sandwich Harbour	24 Feb 1975- 17 Mar 1975	4/3	-		Becker (1977)
4.	Sandwich Harbour	10 Jan 1978	1	-	+	Whitelaw *et al.*(1978)
5.	Langebaan Lagoon	Dec 1950- Mar 1951	1	-		Broekhuysen *et al.* (1958)
6.	Langebaan Lagoon	Apr 1975	2	-		Cape Bird Club (1979)
7.	Dassen Island	31 May 1971- 16 Aug 1971	1	Juv	+	J. Cooper (pers. obs.)
8.	Kommetjie	13 Nov 1938	1	-	+	Cary (1939)
9.	Strandfontein Sewage Works and adjacent coast	19 Dec 1979- 15 May 1980	1	Juv	+	P. Ryan, B. Rose, (pers. comm.)
10.	Plettenberg Bay	Dec 1953	1	-		Edwards (1970)
11.	Keurbooms R. Lagoon	Dec 1954	1	-		de Villiers (1955)
12.	Gamtoos R. mouth	11 Dec 1949- 29 Jan 1950	1	-	+	Stewell (1950)
13.	Gamtoos R. mouth	15 Oct 1972	1	-	+	McLachlan (1972)
14.	Gamtoos R. mouth	16 Sep 1980	1	Juv	+	Pers. obs.
15.	Kabeljous R. mouth	20 Mar 1970	1	-	+	Nixon (1970)
16.	Maitlands R. mouth	7 Dec 1969	1	-	+	Fisher (1969)
17.	Van Stadens R. mouth	26 Dec 1970	2	-	+	Edwards (1971)
18.	Van Stadens R. mouth	15 Dec 1978	2	-	+	Anon (1978), McLachlan *et al.* (1980), Underhill *et al.* (1980), G.J.B. Ross *in litt.*
19.	Cape Recife Sewage Works	4-12 Sep 1971	1	-	+	Blake (1976)
20.	Sundays R. mouth	9 Dec 1979	1	-	+	G.J.B.Ross *in litt.*, A.L.Batchelor (pers. comm.)

TABLE 59. (continued)

Record No.	Locality	Period of Observation	No.	Age	Association	Source
21.	Bushmans R. mouth	30 Apr 1972– 1 May 1972	1	–		Tree (1979)
22.	Kleinmonde	Feb 1892	1	–		Skead (1974)
23.	Kleinmonde	Dec 1968– Jan 1969	1	–		Tree (1979)
24.	East London	7 Dec 1968– 4 Oct 1969	1	Juv		Edwards (1970) Quickelberge (1971)
25.	Durban	2 Nov 1975	1	Juv		Sinclair (1976)
26.	Maputo	4–7 Jun 1957	1	–		Clancey (1971a)
27.	Inhaca Island	Nov 1976	1	–		J.C.Sinclair (pers. comm.)
28.	Inhambane	<u>ca</u>. 1845	1	–		Clancey (1971b)
29.	Bazaruto Island	Jun 1950	2	1 Ad 1 Juv		Van Eyssen (1958)
30.	Bazaruto Island	May 1960	1	–		Wheeler & Brooke (1961)

+ denotes association with the African Black Oystercatcher

Figure 54. Seasonal distribution of records of European Oystercatchers in southern Africa

