Quantifying abundance, breeding and behaviour of the African Black Oystercatcher

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Thesis Presented for the Degree of

DOCTOR OF PHILOSOPHY

in the Department of Statistical Sciences

UNIVERSITY OF CAPE TOWN

January 2006

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Table of contents

to provide an overview of breeding events is introduced and used to facilitate visual comparisons between different seasons and sites.

Oystercatcher density increased over 30 years; in the harbour there were 46 birds/km and 13 birds/km on the beach. The oystercatcher pairs in the artificial shore of the harbour have a similar productivity to an adjacent area of shoreline five times as long as the original shore. Over the three-year study period, the breeding productivity of oystercatchers at Koeberg was below that estimated to maintain a stable population (0.35 fledglings per pair per year). The poor productivity at Koeberg is mainly attributed to egg and chick loss as a result of predation; in addition there were high levels of human disturbance in the 2004/2005 breeding season.

Data from 18 breeding sites around the South African coastline, on different shore types, were grouped into protected island sites, protected mainland sites and unprotected mainland sites. Egg loss resulting from predation caused poor breeding success at protected mainland sites; human disturbance caused chick loss at unprotected mainland sites. Site-specific conditions played the largest role in determining breeding success and reasons for variation in breeding success often remained unclear. However, it is clear that the best place for an oystercatcher to breed is on an island with no predators.

African Black Oystercatchers foraging diurnally on sandy shores of the Western Cape, feed mainly on polychaetes (*Scololepsis, Nephtys* and *Glycera*), also on small crustaceans (especially associated with the drift-line kelp) and *Donax serra.* This sandy shore offered a diverse array of possible prey items throughout the tidal cycle and although specialization was present (particularly for an individual bout of feeding), the adaptable oystercatchers used a variety of techniques and opportunistic behaviours to utilise the available prey.

The effects of several variables on the different behavioural activities of the oystercatcher on rocky and sandy shores on a Western Cape mainland site were quantified. The main difference seen is the dependence of the rocky shore birds on the tide height, especially feeding, sleeping and lying and the relative importance of all the variables (tide, weather conditions, daylength and time of day) on all behaviour activities on the sandy shore birds.

Feeding on the sandy shore occurs throughout the tidal cycle but was more dependent on weather variables.

The Koeberg Nuclear Power Station and Nature Reserve meets the criteria for an Important Bird Area and a Ramsar Wetland of International Importance. The nuclear power station is a National Key Point site having strict security for entry and therefore low human disturbance within the harbour area. Practical conservation recommendations are given.

Acknowledgements

Thank-you to Les Underhill for suggesting the project in the first place and for believing in me. Thanks for letting me learn on my own but always being available for advice and discussion. Thanks also for introducing me to oystercatchers and to stats!

Eskom Koeberg Nuclear Power Station provided access to the study site; Thank-you to Gert Greeff and Hilton Westman, nature conservators at the site, for their help. The project was supported by the National Research Foundation, the Earthwatch Institute, and the University of Cape Town Research Committee.

Thank-you to those who read and commented on draft versions: Leo Bruinzeel, Marienne de Villiers, Charlie Griffiths, Humphrey Sitters and Tony Williams. Thank-you to those who have inspired me to do better: Mike Cranfield, Charlie Griffiths, Theunis Piersma, Humphrey Sitters, Les Underhill, Manfred Waltner and Tony Williams. Thank-you to Sue Kuyper for advice, administration and friendship. Thank-you to Margaret Sandwith for friendly library assistance. Thank-you to René Navarro for help with figures.

Thank-you to my family, especially my mom, Viv Parsons, for their support and love. Thank-you to friends, who helped in so many ways: Lesley Bester, Lizelle Cilliers, Mike Cranfield, Natasha Fleming, Sharon Gelber, Stephnie Jensen, Silvia Kirkman, Brian McCallum, Kim McConkey, Annekie Montgomery, Lindy Oakes, Carolé Olivier, Samantha Petersen and Nicole Wallace.

Introduction

Overview

The African Black Oystercatcher was studied at the Koeberg Nuclear Power Station and Nature Reserve from November 2002 to June 2005 as part of my thesis submitted for the degree of Doctor of Philosophy at the University of Cape Town. Professor Les G. Underhill supervised this study and will be a co-author on the submitted versions of all chapters except Chapter 4, of which I will be the author. He was responsible for most of the statistical analyses and commented on drafts. Each chapter has been written as a paper to be submitted to a journal and therefore there is some repetition. A description of the study site is given below to reduce the amount of repetition of this material between chapters. The taxonomy adopted for the oystercatcher family *Haematopodidae* in this thesis is that of Hockey (1996a). The names of the prey items are from Branch *et al.* (1994). All references are listed at the end of the thesis.

Overall Introduction to the Study Site: The Koeberg Nuclear Power Station and Nature Reserve

Koeberg Nuclear Power Station (33 40'S, 18 25'E) lies 30 km north of Cape Town. It is the only nuclear power station on the continent of Africa, and the most southerly nuclear power plant in the world (Eskom Holdings Limited 2006). Construction began in 1976, and the two pressurized water reactors of French design were linked to the ESKOM power grid in 1984 and 1985. It has an electricity generation capacity of 1 800 MW (Eskom Holdings Limited 2006). On the shore side of the high-security area is a harbour, completed in 1984, which consists of a northern and southern breakwater, and a water outflow channel (Figures 1 and 2). The power station is surrounded by a 3 000 ha nature reserve which consists of West Coast strandveld and duneveld and includes the coastline (Eskom Holdings Limited 2006). In this study, the focus was on the shoreline environment.

The two harbour breakwaters are protected by concrete dolosse on the sea side (Figure 2). The insides of the breakwaters are built up with rocks of assorted sizes to form a gently sloping intertidal area (Figure 3). The rocks are tough and durable Malmesbury hornfels quarried and transported to the site. The function of the harbour is to act as a settling pond to provide sand-free water at the inlet of the pump house for cooling the condensers (Figure 2). The harbour area is fenced off (Figure 2) and provides an area with minimal human disturbance. Koeberg Nuclear Power Station falls under the National Key Points Act 102 of 1980 in terms of South African legislation, imposing heavy penalties for illegal entry. The harbour area thus provides undisturbed opportunities for the breeding of several species of seabirds.

The site also includes two sections of sandy shore north and south of the power station (Figure 1). The north beach (c. 2 km of sandy shore) (northern limit 33 39.183'S, 18 25.003'E) is rarely visited by people and is isolated and inaccessible. The first public access point to the shoreline north of the power station is at Silwerstroomstrand, c 10 km away. The south beach is more sheltered than the north beach, has finer sand and a wider intertidal area than the north beach. The c. 500 m of sandy shore (southern limit 33 41.292'S, 18 26.085'E) is close to two residential areas on the coastline, Duynefontein and Melkbosstrand, approximately 2 km south of the power station. The south beach has sign posts indicating the limits beyond which people and dogs are not permitted to venture, but these are not strictly obeyed and people and their dogs walk right up to the fenced off harbour area. There is therefore some human disturbance on this beach.

There is a wide diversity of predators present at the site. Predators implicated in oystercatcher mortality include the Yellow Mongoose *Cynictis penicillata*, Kelp Gull *Larus dominicanus*, Sacred Ibis *Threskiornis aethiopicus*, Pied Crow *Corvus albus*, various snakes, domestic dogs (south beach) and feral cats *Felis catus* (harbour area).

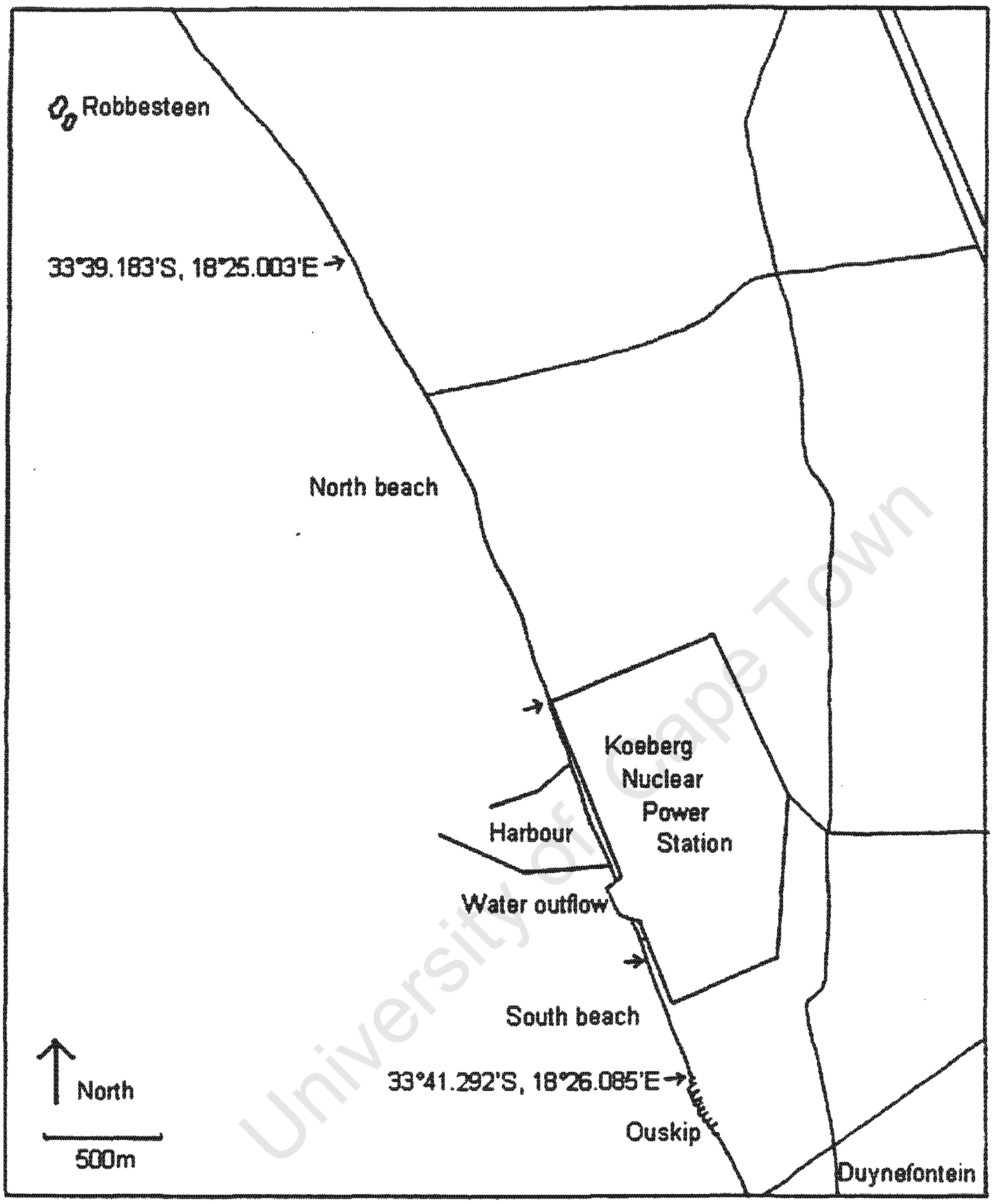


Figure 1. Map of the Koeberg study site.

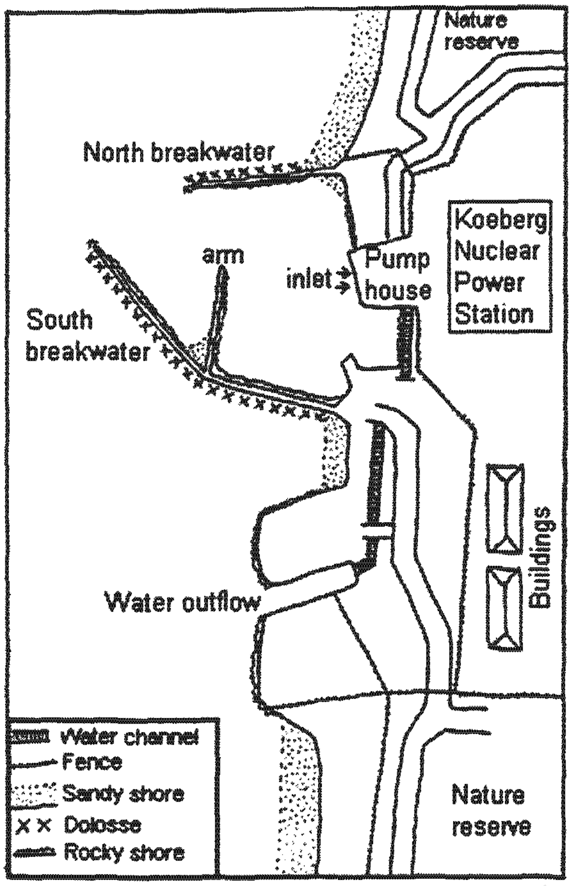


Figure 2. Diagram of the Koeberg harbour area. For security reasons, not drawn to scale.

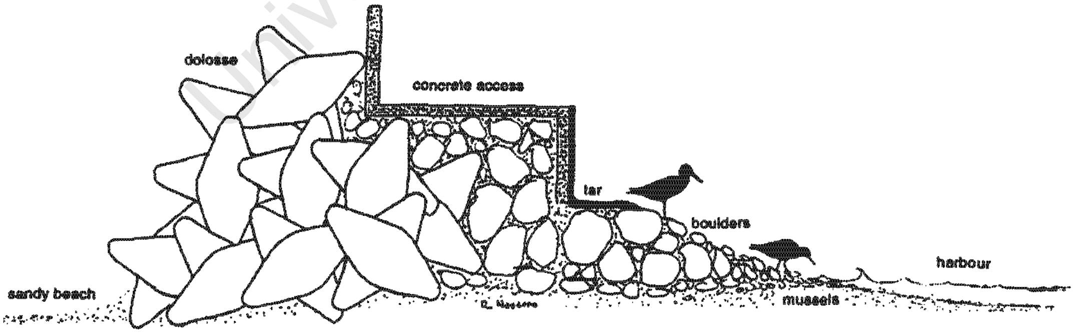
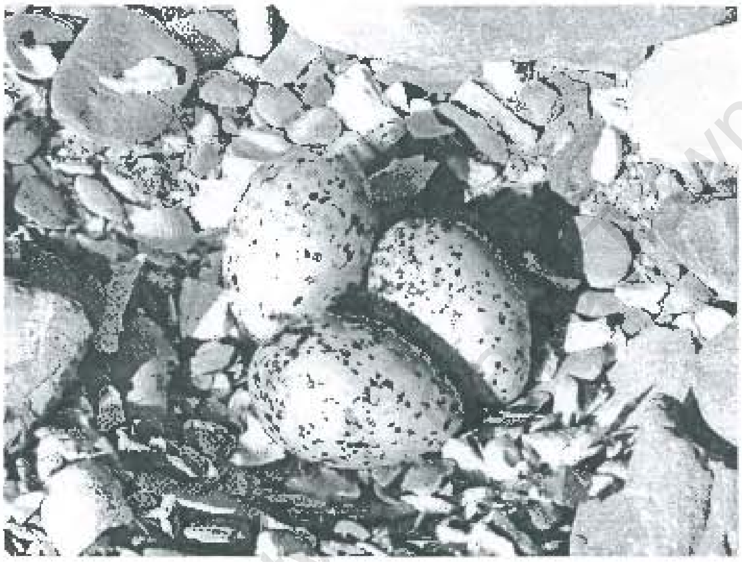
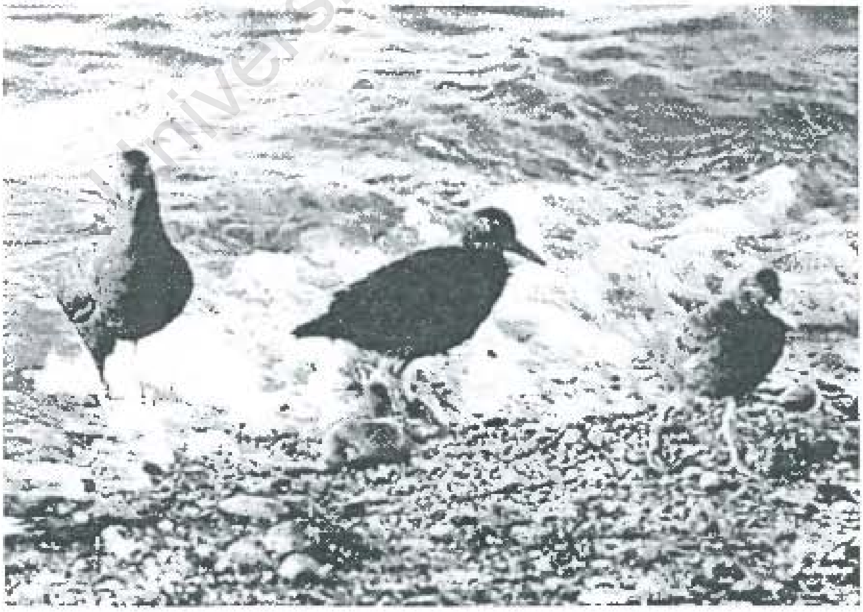


Figure 3. Schematic representation of the cross-section of the harbour wall with the sea side on the left-hand side and inside the harbour on the right-hand side of the figure. Birds not drawn to scale.

Chapter 1

Quantifying and displaying annual investment by parents to breeding, using African Black Oystercatchers *Haematopus moquini* as an example





Introduction

The breeding success of birds is frequently reported as the number of fledglings produced per breeding attempt, or the number of fledglings produced per pair per year (for example in the African Black Oystercatcher *Haematopus moquini*, Hockey 1983b, Calf & Underhill 2002, Jeffery & Scott 2005). Although this approach provides the key information for the production of models of population dynamics (Clutton-Brock 1988), it fails to measure the varying amount of parental effort (Ens *et al.* 1992, Kersten 1997) that is expended to produce a given number of chicks. This potentially has implications for their survival and future fitness (Williams 2005). Lifetime reproductive success of a bird is primarily dependent on its annual breeding productivity and annual survival and their interaction (for example Partridge 1989, Heg 1999) with a trade-off existing between current reproduction and future reproduction (Williams 1966).

In this paper, the annual time investment by parents to the various components of the breeding cycle (incubation, chick rearing, post-fledging care) is quantified. In addition, the biomass investment of the female to the production of eggs is estimated. These statistics provide a method of evaluating parental effort into reproduction. In particular, this approach provides a way to quantify the cumulative costs of repeated breeding attempts on adult birds after the loss of a clutch or brood. The method is discussed with potential to use it in long-term studies of bird reproduction and to evaluate individual lifetime reproductive success.

A graphical overview of breeding events is introduced, providing a visual representation of the timing of these events and facilitating comparisons between areas and between years.

The paper is illustrated using data on the breeding productivity of the African Black Oystercatcher at the Koeberg Nuclear Power Station (33°40' S, 18°25' E), Western Cape, South Africa, over one breeding season, from November 2002 until May 2003. The oystercatcher is long-lived, strongly territorial, mate-faithful and single-brooded with a naturally low reproductive rate (less than one fledgling per pair per year) (Summers & Cooper 1977, Hockey 1983a, b, 1996a, Hockey *et al.* 2005).

A method is introduced here in an attempt to measure the investment into reproduction and relate this to the breeding success of individual birds as well as the breeding success of particular areas or years. This was undertaken due to the observed differences in investment into breeding and breeding success between mainland and island sites. The method was facilitated by regular nest checking and estimating the length of incubation from the egg measurements and mass.

Methods

The African Black Oystercatcher was studied at Koeberg Nuclear Power Station. Koeberg lies 30 km north of Cape Town and is surrounded by a nature reserve including the coastline. A harbour which has created an artificial and sheltered rocky shoreline and the adjacent sandy beaches provide breeding habitat for the oystercatchers (Chapter 2). Counts (pairs, nests, chicks and fledglings) were conducted weekly from November 2002 until May 2003. It was straightforward to follow the breeding fortunes of every pair throughout the breeding season. Nests were searched for regularly and were monitored at three to seven day intervals until hatching. On the first visit to the nest, eggs were weighed and measured (see below). On subsequent visits, the nest contents were checked and eggs weighed. Once the eggs hatched, the chicks were searched for at similar intervals and were weighed and measured until fledging. Fledging was taken as the point at which chicks could fly well, at 35–40 days, when the chicks reach about two-thirds of adult body mass (Hockey 1984a). Oystercatcher fledglings remain with their parents for an extended period. There is no published information on the average length of this period, and we attempted to measure this as accurately as feasible; this information was needed in order to establish relative parental effort during the post-fledging period. For each breeding attempt, the dates of start of incubation, hatching, fledging, final departure and, where appropriate, loss of eggs or chicks, were estimated as the midpoint between visits, unless more precise information was available. This information was presented graphically along a time axis, with one line per breeding pair.

Breeding attempts were first identified after eggs had been laid. Egg length and two breadth measurements, taken at right angles to each other, were made to 0.1 mm accuracy and eggs were weighed to the nearest 0.1 g with an electronic balance (Tanita model 1479). The measurements were used to calculate the fresh mass of the egg using the formula presented in Underhill & Calf (2005). The estimate of the number of days since the start of incubation was calculated from the difference between the fresh mass and the egg mass when the nest was found, based on oystercatcher eggs losing a total of 16% of their fresh mass over an average 32-day incubation period (Hockey 1983b, Underhill & Calf 2005). For nests with more than one egg, the date of start of incubation of the nest was taken as the date calculated for the first-laid egg. The laying period (the time taken to lay the complete clutch) was calculated and included in the incubation period because the African Black Oystercatcher incubates the clutch after the first-laid egg due to high levels of egg predation (Hockey 1996a).

The hatching date was estimated as the mid-date between the last date that an egg was observed and the first date that a chick was observed, unless hatching was witnessed and a more accurate date could be given. Two small chicks were present at the study site when observations started; the dates of start of incubation and hatching were estimated for these from the average incubation period and from the size of the chicks. The fledging date was estimated as the mid-date between the last date that a chick was not flying and the first date that it was seen flying well. The final departure date was estimated as the mid-date between the last date that the fledgling was observed with the parents and the first date that it was not observed. It is possible that the fledgling died and therefore was not observed, but this is unlikely as most oystercatcher chicks die within seven days of hatching (Hockey 1983b) and fledglings are capable of avoiding predators at this stage (Hockey 1984a). The fledgling was usually determined to be present by direct observation; occasionally, it was inferred to be present if the adults alarmed upon the approach by the observer even though the fledgling was not seen.

For each oystercatcher breeding pair, we calculated the total number of days during the breeding season allocated to the three key components (incubation (including the laying period), chick-rearing from hatching to fledging, and chick-rearing from fledging to final departure from the parental breeding territory) of oystercatcher breeding activity. These values were summed across all breeding pairs in the study area, and the average time investment calculated. These averages were set into context by expressing them relative to the "mean" periods for each key breeding component.

The incubation period of the African Black Oystercatcher averages 32 days, with a recorded range of 27–39 days (Hockey 1983b). Chicks fledge at 35–40 days (Hockey 1984a), we used 40 days as the mean period between hatching and fledging. The period for which oystercatcher fledglings remain with their parents was estimated from the 10 chicks that fledged and left the study area in the 2002/2003 breeding season and the two chicks in the 2003/2004 breeding season (Chapter 2). The median post-fledging to leaving period was 50 days for oystercatchers at this site (Chapter 2). Therefore, a mean reproductive period for African Black Oystercatchers at Koeberg was taken to be 32 days incubation, 40 days chick-rearing and 50 days post-fledging with a total time of 122 days.

Results

In the 2002/2003 breeding season at Koeberg, 37 pairs of African Black Oystercatchers bred (i.e. produced at least one egg) and 26 of these pairs produced more than one clutch (Chapter 2). In total, there were 128–130 eggs; of which 24 hatched (Appendix 1). Ten chicks fledged and left the parental territory (Appendix 1). Breeding productivity (fledglings per pair per year) was measured at 0.27 (Chapter 2). Detailed results relating to this breeding season are contained in Chapter 2.

Figure 1 indicates the time investment of breeding pairs to breeding. The overall breeding season extended for 9 months, from the laying of the first eggs in the beginning of October to the departure of the last fledgling from the study area in the beginning of July. The egg-laying period was protracted, extending over seven months. The breeding season was intensive, characterized by high levels of egg loss and replacement clutches. Six pairs produced three or four clutches each but no chicks hatched. Three pairs re-laid after chicks were lost and two pairs re-laid after chicks fledged.

The 37 pairs of breeding oystercatchers spent a total of 1646 days incubating (Table 1). On average, each pair spent a total of 44 days incubating (Table 1); this value is about 40%

longer than the mean incubation period (32 days). A total of 78 clutches were laid (Appendix 1), so that the mean period for which each clutch was incubated was 21 days, therefore the average clutch survived two-thirds of the mean incubation period. The two longest total incubation investments by individual pairs were a) 113 days spent on three clutches (all five eggs failed to hatch) and b) 104 days on three clutches (three of six eggs hatched and two chicks fledged) (Pairs 6 and 3, Appendix 1, Figure 1). The shortest incubation investment was one day; Pair 34 was estimated to have had a single egg for one day only (Appendix 1, Figure 1). Pair 18 had four nests of one egg each and spent a total of 45 days incubating; no eggs hatched (Appendix 1, Figure 1).

The total amount of time devoted to tending chicks between hatching and fledging was 433 days, or 12 days per breeding pair (Table 1). Each pair spent 30% of the mean chick-rearing period (40 days) on this activity. Fourteen pairs succeeded in hatching at least one egg (Appendix 1); these pairs averaged 31 days of chick-rearing (Table 1), 77% of the mean chick-rearing period.

The total post-fledging time was 475 days, or an average of 13 days per breeding pair (Table 1). This is 26% of the mean post-fledging period (50 days). All chicks which fledged survived the post-fledging period; those breeding pairs which produced fledglings allocated 119% of the mean post-fledging period to this activity (eight pairs produced 10 chicks). This value is inflated by the fact that the post-fledging period for one chick of one pair was 104 days (Appendix 1).

The total time investment to reproductive activities from egg laying to final departure by the 37 African Black Oystercatcher breeding pairs at Koeberg in the 2002/2003 breeding season was 2554 days, an average of 69 days per breeding pair (Table 1). Each breeding pair undertook 57% of a mean reproductive period (122 days). The ratio of time spent on each breeding component (incubation:chick-rearing:post-fledging) was 64:17:19 whereas it should be 26:33:41 in a mean reproductive period. With a total production of 10 fledglings in this breeding season, 255 days were invested in reproduction per juvenile produced. Each fledgling therefore was produced in 209% of a mean reproductive period.

The total egg mass produced by individual females over the 2002/2003 breeding season ranged from 48.3 g to 440.7 g with an average of 196.2 g produced per female (Table 1) and an average egg mass of 56.1 g (7176.2/128) (Appendix 2). Using the average female body mass of 722.3 g (Hockey 1981a), the percentage of the female body mass produced in eggs ranged from 8% (one egg produced) to 61% (eight eggs produced) (Table 2). The average female produced 3.5 eggs at 27% of "her" body mass (Table 2).

Discussion

In evaluating lifetime reproductive success (the sum of lifetime breeding productivity and annual survival (Partridge 1989)), annual breeding success must be measured against the cost of reproduction and possible risks. Costs of reproduction include increased exposure to external sources of risk such as predation or parasitism as well as physiological costs such as energy, nutritional and time demands (Partridge 1989, Kersten 1997, Williams 2005). Physiological costs tend to be short-term but probably also have long-term biological consequences (Williams 2005). Lifetime reproductive success is particularly important in long-lived birds with high annual adult survival (such as the African Black Oystercatcher) as birds will tend to not invest in breeding if there is any threat to their survival.

Breeding productivity, as measured by the number of fledglings produced per pair per year, provides an overall indication of successful breeding attempts. This value can be used in population modelling. For African Black Oystercatchers, productivity of 0.35 fledglings per pair per year has been estimated as sufficient to sustain a population (Hockey *et al.* 2005). In the 2002/2003 breeding season at Koeberg, the African Black Oystercatcher breeding productivity of 0.27 fledglings per pair fell below this minimum. However, these results should be evaluated on a long-term basis and variation in parental condition, parental quality and territory quality must all be borne in mind when considering lifetime reproductive success (Clutton-Brock 1988, Ens *et al.* 1992, 1996b, Kersten 1997, Moreno 2003).

This paper examines some factors effecting reproductive effort as a component of parental quality. The variation shown in these results implies that the variability over the birds breeding lifespan may be immense and worth considering in long-term studies.

The difference between the actual ratio of time spent on each breeding component and the mean ratio shows incubation as 40% longer than the mean while chick-rearing and post-fledging times are 30% and 26% of the mean respectively. This reflects the parental investment of time in repeated relaying of eggs after nest losses with few chicks being reared to fledging. This ratio can be used to compare different seasons or locations of breeding birds, although the post-fledging time appears to be site-dependent (Chapter 3). The African Black Oystercatcher lays eggs over eight months from September to April although the peak egg-laying season is between November and January (Hockey *et al.* 2005). At Koeberg, the season extended for seven months from October to April.

Increased time spent incubating places the adults at increased risk because the birds are targets for predator attacks (Drent 1975, Hockey 1983b, 1996a, b, Partridge 1989). Ground-nesting birds, including African Black Oystercatchers, attempt to conceal the fact that they are sitting on eggs by using distraction displays such as false brooding, injury feigning and distraction lure (Hockey 1996b). An African Black Oystercatcher has been observed driving a Small Grey Mongoose *Galerella pulverulenta* away from the nest (Hockey 1996b). Several adult oystercatchers killed at night on Marcus Island during the 1979/1980 breeding season was attributed to predation by the Cape Fox *Vulpes chama* (Hockey 1983b). The additional risk of predation to adults while engaged in chick-rearing is less than the additional risk during incubation and the additional risk during the period of post-fledging care is small, and possibly negligible. The time spent on incubation is therefore, more important than the time spent on chick and fledgling care as it carries a higher predation risk.

Tufte (1983) demonstrated how good visual representations of data are a critical component of understanding complex material. The key advance which enables the construction of Figure 1 is the ability, provided by Underhill & Calf (2005), to be able to backdate African Black Oystercatcher eggs to the date of start of incubation. This figure provides a general overview of the breeding season, the intensity of the breeding attempt, breeding success and the time investment of the parents to breeding which can be used to visually compare different seasons or locations of breeding birds.

Quantifying the egg mass produced by each female as a percentage of "her" mass indicates the effort put into egg production. Large individual variability in egg production and reproductive success was seen in the oystercatchers at Koeberg. Incubation commences after laying of the first egg with both eggs being at equal risk from predators (Hockey 1983b, Hockey 1996b). Therefore, the under-estimation of clutch size in the Eurasian Oystercatcher as reported by Ens (1991), due to 40% of first-laid eggs being lost, is not a factor in the African Black Oystercatcher.

It is difficult to quantify the physiological costs of egg production to female birds especially due to individual variability (Williams 2005). Increased nutrient and energy demands during egg production are likely to be met through re-allocation of female reserves so that the models of energy costs of egg production do not reflect the true costs involved (Williams 2005). The mechanisms involved in re-allocation of reserves target protein depletion mainly from muscle tissue and a reproduction versus immune function trade-off (Williams 2005). In the Eurasian Oystercatcher no energy constraints were found during the pre-laying stage (Kersten 1996). However, Williams (2005) proposes mechanisms that are non-resource based and long-term, such as pleiotropic effects of reproductive hormones.

Kersten (1997) evaluated the parental energy allocation (of the Eurasian Oystercatcher at Schiermonnikoog) into chick-rearing and found that low parental effort was selected for a maximum lifetime reproductive success. This is a result of the high annual survival of the oystercatcher (Kersten 1997). The African Black Oystercatcher has a similarly high adult annual survival rate of 96% (Hockey *et al.* 2005), and presumably this plays a role in the low reproductive rate.

Oystercatcher parents share duties equally (Hockey 1996a, Kersten 1996). This investment in breeding can be divided into incubation time (b_1), chick-rearing time (b_2), post-fledging time (b_3). Females have additional investment in total egg mass laid (b_4). At the level of the individual bird, these investments can be used as explanatory variables in a model of survival probabilities between breeding seasons, ie from the start of one breeding season to the start of the next. For example, using a logit transformation to model survival probability S, we could use:

$$\text{logit}(S) = \log(S/(1-S)) = a + b_1\,(\text{total incubation time investment}) + b_2\,(\text{total pre-fledging time investment}) + b_3\,(\text{total post fledging time investment}) + b_4\,(\text{total mass of eggs laid})$$

for females, with the final term omitted for males. In this study, each of the four explanatory variables had wide ranges (Table 1) giving leverage to this equation. Given a large enough sample of observations of individual birds surviving (or not) from one closely monitored breeding season to the next, a generalized linear model with binomial distribution and logistic link function could be used to establish whether there is statistically significant relationship between these variables, and if so to estimate the regression coefficients a, b_1, b_2, b_3 and b_4 and gain an understanding of the impact, if any, of breeding investment on survival and therefore fitness.

We have attempted to evaluate the effort invested in breeding by birds by measuring time investment and egg production compared to reproductive success. This can potentially be used to evaluate life histories of individuals and their offspring. Together with other factors such as parental energy allocation (Kersten 1997) and parental quality (such as health status and immunocompetence (Moreno 2003)) will surely give a more complete picture of individual lifetime reproduction.

Acknowledgements

Eskom Koeberg Nuclear Power Station provided access to the study site; we especially acknowledge the helpfulness of Gert Greeff and Hilton Westman, nature conservators at the site. Marienne de Villiers commented on a earlier draft. The project was supported by the National Research Foundation, the Earthwatch Institute, and the University of Cape Town Research Committee.

Table 1. Breeding effort of African Black Oystercatchers at Koeberg in the 2002/2003 breeding season. In the chick-rearing and post-fledging time rows, the range is calculated from those pairs with chicks or fledglings, but the mean is calculated from all pairs attempting breeding (brackets indicate mean per pair with chicks or fledglings).

	Total all breeding pairs	**Range of individual pairs**	**Mean (per breeding pair)**
Incubation time	1646 days	1–113 days	44 days
Chick-rearing time	433 days	3–64 days	12 days (31 days)
Post-fledging time	475 days	38–104 days	13 days (59 days)
Total breeding time	2554 days	1–239 days	69 days
Egg mass produced	7176.2 g	48.3–440.7 g	196.2 g

Table 2. Egg mass produced by each female African Black Oystercatcher during the 2002/2003 breeding season at Koeberg. The egg mass is presented as a percentage of the average female body mass (722.3 g) (Hockey 1981a).

No. of females	**No. of eggs**	**Average egg mass produced by each female**	**Percentage female body mass produced in eggs**
4	1	54.8	8%
9	2	114.6	16%
6	3	165.3	23%
10	4	225.4	31%
3	5	290.6	40%
3	6	324.8	45%
1	7	392.2	54%
1	8	440.7	61%
Mean	**3.5**	**196.2**	**27%**

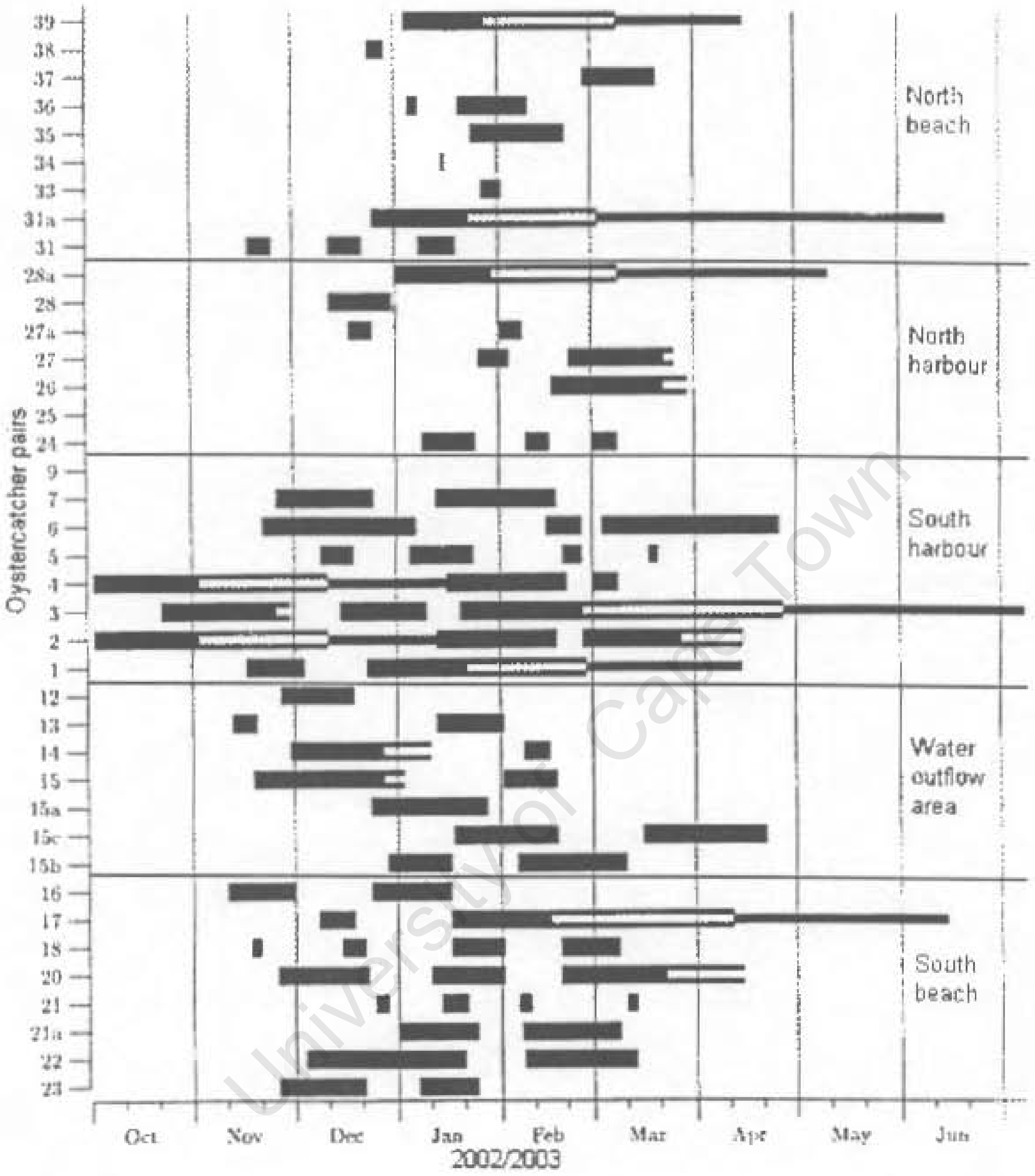


Figure 1. Graphical representation of incubation and chick-rearing of individual pairs of African Black Oystercatchers at Koeberg during the 2002/2003 breeding season. Time spent incubating is represented by a thick black line, time spent rearing chicks to fledging is represented by two parallel lines and time spent chick-rearing post-fledging is represented by a thin black line.

Appendices

Appendix 1. Individual pairs of African Black Oystercatcher with breeding results and time investment in the 2002/2003 breeding season at Koeberg. Pairs 2 and 4 had one chick each at the start of the study, therefore egg numbers and an average of 32 days incubation have been estimated for these pairs. Brackets in the chick-rearing columns indicate days for each chick in clutch, total breeding time is calculated from the higher number.

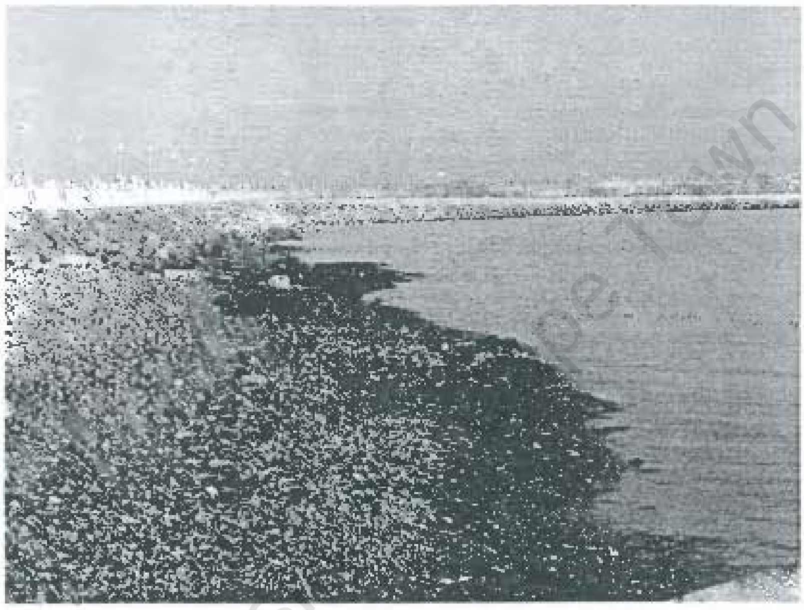
Pair No.	**Breeding attempts (number of nests)**	**Number of eggs**	**Incubation time (days)**	**Number of chicks hatched**	**Chick rearing time (days)**	**Post fledging time (days)**	**Number of chicks fledged and left area**	**Total breeding time (days)**
Harbour area								
1	2	4	51	1	(36)	(48)	1	135
2	3	5–6	99	3	(40) (17,19)	(43)	1	201
3	3	6	104	3	(5) (59,59)	(49,71)	2	239
4	3	4–5	77	1	(40)	(43)	1	160
5	4	8	42					42
6	3	5	113					113
7	2	4	67					67
12	1	2	23					23
13	2	4	29					29
14	2	4	41	2	(17,17)			58
15	2	3	60	1	(9)			69
15a	1	2	36					36
15b	2	3	68	1	(5)			73
15c	2	2	70					70
24	2	4	34					25
26	1	2	33	2	(4,7)			40
27	2	4	38	2	(3,3)			41
27a	2	3	16					16
28	1	2	20					20
28a	1	2	28	2	(8.38)	(63)	1	129
Beach area								
16	2	4	46					46
17	2	3	42	1	(54)	(65)	1	161
18	4	5	45					45
20	3	6	81	2	(7,23)			104
21	4	5	23					23
21a	2	3	56					56
22	3	4	83					83
23	2	4	46					46
31	4	6	30					30
31a	1	2	28	2	(39,39)	(44,104)	2	171
33	1	1	7					7
34	1	1	1					1
35	1	2	29					29
36	2	3	25					25
37	1	1	23					23
38	2	2	7					7
39	1	1	25	1	(39)	(38)	1	102
Total	**78**	**128–130**	**1646**	**24**	**433**	**475**	**10**	**2554**
Range		**1–8**	**1–113**		**3–64**	**38–104**		**1–239**
Pairs			**37**		**14**	**8**		**37**

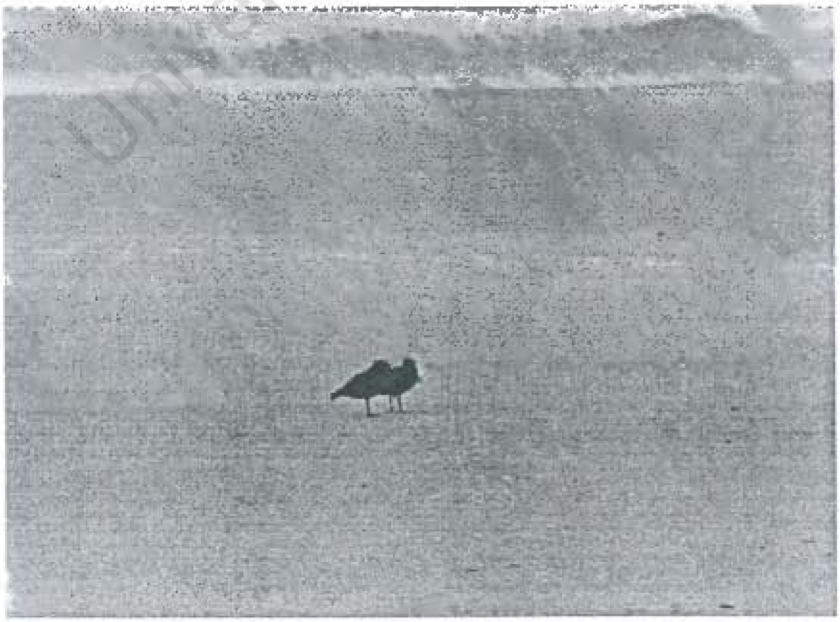
Appendix 2. Total egg mass produced by each female African Black Oystercatcher during the 2002/2003 breeding season at Koeberg Nuclear Power Station. The egg laying-mass was calculated as described in the text. *Two chicks were present at the start of the study (pair 2 and 4) and one egg was not measured (pair 13); for these pairs the mean egg mass was used (Chapter 2).

Pair	Clutch 1		Clutch 2		Clutch 3		Clutch 4		Total no. eggs	Total mass eggs (g)
	Egg mass (g)	Egg mass (g)	Egg mass (g)	Egg mass (g)	Egg mass (g)	Egg mass (g)	Egg mass (g)	Egg mass (g)		
Harbour										
1	57.3	57.0	53.1	56.9					4	224.3
2	55.5*		56.8	58.7	55.5	57.4			5	283.9
3	50.5	51.4	50.0	48.0	53.3	50.4			6	303.6
4	55.5*		59.5	57.3	58.3				4	230.6
5	55.2	54.2	58.0	56.9	54.7	53.8	53.5	54.4	8	440.7
6	60.5	56.8	59.2		58.1	58.5			5	293.1
7	58.1	62.8	61.9	58.0					4	240.8
12	58.6	54.6							2	113.2
13	53.4	51.9	53.3	55.5*					4	214.1
14	57.7	57.3	54.3	51.6					4	220.9
15	54.8		50.8	50.1					3	155.7
15a	49.2	56.7							2	105.9
15b	54.6		55.5	53.8					3	163.9
15c	58.9		59.0						2	117.9
24	52.6	55.7	51.4	51.6					4	211.3
26	57.9	55.3							2	113.2
27	54.9	54.6	50.8	54.8					4	215.1
27a	60.3		59.2	55.5					3	175.0
28	58.9	55.2							2	114.1
28a	59.3	57.7							2	117.0
Beach										
16	58.1	58.8	56.2	57.5					4	230.6
17	52.9		53.7	52.1					3	158.7
18	57.3		57.2	54.8	57.0	58.6	53.0	54.3	7	392.2
20	59.2	58.0	58.0	58.3	55.6	55.0			6	344.1
21	59.8		59.5	58.9	55.9		60.8		5	294.9
21a	55.1		53.4	54.1					3	162.6
22	61.9	61.3	59.7	60.8					4	243.7
23	55.0	56.0	55.0	57.0					4	223.0
31	53.5	53.3	54.9		53.3		57.3	54.4	6	326.7
31a	60.9	64.3							2	125.2
33	48.3								1	48.3
34	52.1								1	52.1
35	52.3	53.5							2	105.8
36	58.5		60.3	56.8					3	175.6
37	63.1								1	63.1
38	59.9		59.6						2	119.5
39	55.8								1	55.8
Total									128	7176.2
Range									1–8	48.3–440.7
Mean									3.5	196.2

Chapter 2

African Black Oystercatchers *Haematopus moquini*: density, breeding productivity and investment over three breeding seasons on a mainland habitat





Introduction

The breeding range of the African Black Oystercatcher *Haematopus moquini* extends along the coast of southern Africa from the Eastern Cape, South Africa, to southern Namibia (Summers & Cooper 1977, Hockey 1983a, Martin 1997, Vernon 2004, Hockey *et al.* 2005). It is classified as "near-threatened" in South Africa and globally (Underhill 2000, BirdLife International 2004). The oystercatcher breeds on rocky and sandy shores and on offshore islands in the austral summer (Summers & Cooper 1977, Hockey 1983a, b, Underhill 2000). Adults are territorial and stay on their breeding territories throughout the year (Summers & Cooper 1977, Hockey 1983a, 1984b). They are long-lived, mate-faithful with a naturally low reproductive rate (less than one fledgling per pair per year) (Summers & Cooper 1977, Hockey 1983b, 1996a).

Oystercatchers are vulnerable to human disturbance (Summers & Cooper 1977, Hockey 1983a, b, 2002, Jeffery 1987, Watson & Kerley 1995, Martin 1997, Leseberg *et al* 2000, Underhill 2000, Hockey *et al.* 2005, Jeffery & Scott 2005). Conserved offshore islands are key to the species' survival showing a high breeding productivity (Hockey 1983a, Hockey *et al.* 2005). Introduced terrestrial predators depress breeding success on islands (Summers & Cooper 1977, Hockey 1983b) and predators cause nest failure on mainland coasts (Ward 1990, Jeffery & Scott 2005).

Several mainland sites support more than 1% of the world population (Hockey 1983a). On the Western Cape mainland, rocky shores support higher densities of birds than sandy shores (Hockey 1983a). Koeberg Nature Reserve consists of both rocky (harbour) and sandy shores; it is a mainland site with little human disturbance and a wide diversity of predators.