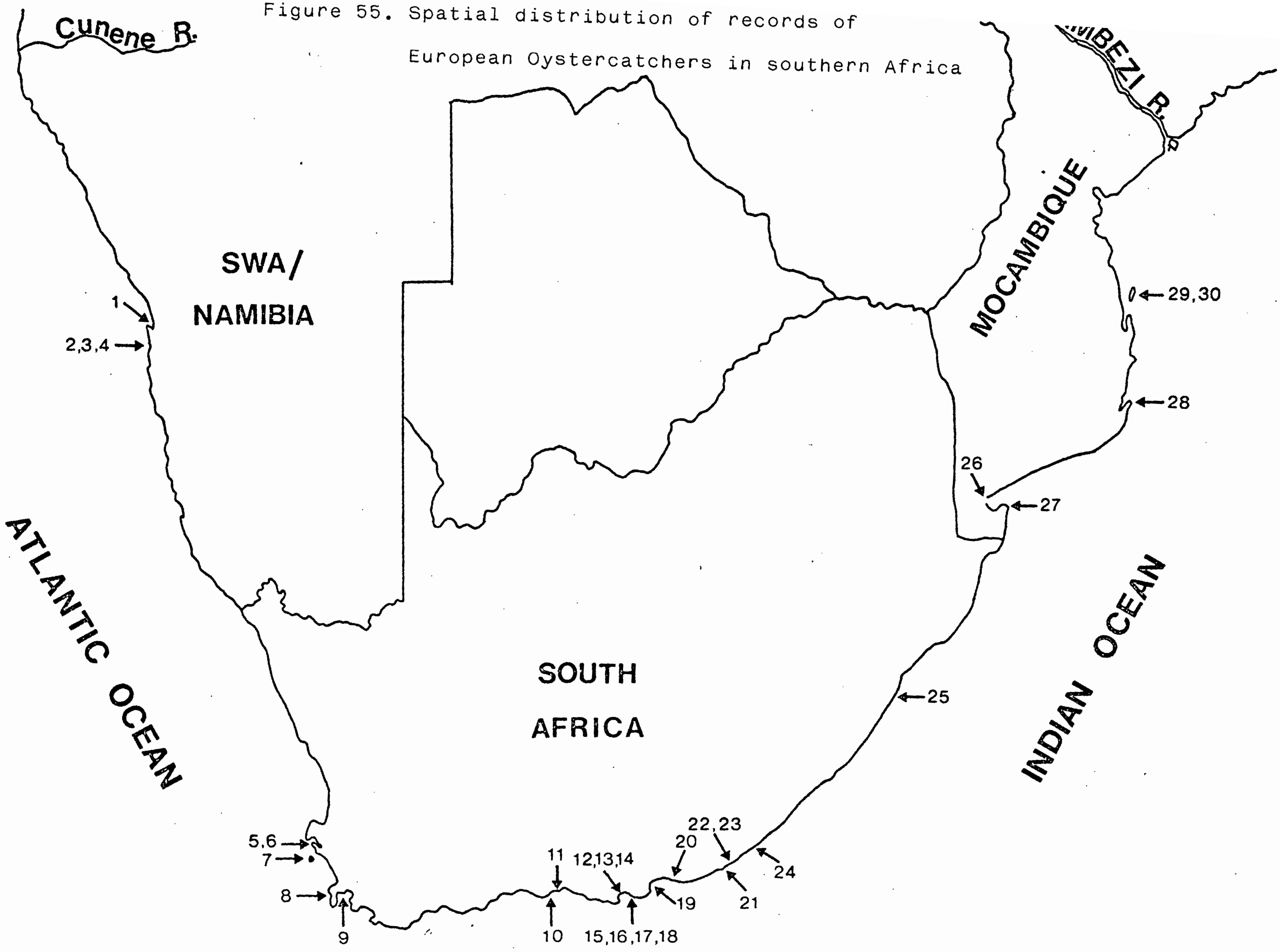


was a juvenile bird first seen in May (No. 7) (Table 59). A greater proportion of juveniles was recorded in the austral winter (April-September) than during summer (Table 59). Although the records are few, this suggests a tendency for young birds to overwinter as occurs in other species in Palaearctic waders in southern Africa (Elliott et al., 1976; Summers & Waltner, 1979).

Sixteen individuals were recorded from the south coast of South Africa between Plettenberg Bay and East London (Fig. 55). The concentration of records here, as well as further west in the southwestern Cape, may be a reflection of the distribution of observers. A record of the European Oystercatcher from Beira (Clancey, 1971a) is uncertain. Haagner (1948) reported an African Black Oystercatcher H. moquini there but gave no details. Clancey (1971a) treated Haagner's record as a European Oystercatcher, presumably on distributional grounds.