This chapter examines the breeding success of African Black Oystercatchers at Koeberg Nuclear Power Station and Nature Reserve over three breeding seasons. We undertook detailed observations of breeding productivity in order to examine the conservation threats of the oystercatcher at this mainland site. Density of birds, breeding productivity and investment to breeding are considered.

Study area

Koeberg Nuclear Power Station (33°40'S, 18°25'E) lies 30 km north of Cape Town and is surrounded by a 3 000 ha nature reserve which includes the coastline (Johnson 1995, Eskom Holdings Limited 2006). On the shore side of the high-security area surrounding the power station is a harbour, which consists of a northern and southern breakwater, and a water outflow channel (Figures 1 and 2 thesis introduction).

The two harbour breakwaters are protected by concrete dolosse on the seaside. The inside of the breakwaters are built up with rocks of assorted sizes to form a gently sloping intertidal area covered with mussels and limpets (Figure 3 thesis introduction). The function of the harbour is to act as a settling pond to provide sand-free water at the inlet of the pump house for cooling the condensers, and therefore has little human disturbance. The harbour area is fenced off and it is a "National Key Point" in terms of South African legislation (Act 102 of 1980), which imposes heavy penalties for illegal entry.

The study area includes two sections of sandy shore north and south of the power station. The north beach is approximately 2 km long (northern limit 33°39.183'S, 18°25.003'E), is rarely visited by people and is isolated and inaccessible. The nearest public access point north of the power station is at Silwerstroomstrand, c. 12 km away. The south beach, approximately 500 m long (southern limit 33°41.292'S, 18°26.085'E), is more sheltered than the north beach, has finer sand and a wider intertidal area (gentler slope) than the north beach. Two residential areas, Duynefontein and Melkbosstrand, are approximately 2 km south of the power station. There is some human disturbance (mainly walkers and dogs) on the south beach.

Methods

Surveys of oystercatchers were conducted on a weekly basis from November 2002 until May 2004 and from November 2004 until March 2005 with numbers of pairs, nests, eggs, chicks and fledglings recorded. Pairs were defined as birds that roosted and fed close to each other and were not necessarily breeding at that time. During the breeding season (November to May), a non-breeding pair was only classified as a pair if they were present together on their territory for more than 25% of the weekly bird counts. Hatching percentage was taken as the percentage of eggs that hatched and fledging percentage was taken as the percentage of chicks that fledged.

From November 2002 until May 2003, October 2003 until May 2004 and from November 2004 until March 2005, nests were searched for twice a week. Once found they were monitored at three- to seven-day intervals until hatching. On the first visit to the nest, eggs were measured to 0.1 mm accuracy and weighed, to the nearest 0.1 g, with an electronic balance (Tanita model 1479). On subsequent visits, nest contents were checked and eggs were re-weighed. For each egg, up to 13 weight measurements were recorded. The eggs were measured to estimate a laying date and the proportion of time through incubation of each egg, as well as to use in comparisons between years and areas. Once the eggs hatched, the chicks were searched for at similar intervals. Whenever found, the chicks were weighed and measured (culmen, head, tarsus, foot, wing and tail) (Appendices 5 and 6) until fledging. Chicks were ringed (11 mm stainless steel rings from SAFRING) on the right leg (placed on the tarsus) once they reached 150 g. Chicks were measured to calculate growth rates and used in comparison between years and areas. Eight chicks were ringed in the 2002/2003 season and three in the 2003/2004 season. Gompertz growth rates were estimated using the method of Underhill (in prep.) for each chick for which two or more mass measurements were available.

From the egg masses and measurements, the estimated fresh mass and the date of start of incubation were estimated using the methods described by Underhill & Calf (2005). These estimated dates were used to generate a probability distribution of incubation starting dates and from this summary, statistics were computed, together with approximate confidence intervals generated by bootstrapping (Underhill submitted). Statistical hypothesis testing for differences between years was performed using randomization tests (Manly 1991, Underhill submitted). For the three study seasons, we tested whether egg mass changed during the breeding season by regressing estimated fresh egg mass against estimated date of start of incubation. Length and breadth were considered similarly.

Sixteen adults were caught and measured (mass, culmen, bill-width, bill-depth, head, tarsus, foot, wing and tail) in the 2002/2003 breeding season by placing a walk-in trap over the nest (where the eggs had been replaced by artificial eggs) (Appendix 7). The birds were ringed with 11 mm stainless steel rings on the right leg (on the tibia) as well as a unique combination of colour bands on the right and left legs (on the tarsus). Adult birds were caught in order to ring with colour bands to determine whether birds moved from their territories, measurement data was collected incidentally and is recorded in the appendices. Pairs were strictly territorial and were identified due to their positions on the coast according to distinctive landmarks.

The Mayfield method (Mayfield 1961, 1975) was used to calculate the daily clutch and chick survival rates. The probability of the nest surviving the incubation period through to hatching was estimated for each year by raising the daily clutch survival probability to the average incubation period (32 days). A similar calculation was done for the pre-fledging period (40 days). The daily survival rates between years were compared using the method of Johnson (1979).

The laying period (the time taken to lay the complete clutch) was calculated and included in the incubation period because the African Black Oystercatcher incubates the clutch after the first-laid egg due to high levels of egg predation (Hockey 1996a). The period between the loss of each clutch and the start of the re-laid clutch was estimated. The hatching date of each egg was estimated as the middle date between the last date that the egg was observed and the first date that the chick was observed, unless hatching was observed and a more accurate date could be given. The fledging date of each chick was estimated as the middle date between the last date that the chick was not flying and the first date that it was seen flying well. Oystercatcher fledglings remain with their parents for an extended period and we attempted to measure this as accurately as possible. The final departure date was estimated as the middle date between the last date that the fledgling was observed with the parents and the first date that it was not observed. The fledgling was usually determined to be present by direct observation, but was assumed to be present if the adults alarmed on the approach of the observer even though the fledgling was not seen. Given that the visits took place at three to seven day intervals, errors in the estimates of dates will be less than six days. The key dates for each pair (start of incubation (including the laying period), hatching date, fledging date, final departure date and, where appropriate, date of loss of eggs or chicks) were represented graphically along a time axis using the method described in Chapter 1.

For each pair, the total number of days during the breeding season allocated to the three key components (incubation (including the laying period), chick-rearing from hatching to fledging, and chick-rearing from fledging to final departure from the parental breeding territory) of oystercatcher breeding activity were calculated. These values were summed across all breeding pairs in the study area, and the average time investments calculated. These averages were set into context by expressing them relative to the mean periods for each key breeding component. A mean reproductive period of oystercatchers at the Koeberg site has a total of 122 days: 32 days incubation (26%), 40 days chick-rearing (33%) to fledging and 50 days from fledging to leaving (41%). The time taken for fledglings to leave the parental territory was taken from the median of 12 chicks measured at Koeberg in 2002/2003 and 2003/2004 breeding seasons (see results, Table 7). In an ideal breeding situation, the allocation to these three components should be 26% incubation, 33% chick-rearing and 41% post-fledging care; the extent of the departure from this ideal (26:33:41) provides a measure of the distortion from the ideal situation.

Results

Density and territoriality

In the 2002/2003 breeding season, the mean numbers of adults seen on weekly counts was close to double the mean numbers of pairs seen (Table 1). In 2003/2004 and 2004/2005, the counts were lower than the previous year and mean number of pairs did not account for all the adults counted (Table 1). Over the three breeding seasons, the highest number of pairs present corresponded to the highest number of pairs counted while incubating eggs. The harbour area (c. 1 km of shoreline) supported 23 pairs (46 birds/km) while the south beach area (c. 500 m of shoreline) supported 8 pairs (32 birds/km) and the north beach area (c. 2 km of shoreline) supported 8 pairs (8 birds/km).

Mean number of adults were higher and mean number of pairs of adults were lower in the non-breeding season compared to the breeding seasons (Table 1). A roosting site in the south harbour (towards the end of the south breakwater jetty) was frequently used, especially in bad weather (rain, southerly winds and a high swell); groups of 4-60 birds were observed.

More than 80% of pairs were present on their territory during the weekly counts in the 2002/2003 breeding season (Table 2). This decreased to 67% and 70% in the overall area in the 2003/2004 and 2004/2005 breeding seasons respectively (Table 2). There was no difference in the percentage of pairs present on their territories between the harbour and the beach areas in 2002/2003 (Table 2). In 2003/2004, there was a lower percentage of birds on their territories in the harbour area compared to the beach area but the opposite was true in 2004/2005 (Table 2).

There were 37 breeding pairs (produced at least one egg) in 2002/2003, 31 breeding pairs in 2003/2004 and 13 breeding pairs in 2004/2005 (Table 4). Sixteen adults were ringed during the 2002/2003 breeding season (Appendix 7).

Egg production

We estimated that in the 2002/2003 breeding season, 95% of all eggs were laid in a 162-day interval from 2 October to 12 March, in 2003/2004, 95% of all eggs were laid in a 81-day interval from 23 November until 12 February and in 2004/2005, 95% of all eggs were laid in a 97-day interval from 17 November to 22 February (Figures 1, 2, 3 and Table 3). The median date for the start of incubation in 2002/2003 was 9 January, this date was 4 January in 2003/2004 and 6 December in 2004/2005 (Table 3). There was a month's difference (8 December and 9 January) in the median date of egg-laying comparing the first clutch with all clutches in 2002/2003, 13 days difference (22 December and 4 January) in 2003/2004 and no difference in 2004/2005 (Table 3). However, there was 43 days difference in the 95% interval between first and all clutches laid in 2004/2005 (Table 3).

Percentage of pairs attempting breeding was markedly lower in 2004/2005 than in the previous two breeding seasons (Tables 4 and 5). In 2002/2003, 128-130 eggs were laid (Table 4) and there were 2.11 nests per breeding pair (Table 5). Twenty-six pairs laid more than one clutch each; eight pairs re-laid more than twice, five pairs re-laid after chicks hatched and two pairs re-laid after chicks fledged (Table 4). In 2003/2004, 84 eggs were laid and there were 1.48 nests per breeding pair, in 2004/2005 there were 26 eggs laid and 1.23 nests per breeding pair (Tables 4 and 5). There were 13 pairs and three pairs which re-laid in 2003/2004 and 2004/2005 respectively (Table 4).

In 2004/2005, 21% of pairs in the harbour area attempted breeding (opposed to 77% and 85% in 2002/2003 and 2003/2004 respectively) (Table 5), 50% of pairs attempted breeding on the beach sections in this year (Table 5). Nests per breeding pair and numbers of pairs laying replacement clutches were similar in the harbour and beach areas in each breeding season (Table 5).

Using the Mayfield method, there was a clutch daily survival rate of 94.97% (63 clutches lost during 1253 nest days), 94.07% (41 losses, 691 nest days) and 89.94% (16 losses, 159 nest days) in the 2002/2003, 2003/2004 and 2004/2005 breeding seasons respectively. These differences were not formally significant; largely because of the small number of nest days in the third season. The probabilities of a clutch surviving a 32-day incubation period were 15%, 10% and 2% in the three successive breeding seasons.

At three nests in 2002/2003, parents continued incubation after eggs rolled down sand dunes. The scrape edges may have been disturbed by the birds or by wind, allowing the eggs to roll down the slope of the dune while neither adult was incubating them, or the eggs may have been blown directly off the nest by the wind. In the first instance, the nest was placed 20 cm from the edge of the dune and the two eggs rolled 5.5 m down the dune (approximately a 70-degree angle to the horizontal) onto the beach. The eggs had been incubated for two weeks before this event and the pair continued to incubate for a further two weeks until the eggs disappeared. In the second instance, the nest was placed on the slope of a dune (approximately a 45-degree angle to the horizontal) and the egg gradually rolled 2 m down the dune. The egg was incubated for approximately 43 days and the chick died during hatching. In the third instance, the nest was 5 cm from the edge of a nearly vertical dune (approximately 85-degree angle to the horizontal). This nest was originally a two-egg clutch from which one egg disappeared 2.5 weeks into incubation; the remaining egg was damaged after 3.5 weeks of incubation and rolled 11 m down the dune to land on the beach after 4.5 weeks of incubation. The pair continued to incubate the damaged egg for another three weeks.

There were six non-breeding pairs in the south harbour area in the 2002/2003 breeding season. There were no suitable nest sites along the south arm (the tarred section extended from the water to the concrete access). Three tyres filled with sand were fixed to the tarred section of the slope of the jetty (Figure 3 thesis introduction) in 2003 to provide a suitable nesting environment. Clutches were laid in two of these tyres in the 2003/2004 breeding season, with one chick hatching. One of the tyres washed away during the winter of 2004. No birds laid eggs in the two remaining tyres in the 2004/2005 season.

The estimated mean fresh masses of eggs at Koeberg in the 2002/2003, 2003/2004, 2004/2005 breeding seasons were 56.1 g, 56.0 g and 56.0 g respectively, and 56.0 g overall (Table 6); the inter-year differences were not statistically significant (ANOVA $F_{2,225} = 0.11$, P=0.89). The difference between the estimated mean fresh masses of eggs from first clutches and from replacement clutches was not significant (t_{226}=–0.23, P=0.82). There was no significant change in fresh egg mass during the breeding season (estimated to be a 0.17 g increase per 100 days, P=0.81), with similar results for length (P=0.85) and breadth (P=0.73). Lengths and breadths of eggs in all breeding seasons were similar with an overall mean length of 59.6 mm and overall mean breadth of 41.7 mm (Table 6), and their differences were not significant.

Chick-rearing and fledging

In 2002/2003, 24 eggs hatched, a hatching success of 19% and 0.64 hatchlings per breeding pair (Tables 4 and 5). In 2003/2004, 6 eggs hatched, hatching success of 7% and 0.19 hatchlings per breeding pair (Tables 4 and 5). No chicks hatched in the 2004/2005 breeding season (Table 4, Figure 3). In 2002/2003, 10 chicks fledged and left the area, a fledging success of 42% and 0.27 fledglings per breeding pair (Tables 4 and 5, Figure 1). In 2003/2004, two chicks fledged and left the area, a fledging success of 33% and 0.06 fledglings per breeding pair (Tables 4 and 5, Figure 2).

At Koeberg 2002/2003, the median of the 10 estimated growth rates was higher than that at Dyer Island 2002/2003 (Appendix 5, Chapter 3). The median time that a fledgling chick remained with its parents before departing the area was 50 days (49 in table) (range 38–104 days) (Table 7) based on 12 oystercatcher fledglings at Koeberg over the 2002/2003 and 2003/2004 breeding seasons.

In 2002/2003 there was a hatching success of 24% and a fledging success of 33% in the harbour as opposed to values of 11% and 66% respectively in the beach area (Table 5), indicating a relatively higher egg loss on the beach and a relatively higher chick loss in the harbour. In 2003/2004 both areas had high egg losses and the beach area pairs also had high chick losses (Table 5). In 2004/2005 there were no chicks or fledglings produced.

Using the Mayfield method, there was a chick daily survival rate of 97.96% and 97.71% in the 2002/2003 and 2003/2004 breeding seasons respectively, which translates in 44% and 40% of hatchlings surviving the 40-day pre-fledging period. In each of these breeding seasons, the daily rate of chick survival was significantly greater than the rate of clutch survival (in 2002/2003, $z=3.16$, $P<0.001$, and in 2002/2003, $z=2.30$, $P=0.011$).

In 2002/2003, birds in the south harbour started breeding early, with two nests hatched in early October and subsequently the two pairs successfully produced one fledgling each before re-laying (Figure 1). Both chicks fledged in the second week of December 2002 and left the area towards the end of January 2003, by which time both pairs were incubating more eggs. Pair 2 incubated an unsuccessful clutch from 12 January until 17 February 2003 and a successful clutch from 25 February to 27 March 2003, although the two chicks disappeared on 14 April 2003. Pair 4 incubated two more unsuccessful clutches from 15 January to 20 February and from 28 February to 8 March 2003.

Egg and chick loss

Sixty-two clutches and 104 eggs were lost in 2002/2003, 41 clutches and 78 eggs were lost in 2003/2004 and all 16 nests and 26 eggs were lost in 2004/2005 (Tables 4 and 8). Predation probably accounted for 59% of eggs lost in 2002/2003; this value was 78% in 2003/2004 and 88% in 2004/2005 (Table 8). The percentages of eggs presumed to have been predated in the harbour area were 38%, 73% and 100% in 2002/2003, 2003/2004 and 2004/2005 respectively; in the beach area these values for the same years were 82%, 85% and 83% (Table 8).

On the sandy shore, predators of oystercatcher eggs were determined from the footprints that were found at the empty nest; Kelp Gulls *Larus dominicanus*, Sacred Ibises *Threskiornis aethiopicus* and Yellow Mongooses *Cynictis penicillata* were identified as definite predators in this way. A Pied Crow *Corvus albus* was observed removing an egg from a nest on the beach and flying away with it. Other potential predators that were seen in the study area included domestic dogs, feral cats *Felis catus* and various snakes. A Yellow Mongoose was seen feeding on Swift Tern *Sterna bergii* eggs in March 2003 in the Koeberg water outflow area where up to 700 nests were deserted as a result. Predated Swift Tern eggs were seen in May 2005 with bite marks assumed to be from a feral cat.

In the 2002/2003 season, seven eggs were washed away in a surge high tide event that took place at around 03h00 on 17 February 2003. Human disturbance caused losses of eggs in the harbour area during busy times of maintenance (people disturbed the adults preventing them from feeding the chick) or by storm water from outflow pipes washing away eggs. Eggs were also lost when buried by windblown sand.

Fourteen chicks (from a total of 24 chicks) were lost in 2002/2003; nine of these were lost at eight days of age or younger. Two chicks were lost at 15 days old, two chicks at 19 days old and one chick at 24 days old. Four out of six chicks were lost in 2003/2004; three of these were under eight days old and one chick was 47 days old.

Human disturbance caused by nest checking may have aided predators in finding nests as described by Hockey (1983b) where Kelp Gulls were seen as opportunistic scavengers rather than active predators on Marcus Island. Kelp Gulls were present at this site but were never observed predating eggs or chicks, however Pied Crows were observed following the researcher. On one occasion a Pied Crow removed an egg from an unprotected nest while the adult was disturbed by the researcher. On most visits, nests were not checked if Pied Crows were in the vicinity. Egg and chick predation caused by mongooses, cats and snakes was unlikely to have been aided by human disturbance as these predators were wary of people.

Time investment to breeding

The 37 pairs which laid eggs in 2002/2003 spent on average 44 days incubating per pair (Table 9), about 40% longer than the mean incubation period of 32 days. A total of 78 clutches were laid (Table 4), so that the mean period for which each clutch was incubated was 21 days, 60% of the mean incubation period. In 2003/2004, 31 pairs spent on average 29 days incubating per pair (Table 9), slightly shorter than the mean incubation. A total of 46 clutches were laid (Table 4), so that the mean period for which each clutch was incubated was 20 days, 60% of the mean incubation period. In

2004/2005, 13 pairs spent on average 18 days incubating per pair (Table 9), slightly more than half the mean incubation period. A total of 16 clutches were laid (Table 4), the mean period for which each clutch was incubated was 15 days, 50% of the mean incubation period.

In 2002/2003, pairs spent 12 days per breeding pair on rearing chicks from hatching to fledging, and 13 days per breeding pair on fledging to final departure of the juveniles (Table 9). In 2003/2004, pairs spent five days per breeding pair on rearing chicks from hatching to fledging, and three days per breeding pair on fledging to final departure of the juveniles (Table 9). No chicks hatched in the 2004/2005 breeding season.

The total time investment by breeding pairs to reproductive activities from egg laying to final departure in 2002/2003 was 69 days per pair and therefore undertook 57% of a mean reproductive period (Table 9). The allocation of parental breeding effort was summarized by the ratio 64:17:16 for incubation; chick-rearing; post-fledging care, a large departure from the ideal ratios (26:33:41). In 2003/2004, the total time investment to breeding was 37 days per pair, 30% of mean (Table 9). The allocation of parental breeding effort in this season was summarized by the ratio 79:13:9, a larger departure from the ideal situation than in 2002/2003. In 2004/2005, the total time investment to breeding was 18 days per pair, 14% of mean (Table 9). The allocation of parental breeding effort in this season was summarized as the extreme ratio 100:0:0.

With a total production of 10 fledglings in 2002/2003, 255 days were invested in reproduction per juvenile produced, 209% of a standard reproductive period (Table 9). In 2003/2004, two fledglings were produced, 577 days were invested in reproduction per juvenile, 473% of a standard reproductive period (Table 9). No juveniles were produced in 2004/2005.

A total of 53 replacement clutches were found between November 2002 and March 2005 (Table 10). There were up to four clutches laid by an individual pair (Chapter 1). The mean interval between egg or chick loss and re-laying was 20.1 days (5-56 days) (Table 10). In 2002/2003, two pairs attempted to rear a second brood, producing second clutches after fledging chicks (Figure 1, Table 4).

Of the pairs that we can evaluate over the three years (some of the north harbour pairs are excluded) there were 34 that attempted breeding in the 2002/2003 breeding season. Of the 12 pairs that hatched chicks in 2002/2003, 10 pairs attempted breeding in 2003/2004 and five pairs in 2004/2005. In 2003/2004 there was one pair that had not attempted breeding the year before. There were 11 pairs that attempted breeding in all three seasons, with two pairs hatching (and fledging) chicks in the first two years.

Discussion

Bird density and territoriality

The beach sections at Koeberg differ in that the south beach is more sheltered, has a gentle gradient with a wide inter-tidal area and has more human disturbance than the north beach which is isolated and inaccessible. The south beach had a density of 32 birds/km compared to 8 birds/km on the north beach. Hockey (1983a) recorded a oystercatcher density of 3.21 birds/km (breeding season) for the mainland shore between Slipper Bay (St. Helena Bay) and Bloubergstrand of which the study area forms part, although the density on sandy beaches for this area was 2.17 birds/km. Hockey *et al.* (2005) reports a typical density of 1–4 birds/km on the mainland. Summers *et al.* (1976) found no African Black Oystercatchers on this section of shoreline (Melkbostrand to Robbesteen) in summer 1975/1976. The oystercatcher density on this mainland area has therefore increased over 30 years.

The fenced in harbour and water outflow area covers c. 500 m of what was originally a sandy shore. At a density of 32 birds/km, it would have supported eight pairs of oystercatchers. This area, which now includes 1 km of artificial rocky shoreline in the harbour, supports 46 birds, a 44% increase as a result of the habitat transformation. Hockey (1983a) recorded a density of 2.58 birds/km (breeding season) on rocky shores in the St. Helena Bay to Bloubergstrand area. There was a higher density of breeding oystercatchers in the harbour area compared to the adjacent beaches and a similar number of breeding pairs in the harbour area as in the whole beach area. The artificially-created sheltered rocky shore inside the harbour provides excellent breeding habitat for oystercatchers.

Numbers of oystercatchers have increased at other mainland breeding sites in the Western Cape and Eastern Cape (Ward 1990, Leseberg *et al.* 2000, Hockey 2002, Vernon 2004, Jeffery & Scott 2005). Hockey *et al.* (2005) state that the total African Black Oystercatcher population is now probably more than 6 000, due in part to the invasion of the Mediterranean Mussel *Mytilus galloprovincialis* along the rocky shores.

The counts of oystercatchers, the percentage present on their territories and the number of breeding pairs in the 2002/2003 breeding season were higher than in the following two breeding seasons; this corresponded to an overall higher breeding success in this season as opposed to the later seasons. The higher percentage of pairs present on territories on the beach compared to the harbour in 2002/2003 and on the harbour compared to the beach in 2003/2004 does not correlate with higher breeding success in these areas during the two breeding seasons and therefore must be coincidental.

There was a partial relaxation of territoriality over the non-breeding season as was seen in higher numbers of adults and lower numbers of pairs counted weekly, as well as the roost formed on the south harbour jetty. The birds that roosted were probably birds that were living and breeding in the area because several of the colour-ringed adults were regularly observed there. None of the hundreds of juveniles ringed and colour-ringed elsewhere in the breeding range as part of the Oystercatcher Conservation Programme were observed at the roost (or anywhere else within the study area), although a careful watch was maintained for them.

African Black Oystercatchers are territorial (Summers & Cooper 1977, Hockey 1983a, 1984b, Hockey *et al.* 2005) and unbanded pairs in this study were assumed to stay on their territory although this could only be confirmed from banding all the birds. Of the 16 banded birds, all but one stayed on their territories.