Vaurie (1965) has recognized three subspecies of European Oystercatcher: the nominate race breeding in the western Palaearctic, H. o. longipes in the central Palaearctic and H. o. osculans in the eastern Palaearctic. A specimen from Inhambane, Mocambique (No. 28) has been identified as longipes (Clancey, 1971b). The bird at the Cape Recife Sewage Works (No. 19) was photographed and attributed to this subspecies (Blake, 1976). The Strandfontein Sewage Works and Gamtoos River mouth individuals (Nos. 9 and 14) showed characteristics of longipes (pers. obs.). The Durban bird (No. 24) was thought to be H. o. buturlini (Sinclair, 1976), a synonym of longipes (Vaurie, 1965). The fact that all east and south coast European Oystercatchers that have been subspecifically identified are longipes shows that southern Africa is the southerly limit of this population's wintering

Figure 55. Spatial distribution of records of European Oystercatchers in southern Africa



range. However, records from the west coast of southern Africa may be attributable to the nominate race, which is known to occur as far south as Sierra Leone (Bannerman, 1951). Sight records of the species exist from Ghana (Bannerman, 1951) and Nigeria (Smith, 1966).

European Oystercatchers in southern Africa show a preference for sheltered areas with a sandy substrate such as river mouths and lagoons (Table 59). This contrasts markedly with the habitat preference of the African Black Oystercatcher which is most abundant at rocky offshore islands, and on the mainland prefers mixed (rocky and sandy) or rocky shores. This species occurs at a low density on predominantly sandy shores (Summers & Cooper, 1977). However, on fourteen occasions, when details were given, European Oystercatchers were found in association with African Black Oystercatchers.

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Appendix 1.2. Haematopus ostralegus in Africa, a summary.

In: Urban, E.K., Fry, C.H. &
Keith, G.S. The Birds of Africa,
Vol. 2. London: Academic Press.
(In press)

Haematopus ostralegus Linnaeus, 1758. Syst. Nat., 10th ed., p. 152; Europe; restricted type locality Öland Island, Sweden.

Range and Status. Palaearctic winter migrant, occasionally over-summering. Occurs around the African coast, although not yet recorded between Cameroon and Walvis Bay, Namibia. Common to abundant in suitable habitat in Morocco and Mauritania (estimated midwinter population 10-11 000 birds), frequent to uncommon Ethiopia and Somalia, uncommon to rare elsewhere. Possible wintering population of several thousand in unsurveyed areas of Guinea-Bissau (W.J.A. Dick, pers. comm.). On the east coast most regular at offshore islands, but at least seven records inland E. Africa. (Breeds W. and central Palaearctic with an isolated population in E. USSR).

Description. ADULT M (breeding) H. o. ostralegus (Linnaeus) : N. and NW Africa. Upperparts and head glossy black; lower back, rump and uppertail-coverts white. Breast black, rest of underparts white. Bill orange-red; eye red with orange-red orbital ring, legs pink. ADULT M (non-breeding) : as breeding but upperparts duller black; neck with irregular white collar. Orbital ring and bill duller orange; bill often slightly dusky towards tip; legs sometimes suffused with grey. ADULT F. As M but bill longer and more pointed. SIZE : wing, M (n=34) 245-272 (259), F (n=30) 249-277 (260); tail, M (n=22) 101-118 (107.6), F (n=20) 105-119 (110.3); tarsus, M (n=34) 47-56 (50.6), F (n=33) 46-54 (49.7); culmen M (n=84) 64-81 (71.4), F (n=82) 65-87 (79.8). WEIGHT (breeding): M (n=18) 425-560 (500), F (n=20) 445-590 (536).

IMMATURE: upperparts brownish black with buff fringes to feathers; broad white neck collar. Eye brown, becoming yellowish; bill orange, distal half brown; legs grey becoming slate.