Egg production

The total egg-laying period in 2002/2003 was double that in 2003/2004. The length of the egg-laying period in 2004/2005 can be explained by one replacement clutch that was laid 43 days after the previous laid clutch. The longer egg-laying period in 2002/2003 corresponds with more eggs produced and more time spent incubating than in the following two breeding seasons. The median date of egg-laying (ie. the peak of egg-laying) was similar in the first two seasons but was a month earlier in 2004/2005, reflecting few replacement clutches laid. This was due to few birds attempting breeding in this year and little attempt made to continue breeding once the first clutch had been lost.

The number of eggs produced, the number of replacement clutches laid and the eggs per breeding pair decreased from 2002/2003 to 2004/2005. This corresponds with an overall decrease in breeding productivity over these years. The number of pairs attempting breeding decreased from 80% in the first two years to 35% in 2004/2005. The egg mass and dimensions did not differ significantly between years, between first-laid or replacement clutches or throughout each breeding season. Hockey (1983b) also found no significant change in egg size or mass throughout the breeding season and with first or replacement clutches.

There was a high level of replacement clutches laid, especially in the 2002/2003 breeding season with up to four clutches laid by an individual pair. Jeffery & Scott (2005) also found oystercatchers at Cape Agulhas laying a fourth clutch in some years although Hockey *et al.* (2005) state that up to three replacement clutches are laid. Replacement clutches correlate with a high egg loss and a high breeding effort (see Chapter 1).

There was no difference in egg production between harbour and beach areas in 2002/2003 and 2003/2004, but fewer pairs attempted breeding in the harbour area than in the beach area in 2004/2005. There was considerable human disturbance in the harbour in this year as well as a high level of predation caused by the presence of a feral cat, which was not present in the previous two years. There was no difference between nests per breeding pair between harbour and beach areas in this year.

Three pairs continued incubation after eggs rolled down sand dunes in 2002/2003. A similar event was recorded by Hall (1959). The tyres fixed to the harbour jetty in 2003 provided suitable nesting habitat; clutches were laid in two of these tyres in the following breeding season. One chick hatched but died, probably as a result of disturbance caused by extensive maintenance work performed in this section of the harbour at this time. One tyre was washed away in winter 2004. Placing suitable nesting habitat in harbours may be a conservation tool to increase breeding productivity of oystercatchers.

There was a much decreased attempt at breeding made in 2004/2005, presumably due to a threat to the birds survival. This can be explained by the high adult annual survival of the African Black Oystercatcher, therefore, the birds do not invest time or energy in breeding if it may decrease their lifetime reproductive success.

Chick-rearing and fledging

There was a decrease in hatching success, hatchlings per breeding pair, fledging success and fledglings per breeding pair from 2002/2003 to 2003/2004. No chicks hatched in 2004/2005. This corresponds to other breeding parameters already discussed. There were similar fledglings per breeding pair between harbour and beach areas in both seasons, although the hatching and fledging success differed.

The median time from fledging to leaving for oystercatcher chicks at Koeberg was quantified as being 50 days (seven weeks), compared to reported times of 2-6 months (8–24 weeks) (Hockey 1996a, Martin 1997; Hockey *et al.* 2005). However, this period was shorter and the chick growth rates were faster than that measured at Dyer Island (Chapter 3, Wortel *et al.* 2003) and may be different for different sites and conditions. Territorial species of Charadriiformes have early fledging times probably as an anti-predator strategy (Drent & Daan 1980, Hockey 1984a, 1996b). Our observations show that juveniles leave parental territories earlier on the mainland than on islands presumably due to high levels of predation, compared to the opposite situation reported by Hockey (1983b). He stated that juveniles are ousted earlier from parental territories at islands than on the mainland due to competition for feeding territories in the non-breeding season.

There were two attempts to fledge a second brood of chicks in the 2002/2003 breeding season; the second report of attempting to raise a second brood for the African Black Oystercatcher. The first record of double-brooded African Black Oystercatchers is at Possession Island, Namibia, where a pair reared two broods in two seasons (Hockey 2002, Hockey *et al.* 2005). The African Black Oystercatcher normally rears one brood per year (Hockey 1996a, Hockey *et al.* 2005).

Egg and chick loss

There were high levels of egg predation at this site in all three breeding seasons but increasing from 2002/2003 to 2004/2005 with the daily clutch survival rate decreasing over the three breeding seasons. There was higher egg predation on the beach compared to the harbour area in 2002/2003 although beach and harbour areas showed similar levels of egg predation in 2003/2004 and 2004/2005. There is a diversity of predators present at this mainland site, especially on the beach sections. The harbour area is completely fenced-in and has a medium level of human disturbance which helps to deter predators from entering the area, although a Yellow Mongoose was seen in 2003 and a feral cat in 2004. The presence of the feral cat accounted for the high level of predation in the 2004/2005 season and possibly also in the 2003/2004 season.

Eggs were lost in the surge high-tide event in February 2003, eggs and chicks being monitored were also lost in this event at Robben Island, Bettys Bay and Dyer Island (Calf & Underhill 2005b, S Starke and NME Wortel pers. comms).

Hockey (1983b) reported 87.5% of chick deaths (n=20) occurring in the first week of age at Marcus Island in the 1979/1980 breeding season. At Koeberg, 67% of chick deaths (n=18) occurred within eight days of age. Of these chick deaths, only two are probably related to human disturbance. Predation probably accounts for the rest of the chick mortality although we were not able to confirm this. There was no difference in the chick survival rate between years.

The results at Koeberg showed that predators depressed breeding productivity on this protected mainland shoreline, causing egg and chick loss, although Hockey (2001, 2002) stated that low fledgling production is caused by loss of chicks mainly attributed to human disturbance. This study showed that the daily rate of clutch loss was significantly greater than that of chick loss, suggesting that the nest period is the crucial stage in productivity. Pond (1999) found high egg loss due to predation and high chick loss due to human disturbance, but the proportion of clutches lost was greater than the proportion of chicks lost.

Time investment to breeding

The time spent on incubation decreased from 2002/2003 to 2003/2004 to 2004/2005, as well as the length of the egg-laying period, the number of eggs laid, the number of replacement nests and the number of nests per breeding pair. In all years, there was an increased proportion of the total reproductive period spent on incubation as a result of the high level of egg loss and high number of replacement clutches laid. There was a large departure from the ideal situation of time spent on breeding activities in all three years; the ratio of 26:33:41 (incubation:chick-rearing:post-fledging) was 64:17:16 in 2002/2003, 79:13:9 in 2003/2004 and 100:0:0 in 2004/2005.

Thirty-four of 35 pairs that can be evaluated over the three seasons attempted breeding in the first year. Of these, eight pairs successfully reared chicks to fledging. This was the best breeding productivity at the site over the three years studied and it stands to reason that those birds that were unsuccessful in this year, carry a higher burden than those failing to breed successfully in subsequent years. In the second year, the two pairs that successfully fledged chicks had been successful in the previous year, indicating the most-highly productive birds at the site, these two pairs also attempted breeding in the third year. A longer term dataset is necessary to fully evaluate individual variation in breeding success.

Conservation implications

There are substantial numbers of African Black Oystercatchers at Koeberg, especially in the harbour area. The harbour area provides a sheltered rocky shoreline with a wide inter-tidal feeding area with potentially little human disturbance and predation. This is therefore an ideal feeding and breeding area for oystercatchers, as was seen by two pairs attempting to rear a second brood in the south harbour area in 2002/2003. Human disturbance in the harbour is limited to routine harbour maintenance and operation and maintenance of the dredging machine (which is not present in all years). There was a high level of human disturbance over the 2004/2005 season due to the removal of the dredging machine in 2004 and the renovation of the south breakwater in 2004 and 2005. This is the first time that the breakwater has been renovated since construction (completed in 1984) and therefore doesn't represent a permanent disturbance.

There was substantially poorer success in the 2004/2005 breeding season, where few pairs attempted breeding and no chicks hatched. This is important because the factors causing this poor productivity can have conservation implications for the oystercatchers breeding at this site. The increased human disturbance in the south harbour and outflow area definitely prevented birds from attempting breeding. There was also a feral cat present in the harbour in this season which caused egg predation.

Regular maintenance should be limited to the winter or non-breeding season which would potentially increase breeding productivity in the harbour oystercatchers. The fences surrounding the harbour area (and power station) have been improved over the course of these three years and this should help to deter terrestrial predators, however predators already present in the harbour area, need to be removed.

The beach areas are part of a nature reserve, mostly protected from human disturbance but with a large diversity of predators. The poor breeding productivity of oystercatchers in these areas is therefore a natural problem and cannot be easily corrected. Human disturbance on the south beach can be limited by security measures and dogs should not be allowed on this section.

Conclusion

The breeding success of the African Black Oystercatcher at Koeberg Nuclear Power Station decreased from 2002/2003 to 2003/2004 to 2004/2005, as well as a marked decrease in investment to breeding over these years. This was seen in fewer pairs breeding, fewer eggs laid, fewer chicks and lower hatching and fledging success. The poor success in the 2004/2005 season can be partly attributed to the disturbance in the south harbour and the presence of a feral cat in the harbour area but this does not explain the poor breeding success and low investment to breeding elsewhere at the site. There was lower breeding success on Dyer Island in 2004/2005 compared to the 2002/2003 breeding season (Chapter 3), also with no explanation. Poor breeding success was seen on Robben Island in 2004/2005 but was attributed to egg predation (mainly from the presence of feral cats) (Chapter 3). It stands to reason that there is a natural annual variation in breeding success of a long-lived bird such as the African Black Oystercatcher and the reasons for this variation may not always be apparent.

Further study is needed to determine the scale on which these fluctuations in breeding productivity occur (local or regional) and it is important to continue long-term monitoring to determine whether the downward trend observed over this three year period at Koeberg represents part of a long-term decline, or whether it can be dismissed as part of random fluctuations.

There were 0.27, 0.06 and 0 fledglings produced per breeding pair in 2002/2003, 2003/2004 and 2004/2005 respectively. Hockey *et al.* (2005) stated that 0.35 fledglings per pair per year are needed to maintain a stable population. In all years, productivity was below this value; the year with the best productivity was 2002/2003, when it was 77% of the maintainance value. Hockey (2001) reported an average breeding productivity level of 0.25 fledglings per pair per year for unprotected mainland areas; this is similar to 0.27 fledglings per pair per year of 2002/2003 although the area is a protected site. The African Black Oystercatcher is a long-lived bird and it is therefore not possible to evaluate the long-term impact of low breeding success in a three-year period.

There was similar overall breeding success between the birds in the sheltered harbour (c. 1 km shore length) and on the entire beach section (c. 2.5 km shore length) in the three breeding seasons. In 2002/2003 there was a higher level of egg loss on the beach area and a higher level of chick loss in the harbour area. In 2004/2005 there were fewer attempts at breeding made in the harbour area compared to the beach area; the most likely explanations for this are discussed above.

There was a large breeding effort from the oystercatchers in all years into egg production and time spent on incubation. The hatching success was lower than the fledging success in the 2002/2003 and 2003/2004 breeding seasons and no chicks hatched in the 2004/2005 season indicating that at this site, incubation is the critical stage of the oystercatchers' breeding cycle and predation depresses breeding productivity.

Acknowledgements

Eskom Koeberg Nuclear Power Station provided access to the study site; we especially acknowledge the helpfulness of Gert Greeff and Hilton Westman, nature conservators at the site. Several volunteers helped with data collection, in particular Manfred Waltner. Tony Williams gave valuable comments on a earlier draft. The project was supported by the National Research Foundation, the Earthwatch Institute, and the University of Cape Town Research Committee.

Table 1. Means of weekly counts of African Black Oystercatchers on the shoreline at Koeberg Nuclear Power Station during three breeding seasons and one non-breeding season (summarised from Appendices 1 to 4).

	Mean number of adults	**Mean number of pairs of adults**
Breeding season		
November 2002 – April 2003	81	37
November 2003 – April 2004	74	26
November 2004 – March 2005	72	28
Non-breeding season		
May 2003 – October 2003	89	21

Table 2. Percentage of African Black Oystercatcher pairs present on their territories at Koeberg Nuclear Power Station counted on weekly surveys during three breeding seasons.

	Year	**Harbour area**	**Beach area**	**Overall**
Number of pairs holding territories	02/03	26	20	46
	03/04	20	19	39
	04/05	19	18	37
Average percentage of pairs present on territory	02/03	87%	81%	84%
	03/04	63%	71%	67%
	04/05	77%	64%	70%

Table 3. Percentiles of the dates of the start of incubation for African Black Oystercatchers at Koeberg Nuclear Power Station for three breeding seasons. The two columns for each breeding season refer to the first clutches and all clutches, including relays. The dates in the table are those by which the percentage of eggs given in the row had started incubation. The figures below the dates are the bootstrapped 90% confidence intervals for each percentile, given as days only; if the two numbers are increasing, then the month for both is that for the date in the line above, otherwise one is for the month before or after, as determined by the context (e.g.16–29 under 19 Nov means 16 Nov–29 Nov, and 28–11 under 2 Oct can only mean 28 Sept–11 Oct). The final six rows of the table give the estimated lengths of the periods (in days) during which the central 50%, 90% and 95% of incubation started; the second row for each period is the 90% bootstrapped confidence interval.

	2002/2003		**2003/2004**		**2004/2005**	
Percentile	**First**	**All**	**First**	**All**	**First**	**All**
2.5%	28 Sept	2 Oct	19 Nov	23 Nov	16 Nov	17 Nov
	26–25	28–11	16–29	17–30	15–21	15–22
5%	1 Oct	9 Nov	26 Nov	29 Nov	18 Nov	18 Nov
	28–10	3–16	18–1	20–4	16–22	16–23
25%	20 Nov	10 Dec	9 Dec	15 Dec	25 Nov	26 Nov
	16–26	11–12	5–13	10–21	21–1	23–2
50%	8 Dec	9 Jan	22 Dec	4 Jan	4 Dec	6 Dec
	30–18	4–14	16–29	28–12	28–9	30–14
75%	2 Jan	4 Feb	7 Jan	4 Jan	13 Dec	18 Dec
	24–12	27–9	1–14	19–27	7–28	11–30
95%	4 Feb	4 Mar	1 Feb	9 Feb	5 Jan	20 Feb
	26–26	24–11	23–2	3–12	25–9	29–22
97.5%	25 Feb	12 Mar	3 Feb	12 Feb	8 Jan	22 Feb
	30–2	3–18	30–4	7–24	28–10	8–23
50%	42 days	56 days	29 days	45 days	18 days	22 days
	34–51	45–65	23–36	34–45	11–32	15–30
90%	121 days	115 days	66 days	72 days	49 days	94 days
	86–148	103–148	57–75	64–79	35–53	40–96
95%	148 days	162 days	75 days	81 days	54 days	97 days
	120–155	117–169	65–79	72–91	39–56	51–99

Table 4. Productivity statistics for African Black Oystercatchers over three breeding seasons at Koeberg Nuclear Power Station.

Factor	**2002/2003**	**2003/2004**	**2004/2005**
Number of pairs	46	39	37
Number of breeding pairs	37	31	13
Number of nests	78	46	16
(1 egg clutch)	26-28	10	6
(2 egg clutch)	50-52	34	10
(3 egg clutch)	0	2	0
Number of eggs	128-130	84	26
Number of clutches lost	62	41	16
Number of chicks hatched	24	6	0
Number of chicks lost	14	4	-
Number of fledglings	10	2	-
(1 egg clutch)	1–3	0	-
(2 egg clutch)	7–9	2	-
Pairs raised one or more fledglings	8	2	-
Pairs raised two fledglings	2	0	-
Pairs re-laid (total)	26	13	3
(Pairs re-laid 3 or more times)	8	2	0
(Pairs re-laid after chicks hatched)	5	1	-
(Pairs re-laid after chicks fledged)	2	0	-

Table 5. Breeding productivity of the African Black Oystercatcher during three breeding seasons at Koeberg Nuclear Power Station.

Factor	**Year**	**Harbour area**	**Beach area**	**Overall**
Percentage of pairs attempting breeding	02/03	77%	85%	80%
	03/04	85%	74%	79%
	04/05	21%	50%	35%
Nests per breeding pair	02/03	2.05	2.18	2.11
	03/04	1.47	1.50	1.48
	04/05	1.25	1.22	1.23
Hatching Success (percentage eggs hatched)	02/03	24%	11%	19%
	03/04	4%	11%	7%
	04/05	0%	0%	0%
Hatchlings per breeding pair	02/03	0.9	0.35	0.64
	03/04	0.35	0.29	0.19
	04/05	0	0	0
Fledging Success (percentage chicks fledged)	02/03	33%	66%	42%
	03/04	50%	25%	33%
	04/05	-	-	-
Fledglings per breeding pair	02/03	0.30	0.24	0.27
	03/04	0.06	0.07	0.06
	04/05	0	0	0

Table 6. Dimensions and estimated fresh mass of African Black Oystercatcher eggs at Koeberg Nuclear Power Station in three breeding seasons.

		2002/2003	**2003/2004**	**2004/2005**	**Overall**
		n=125	n=80	n=24	n=229
Length (mm)	Mean	59.6	59.6	59.8	59.6
	Range	54.6–63.7	53.5–64.2	56.6–64.3	53.5–64.3
	S.D.	1.94	1.73	1.94	1.86
Breadth (mm)	Mean	41.7	41.7	41.8	41.7
	Range	38.6–43.8	38.5–44.6	38.9–44.2	38.5–44.6
	S.D.	0.99	1.11	1.23	1.06
Fresh mass (g)	Mean	56.1	56.0	56.0	56.0
	Range	48.0–64.3	47.7–64.5	46.3–66.8	46.3–66.8
	S.D.	3.25	3.52	4.29	3.45

Table 7. Chick-rearing time from hatching to leaving the parental territory for individual African Black Oystercatcher chicks at Koeberg Nuclear Power Station during the 2002/2003 and 2003/2004 breeding seasons (summarised from Appendices 5 and 6).

Chick Number	**Hatching Date**	**Fledging Date**	**Age of chick at fledging (days)**	**Leaving Date**	**Time from fledging to leaving (days)**
2-1	1 Nov 2002	10 Dec 2002	40	22 Jan 2003	43
4-1	1 Nov 2002	10 Dec 2002	40	22 Jan 2003	43
1 -1	21 Jan 2003	26 Feb 2003	36	15 Apr 2003	48
31a-1	22 Jan 2003	2 Mar 2003	39	14 June 2003	104
31a-2	22 Jan 2003	2 Mar 2003	39	15 Apr 2003	44
39-1	28 Jan 2003	8 Mar 2003	39	15 Apr 2003	38
28a-2	29 Jan 2003	8 Mar 2003	38	10 May 2003	63
17-1	15 Feb 2003	10 Apr 2003	54	14 June 2003	65
3-2	26 Feb 2003	26 Apr 2003	59	14 June 2003	49
3-3	26 Feb 2003	26 Apr 2003	59	6 July 2003	71
2-1	18 Jan 2004	29 Feb 2004	51	2 Apr 2004	49
39-1	7 Mar 2004	18 Apr 2004	41	31 May 2004	44
Mean			**45**		**55**
Median			**40**		**49**

Table 8. Causes and numbers of egg losses of the African Black Oystercatcher at Koeberg Nuclear Power Station during three breeding seasons.

Causes of egg losses	**2002/2003**		**2003/2004**		**2004/2005**	
	Harbour	**Beach**	**Harbour**	**Beach**	**Harbour**	**Beach**
Human disturbance	9	0	2	0	0	0
Extreme high tide event	5	2	0	2	0	2
Covered by windblown sand	0	4	0	0	0	0
Eggs not viable	8	0	3	0	0	0
Eggs damaged	5	1	5	1	0	0
Adult died while incubating	2	0	0	1	0	0
Died or disappeared in hatching	5	2	2	1	0	1
Predated	0	15	2	3	1	2
Disappeared (probably predated)	21	25	31	25	7	13
Total	**55**	**49**	**45**	**33**	**8**	**18**

Table 9. Time investment and breeding intensity of African Black Oystercatchers at Koeberg Nuclear Power Station during three breeding seasons. The mean reproductive cycle was taken as 32 days incubation, 40 days chick rearing, 50 days post fledging with a total duration of 122 days (see text).

Factor	**2002/2003**	**2003/2004**	**2004/2005**
Total incubation time (days)	1646	911	236
Mean incubation time per breeding pair (days)	44	29	18
Median incubation time per breeding pair (days)	38	30	16
Incubation time per breeding pair as percentage of mean	138%	91%	56%
Total chick-rearing time (days)	433	150	0
Mean chick-rearing time per breeding pair (days)	12	5	0
Median chick-rearing time per pair that produced chicks (days)	37	41	0
Chick rearing time per breeding pair as percentage of mean	30%	13%	-
Total post-fledging time (days)	475	93	0
Mean post-fledging time per breeding pair (days)	13	3	0
Median post-fledging time per pair that produced chicks (days)	55	47	0
Post fledging time per breeding pair as percentage of mean	26%	6%	-
Total breeding investment (days)	2554	1154	236
Mean breeding investment per breeding pair (days)	69	37	18
Total breeding investment per breeding pair as percentage of mean	57%	30%	14%
Total breeding investment per juvenile fledged (days)	255	577	-
Total breeding investment per juvenile fledged as percentage of mean	209%	473%	-

Table 10. Length of time spent incubating unsuccessful clutches and time before re-laying of individual pairs of African Black Oystercatchers at Koeberg Nuclear Power Station during three breeding seasons. Only pairs that laid replacement clutches are considered here.

		2002/2003	**2003/2004**	**2004/2005**	**Overall**
Time spent incubating unsuccessful clutches		n=51	n=26	n=6	n=83
	Mean	21.7	19.5	10.0	20.3
	Median	20.0	19.5	8.0	19.0
	Range	3–54	5–44	4–24	3–54
	S.D.	12.76	9.45	7.32	11.66
Time before re-laying clutches		n=36	n=14	n=3	n=53
	Mean	19.6	19.1	30.3	20.1
	Median	17.0	16.5	20.0	17.0
	Range	5–53	6–35	15–56	5–56
	S.D.	10.44	8.98	22.37	10.89

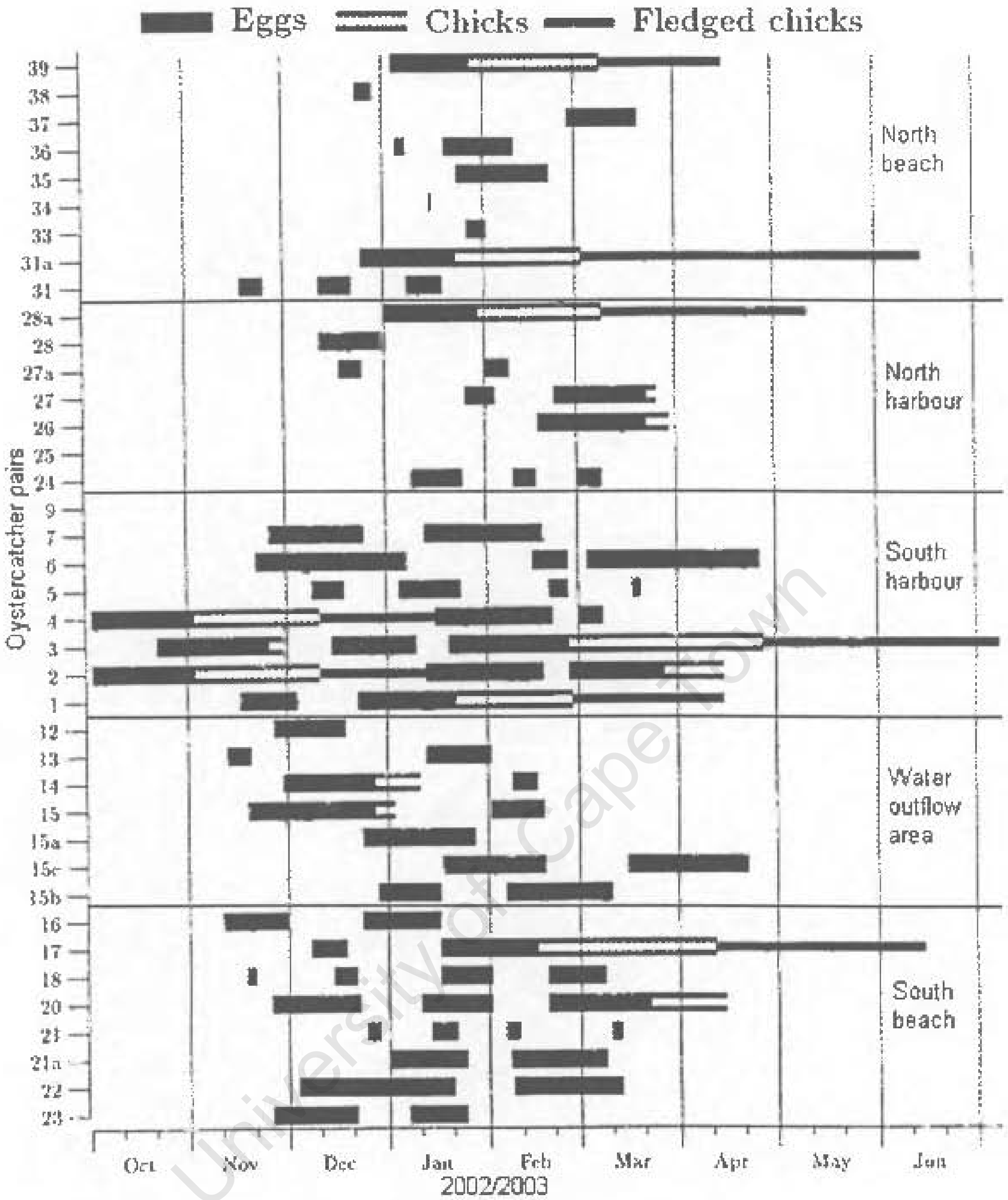


Figure 1. Graphical representation of incubation and chick-rearing of individual pairs of African Black Oystercatchers in relation to date at Koeberg Nuclear Power Station during the 2002/2003 breeding season. Time spent incubating is represented by a thick black line, time spent rearing chicks to fledging is represented by two lines and time spent chick-rearing post-fledging is represented by a thin black line.