H. o. longipes (Buturlin). Ethiopia and Somalia south to South Africa. SIZE: culmen, M (n=29) 68.5-81.9 (75.4), F (n=17) 77.0-90.9 (86.6).

Field Characters. Unmistakable; a striking, medium-sized pied wading bird. No other wader in Africa has the combination of black upperparts white underparts, long orange bill and pink or grey legs. White rump and wing bar conspicuous in flight. Immature browner than adult with bill dull distally.

Voice. Recorded in Europe, but not in Africa. Normally a loud, clear, shrill "Klee-eep, Klee-eep" or "Kleep-Kleep". When agitated also a "Kleep-a, Kleep-a" or a short, sharp "Pic .. pic". In flight a lower, quieter "Kip .. kip .. kip ....". More involved vocalizations, such as given during piping displays, associated with breeding.

General Habits. Little known in Africa; intimately known in Europe. In Africa generally prefers sandy shores, estuaries and lagoon, but in tropical E. Africa appears to favour rocky offshore islands. Roosts communally at high tide and has been recorded roosting in association with H. moquini. The scarcity of inland records indicates it is almost exclusively a coastal migrant. In E. Africa most records July-Sept, in South Africa and Namibia, Dec-Mar. Breeding birds from W. Palaearctic migrate mainly to NW Africa, while those from central Palaearctic migrate to NE, E and probably southern Africa. Birds ringed Wales and Netherlands recovered Morocco.

Food. In Mauritania feeds almost exclusively on the bivalve Arca *senilis* (Altenberg *et al*., 1982). In Europe preys principally on cockles, mussels, limpets, whelks and terrestrial invertebrates.

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Appendix 1.3. The taxonomic status of the Canary Islands Oystercatcher *Haematopus meadewaldoi*.

Bull Brit Orn Club 102 (1982): 77-84

INTRODUCTION

The taxonomic status of Meade-Waldo's Black Oystercatcher or Canarian Black Oystercatcher *Haematopus niger meadewaldoi* Bannerman (1913) of the Canary Islands remains an enigma. Apart from a white patch in the wing, the bird is similar in plumage and soft part coloration to the African Black Oystercatcher *H. moquini* (Bannerman, 1913). Three hypotheses have been proposed to explain its taxonomic status: either it is a melanistic subspecies of *H. ostralegus* (Stresemann, 1927), a distinct subspecies of the African Black Oystercatcher *H. moquini* Bonaparte (1856) (Bannerman, 1913, 1963) or individuals recorded in the Canary islands represent long-distance vagrants of the southern African population of *H. moquini* (Etchécopar & Huë, 1964). This paper aims to examine these 3 hypotheses by considering a) the extent of vagrancy and the distribution of extralimital records of *H. moquini*; b) mensural and plumage differences between *moquini* and *meadewaldoi*; and c) habitat preference and biology of the 2 populations.

NOMENCLATURE

Meade-Waldo's Black Oystercatcher originally was referred to as *H. capensis*, now a synonym of *H. moquini* (Table 60) (Meade-Waldo, 1889). Bannerman (1913), on the basis of 4 specimens collected between 1890 and 1913, named the form *H. niger meadewaldoi*, *H. niger* also now being a synonym of *H. moquini*. Stresemann (1927) and Peters (1934), on the contrary, considered both *moquini* and *meadewaldoi* to be subspecies of the European *H. ostralegus*. In recent literature, the Canary Island oystercatcher has been referred to as *H. moquini meadewaldoi* (Vaurie, 1965; Bannerman, 1963; King, 1979).

TABLE 60 . SYNONOMY OF *HAEMATOPUS MOQUINI* BONAPARTE

Haematopus niger Cuvier 1816 *Règné Anim*. 1: 469 - Cape of Good Hope. *Nec H. niger* Pallas 1811 *Zoogr. Ross. - Asiat*. 2: 131 = *H. bachmani* Audubon 1838 *Birds Amer*. ed. 4, pl. 427.