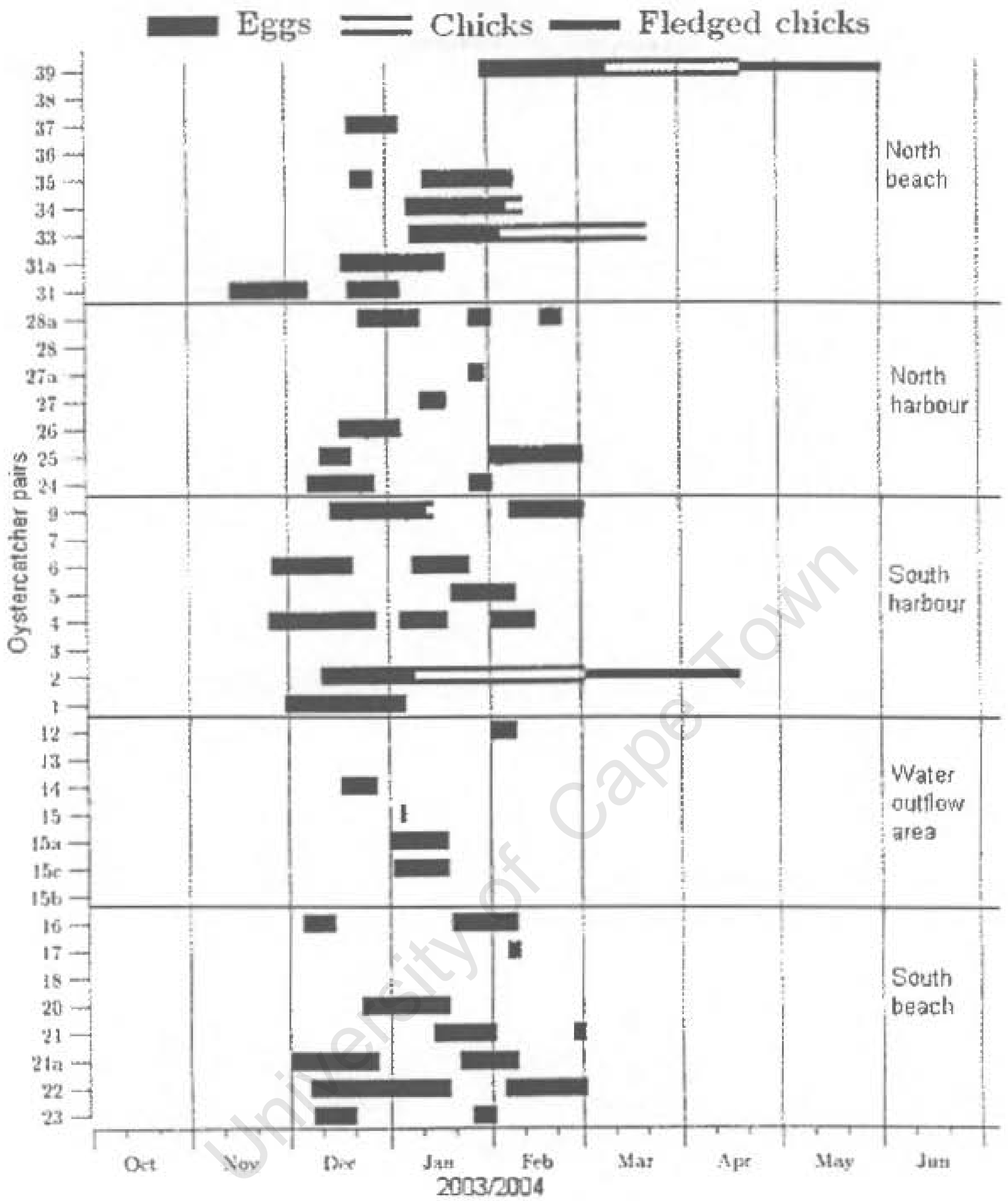


Figure 2. Graphical representation of incubation and chick-rearing of individual pairs of African Black Oystercatchers in relation to date at Koeberg Nuclear Power Station during the 2003/2004 breeding season. Time spent incubating is represented by a thick black line, time spent rearing chicks to fledging is represented by two lines and time spent chick-rearing post-fledging is represented by a thin black line.

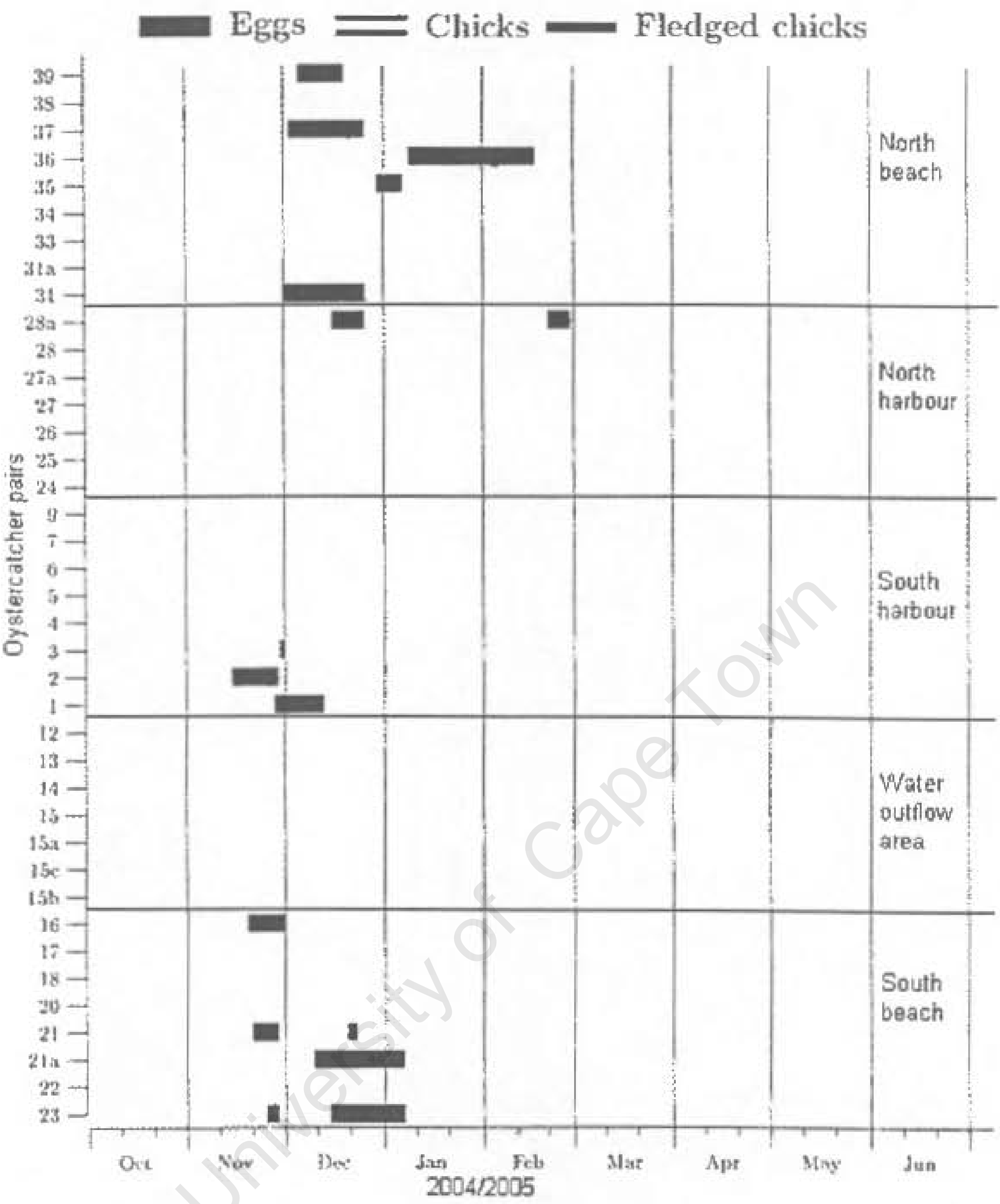


Figure 3. Graphical representation of incubation and chick-rearing of individual pairs of African Black Oystercatchers in relation to date at Koeberg Nuclear Power Station during the 2004/2005 breeding season. Time spent incubating is represented by a thick black line, time spent rearing chicks to fledging is represented by two lines and time spent chick-rearing post-fledging is represented by a thin black line.

Appendices

Appendix 1. Counts of African Black Oystercatchers on the shoreline at Koeberg Nuclear Power Station during the 2002/2003 breeding season, November 2002–April 2003.

Date	**Total number of adults**	**Number of pairs of adults**	**Number of pairs with eggs**	**Number of pairs with chicks**	**Number of pairs with fledglings**
05 Nov 2002	75	36	1	2	
13 Nov 2002	82	33	2	2	
22 Nov 2002	85	38	6	2	
29 Nov 2002	98	40	7	3	
06 Dec 2002	76	31	9	2	
18 Dec 2002	84	35	15		2
31 Dec 2002	86	39	7	2	2
07 Jan 2003	82	40	13	1	2
14 Jan 2003	85	40	18		2
21 Jan 2003	98	44	17	1	2
28 Jan 2003	82	40	14	3	
06 Feb 2003	87	39	13	4	
14 Feb 2003	78	39	13	4	
25 Feb 2003	90	43	11	5	
04 Mar 2003	71	34	8	4	2
11 Mar 2003	86	40	7	3	4
18 Mar 2003	79	35	8	2	4
25 Mar 2003	79	39	3	4	4
01 Apr 2003	66	33	2	4	4
08 Apr 2003	73	34	2	4	4
23 Apr 2003	75	28	1	1	3
30 Apr 2003	73	27			4
Mean	**81**	**37**			

Appendix 2. Counts of African Black Oystercatchers on the shoreline at Koeberg Nuclear Power Station during the 2003/2004 breeding season, November 2003–April 2004.

Date	**Total number of adults**	**Number of pairs of adults**	**Number of pairs with eggs**	**Number of pairs with chicks**	**Number of pairs with fledglings**
05 Nov 2003	88	23			
12 Nov 2003	70	26	1		
19 Nov 2003	70	28	1		
26 Nov 2003	80	28	2		
03 Dec 2003	75	25	4		
10 Dec 2003	73	30	9		
17 Dec 2003	105	33	11		
23 Dec 2003	98	36	12		
31 Dec 2003	88	34	11		
07 Jan 2003	62	25	12		
14 Jan 2004	78	29	12	2	
21 Jan 2004	87	35	8	1	
29 Jan 2004	71	28	12	1	
04 Feb 2004	72	26	11	2	
11 Feb 2004	63	25	4	3	
18 Feb 2004	73	23	5	2	
25 Feb 2004	59	23	5	2	
03 Mar 2004	69	25	1	1	1
10 Mar 2004	57	19		2	1
16 Mar 2004	82	26		2	1
24 Mar 2004	67	18		1	1
31 Mar 2004	69	24		1	1
07 Apr 2004	67	20		1	
14 Apr 2004	68	21		1	
21 Apr 2004	49	13			1
27 Apr 2004	73	23			1
Mean	**74**	**26**			

Appendix 3. Counts of African Black Oystercatchers on the shoreline at Koeberg Nuclear Power Station during the 2004/2005 breeding season, November 2004–March 2005.

Date	**Total number of adults**	**Number of pairs of adults**	**Number of pairs with eggs**	**Number of pairs with chicks**	**Number of pairs with fledglings**
9 Nov 2004	82	35			
16 Nov 2004	64	31			
24 Nov 2004	87	33	3		
1 Dec 2004	87	30	2		
8 Dec 2004	75	30	3		
15 Dec 2004	87	28	4		
22 Dec 2004	79	31	4		
27 Dec 2004	72	27	2		
31 Dec 2004	60	24	3		
12 Jan 2005	45	18	1		
19 Jan 2005	56	20	1		
26 Jan 2005	45	16	1		
1 Feb 2005	74	30	1		
9 Feb 2005	60	26	1		
16 Feb 2005	75	30	1		
23 Feb 2005	57	20	1		
2 Mar 2005	60	23			
9 Mar 2005	72	27			
Mean	**72**	**28**			

Appendix 4. Counts of African Black Oystercatchers on the shoreline at Koeberg Nuclear Power Station during the non-breeding season in 2003, May–October.

Date	**Total number of adults**	**Number of pairs of adults**	**Number of adults in "roost"**
06 May 2003	96	35	14
13 May 2003	114	21	19
23 May 2003	96	22	25
28 May 2003	92	19	35
04 June 2003	98	13	39
11 June 2003	134	23	62
18 June 2003	95	23	40
25 June 2003	137	13	63
04 July 2003	96	20	35
09 July 2003	80	25	17
18 July 2003	84	28	21
25 July 2003	112	25	26
30 July 2003	43	12	6
08 Aug 2003	57	20	4
15 Aug 2003	102	26	31
22 Aug 2003	115	17	41
29 Aug 2003	69	24	4
05 Sept 2003	108	27	34
10 Sept 2003	84	17	0
01 Oct 2003	64	18	3
08 Oct 2003	74	16	7
17 Oct 2003	76	16	6
24 Oct 2003	67	31	15
29 Oct 2003	52	12	4
Mean	**89**	**21**	**23**

Appendix 5. Individual measurements of African Black Oystercatcher chicks measured at Koeberg Nuclear Power Station in the 2002/2003 breeding season.

Chick Number	**Safring**	**Date**	**Mass (g)**	**Culmen (mm)**	**Head (mm)**	**Tarsus (mm)**	**Foot (mm)**	**Wing (mm)**	**Tail (mm)**	**Estimated age of chick (days)**	**Estimated hatching date**	**Estimated fledging date**
2-1	K23825	22 Nov 2002	388	41.0	80.6	54.9	97	140	50	21	01 Nov 2002	10 Dec 2002
3-1		27 Nov 2002	34	15.9	38.2	24.5	50			2	25 Nov 2002	-
14-1		31 Dec 2002	45	15.4	43.4	34.5	55	25	15	4	27 Dec 2002	-
14-2		31 Dec 2002	40	14.4	40.5	30.8	51	22	14	4	27 Dec 2002	-
15-1		31 Dec 2002	37	14.8	39.5	31.0	47	20	15	4	27 Dec 2002	-
1-1	K23830	21 Jan 2003	40	15.3	41.5	28.2	50	28	18	0	21 Jan 2003	26 Feb 2003
		06 Feb 2003	239	32.5	72.2	42.9	88	72		16		
31a-1	K26065	24 Jan 2003	41	16.3	38.8	29.0	57	28	13	2	22 Jan 2003	2 Mar 2003
		27 Jan 2003	66	17.4	46.7	28.0	60	28	16	5		
		31 Jan 2003	100	21.6	49.1	32.9	60	30	27	9		
		07 Feb 2003	178	24.4	62.0	38.6	76	50	20	16		
		11 Feb 2003	200	27.2	64.8	41.5	81	70	41	20		
		18 Feb 2003	311	33.3	74.2	45.0	89	108	50	27		
		28 Feb 2003	436	38.1	83.9	51.9	95	171	70	37		
31a-2	K26066	24 Jan 2003	39	16.3	41.2	28.3	56	26	12	2	22 Jan 2003	2 Mar 2003
		27 Jan 2003	81	19.6	49.6	30.6	61	30	18	5		
		31 Jan 2003	123	22.4	52.9	32.0	67	36	28	9		
		07 Feb 2003	220	28.1	63.9	41.8	82	70	30	16		
		11 Feb 2003	252	29.7	71.3	44.9	85	92	45	20		
		18 Feb 2003	360	35.4	78.7	46.6	92	140	60	27		
		28 Feb 2003	460	44.8	88.8	52.1	95	195	82	37		
28a-1		31 Jan 2003	38	14.5	38.8	25.7	52	26	20	2	29 Jan 2002	-
28a-2	K26060	31 Jan 2003	40	17.2	42.7	25.5	54	25	25	2	29 Jan 2003	8 Mar 2003

		11 Feb 2003	175	29.8	66.8	40.6	80	58	30	13		
		21 Feb 2003	364	38.4	81.1	49.0	95	112	55	23		
		28 Feb 2003	418	47.9	90.5	54.3	100	160	54	30		
39-1	K26067	31 Jan 2003	35	16.3	42.4	27.6	55	26	15	3	28 Jan 2003	8 Mar 2003
		07 Feb 2003	123	23.9	54.4	34.5	70	40	17	10		
		11 Feb 2003	182	26.2	63.2	41.7	81	67	30	14		
		18 Feb 2003	283	34.9	72.0	47.1	90	105	50	21		
		04 Mar 2003	424	42.5	86.6	53.2	101	195	76	35		
17-1	K26055	28 Feb 2003	122	24.8	59.9	37.7	71	40		13	15 Feb 2003	11 Mar 2003
		11 Mar 2003	238	32.7	73.7	46.1	85	97	50	24		
		18 Mar 2003	318	35.9	77.9	48.8	91	144	50	31		
		25 Mar 2003	310	39.1	84.2	49.1	95	180	68	38		
3-2		28 Feb 2003	42	14.5	42.6	26.4	51	25		2	26 Feb 2003	26 Apr 2003
3-3	K26056	28 Feb 2003	50	16.1	44.6	26.8	54	25		2	26 Feb 2003	26 Apr 2003
		11 Mar 2003	214	27.2	66.2	46.1	84	70	30	13		
		18 Mar 2003	289	33.2	75.6	48.9	90	110	50	20		
		28 Mar 2003	400	37.5	85.8	51.8	97	172	65	30		
		08 Apr 2003	480	46.0	92.5	55.5	101	225	94	41		
15b-1		11 Mar 2003	39	16.4	40.4	26.9	52	25		1	10 Mar 2003	-
26-1		25 Mar 2003	35	13.4	42.6	26.3	53	28		3	22 Mar 2003	-
26-2		25 Mar 2003	42	17.2	46.5	26.8	55	26		3	22 Mar 2003	-
		28 Mar 2003	64	18.7	50.4	29.4	55	24		6		
20-1		25 Mar 2003	40	16.5	44.5	25.9	51	24		3	22 Mar 2003	-
		01 Apr 2003	89	21.6	55.9	34.2	60	30		10		
		08 Apr 2003	149	27.3	62.1	37.6	69	42	20	17		
20-2		25 Mar 2003	31	16.1	42	27.9	50	25		3	22 Mar 2003	-
2-2		28 Mar 2003	41	14.1	40.4	27.6	51	23		1	27 Mar 2003	-
		08 Apr 2003	166	27.0	62.1	41.7	78	50	18	12		
2-3		08 Apr 2003	123	20.9	57.3	38.6	71	40	15	10	29 Mar 2003	-

Appendix 6. Individual measurements of African Black Oystercatcher chicks measured at Koeberg Nuclear Power Station in the 2003/2004 breeding season.

Chick Number	Safring	Date	Mass (g)	Culmen (mm)	Head (mm)	Tarsus (mm)	Foot (mm)	Wing (mm)	Tail (mm)	Estimated age of chick (days)	Estimated hatching date	Estimated fledging date
2-1	K24991	09 Jan 2004	32	15.2	40.4	25.2	50	20		1	8 Jan 2004	29 Feb 2004
		14 Jan 2004	50.2	18.1	44.4	27.8	53	25		6		
		21 Jan 2004	144	25.1	59.1	38.1	73	37		13		
		29 Jan 2004	250	31.8	72.4	46.5	86	75	35	21		
		04 Feb 2004	332	37.0	78.4	49.2	94	115	50	27		
		11 Feb 2004	372	42.3	83.7	51.4	98	155	60	34		
9-1		14 Jan 2004	30.6	13.5	39.6	24.8	50	20		2	12 Jan 2004	-
33-1	K24992	04 Feb 2004	34.6	16.8	41.5	25.8	53	25		2	2 Feb 2004	-
		11 Feb 2004	68	22.0	52.6	29.1	60	30		9		
		18 Feb 2004	122	26.7	60.6	34.3	70	45		16		
		25 Feb 2004	196	30.3	68.8	38.6	76	65		23		
		10 Mar 2004	352	41.1	80.7	46.2	91	150	65	37		
34-1		11 Feb 2004	76	20.6	52.3	31.5	62	30		5	6 Feb 2004	-
39-1	K24993	10 Mar 2004	70	22.0	48.3	31.0	60	28		3	7 Mar 2004	18 Apr 2004
		16 Mar 2004	135	23.9	58.2	36.1	71	40		9		
		24 Mar 2004	236	30.0	68.1	42.5	82	85	40	17		
		31 Mar 2004	292	33.5	74.5	45.4	87	120	55	24		
		07 Apr 2004	363	38.2	78.3	48.9	93	162	65	31		

Appendix 7. Individual measurements of adult African Black Oystercatchers ringed at Koeberg Nuclear Power Station in the 2002/2003 breeding season (adults were caught in a trap-door trap during incubation). Measurements are ordered in increasing culmen length. In two pairs, both adults were banded (* and °) and male and female identified based on measurements.

Safring	**Mass (g)**	**Culmen (mm)**	**Bill width (mm)**	**Bill depth (mm)**	**Head (mm)**	**Tarsus (mm)**	**Foot (mm)**	**Wing (mm)**	**Tail (mm)**	**Habitat type**	**Gender**
K23829	621	62.2			114.9	53.4	102	264	106	Sandy	
K26069	645	63.1	17.7	16.4	113.8	52.3	110	265	106	Rocky	
K26062*	670	63.2	16.1	17.3	117.8	53.6	118	284	108	Rocky	Male
K26070	670	65.2	17.4	16.8	118.5	58.3	108	272	113	Sandy	
K23826°	673	67.5			122.1	55.1	108	276	107	Sandy	Male
K23824	634	67.6			119.7	55.0	110	259	110	Sandy	
K23823	652	69.9			122.7	50.7	102	270	108	Rocky	
K26068	730	70.3	15.9	16.8	122.9	56.0	110	265	110	Sandy	
K23827	765	70.6			125.2	53.2	113	285	112	Rocky	
K23828	690	70.8			125.4	55.0	109	270	104	Rocky	
K26064	724	72.4	13.9	14.4	125.4	57.0	112	279	112	Sandy	
K26059	705	72.5	16.6	16.1	125.4	56.5	109	274	112	Sandy	
K26058	773	74.0	17.4	17.7	127.9	60.1	110	278	120	Sandy	
K26057°	778	75.6	17.4	17.7	128.8	68.4	112	285	115	Sandy	Female
K26061*	775	75.9	16.3	16.2	127.7	58.2	112	273	113	Rocky	Female
K26063	785	79.3	16.8	17.6	131	55.3	110	286	112	Sandy	

Chapter 3

Between-site variability of breeding productivity of the African Black Oystercatcher *Haematopus moquini*

Introduction

In understanding the population dynamics of a species, it is important to understand the extent of the variability in breeding success between sites. For example, to run models of the long-term dynamics of a population, such as VORTEX (Lacy 1993), requires extensive quantitative information for a suite of input parameters related to breeding. The broader and more detailed this knowledge, the more realistically potential conservation interventions can be evaluated. For example: the effects of reducing predation or limiting human disturbance can only be considered if there is insight into the extent to which these factors cause reductions in breeding success.

The African Black Oystercatcher is distributed along the coast of South Africa and Namibia (Summers & Cooper 1977, Hockey 1983a, Martin 1997, du Toit *et al* 2003, Hockey *et al.* 2005) and is classified as "near-threatened" in South Africa and globally (Underhill 2000, BirdLife International 2004). Oystercatchers breed on rocky and sandy shores and on offshore islands in the austral summer (Summers & Cooper 1977, Hockey 1983a, b, Underhill 2000, du Toit *et al* 2003, Hockey *et al.* 2005). Adults are territorial and stay on their breeding territories throughout the year (Summers & Cooper 1977, Hockey 1983a, 1984b, du Toit *et al* 2003, Hockey *et al.* 2005). They are long-lived, mate-faithful with a naturally low reproductive rate (less than one fledgling per pair per year) (Summers & Cooper 1977, Hockey 1983b, 1996a, Hockey *et al.* 2005). Eggs and chicks are lost to natural causes such as storms (causing flooding of sites or causing nests to be covered by sand) and predation by birds, mammals and reptiles as well as being vulnerable to human disturbance (Summers & Cooper 1977, Hockey 1983a, b, Jeffery 1987, Ward 1990, Watson and Kerley 1995, Martin 1997, Adams *et al* 1999, Pond 1999, Leseberg *et al* 2000, Underhill 2000, du Toit *et al.* 2003, Calf 2004, Williams *et al.* 2004, Calf & Underhill 2005b, Hockey *et al.* 2005, Jeffery & Scott 2005).

This paper compares breeding productivity of the African Black Oystercatcher at 18 different sites. The sites differ with respect to access by land-based mammals (island versus mainland sites) and by their management status (protected versus unprotected sites). An attempt is made to assess the variability in breeding success of the oystercatcher at these different sites, using data collected or previously published, in order to establish factors that have a real impact on breeding levels. A generalised linear model is used to statistically evaluate the data.

Breeding sites used in study

Breeding sites for which the published information contained at least some comparable breeding productivity data were selected for this study. The breeding sites are arranged in order from west to east around the South African coast (Figure 1). The references used for the breeding data for each study area as well as references used for a description of the site are listed after the site name. Table 1 summarizes the different sites in terms of area status, shore type and levels of human disturbance and predation.

St. Helena Bay (Hockey 2001)
St. Helena Bay (32°46' S 18°05'W) is an unprotected mainland site. A description of the site as well as levels of human disturbance and possible predators are not mentioned in Hockey (2001). The number of breeding pairs and time-span of the study were also not mentioned.

Marcus Island (Hockey 1983b, Barnes 1998)
Marcus Island (33°03'S, 17°58'E) is an 17 ha island with a 1.9 km rocky shoreline and is connected to the mainland at Saldanha by a causeway, constructed in 1976. The West Coast National Park and the associated Saldanha Bay islands, including Marcus Island, are recognised together as an Important Bird Area. Because of the causeway, it is effectively a protected mainland site; there is some human disturbance caused by researchers. The Kelp Gull *Larus dominicanus* is the only predator that occurs naturally; other predators that have been recorded as a result of the link to the mainland include Cape Grey Mongoose *Herpestes pulverulentus*, Yellow Mongoose *Cynictis penicillata,* Water Mongoose *Atilax paludinosus*, Small Spotted Genet *Genetta genetta,* Cape Fox *Vulpes chama*, feral cats *Felis catus* and rats *Rattus* spp. High tide events have caused loss of nests and chicks.
There were 55 breeding pairs studied over one season (1979/1980).

Dassen Island (Barnes 1998, Hockey 2001)

Dassen Island (33°25'S 18°05'E) is a 273 ha island 9 km offshore with c. 10 km of mostly rocky shoreline with various degrees of exposure, dependent on the extent of the offshore reefs. Dassen Island is a Provincial Nature Reserve (protected island site) with little human disturbance. It is recognised as an Important Bird Area and holds up to 4.6% of the global population of the African Black Oystercatcher. The only avian predator is the Kelp Gull and there are no terrestrial predators, feral cats having been eliminated during the 1990s (AC Wolfaardt pers. comm.).

The study took place over two years; there is no mention in the reference of number of breeding pairs studied.

Koeberg Nuclear Power Station (Chapter 2)

Koeberg Nuclear Power Station (33 40'S, 18 25'E) lies 30 km north of Cape Town and is surrounded by a 3 000 ha nature reserve including the coastline. It is a protected mainland site with little human disturbance. The study area consists of a fenced-off harbour with northern and southern breakwaters (c. 1 km) that are protected by concrete dolosse on the seaside and built up with rocks of assorted sizes to form a gently sloping intertidal area on the inside of the harbour. The study area included two sections of sandy shore north (c. 2 km) and south (c. 0.5 km) of the power station. The south beach is more sheltered than the north beach; and has finer sand and a wider intertidal area than the north beach. The south beach also allows access to people and dogs. Predators occurring at the site include Yellow Mongoose, Kelp Gull and Sacred Ibis *Threskiornis aethiopicus* (footprints observed at depredated nests), Pied Crow *Corvus albus* (observed depredating a nest), various snakes, domestic dogs and feral cats (observed inside harbour area in the 2004/2005 breeding season). This area is exposed to strong onshore winds and high tide events have caused nest loss.

There were 13–37 breeding pairs studied over three years (2002/2003–2004/2005).

Robben Island (Barnes 1998, Crawford & Dyer 2000, Underhill *et al.* 2001, Calf & Underhill 2002, 2003, 2005a, b, Calf *et al.* 2003, Calf 2004, J. Braby *in litt.*)

Robben Island (33°49'S, 18°22'E) lies in Table Bay, 7 km offshore and 11 km from the port of Cape Town and has an area of 507 ha. The c. 10 km shoreline is mostly rocky with

various degrees of exposure, dependent on the extent of the offshore reefs. Robben Island is a World Heritage Site and tourist attraction (protected island site). It is classified as an Important Bird Area and is estimated to hold over 1% of the world population of the African Black Oystercatcher. There is extensive human disturbance in limited areas and possible predators include Kelp Gull, Sacred Ibis, Mole snake *Pseudaspis cana*, domestic dogs, feral cats and rats. High tide events have caused nest and chick loss.
There were 57–63 pairs studied over four years (2001/2002 and 2004/2005).

Noordhoek beach (Pond 1999)
Noordhoek beach (34°08'S, 18°21'E) is a 2.4 km section of mixed sandy-rocky shoreline along the Atlantic Ocean. It is an unprotected mainland site with extensive human disturbance (holiday-makers) and horse-riding. Predators include Kelp Gull, domestic dogs and feral cats. This area is exposed to strong winds and high tide events.
Ten breeding pairs were studied over one breeding season (1998/1999).

Cape Point (Pond 1999)
The Cape Point (34°13'S, 18°22'E) site is a 7 km section of mixed sandy-rocky shore in the Cape Peninsula National Park (protected mainland site) along the Atlantic Ocean. There is little human disturbance and possible predators include Chacma Baboon *Papio ursinus*, Cape Clawless Otter *Aonyx capensis*, Caracal *Felis caracal*, Kelp Gull, foxes, genets, mongooses and snakes. The area is exposed to strong winds and high tide events.
There were 12 breeding pairs studied over one season (1998/1999).

Betty's Bay (Hockey 2001)
Betty's Bay (34°21'S 18°18'E) is an unprotected mainland site and consists of a wide sandy beach backed by dunes. There is a high level of human disturbance from residents and holiday-makers. Possible predators include Kelp Gull, White-necked Raven *Corvus albicollis,* Cape Grey Mongoose, Water Mongoose, Caracal and domestic dogs.
There is no mention in the reference of number of breeding pairs or time-span of the study.

Dyer Island (Barnes 1998, Venter *et al.* 2002, Wortel *et al.* 2003, L. Waller *in litt.*)

Dyer Island (34°41'S, 19°25'E) lies in the Atlantic Ocean 4 km offshore from Gansbaai, has an area of 20 ha. and the entire c. 4 km of shoreline is rocky. The island is the raised portion of a shallow rocky bank; the inshore waters are characterized by reefs and dense forests of kelp that reduce the magnitude of wave action on the shoreline. Dyer Island is a Provincial Nature Reserve (protected island site) with little human disturbance. Dyer Island is classified as an Important Bird Area and is estimated to hold over 1% of the world population of African Black Oystercatcher. The only avian predator is the Kelp Gull and there are no terrestrial predators.

There were 21–22 breeding pairs studied over two years (2002/2003 and 2004/2005).

Cape Agulhas (Jeffrey 1987, Jeffery & Scott 2005)

The Cape Agulhas (34°49'S 20°02'E) site is a 12 km section of coast north-west of Cape Agulhas, with sandy beach and low rocky areas along-side low cliffs and extensive sand dunes. It is an unprotected mainland site. Because the area is remote, there is limited human disturbance. Possible predators include Kelp Gull, Egg-eater Snake *Dasypeltis scabra,* genets and mongooses. Up to the end of the study period, there was considerable traffic along the coast by off-road vehicles causing damage to the dunes and disturbance to the birds. High tide events caused loss of nests.

There were an average of 16 breeding pairs (8–22) studied over 24 years (1978/1979–2001/2002).

De Hoop Nature Reserve (Barnes 1998, Hockey 2001)

De Hoop Nature Reserve (34°29'S, 20°30'E) is situated to the east of Cape Agulhas and comprises 40 000 ha of mountain range, coastal lake and rugged coastline. It is a protected mainland site with little human disturbance and is classified as an Important Bird Area. The coastline is a mixed shore with wave cut platforms and backed by sandstone cliffs.

There is no mention in the reference of number of breeding pairs or time-span of the study.

Dana Bay (Swanepoel 2003)

Dana Bay (34°13'S 22°01'E) is a c. 6 km stretch of wide sandy beach backed by dunes with low rocky reefs exposed at low tide. It is an unprotected mainland site with high levels of human disturbance (residents, holiday-makers and fishermen). Possible predators include Kelp Gull, genets and domestic dogs. Weather causes egg and chick loss when strong winds blow sand over nests.

There were 17 breeding pairs studied over one breeding season (2002/2003).

Goukamma Nature Reserve (Barnes 1998, Leseberg *et al* 2000, Hockey 2001)

Goukamma Nature Reserve (34°04'S, 22°50'E) has an area of 2 230 ha. made up of river estuary, a freshwater lake and 11 km of coastline. It is a protected mainland site with little human disturbance. It falls within the Wilderness-Sedgefield Lakes complex which is recognised as an Important Bird Area. The coastline is a mixed shore with wave cut platforms and backed by extensive sand dunes.

There is no mention of number of breeding pairs studied; a time-span of 10 years is mentioned in the reference.

Sedgefield (Elwell 2005)

The Sedgefield site (33°55'S 22°55'E) is 7 km of shoreline east of Sedgefield and consists of 2 km of wide sandy beach backed by dunes and 5 km of narrow beach backed by sandstone cliff with a wide tidal rock shelf. It is an unprotected mainland site. There is a high level of human disturbance by holiday-makers, fishermen and bait-collectors. Possible predators include Kelp Gull, genets and domestic dogs. The sand cliff collapses after heavy rains and covers the rock shelf, possibly limiting the oystercatcher food supply.

An average of nine (7–11) breeding pairs were studied over nine years (1996/1997–2004/2005).

Brenton-on-Sea (Hockey 2001, Elwell 2005)

Brenton-on-Sea (34°04'S 23°01'E) is a holiday centre 17 km south of Knysna and an unprotected mainland site. The site consists of 4 km of wide beach backed by dunes west of Brenton-on-Sea and 4 km of rocky shore backed by cliff to the east. There is a high level of human disturbance by holiday-makers and fishermen and possible predators include mongooses, genets and domestic dogs.

There is no mention in Hockey (2001) of number of breeding pairs or time-span of the study.

Knysna Lagoon (Elwell 2005)

The Knysna Lagoon site (34°03'S 23°02'E) consists of a 17 km long tidal lagoon that is effectively an unprotected mainland site. Low tide exposes large areas of salt marsh and mud flat. There is human disturbance in the form of fishermen, bait collectors and holiday-makers. Possible predators include Kelp Gull, domestic dogs, feral cats and rats. Run-off from storm water drains pollute the lagoon in floods.

An average of 12 (9–16) breeding pairs were studied over seven years (1998/1999–2004/2005).

Sundays River (Ward 1990)

The Sundays River site (33°48'S, 25°46'E) consists of 40 km of exposed sandy beach east of the Sundays River mouth, Algoa Bay, along the Indian Ocean. It is an unprotected mainland site although the level of human disturbance is not mentioned (moderate disturbance from off-road vehicles was likely) and predators include Black-backed Jackal *Canis mesomelas* and Kelp Gull.

This study took place over one breeding season (1987/1988) but there is no mention of the number of breeding pairs in the reference.

East London (Hockey 2001, Vernon 2004)

East London (33°00'S, 27°55'E) is an unprotected mainland site. A description of the site, levels of human disturbance and possible predators are not mentioned in the reference. This site is near the eastern limit of the breeding range of the species

There is no mention in the reference of number of breeding pairs or time-span of the study.

Methods

Koeberg Nuclear Power Station

Counts were conducted at the Koeberg site on a weekly basis from November 2002 until May 2004 and from November 2004 until March 2005 with numbers of pairs, nests, chicks and fledglings recorded. Pairs were defined as birds that roosted and fed close to each other but were not necessarily breeding at that time. Pairs were strictly territorial and were identified due to their position on the coast (using distinctive landmarks).

From November 2002 until May 2003, October 2003 until May 2004 and from November 2004 until March 2005, nests were searched for regularly. Once found they were monitored until hatching at three- to seven-day intervals. On the first visit to the nest, eggs were measured to 0.1 mm accuracy and weighed, to the nearest 0.1 g, with an electronic balance. On subsequent visits, nest contents were checked and eggs were re-weighed. Once the eggs hatched, the chicks were searched for at similar intervals. Whenever found, the chicks were weighed and measured (culmen, total head, tarsus, foot, wing and tail) until fledging, taken as the point at which chicks can fly well, at an age of about 35-40 days, when the chicks reach c. 65% of adult body mass (Hockey 1984a). Gompertz growth rates were estimated using the method of Underhill (submitted) for each bird for which two or more mass measurements were available. Oystercatcher fledglings remain with their parents for an extended period, and we attempted to measure this as accurately as possible. From the egg masses and measurements, the date of start of incubation was estimated using a method based on the daily mass loss of eggs through incubation (Underhill & Calf 2005). The key dates for each nest (start of incubation (including laying date), hatching date, fledging date, final departure date and, where appropriate, date of loss of eggs or chicks) were represented graphically.

Dyer Island 2002/2003 (Wortel *et al.* 2003)

Weekly counts were undertaken throughout this period except for some interruptions during an Avian Cholera *Pasteurella multocida* outbreak (October 2002) and from security arrangements to control poaching activities (March to April 2003). From November 2002 to May 2003, nests were searched for regularly and monitored as detailed above except for the use of a Pesola 100 g spring balance instead of an electronic balance.

Robben Island and Dyer Island 2004/2005 (J. Braby *in litt.*, L. Waller *in litt.*)

Unpublished data for these two sites was obtained: details included weekly bird counts, nest monitoring, egg measurements and mass, chick measurements and mass and chick outcome. This data was evaluated in the same way as described above except it was not possible to determine the key dates for each nest (start of incubation, hatching date, fledging date, final departure date and date of loss of eggs or chicks).

Other breeding sites

Data for the other 15 breeding sites were obtained from published papers or reports. The amount of information for each site varied and some values were calculated to use as a comparison in this study. Where available the egg measurements were used to calculate the fresh mass using the method described by Underhill & Calf (2005). If there was no information on the number of breeding pairs at a breeding site, values from Barnes (1998) (Important Bird Areas including Dassen Island, De Hoop Nature Reserve, Goukamma Nature Reserve), values calculated from density values (Sundays River (Ward 1990), East London (Vernon 2004)) and values estimated from a knowledge of the area (St. Helena Bay, Betty's Bay, Brenton-on-Sea) were used in the statistical analysis.

Statistical Methods

The data for each breeding sites were analysed using a multiple regression models with factor variables. Breeding productivity results (eggs per pair, hatchlings per pair, hatching success, fledglings per pair and fledging success were modelled using area status, shore type, position along the coast, level of human disturbance and level of predation as explanatory variables (as summarised in Table 1). Date of start of egg-laying and egg mass could not be used as explanatory variables because these data were available for only a small subset of sites. The square root of the number of breeding pairs at a particular site were used as weights in the regression models. The models were fitted using GenStat 8 (GenStat Committee 2005).

Factor variables were entered successively into the model. For a variable to be accepted into the model, it needed both to be statistically significant using the conventional model selection approaches, and it needed to reduce the value of the Akaike Information Criterion (AIC). Several of the factor variables were changed from three to two levels because these generated better fitting models; area status was evaluated as mainland (protected and unprotected) or island, shoretype was evaluated as sandy or mixed and rocky, human disturbance was evaluated as high (high and medium) or low and predation was evaluated as high or low (medium or low). Position along the coast was evaluated as the west coast (Benguela current) as far as Cape Point, between Cape Point and Cape Agulhas and the east coast (Agulhas current) from Cape Agulhas eastward. Interactions between explanatory variables were also considered. We express the fit of the model using the concept "percentage of variance explained", as calculated by Genstat 8 (Genstat Committee 2005). We tabulate the detailed results for the best fitting models.

Results

Egg production

At Koeberg in the 2002/2003 season, 95% of all eggs were laid in a 162-day interval between 2 October and 12 March, in the 2003/2004 and 2004/2005 breeding seasons the same percentage of eggs were laid in a 81-day interval from 23 November until 12 February and in a 97-day interval from 17 November to 22 February respectively (Table 2, Figures 1, 2 and 3 in Chapter 2). At Dyer Island in the 2002/2003 breeding season, 95% of all eggs were laid in 80 days between 10 November and 29 January (Table 2, Figure 2). At the Koeberg site, the median date for all clutches laid was 9 January, 4 January and 6 December for the 2002/2003, 2003/2004 and 2004/2005 breeding seasons respectively (Table 2, Chapter 2). On Dyer Island 2002/2003 the median date for all clutches laid was 22 December (Table 2).

Egg-laying started in November at most breeding sites studied, but was early (October) at Koeberg in 2002/2003, Noordhoek in 1998/1999 and occasionally at Cape Agulhas (1978/1979–2001/2002) (Table 3). At Cape Agulhas, 23% of all nests were laid in October–November (Jeffery & Scott 2005). Egg-laying started later; in December at Marcus Island in 1979/1980 and in January at Sundays River in 1987/1988 (Table 3). The peak egg-laying period at most breeding sites studied was between mid-December and mid-January (Table 3). The Koeberg 2004/2005 and Dyer Island 2002/2003 seasons were early (peaking a month earlier), while the Robben Island 2001/2002 and 2002/2003 seasons peaked in the middle of January and the Koeberg 2002/2003 peak egg-laying period extended until February (Table 3).

Mean clutch size varied from 1.58 eggs (Cape Point 1998/1999) to 2.01 eggs (Robben Island 2001/2002) and the mean value from the 13 single-season studies was 1.77 (Table 3). The mean value for the 24-year study (1978/1979–2001/2002) at Cape Agulhas was 1.68 (Jeffery & Scott 2005). Three-egg clutches were recorded at four sites: Koeberg, Robben Island, Cape Point and Cape Agulhas (Table 3). At Robben Island in 2001/2002, 8% of all clutches had three eggs, 85% had two eggs and 7% had one egg with a mean clutch size of 2.01 eggs, while at Cape Point in 1998/1999 although 7% of all clutches had three eggs, 45% had two eggs and 48% had one egg with a mean clutch size 1.58 eggs (Table 3).

Two sites had more than 50% of the pairs laying replacement clutches (Koeberg 2002/2003 and Cape Point 1998/1999) as well as more than one pair each that laid four clutches (Table 3). Four clutches per breeding pair were also recorded in five years at Cape Agulhas (1978/1979–2001/2002) (Table 3). Three clutches per breeding pair were seen at Marcus Island 1979/1980, Koeberg 2003/2004, Robben Island 2002/2003, 2003/2004 and Noordhoek 1998/1999 (Table 3).

In Table 4, the mean estimated fresh mass ranged from 53.1 g at Cape Agulhas (1978/1979–2001/2002) to 58.7 g at Robben Island 2004/2005 and the mean value from the eight single-season studies was 55.9 g. The mean egg length ranged from 59.6 mm at Koeberg 2003/2004 to 61.6 mm at Robben Island 2004/2005 and the mean value from the eight single-season studies was 60.6 mm (Table 4). The mean egg breadth ranged from 40.6 mm at Cape Agulhas (1978/1979–2001/2002) to 42.3 mm at Robben Island 2004/2005 and the mean value from the eight single-season studies was 41.6 mm (Table 4). These measurements are for all eggs measured at a site, because no significant difference was recorded between first-laid clutches and replacement clutches (Hockey 1983b, Chapter 2). The estimated mean fresh masses of eggs at Koeberg and Dyer Island in the 2002/2003 breeding season were 55.5 g and 54.6 g, respectively; this difference was not statistically significant (t_{157}=1.27, P=0.21, ns). However, eggs at Dyer Island in the 2002/2003 breeding season were 2.7% longer than those at Koeberg (t_{157}=3.53, P<0.001), but 2.0 % narrower (t_{157}=–4.32, P<0.001).

There were six areas where the average female oystercatcher produced more than 15% (the median value) of the average female mass in eggs: Marcus Island 1979/1980, Koeberg 2002/2003, 2003/2004, Noordhoek 1998/1999, Cape Point 1998/1999 and Cape Agulhas 1978/1979–2001/2002 (Table 5). These areas all had more than 25% of pairs that laid replacement clutches (Table 3).

At Koeberg in 2002/2003, 2003/2004 and 2004/2005 egg losses were attributed to predation in 59%, 78% and 88% of the total numbers of eggs lost (Chapter 2). The main culprits were deemed to be the Yellow Mongoose, Kelp Gull, Sacred Ibis and feral cats (Chapter 2). On Marcus Island in 1979/1980, 76% of total egg loss was attributed to predation, especially the Kelp Gull (opportunistically predating eggs when birds were disturbed by human presence) and the Cape Fox (Hockey 1983b). On Robben Island in 2004/2005, 95% of total egg loss was attributed to predation by feral cats (J. Braby, LGU pers. comm.). Other areas that experienced a high level of egg loss from predators were: Cape Point 1998/1999 (Chacma Baboon, mongooses and others) (Pond 1999), Cape Agulhas 1978/1979–2001/2002 (Kelp Gull, genets and mongooses) (Jeffery & Scott 2005), Dana Bay 2002/2003 (Kelp Gull, genets) (Swanepoel 2003) and Sundays River 1987/1988 (Black-backed Jackal, Kelp Gull) (Ward 1990). Table 1 estimates relative levels of predation at the different sites in the study.

Chick-rearing and post-fledging care

At Koeberg in 2002/2003 and 2003/2004, the median of the 13 estimated growth rates was 0.0538, with values ranging from 0.0374 for the slowest growing chick to 0.0637 for the fastest (Table 6). At Dyer Island in 2002/2003, the median growth rate was 0.0471, with values ranging from 0.0106 to 0.0602 (Table 6). The value of 0.0106 was based on a chick which grew from 215 g to 269 g over 20 days (Table 6), a particularly slow growth rate. Even if this chick is removed as an outlier, the median of the remaining nine values is also 0.0471. A Mann-Whitney test was used to test whether growth rates at the two study sites differed (U=52, P=0.22, one-sided test with n_1=13, n_2=10). The difference is not formally significant, however, the two sample sizes are small, and the power of the test is low.

The median time that a fledgling chick remained with its parents before departing the area was 50 days at Koeberg based on 12 oystercatcher fledglings during the 2002/2003 and 2003/2004 breeding seasons (Chapter 2). At Dyer Island in 2002/2003, the median post-fledging time was 77 days, calculated from 17 chicks (Table 7). This difference is statistically significant (Mann-Whitney test, U=33, P<0.001).

Chick loss was often attributed to human disturbance. Sites where human disturbance was considered an important factor were St. Helena Bay, Betty's Bay, Brenton-on-Sea and East London (Hockey 2001) as well as Sedgefield (Elwell 2005), Knysna (Elwell 2005) and Noordhoek (Pond 1999). These areas had fledging successes (and therefore chick loss) ranging from 15% to 64%.