Haematopus ostralegus capensis A. Lichtenstein 1823 *Verz. Doubl. Zool. Mus. Berol*. p. 73 - Cape of Good Hope. *Nomen nudum*.

Haematopus moquini Bonaparte 1856 *Comp. Rend. Acad. Sci. Paris* 43: 1020 - Africa. *Nom. nov. pro H. niger* Cuvier *nec* Pallas. Type locality restricted to Cape of Good Hope by Traylor 1960 *Publ. cult. Co. Diam. Ang*. 51: 147.

Haematopus capensis Sharpe in 1884 Sharpe and Layard's *Birds S. Africa* p. 672 - Cape of Good Hope. By providing a description Sharpe made Lichtenstein's name available, but its authorship and date is Sharpe 1884.

VAGRANCY IN H. MOQUINI

The breeding range of H. moquini extends from Seal Island, South West Africa/Namibia (26 37S; 15 19E) (Cooper et al., 1980) round the coast to Mazeppa Bay, Transkei (32 29S; 28 39E) (Summers & Cooper, 1977).

The northern limit of its normal non-breeding range may be considered as the Hoanib estuary, South West Africa/Namibia (19 30S; 12 50E), where 9 birds were seen in October 1978 and January 1979 (R. Loutit, in litt.). East of the Transkei there are only six records which unequivocally refer to H. moquini, all in Natal, the most northerly being that of a single bird at Dawson's Rocks (28 38S; 32 18E) on 31 July 1981 (Part 1.2).

Only 5 black oystercatchers have been seen in Africa north of the normal non-breeding range: 3 in Angola: 2 as far as north as Lobito (12 35S; 13 25E) in May 1973 (Summers & Cooper, 1977) and one at at Foz do Cunene (17 15S; 11 45E) in January 1975 (W.R.J. Dean, in litt.) (all seen by competent observers); and one, even more northerly, old record from the west coast of Africa, in Gabon (Hartlaub, 1857). Vincent (1949) actually restricted the type locality of H. moquini to Gabon, based on the fact that this is the first locality cited; but Hartlaub's record is based on a Verreaux specimen according to Traylor (1960), and the specimen has not been traced and may no longer exist. Bannerman (1931) was noncommittal about this record, but it has been omitted by subsequent authors. It probably refers to a mislabelled specimen from the Cape, where the Verreaux brothers had strong connections.

There are 2 records from the east coast of Africa outside the normal non-breeding range. Haagner (1948) lists the bird from

Beira (20S, 35E), Mocambique, without details, a record which is considered by Clancey (1971) to refer to the European Oystercatcher H. ostralegus. Clancey does not justify his decision and in view of the northerly record on the west coast from Lobito, it seems possible that a vagrant might have reached Mocambique. A very strange record is from the Dahlak Archipelago, in the southern part of the Red Sea, where a black oystercatcher of some form was collected, but not preserved, by Rüppell (1845).

The paucity of extralimital records, all in excess of 4 000 km distance from the Canary Islands, renders it very unlikely that Canary Island birds are vagrant H. moquini. Adult breeding H. moquini are essentially sedentary, though juveniles may disperse some distance from their birthplaces (Part 1.2). No age class data are available for the extralimital mainland and Dahlak Island birds, but all specimens taken on the Canary Islands have been adults (Bannerman, 1913).

MEASUREMENTS AND PLUMAGE

Bannerman (1913) based his separation of meadewaldoi solely on aspects of plumage and measurements, meadewaldoi being smaller and with a distinct white patch in the wing, a feature not shared by moquini. At the time, few specimens and hence few mensural data were available for moquini. More data are now available and comparative measurements of moquini and meadewaldoi are given in Table 61. The low probabilities (%) of each measurement of each specimen of meadewaldoi belonging to a bird from the southern African population of moquini demonstrate that although the two populations may be related at subspecific level, where size is not necessarily a critical factor, they definitely do not belong to

TABLE 61 . CULMEN, TARSUS AND WING MEASUREMENTS COMPARED BETWEEN *HAEMATOPUS MOQUINI* AND THE FOUR EXISTING SPECIMENS OF *H. MEADEWALDOI*. "P" IS THE PROBABILITY OF EACH MEASUREMENT OF EACH MEADEWALDOI SPECIMEN BELONGING TO THE SOUTHERN AFRICAN POPULATION OF *MOQUINI*.