There were several reports of oystercatchers being tolerant of people and human disturbance (Pond 1999, Jeffery & Scott 2005). At Noordhoek Beach in 1998/1999, Pond (1999) reported that one pair consistently continued to incubate eggs while people and dogs passed within 4 m of the nest; Jeffery & Scott (2005) reported a pair that did not move from the nest when vehicles drove within 2 m of the nest. At Koeberg in 2002/2003, one pair successfully raised one chick to fledging even though the 2-egg nest was within 2 m of an informal braai (barbecue) area (NJP pers. obs.).

Breeding productivity

Breeding outcome for African Black Oystercatchers at 11 breeding sites is summarised in Table 8 and breeding productivity at 18 breeding sites is summarised in Table 9.

Number of eggs produced per breeding pair per season ranged from 1.9 (Robben and Dyer Islands 2004/2005) to 4.1 (Cape Point 1998/1999) (Table 9) and is a function of clutch loss. Based on 23 values, the overall mean was 2.57 eggs per breeding pair per season; the median was 2.5. Number of hatchlings measured per breeding pair per season ranged from 0 (Koeberg 2004/2005) and 0.08 (Cape Point 1998/1999) to 1.40 (mean at Dassen Island for *n*=2 breeding seasons) and 1.53 (mean at Brenton-on-Sea, no value given for number of seasons studied) (Table 9). The overall mean was 0.79 hatchlings per breeding pair per season and the median was 0.72 (*n*=22). Breeding productivity, measured as fledglings per breeding pair, ranged from 0 (Koeberg 2004/2005) and 0.06 (Koeberg 2003/2004) to 0.82 (mean at Dassen Island for *n*=2 breeding seasons), 0.86 (Dyer Island 2002/2003) and 0.94 (Robben Island 2001/2002) (Table 9). The mean was 0.37 fledglings per breeding pair per season and the median was 0.31 (*n*=23). Number of fledglings produced per egg ranged from 0 (Koeberg 2004/2005) and 0.02 (Koeberg 2003/2004 and Cape Point 1998/1999) to 0.42 (Dyer Island 2002/2003) (Table 9). The mean was 0.15 fledglings per egg and the median was 0.12 (*n*=24).

Hatching success, measured as the percentage of eggs which hatched, ranged from 0% (Koeberg 2004/2005) and 2% (Cape Point 1998/1999) to 60% (Dyer Island 2004/2005), 61% (mean at Dassen Island for *n*=2 breeding seasons) and 63% (Dyer Island 2002/2003) (Table 9) There was a mean hatching success of 32% and a median hatching success of 30% based on 23 values. Fledging success, measured as the percentage of chicks that survived from hatching to fledging, ranged from 15% (mean at St. Helena Bay, no value given for number of seasons studied) and 16% (mean at Brenton-on-Sea, no value given for number of seasons studied) to 81% (mean at De Hoop Nature Reserve, no value given for number of seasons studied) and 100% (Cape Point 1998/1999) (Table 9). There was a mean fledging success of 48% and a median fledging success of 45% based on 22 values.

Hatching success was lower than fledgling success for 17 of the 22 entries for which these data were available in Table 9. The sign test, used as a conservative approach to testing the null hypothesis that fledging and hatching success are equal, points to this difference being significant (*P*=0.005).

Investment to breeding and breeding intensity

In this section, a detailed comparison is made between the oystercatchers breeding at Koeberg Nuclear Power Station, one of the low breeding productivity sites, and Dyer Island, a high productivity site during the 2002/2003 breeding season (Table 9). An overview of breeding events can be seen in Figure 1 in Chapter 2 (Koeberg) and Figure 2 (Dyer Island).

Periods of 32 days for incubation (Hockey 1983b) and 40 days for chick-rearing until fledging (Hockey 1984a) are taken as average values. The time from fledging until leaving was determined to be 50 days for the chicks at Koeberg (Chapters 1 and 2) and 77 days for the chicks at Dyer Island (Table 7). The total reproductive period, used as a mean in this paper, was therefore 122 days at Koeberg and 149 days at Dyer Island. In a standard reproductive period at Koeberg, 26% of the time should be spent on incubation, 33% on chick-rearing and 41% on post-fledging care (a ratio of 26:33:41) (Chapter 1). At Dyer Island this ratio is 21:27:52.

The incubation time per breeding pair at Koeberg was almost 40% more than normal, compared to Dyer Island where it was close to normal (Table 10). At Koeberg, incubation took up 64% of the total breeding time, compared to of 24% at Dyer Island (Table 10). At Koeberg, 70% of pairs laid repeat clutches, compared to 10% at Dyer Island (Table 3), and four of the pairs that re-laid three or more times, spent more than 60 days (113 days, 67 days, 70 days and 83 days) incubating eggs but without producing any chicks (Chapter 2).

There was a 19% hatching success at Koeberg, compared to 63% at Dyer Island (Table 9). At Dyer Island, the time spent on chick rearing (pre-fledging) per breeding pair was more than twice the time spent by Koeberg birds (Table 10). At Koeberg, time spent on chick rearing as a percentage of the total breeding investment was 17%, compared to the mean of 33%, and at Dyer Island this value was 24%, compared to the mean of 27% (Table 10).

There was a fledging success of 42% at Koeberg, compared to 67% at Dyer Island (Table 9). At Dyer Island, the time spent on rearing fledglings until they leave the parents (post-fledging) per breeding pair was five times the time spent by Koeberg birds (Table 10). The value for fledglings per breeding pair per year is significantly different; 0.27 at Koeberg and 0.86 at Dyer Island (Table 9). The Dyer Island chicks stayed significantly longer with their parents before leaving the site. At Koeberg, time spent on post-fledging as a percentage of the total breeding investment was 19% compared to the mean of 41%, and at Dyer Island this value was 52% compared to the mean of 51% (Table 10).

The total breeding investment per breeding pair at Koeberg was half the time spent at Dyer Island (Table 10). At Koeberg there were 10 fledglings with 255 days invested in reproduction per juvenile produced (Table 10). Each fledgling was produced in 209% of the mean reproductive period for the site (Table 10). At Dyer Island there were 18 fledglings with 149 days invested in reproduction per juvenile produced (Table 10). Each fledgling was produced in 100% of the mean reproductive period for the site (Table 10).

At the other sites, where less detailed studies were done, the success of breeding relative to the effort given to egg production can be seen in the value of fledgings per egg. There were eight sites where this value was under 0.10 (St. Helena Bay, Marcus Island 1979/1980, Koeberg 2002/2003, 2003/2004, 2004/2005, Robben Island 2004/2005, Cape Point 1998/1999, Betty's Bay, Brenton-on-Sea and East London) and four sites where is was above 0.30 (Dassen Island, Robben Island 2001/2002, Dyer Island 2002/2003 and De Hoop Nature Reserve) (Table 9).

Modelled comparison of sites

Of the regression models considered to model the response variable "eggs produced per breeding pair", the model with area status and shoretype as explanatory variables provided the most parsimonious fit, and accounted for 20.4% of the variance (Table 11). Breeding sites located on islands and sites with shoretypes which were mixed or rocky shoretypes had a negative effect on the number of eggs produced per breeding pair of oystercatcher (Table 11). The response variable "hatchlings produced per breeding pair" was best modelled by area status and predation stuatus; the chosen model accounted for 53.1% of the variance (Table 12). Sites with low predation had, on average, 0.66 extra hatchlings per year than sites with medium or high predation, and sites located on islands had 0.41 extra hatchlings per year than mainland sites (Table 12). The response variable "percentage of eggs which produced hatchlings" was also best modelled by area status and predation stuatus; the chosen model accounted for 62.0% of the variance (Table 13). Sites with low predation had, on average, a 25% higher hatching percentage, and sites located on islands a 25% higher hatching success (Table 13). The most important response variable is "fledglings produced per breeding pair". Once again, this was best modelled by area status and predation stuatus; the chosen model accounted for 27.9% of the variance (Table 14). Sites with low predation had, on average, 0.34 extra fledglings per year than sites with medium or high predation, and sites located on islands had 0.33 extra fledglings per year than mainland sites (Table 14). One further response variable was considered: "the percentage of hatchlings which fledged", no significant explanatory variables were found.

Discussion

This study aimed to compare breeding productivity of the African Black Oystercatcher at sites around the South African coast. There was some difficulty establishing these comparisons as the data collected occurred over different years, different periods, different sample sizes using different methods and formats. In general, the data do not lend themselves to formal statistical hypothesis testing. Carefully designed fieldwork will be necessary to evaluate these patterns.

Egg production

At Dyer Island in 2002/2003, the egg-laying period was half that at Koeberg in the same breeding season, where there was a month's difference in the median date for the first clutch (8 December) and all clutches laid (9 January). This demonstrated the high level of egg loss and large proportion of birds laying replacement clutches at Koeberg. At most sites, egg-laying started in November and peaked mid-December to mid-January comparable to previously published times (Summers & Cooper 1977, Hockey 1983b, 1996, Hockey *et al.* 2005). Two pairs at Koeberg in 2002/2003, laid their first eggs in October, reared those chicks to fledging and then attempted rearing a second brood.

The mean clutch size for the 13 single-year studies was 1.77 eggs, comparable to the figure of 1.74 eggs given by Hockey (1983b). The 24-year study at Cape Agulhas had a mean clutch size of 1.68 eggs (Jeffery & Scott 2005), comparable to 1.67 eggs given for the south coast of the Western Cape (Hockey *et al.* 2005). Hockey *et al.* (2005) stated that there has been an increase in clutch size from 1.74 eggs pre-1983 (Hockey 1983b) to 1.92 eggs from 1997–2002, and attributed this to the invasion of the alien mussel *Mytilus galloprovincialis* (see also Hockey & van Erkom Schurink (1992)). The only study from before 1983 included in this comparative study, was the original Hockey (1983b) study; the results of our study therefore contradict Hockey *et al.* (2005). An explanation for this could be the inclusion of sandy shore breeding sites where the birds do not feed on the alien mussel (Chapter 4, McLachlan *et al.* 1980, Hockey 1981b, Ward 1990).

Three-egg clutches were recorded at Koeberg, Robben Island, Cape Point and Cape Agulhas although the reasons for this occurrence are not known and no patterns could be seen from our data. Jeffery & Scott (2005) and Hockey (2002) also noted that three-egg clutches are becoming increasingly common. Fraser & McMahon (1990) reported a pair attempting to rear three chicks at Olifantsbos (Cape Point Nature Reserve).

Hockey *et al.* (2005) stated that up to three replacement clutches are laid. However, four clutches per breeding pair have been reported at Cape Point (Pond 1999), at Cape Agulhas by (Jeffery & Scott 2005) and at Koeberg (Chapter 2). At Cape Point 1998/1999 and Koeberg 2002/2003, these results corresponded with a high levels of predation, a large percentage of pairs producing replacement clutches, low hatching success and ultimately a low breeding productivity. Hatching success cannot be calculated from data presented by Jeffery & Scott (2005) in the Cape Agulhas study; however, in the five years in which four replacement clutches were laid; only one year had a breeding productivity of more than 0.35 (0.70 fledglings per pair per year in 1994/1995) (Jeffery & Scott 2005).

The mean African Black Oystercatcher egg dimensions are given as 60.7×41.0 mm and egg mass of 55.8 g (Hockey 1983b, Hockey *et al.* 2005). Egg dimensions varied at different sites and in different years; eggs at Robben Island 2004/2005 and Sundays River 1987/1988 were larger and heavier and eggs at Cape Agulhas 1978/1979–2001/2002 were smaller and lighter. The differences in egg dimensions between Koeberg and Dyer Island in 2002/2003 were statistically significant; eggs were shorter and broader at Koeberg and longer and thinner at Dyer Island. The biological importance of these intra-species differences in shape and mass between different sites is unknown and should be explored. In birds in general, larger eggs require longer incubation (Drent 1975) and chicks that hatch at a higher mass (ie. larger eggs) have an increased chance of survival (for example Clark & Wilson (1981)). However, the survival value of intra-species shape differences has not been examined.

The median value of egg mass produced as a percentage of female body mass was 15% for 12 single-year studies. All the sites that had values above the median, also had large proportions of pairs laying replacement clutches. Hockey (1983b) described an individual female at Marcus Island in 1979/1980 that produced 40% of its body mass in eggs in 72 days. At Koeberg in the 2002/2003 season, one bird that laid eight eggs produced 61% of the average female body mass (722.3 g Hockey (1983b)) in eggs in approximately 105 days, another laid seven eggs and produced 54% of the average female body mass in eggs in approximately 115 days (Chapter 1).

In general, high levels of egg loss were attributed to predation (Marcus Island, Koeberg, Robben Island, Cape Point, Betty's Bay, Cape Agulhas, Dana Bay and Sundays River). Egg loss was also attributed to high-tide events (Marcus Island, Koeberg, Robben Island, Noordhoek, Cape Point, Betty's Bay, Dyer Island and Cape Agulhas) (for example Calf & Underhill (2005b)), off-road vehicles (Cape Agulhas and Sundays River), blown sand or sand-cliff collapse (Koeberg, Dana Bay and Sedgefield) and flooding with storm-water pollution (Knysna Lagoon).

Chick-rearing

Although the difference between growth rates was not significant, the median growth rate of chicks at Koeberg was 14% larger than that for chicks at Dyer Island (Table 10) lending support to the alternative hypothesis that chicks at Koeberg grew faster than chicks at Dyer Island.. The comparison between growth rates of chicks on the two study sites should be investigated further. This could be a response to the higher predation rates at the mainland study site than on Dyer Island, which is free of terrestrial predators. Growth rates in ground-nesting birds are hypothesised to increase in the presence of high predation risk (Drent & Daan 1980, Hockey 1984a, 1996b) so that chicks have a reduced period of exposure to predators before they are able to fly.

The median post-fledging period was quantified as being 50 days at Koeberg and 77 days at Dyer Island. Our observations show that juveniles leave parental territories earlier on the mainland than on islands, probably due to the higher growth rate and higher predation pressure (see above). This is contrary to the statement by Hockey (1983b) that juveniles are ousted earlier from parental territories at islands than on the mainland due to higher competition for feeding territories in the non-breeding season.

Chick loss has mainly been attributed to human disturbance: Leseberg *et al.* (2000) and Hockey (2001) stated that human disturbance causes chick loss when hiding chicks drown on the rising tide, chicks starve when disturbance prevents their parents from feeding them adequately and when unattended susceptible chicks are predated. Direct effects of human disturbance include destruction of nests by walkers and off-road vehicles (also mentioned in Jeffery & Scott 2005) and predation of chicks by uncontrolled dogs (Leseberg *et al.* (2000) and Hockey (2001)). At Koeberg, no direct human disturbance was observed although uncontrolled dogs disturbed birds on the south beach. Pond (1999) noted that nests and chicks were trampled by horses on Noordhoek beach. Chick loss can also be attributed to high-tide events (see above) and to predation at sites with minimal human disturbance.

Although human disturbance generally causes egg and chick loss, there were several reports of oystercatchers being tolerant of the presence of people, also recorded by Underhill (1991) at Pringle Bay.

Breeding productivity

A high value for eggs per breeding pair correlates with a large effort given to producing eggs and a low value for hatching success correlates with a high level of egg loss. Egg loss was mainly attributed to predation as well as environmental, climatic or tidal events (see above). The four extremes of these two variables from the 18 sites in Table 9 can be represented as follows:

1) eggs per breeding pair low: hatching success high: Dyer Island, 2002/2003, 2004/2005
2) eggs per breeding pair high: hatching success low: Cape Point 1998/1999

3) eggs per breeding pair low: hatching success low: Koeberg 2004/2005
4) eggs per breeding pair high: hatching success high: St. Helena Bay, Brenton-on-Sea
1) The results at Dyer Island in 2002/2003 (Wortel *et al.* 2003) and 2004/2005 (L. Waller *in litt.*) can be related to few replacement clutches laid, little egg loss and low levels of predation. 2) The large effort given by the oystercatchers at Cape Point in 1998/1999 to producing eggs was the result of 75% of pairs producing replacement clutches, as well as two clutches of three eggs each. A high level of egg predation was noted here as causing the low hatching success (Pond 1999). 3) At Koeberg in 2004/2005, there was a high level of egg loss but not associated with a high level of effort into egg production. Egg loss was attributed to high levels of predation (Chapter 2). 4) Both St. Helena Bay and Brenton-on-Sea are unprotected mainland sites and have high levels of human disturbance (Hockey 2001) and although there is some egg loss and replacement clutches laid, there is also a relatively high hatching success.

Hatching success has been discussed above. A low value for fledging success correlates with a high level of chick loss. Chick loss is mainly attributed to human disturbance, as well as high-tide events and predation (see above). The four extremes of these variables from the 18 sites in Table 9 can be represented as follows:
1) hatching success high: fledging success high: Dyer Island 2002/2003, Robben Island 2001/2002
2) hatching success high: fledging success low: Brenton-on-Sea
3) hatching success low: fledging success high: Knysna 1998/1999–2004/2005
4) hatching success low: fledging success low:
1) There were low levels of predation and human disturbance on Dyer Island in 2002/2003 (Wortel *et al* 2003 and L. Waller *in litt.*) and at Robben Island in 2001/2002 (Calf & Underhill 2002). 2) There were low levels of egg loss (low levels of predation) and high levels of chick loss (high levels of human disturbance) at Brenton-on-Sea (Hockey 2001). 3) At Knysna 1998/1999–2004/2005, there were high levels of egg loss and a low level of chick loss. This area is subject to flooding and high tide events (Elwell 2005) which, together with medium levels of predation, cause low hatching success. There was high fledging success in spite of high levels of human disturbance. 4) The egg loss at Koeberg in

2003/2004 was attributed to high levels of predation; only one chick (out of four lost in total) was lost due to human disturbance (Chapter 2).

Breeding productivity is measured by the number of fledglings per breeding pair and a value of 0.35 has been estimated as being needed to maintain a stable population (Hockey *et al.* 2005). In the data from the 18 sites in Table 9, the lowest value for fledglings per breeding pair was 0 at Koeberg Nuclear Power Station in 2004/2005 where there was a high level of egg loss as well as little effort put into egg production and no chicks hatched. Values under 0.10 were recorded at Marcus Island 1979/1980 (0.07), Koeberg 2003/2004 (0.07), Robben Island 2004/2005 (0.09) and Cape Point 1998/1999 (0.08). Low productivity at these sites were mainly attributed to predation. The highest values for breeding productivity were measured at Robben Island 2001/2002 (0.94 fledglings per breeding pair), Dyer Island 2002/2003 (0.86) and Dassen Island mean (0.82). These are all protected island sites and therefore have few predators (except for feral cats on Robben Island but these did not cause much problem in the 2001/2002 season) and little human disturbance.

Adult annual survival is 96% (Hockey *et al.* 2005); adult mortality is caused by predation, Avian Cholera and paralytic shellfish poisoning (Hockey & Cooper 1980, Hockey 1983b, 1996b). Numerous harmful algal blooms have been reported, mostly to the west of Cape Agulhas (Pitcher & Calder 2000), but there have been no other reports of oystercatcher mortality caused by shellfish poisoning.

Investment to breeding and breeding intensity

When evaluating the comparison between the African Black Oystercatcher breeding at Dyer Island and Koeberg Nuclear Power Station over the 2002/2003 breeding season, it can be seen that the breeding productivity at Dyer Island is well above that estimated as being needed to keep the population stable (0.35 fledglings per pair per year (Hockey *et al.* 2005)). The time that each breeding pair at Dyer Island spent on reproduction per juvenile produced is the same as the mean reproductive period. Dyer Island is therefore an ideal breeding site for the oystercatcher. However, at Koeberg the breeding productivity is below the mean value. The time that each breeding pair spends on reproduction per juvenile produced is almost twice the mean reproductive period. This is attributed to a large proportion of the reproductive period spent on incubation and a low breeding productivity.

At sites with less detailed data, a value of fledglings per egg gives a measure of breeding productivity relative to effort put into egg production. The ideal situation would be indicated by a higher value (successful breeding with little effort). The areas with the highest breeding productivity (fledglings per pair) can be compared using the fledglings per egg value: birds put less effort into breeding at Dyer Island 2002/2003 than at Robben Island 2001/2002 and Dassen Island. Likewise sites with poor breeding productivity can be compared: birds put more effort into breeding at Koeberg 2002/2003 than at Dana Bay 2002/2003.

Modelled comparison of site

In the statistical modelling, the position along the coast as well as the level of human disturbance did not have any significant effects on the breeding parameters evaluated. Mixed or rocky shoretypes decreased the number of eggs per breeding pairs, this can be explained by the high level of replacement clutches laid at the sites with sandy shores (Koeberg beach, Betty's Bay and Knysna Lagoon). Island areas also decreased the number of eggs per breeding pairs, this can be explained by the low level of replacement clutches laid on island sites. Both these factors interact as the island sites all have rocky shores. Island areas and low levels of predation positively effected the other breeding parameters (hatchlings per breeding pair, hatching success and fledglings per breeding pairs). These two factors also interact as there are few predators on the islands.

Synthesis

Grouping the 18 sites into protected island sites, protected mainland sites and unprotected mainland sites provided insight into the breeding productivity of oystercatchers in these different categories. The sites with highest hatching success, fledging success and fledglings per breeding pair (0.50-0.87) were undoubtedly the protected island sites that have few predator species and little human disturbance. There was poor breeding productivity at Robben Island in the 2003/2004 and 2004/2005 breeding seasons because there was heavy predation by feral cats in these years (Calf & Underhill 2005a, J. Braby *in litt.*). The protected mainland sites generally had lower hatching success and higher fledging success with variable breeding productivity depending on the individual site. This can be attributed to high levels of egg predation caused by many terrestrial predators and relatively little human disturbance resulting in relatively good chick survival. De Hoop and Goukamma Nature Reserves had higher hatching success and good breeding productivity (more than 0.35). Some unprotected mainland sites (St. Helena Bay, Noordhoek, Brenton-on-Sea and East London) had higher hatching success and lower fledging success and this can be attributed to human disturbance causing chick loss as detailed above as well as fewer terrestrial predators depredating eggs. Some unprotected mainland sites (Betty's Bay, Dana Bay, Sedgefield and Knysna) had lower hatching success and higher fledging success. At Betty's Bay this was attributed to both high levels of egg predation and chick loss while at Knysna high egg loss was attributed to flooding events and storm-water of-flow.

From the statistical analysis, the position along the coast of South Africa, the levels of human disturbance and the management level of mainland sites were not significant. However, it was clear that the island sites and areas with low or medium predation levels had better breeding productivity than the mainland sites and those areas with high predation levels.

Hatching success was significantly lower than fledging success for most of the African Black Oystercatcher breeding sites, indicating that the incubation period is the critical phase in the breeding cycle. This is contrary to Hockey (2001)'s hypothesis that the chick-rearing phase is the most critical although it correlates with the general pattern of all oystercatcher species (Hockey 1996a, b).

Conservation of the African Black Oystercatcher should especially focus on preventing or removing predators from island sites. At mainland sites, limiting the disturbance of the birds during the incubation period seems to be the most critical and decreasing levels of predation if possible. Access by people to beaches with breeding oystercatchers could be limited at various sites where human disturbance is the limiting factor.

Acknowledgements

Eskom Koeberg Nuclear Power Station provided access to the study site; we especially acknowledge the helpfulness of Gert Greeff and Hilton Westman, nature conservators at the site. J. Braby, L. Waller, U. Pond, A. Swanepoel and N. Elwell provided reports of oystercatcher breeding sites. The Avian Demography Unit provided research reports for Dyer Island and Robben Island. Leo Bruinzeel commented on a draft copy. The project was supported by the National Research Foundation, the Earthwatch Institute, and the University of Cape Town Research Committee.

Table 1. Factors influencing breeding of the African Black Oystercatcher at different sites along the coast of South Africa. The source of information for each locality is given in Table 9. Levels of disturbance (high, medium and low) were estimated from the importance given to that factor in the text and compared to other localities. High tide events were assumed to play a role at all sites.