		Culmen (mm)			Tarsus (mm)			Wing (mm)		
		length	+standard deviation units	P(%)	length	+standard deviation units	P(%)	length	+standard deviation units	P(%)
MALES	*H. moquini*	63.2 ± 2.8			56.1 ± 2.1			275.2 ± 5.2		
	H. meadewaldoi (a)	72.5	3.3	0.1	54.0	1.0	31.7	262	2.5	1.2
	H. meadewaldoi (b)	77.0	4.9	0.01	49.2	3.3	0.1	259	3.1	0.2
FEMALES	*H. moquini*	71.6 ± 2.6			57.8 ± 1.9			278.5 ± 5.1		
	H. meadewaldoi (a)	79	2.9	0.4	52	3.1	0.2	250	5.6	0.01
	H. meadewaldoi (b)	81	3.6	0.02	52	3.1	0.2	257	4.3	0.01

+ Standard Deviation Units = the difference between *moquini* means and individual *meadewaldoi* measurements divided by the *moquini* standard deviation of the mean.

the same population. Culmen to tarsus ratios for 17 species and subspecies of oystercatcher are detailed in Table 62. It is clear that moquini is an unusual oystercatcher in that both sexes are comparatively short billed; meadewaldoi, on the other hand, is relatively long billed and shows less variation between sexes than other black oystercatchers - a feature common to most of the pied ostralegus group.

Bannerman (1963), in describing meadewaldoi, noted that: "The white patch formed by the basal portion of the inner webs of the primaries is very pronounced, while in the Cape bird (moquini) there is scarcely any white at the base of the quills though the primaries become lighter towards the base". Although moquini exhibits a pale patch in the wing (when seen from below) at certain times of the year, there is never, contrary to the opinion of Prater et al. (1977), a white patch in the wing. I have occasionally observed asymmetric partial albinism in the wing of moquini, but this never involves more than one or two feathers. The white patch in the wing of meadewaldoi is most evident in fresh plumage, whereas in moquini a pale patch is only evident as a result of feather wear and moult (Bannerman, 1963; pers. obs.).

HABITAT PREFERENCE AND BIOLOGY

In southern Africa, H. moquini is primarily a species of rocky shores, especially undisturbed offshore islands, contrasting strongly with the preferred sandy and muddy foraging substrates of H. ostralegus (Appendix 1.1). It is highly territorial and almost always occurs in pairs (Part 4.2), normally laying 2 eggs, but not often fledging more than one chick, which may remain with its parents for several months after fledging (pers. obs.). So few ornithologists have ever seen meadewaldoi that information

TABLE 62 . CULMEN TO TARSUS RATIOS EXPRESSED AS PERCENTAGES FOR 17 SPECIES AND SUBSPECIES OF OYSTERCATCHERS

Black forms	Culmen/tarsus ratios Males	 Females	Primary data source
H. moquini	112.7	123.9	This study
H. ater		136.0	Jehl 1978
H. fuliginosus ophthalmicus	128.4	145.9	McKean 1978
H. f. fuliginosus	134.7	153.0	McKean 1978
H. unicolor	139.5	153.3	Baker 1975
H. bachmani	141.6	160.6	Ridgway 1919
H. meadewaldoi	145.0	153.8	Bannerman 1913
Pied forms			
H. ostralegus chathamensis	132.2	143.0	Baker 1975
H. o. ostralegus	136.7	143.3	Prater *et al*. 1977
H. palliatus pitanay	138.5	144.1	Wetmore 1965
H. o. occidentalis	141.1	160.6	McKean 1978
H. leucopodus		159.9	Jehl 1978
H. p. frazari	142.7	149.9	Ridgway 1919
H. p. palliatus	143.1	150.2	Ridgway 1919
H. p. prattii	148.3	158.7	Ridgway 1919
H. p. galapagensis	158.8	156.2	Ridgway 1919
H. o. finschi	162.1	177.9	Baker 1975

concerning its biology is very scanty. No nest has ever been reported and the breeding biology is unknown. It has been recorded on both rocky and sandy shores, though rocky shores are probably favoured and these are dominant in the areas where the bird has been recorded (Bannerman, 1922, 1963). It occurs in pairs, and natives reported to von Thanner in the early 20th century that often 3 birds were present together in the summer, suggesting a family group; but it appears that the Canary Islands population underwent a decline in the second half of the 19th century, and probably earlier, and was very rare by the beginning of the 20th century (Bannerman, 1963). The reason for the decline is unknown, but it is possible that introduced mammalian predators, such as cats and rats, may have been the cause. Feral cats and other terrestrial mammals are known to prey upon H. moquini (Part 3.2). Subsequent to Bannerman procuring a specimen in 1913, there is only one sight record, a single bird seen in Tenerife in July 1968, the only previous record of its occurrence in Tenerife being by Du Cane Godman in 1872, a record previously doubted (Bannerman, 1963, 1969). An expedition to the Canary Islands in 1970 failed to locate the bird and concluded that it was probably extinct (Lovegrove, 1971).

DISCUSSION

Evidence presented here strongly suggests that the black oystercatchers of the Canary Islands are not vagrants of the southern African population of H. moquini, and, based on plumage and proportions, that the Canary Island bird is not a subspecies of H. moquini.

The question remains to be considered whether meadewaldoi represents an isolated melanistic population of the European

Oystercatcher H. ostralegus, its geographically closest congener, as suggested by Stresemann (1927). Although albinism has been recorded in H. ostralegus and in the South Island Pied Oystercatcher H. o. finschi of New Zealand, there is no record of melanism in Palaearctic ostralegus subspecies. The Variable Oystercatcher H. unicolor of New Zealand and Frazar's Oystercatcher H. bachmani x H. palliatus of central America exhibit a range of plumages, but the phenomenon is restricted to these two species (Larson, 1957; Baker, 1973). Baker (1977) performed cluster analysis, based on 7 operational taxonomic units, on a number of oystercatcher populations and his results indicate considerable dissimilarity between moquini and meadewaldoi. However, his sample sizes were small and this can only be considered as a supporting argument in differentiating the two populations.

Larson (1957) suggested that all oystercathers originated from Tertiary melanistic Haematopus populations in the Boreal area. With the exception of the American Black Oystercatcher H. o. bachmani (whose status as an ostralegus subspecies should be questioned (Heppleston, 1973)) and meadewaldoi, all other northern hemisphere oystercatchers are pied forms (ostralegus/palliatus). The Atlantic and Pacific gene communication between Eurasian and North American populations was cut off by the middle Pliocene, and it is possible that meadewaldoi is (or was) a relict population of the original dark mutant of the Tertiary, perhaps related to H. (o.) bachmani. It is the only melanistic oystercatcher population in the Palaearctic region, probably surviving by virtue of freedom from competition with vigorous secondary pied mutants, and, if this is the case, then meadewaldoi represents the stock from which moquini, as well as other southern black forms, arose (see Heppleston, 1973; Part 1.1). The two populations have therefore probably been genetically isolated since the Pliocene. Reichenbach (1852) considered moquini discrete enough even to warrant generic status and created the genus Melanibyx. However, no subsequent authors have subscribed to this belief.

CONCLUSION

On the evidence presented in this paper, I propose that H. meadewaldoi be accorded specific status and be referred to as Haematopus meadewaldoi, Meade-Waldo's Black Oystercatcher. As a corollary, Haematopus moquini must be treated binomially.

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