Area and breeding season	**Area Status**	**Density of birds (pairs/km)**	**Shore type**	**Human disturbance**		**Predation**		**Other**
				Level	**Caused by:**	**Level**	**Caused by:**	
St. Helena Bay*	Unprotected mainland	No data	Mixed	High	Residents, dogs Holiday-makers Fishermen	Low	Kelp Gulls Feral cats	
Marcus Island 1979/1980	Protected mainland	30.6	Rocky	Medium	Conservation personnel	High	Many avian and terrestrial predators (see text)	
Dassen Island*	Protected island	11.6	Rocky	Low	Conservation personnel	Low	Kelp Gulls	
Koeberg 2002/2003	Protected mainland	10.6	Harbour Sandy	Medium	Residents, dogs Harbour personnel	High	Many avian and terrestrial predators (see text)	Wind blown sand
Koeberg 2003/2004	Protected mainland	8.8	Harbour Sandy	Medium	Residents, dogs Harbour personnel	High	Many avian and terrestrial predators (see text)	Wind blown sand
Koeberg 2004/2005	Protected mainland	3.7	Harbour Sandy	Medium	Residents, dogs Harbour personnel Harbour construction	High	Many avian and terrestrial predators (see text)	Wind blown sand
Robben Island 2001/2002	Protected island	6.3	Rocky	Medium	Residents, dogs Tourists	Low	Some avian and terrestrial predators (see text)	
Robben Island 2002/2003	Protected island	6.8	Rocky	Medium	Residents, dogs Tourists	Medium	Some avian and terrestrial predators (see text)	
Robben Island 2003/2004	Protected island	4.9	Rocky	Medium	Residents, dogs Tourists	High	As above but especially feral cats	
Robben Island 2004/2005	Protected island	6.3	Rocky	Medium	Residents, dogs Tourists	High	As above but especially feral cats	
Noordhoek 1998/1999	Unprotected mainland	3.3	Mixed	High	Residents, dogs, horses Holiday-makers Fishermen	Low	Kelp Gulls Feral cats	Wind blown sand
Cape Point 1998/1999	Protected mainland	1.7	Mixed	Low	Conservation personnel	High	Many avian and terrestrial predators (see text)	Wind blown sand

Betty's Bay*	Unprotected mainland	No data	Sandy	High	Residents, dogs Holiday-makers	High	Many avian and terrestrial predators (see text)	
Dyer Island 2002/2003	Protected island	8.4	Rocky	Low	Conservation personnel	Low	Kelp Gulls	
Dyer Island 2004/2005	Protected island	8.8	Rocky	Low	Conservation personnel	Low	Kelp Gulls	
Cape Agulhas mean 1978/1979–2001/2002	Unprotected mainland	1.3	Mixed	Medium	Residents, dogs Off-road vehicles	Medium	Some avian and terrestrial predators (see text)	
De Hoop Nature Reserve*	Protected mainland	No data	Mixed	Low	Conservation personnel	Medium ?	No data	
Dana Bay 2002/2003	Unprotected mainland	2.8	Mixed	High	Residents, dogs Holiday-makers Fishermen	Low	Kelp Gulls Genets	Wind blown sand
Goukamma Nature Reserve*	Protected mainland	No data	Mixed	Low	Conservation personnel	Medium ?	No data	
Sedgefield mean 1996/1997–2004/2005	Unprotected mainland	1.0	Mixed	High	Residents, dogs Holiday-makers Fishermen	Low	Kelp Gulls Genets	Sand cliff collapse
Brenton-on-Sea*	Unprotected mainland	0.5	Mixed	High	Residents, dogs Holiday-makers Fishermen	Low	Kelp Gulls	
Knysna Lagoon mean 1998/1999–2004/2005	Unprotected mainland	0.9	Salt marsh Mud flat	High	Residents, dogs Holiday-makers Fishermen	Medium	Kelp Gulls Dogs, Feral cats	Storm water off-flow
Sundays River 1987/1988	Unprotected mainland	1.4	Sandy	Low	No data	Low	Kelp Gulls Black-backed Jackals	
East London*	Unprotected mainland	0.4	No data		No data		No data	

Table 2. Percentiles of the dates of the start of incubation for African Black Oystercatchers at Koeberg Nuclear Power Station and Dyer Island for the 2002/2003 breeding season. The two columns for each breeding site refer to the first clutches and all clutches, including replacement clutches. The dates in the table are those by which the percentage of eggs given in the row had started incubation. The figures below the dates are the bootstrapped 90% confidence intervals for each percentile, given as days only; if the two numbers are increasing, then the month for both is that for the date, otherwise one is for the month before or after, as determined by the context (e.g. 3-16 under 9 Nov means 3 Nov–16 Nov, and 28–11 under 2 Oct can only mean 28 Sept–11 Oct). The final six rows of the table give the estimated lengths of the periods (in days) during which the central 50%, 90% and 95% of incubation started; the second row for each period is the 90% bootstrapped confidence interval.

	Koeberg		**Dyer Island**	
Percentile	**First**	**All**	**First**	**All**
2.5%	28 Sept	2 Oct	10 Nov	10 Nov
	26 - 25	28 - 11	8 – 15	9 – 6
5%	1 Oct	9 Nov	12 Nov	13 Nov
	28 – 10	3 – 16	10 – 18	10 – 18
25%	20 Nov	10 Dec	9 Dec	9 Dec
	16 – 26	11 – 12	20 – 15	20 – 16
50%	8 Dec	9 Jan	21 Dec	22 Dec
	30 – 18	4 – 14	15 – 25	16 – 25
75%	2 Jan	4 Feb	28 Dec	30 Dec
	24 – 12	27 – 9	25 – 1	26 – 16
95%	4 Feb	4 Mar	21 Jan	26 Jan
	26 – 26	24 – 11	3 – 22	19 – 29
97.5%	25 Feb	12 Mar	22 Jan	29 Jan
	30 – 2	3 – 18	18 – 23	22 – 31
50%	42 days	56 days	20 days	20 days
	34 – 51	45 – 65	14 – 39	15 – 40
90%	121 days	115 days	69 days	74 days
	86 – 148	103 – 148	52 – 72	65 – 79
95%	148 days	162 days	73 days	80 days
	120 – 155	117 – 169	66 – 75	71 - 83

Table 3. Egg-laying parameters of African Black Oystercatchers at eight breeding sites along the South African coast. The source of information for each locality is given in Table 9.

Area and breeding season	First egg laid	Peak egg-laying period	Mean clutch size	Clutch size (% of total no. of clutches)			Percentage of pairs that laid repeat clutches	Max no. clutches per pair
				1 egg	2 egg	3 egg		
Marcus Island 1979/1980	Dec	mid-Dec to mid-Jan	1.74	26%	74%		29%	3 (1 pair)
Koeberg 2002/2003	Oct	mid-Dec to beg Feb	1.64	36%	64%		70%	4 (4 pairs)
Koeberg 2003/2004	Nov	mid-Dec to mid-Jan	1.83	22%	74%	4%	42%	3 (2 pairs)
Koeberg 2004/2005	Nov	mid-Nov to mid-Dec	1.63	38%	62%		23%	2
Robben Island 2001/2002	Nov	mid-Jan	2.01	7%	85%	8%	15%	2
Robben Island 2002/2003	Nov	mid-Jan	1.97	10%	85%	5%	21%	3 (4 pairs)
Robben Island 2003/2004			1.98	5%	91%	4%	9%	3 (1 pair)
Robben Island 2004/2005	Nov	mid-Dec to mid-Jan	1.61	39%	61%		16%	2
Noordhoek 1998/1999	Oct	mid-Dec to mid-Jan	1.67	33%	67%		40%	3 (1 pair)
Cape Point 1998/1999	Nov	mid-Dec to mid-Jan	1.58	48%	45%	7%	75%	4 (2 pairs)
Dyer Island 2002/2003	Nov	mid-Dec	1.87	13%	87%		10%	2
Dyer Island 2004/2005	Nov	mid-Dec to mid-Jan	1.83	17%	83%		5%	2
Cape Agulhas 1978/1979-2001/2002	Oct	mid-Dec to mid-Jan	1.68	33%	66%	1%	36%	4 (5 pairs)
Sundays River 1987/1988	Jan		1.77	32%	68%		4 pairs	2

Table 4. Dimensions and estimated fresh mass (see text) of African Black Oystercatcher eggs. The estimated fresh mass for all the areas has been calculated by the method described by Underhill & Calf (2005). The source of information for each locality is given in Table 9.

Area and season		**Length (mm)**	**Breadth (mm)**	**Fresh mass (g)**
Marcus Island 1979/1980	Mean	60.7	41.0	54.4
(*n* = 105)	Range	55.8–65.2	37.9–43.7	
	SD			
Koeberg 2002/2003	Mean	59.7	41.7	55.5
(*n* = 125)	Range	54.6–69.4	38.7–43.8	47.4–70.8
	SD	2.1	1.0	3.5
Koeberg 2003/2004	Mean	59.6	41.7	55.3
(*n* = 80)	Range	53.5–64.27	38.5–44.5	47.1–63.7
	SD	1.7	1.1	3.5
Koeberg 2004/2005	Mean	59.8	41.8	55.7
(*n* = 24)	Range	56.6–64.3	39.0–44.2	45.8–66.8
	SD	1.9	1.2	4.3
Robben Island 2004/2005	Mean	61.6	42.3	58.7
(*n* = 111)	Range	57.2–67.5	39.6–45.2	49.8–69.3
	SD	2.1	1.1	3.8
Dyer Island 2002/2003	Mean	61.3	40.9	54.6
(*n* = 34)	Range	55.4–66.9	37.9–43.1	46.8–65.8
	SD	2.6	1.1	3.9
Dyer Island 2004/2005	Mean	60.4	41.6	55.8
(*n* = 20)	Range	56.7–64.9	39.3–44.6	51.4–64.5
	SD	2.3	1.0	3.5
Cape Agulhas mean	Mean	60.4	40.6	53.1
1978/1979–2001/2002	Range	50.4–69.5	38.0–43.9	
(*n* = 322)	SD			
Sundays River 1987/1988	Mean	61.3	41.8	57.1
(*n* = 21)	Range			
	SD			

Table 5. Egg production in terms of mass produced by female African Black Oystercatchers at seven breeding localities along the South African coast. The average oystercatcher female body mass is taken as 722.3 g (Hockey 1981a) and the average egg mass* (used when no egg measurement data was available) is taken as 55.8 g (Hockey 1983b). The estimated fresh mass has been calculated by the method described by Underhill & Calf (2005). The source of information for each locality is given in Table 9.

Area and breeding season	**No. eggs**	**No. Breeding pairs**	**Eggs per breeding female**	**Mean Fresh mass (g)**	**Egg mass produced by each female (g)**	**Egg mass produced by each female as % of average female mass**	**Fledglings per egg**
Marcus Island 1979/1980	125	55	2.3	54.4	128.3	18%	0.03
Koeberg 2002/2003	128	37	3.5	55.5	194.3	27%	0.08
Koeberg 2003/2004	84	31	2.7	55.3	149.8	21%	0.02
Koeberg 2004/2005	26	13	2.0	55.7	111.4	15%	0
Robben Island 2001/2002	151	63	2.0	55.8*	111.6	15%	0.39
Robben Island 2002/2003	169	68	2.0	55.8*	111.6	15%	0.21
Robben Island 2003/2004	107	49	2.0	55.8*	111.6	15%	0.18
Robben Island 2004/2005	119	63	1.9	58.7	110.9	15%	0.05
Noordhoek 1998/1999	25	10	2.5	55.8*	139.5	19%	0.16
Cape Point 1998/1999	49	12	4.1	55.8*	227.8	32%	0.02
Dyer Island 2002/2003	43	21	2.0	54.6	111.8	15%	0.42
Dyer Island 2004/2005	42	22	1.9	55.8	106.5	15%	0.26
Cape Agulhas mean 1978/1979–2001/2002	42	16	2.6	53.1	139.4	19%	0.12

Table 6. Gompertz growth rates for the African Black Oystercatcher chicks at Dyer Island during the 2002/2003 breeding season and Koeberg Nuclear Power Station during the 2002/2003 and 2003/2004 breeding seasons.

Chick no	Growth rate	Number of days	First mass (g)	Last mass (g)
Dyer island chicks				
1	0.0106	20	215	269
2	0.0444	25	38	273
3	0.0453	31	49	370
4	0.0460	27	48	323
5	0.0470	30	52	369
6	0.0471	30	67	392
7	0.0496	31	36	370
8	0.0500	29	114	439
9	0.0563	32	62	450
10	0.0602	24	74	406
Median	**0.0471**			
Koeberg Nuclear Power Station chicks				
1	0.0374	25	122	310
2	0.0432	34	35	352
3	0.0438	28	70	363
4	0.0441	14	40	149
5	0.0454	39	50	480
6	0.0504	35	41	436
7	0.0538	35	39	460
8	0.0540	28	50	372
9	0.0550	3	42	64
10	0.0584	32	35	424
11	0.0616	16	40	239
12	0.0619	11	41	166
13	0.0637	28	40	418
Median	**0.0538**			

Table 7. Chick-rearing time from hatching to leaving for individual chicks at Dyer Island from November 2002 until May 2003. The date for fledging was estimated to be 40 days after hatching (Hockey 1984a).

Chick Number	**Hatching Date**	**Estimated Fledging Date**	**Age of chick at fledging (days)**	**Leaving Date**	**Time from fledging to leaving (days)**
1-1	22 Dec 2002	31 Jan 2003	40	11 May 2003	100
2-1	18 Dec 2002	26 Jan 2003	40	12 May 2003	106
3-1	23 Dec 2002	1 Feb 2003	40	21 May 2003	110
4-1	13 Dec 2002	21 Jan 2003	40	3 March 2003	42
4-2	13 Dec 2002	21 Jan 2003	40	3 March 2003	42
5-1	15 Jan 2003	23 Feb 2003	40	22 May 2003	120
6-1	12 Jan 2003	20 Feb 2003	40	17 May 2003	118
6-2	12 Jan 2003	20 Feb 2003	40	17 May 2003	118
7-1	18 Jan 2003	26 Feb 2003	40	22 May 2003	117
9-1	11 Jan 2003	19 Feb 2003	40	4 May 2003	75
10-1	21 Jan 2003	1 March 2003	40	22 May 2003	83
11-1	27 Jan 2003	7 March 2003	40	20 May 2003	75
12-1	27 Jan 2003	7 March 2003	40	20 May 2003	75
13-1	26 Jan 2003	6 March 2003	40	21 May 2003	77
15-1	3 Feb 2003	14 March 2003	40	22 May 2003	70
16-1	2 Feb 2003	13 March 2003	40	20 May 2003	69
17-1	27 Jan 2003	7 March 2003	40	17 May 2003	72
Mean					**86**
Median					**77**

Table 8. Outcome of African Black Oystercatcher breeding seasons at 11 breeding localities along the South African coast. Areas are arranged in geographical order from west to east around the South African coast.

Area and breeding season	**Breeding pairs**	**No. nests**	**No. eggs**	**No. chicks hatched**	**No. chicks fledged**	**Source of information**
Marcus Island 1979/1980	55	72	125	20	4	Hockey 1983b
Koeberg 2002/2003	37	78	128	24	10	Chapter 2
Koeberg 2003/2004	31	46	84	6	2	Chapter 2
Koeberg 2004/2005	13	16	26	0	0	Chapter 2
Robben Island 2001/2002	63	75	151	79	59	Calf & Underhill 2002
Robben Island 2002/2003	68	86	169	78	35	Calf & Underhill 2003
Robben Island 2003/2004	49	54	107	34	19	Calf & Underhill 2005a
Robben Island 2004/2005	63	74	119	17	6	J. Braby *in litt.*
Noordhoek 1998/1999	10	15	25	9	4	Pond 1999
Cape Point 1998/1999	12	30	49	1	1	Pond 1999
Dyer Island 2002/2003	21	23	43	27	18	Wortel *et al.* 2003
Dyer Island 2004/2005	22	23	42	25	11	L. Waller *in litt.*
Cape Agulhas mean 1978/1979-2001/2002	16	25	42	No data	5	Jeffery & Scott 2005
Dana Bay 2002/2003	17	21	41	9	5	Swanepoel 2003
Sedgefield mean 1996/1996-2004/2005	9		23	6	3	Elwell 2005
Knysna Lagoon mean 1998/1999-2004/2005	12		41	11	7	Elwell 2005
Sundays River 1987/1988		22	37	10	4	Ward 1990

Table 9. Breeding productivity of the African Black Oystercatcher at 18 breeding localities along the South African coast. Hatching Success is measured as the percentage of eggs that hatched. Fledging success is measured as the pecentage of chicks that fledged. *In one study mean values for the sites were given. Areas are arranged in geographical order from west to east around the South African coast.

Area and breeding season	**Eggs per breeding pair**	**Hatching Success**	**Hatchlings per breeding pair**	**Fledging success**	**Fledglings per breeding pair**	**Fledglings per egg**	**Source of information**
St. Helena Bay*	3.0	45%	1.34	15%	0.20	0.07	Hockey 2001
Marcus Island 1979/1980	2.3	16%	0.36	20%	0.07	0.03	Hockey 1983b
Dassen Island*	2.3	61%	1.40	59%	0.82	0.36	Hockey 2001
Koeberg 2002/2003	3.5	19%	0.64	42%	0.27	0.08	Chapter 2
Koeberg 2003/2004	2.7	7%	0.19	33%	0.06	0.02	Chapter 2
Koeberg 2004/2005	2.0	0%	0	–	0	0	Chapter 2
Robben Island 2001/2002	2.4	52%	1.25	75%	0.94	0.39	Calf & Underhill 2002
Robben Island 2002/2003	2.49	46%	1.15	45%	0.51	0.21	Calf & Underhill 2003
Robben Island 2003/2004	2.18	32%	0.69	56%	0.39	0.18	Calf & Underhill 2005a
Robben Island 2004/2005	1.9	14%	0.27	35%	0.09	0.05	Braby *in litt.*
Noordhoek 1998/1999	2.5	36%	0.90	44%	0.40	0.16	Pond 1999
Cape Point 1998/1999	4.1	2%	0.08	100%	0.08	0.02	Pond 1999
Betty's Bay*	2.9	23%	0.67	33%	0.22	0.08	Hockey 2001
Dyer Island 2002/2003	2.0	63%	1.29	67%	0.86	0.42	Wortel *et al.* 2003
Dyer Island 2004/2005	1.9	60%	1.14	44%	0.50	0.26	Waller *in litt.*
Cape Agulhas mean 1978/1979–2001/2002	2.6	No data	No data	No data	0.31	0.12	Jeffery & Scott 2005
De Hoop Nature Reserve*	2.2	43%	0.95	81%	0.77	0.35	Hockey 2001
Dana Bay 2002/2003	2.4	22%	0.53	56%	0.29	0.12	Swanepoel 2003
Goukamma Nature Reserve*	2.5	30%	0.75	55%	0.41	0.16	Hockey 2001
Sedgefield mean 1996/1997–2004/2005	2.6	26%	0.67	50%	0.33	0.13	Elwell 2005
Brenton-on-Sea*	2.9	53%	1.53	16%	0.25	0.09	Hockey 2001
Knysna Lagoon mean 1998/1999–2004/2005	3.4	27%	0.92	64%	0.58	0.17	Elwell 2005
Sundays River 1987/1988	No data	27%	No data	40%	No data	0.11	Ward 1990
East London*	2.2	30%	0.67	19%	0.13	0.06	Hockey 2001

Table 10. Comparison of time investment to breeding of the African Black Oystercatcher at Koeberg Nuclear Power Station and Dyer Island during the 2002/2003 breeding season. A normal reproductive cycle is taken as 32 days incubation, 40 days chick rearing, 50 days post fledging with a total of 122 days for Koeberg and 32 days incubation, 40 days chick-rearing, 77 days post-fledging with a total of 149 days for Dyer Island. The ratio of time spent on each stage of reproduction (incubation:chick-rearing:post-fledging) should be 26:33:41 at Koeberg and 21:27:52 at Dyer Island.

Factor	**Koeberg (days)**	**Percentage of normal**	**Percentage of total breeding period**	**Dyer Island (days)**	**Percentage of normal**	**Percentage of total breeding period**
Total incubation time	1646		64%	618		24%
Incubation time per breeding pair	44	138%		31	97%	
Total chick-rearing time	433		17%	612		24%
Chick-rearing time per breeding pair	12	30%		31	78%	
Total post-fledging time	475		19%	1309		52%
Post-fledging time per breeding pair	13	26%		65	84%	
Total breeding investment	2554			2539		
Breeding investment per breeding pair	69	57%		127	85%	
Total breeding investment per juvenile fledged	255	209%		149	100%	

Table 11. Results of the multiple linear regression model for the response variate eggs produced per pair for the African Black Oystercatcher breeding at various sites along the South African coast. (n=63).

Percentage of variance explained			20.4%
Explanatory variable	Estimate	Standard error	P
Constant	3.211	0.181	<0.001
Island status	−0.466	0.177	0.011
Mixed and rocky shoretype	−0.542	0.200	0.009

Table 12. Results of the multiple linear regression model for the response variate hatchlings produced per pair for the African Black Oystercatcher breeding at various sites along the South African coast (n=38).

Percentage of variance explained			53.1%
Explanatory variable	Estimate	Standard error	P
Constant	0.154	0.110	0.170
Low predation	0.655	0.115	<0.001
Island status	0.410	0.101	<0.001

Table 13. Results of the multiple linear regression model for the response variate hatching success for the African Black Oystercatcher breeding at various sites along the South African coast (n=39) .

Percentage of variance explained			62.0%
Explanatory variable	Estimate	Standard error	P
Constant	3.210	4.27	0.456
Low predation	25.08	4.43	<0.001
Island status	24.92	3.88	<0.001

Table 14. Results of the multiple linear regression model for the response variate fledglings produced per pair for the African Black Oystercatcher breeding at various sites along the South African coast. (n=62)

Percentage of variance explained			27.9%
Explainatory variable	Estimate	Standard error	P
Constant	0.0155	0.0904	0.864
Low predation	0.3422	0.0923	<0.001
Island status	0.3311	0.0784	<0.001

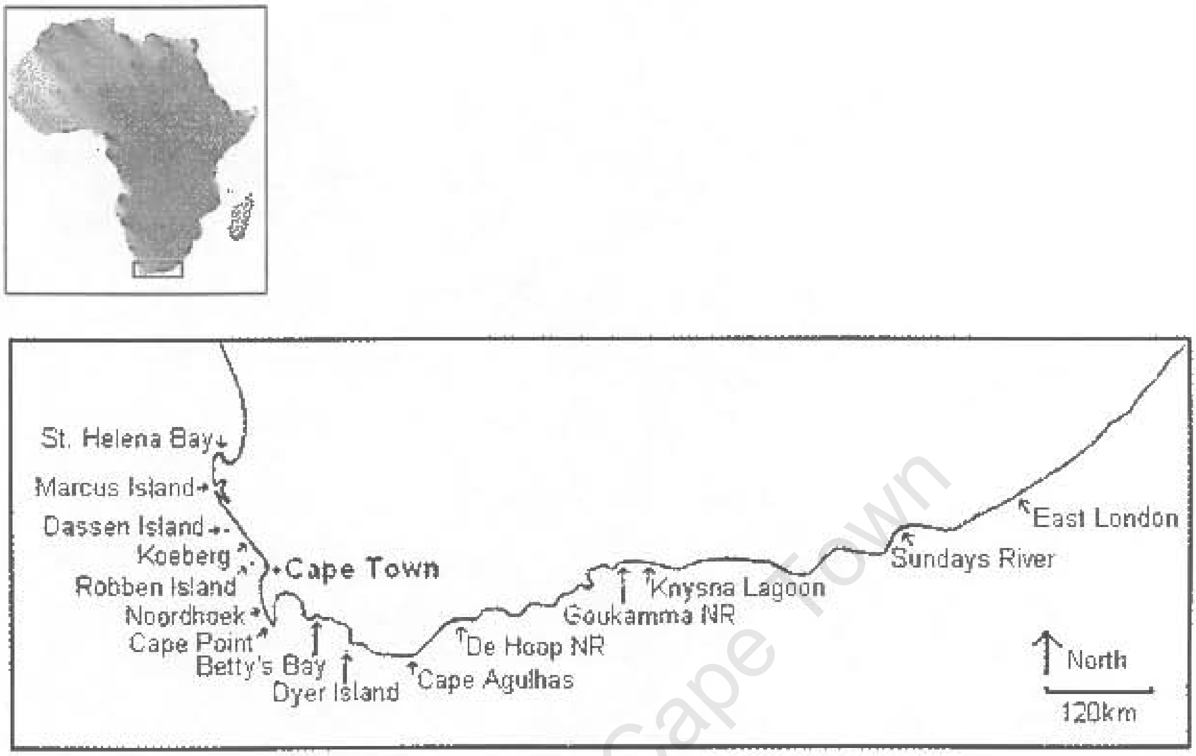


Figure 1. Map of Africa with detail showing the southern coast of South Africa, with approximate positions of the African Black Oystercatcher breeding localities used in this study.

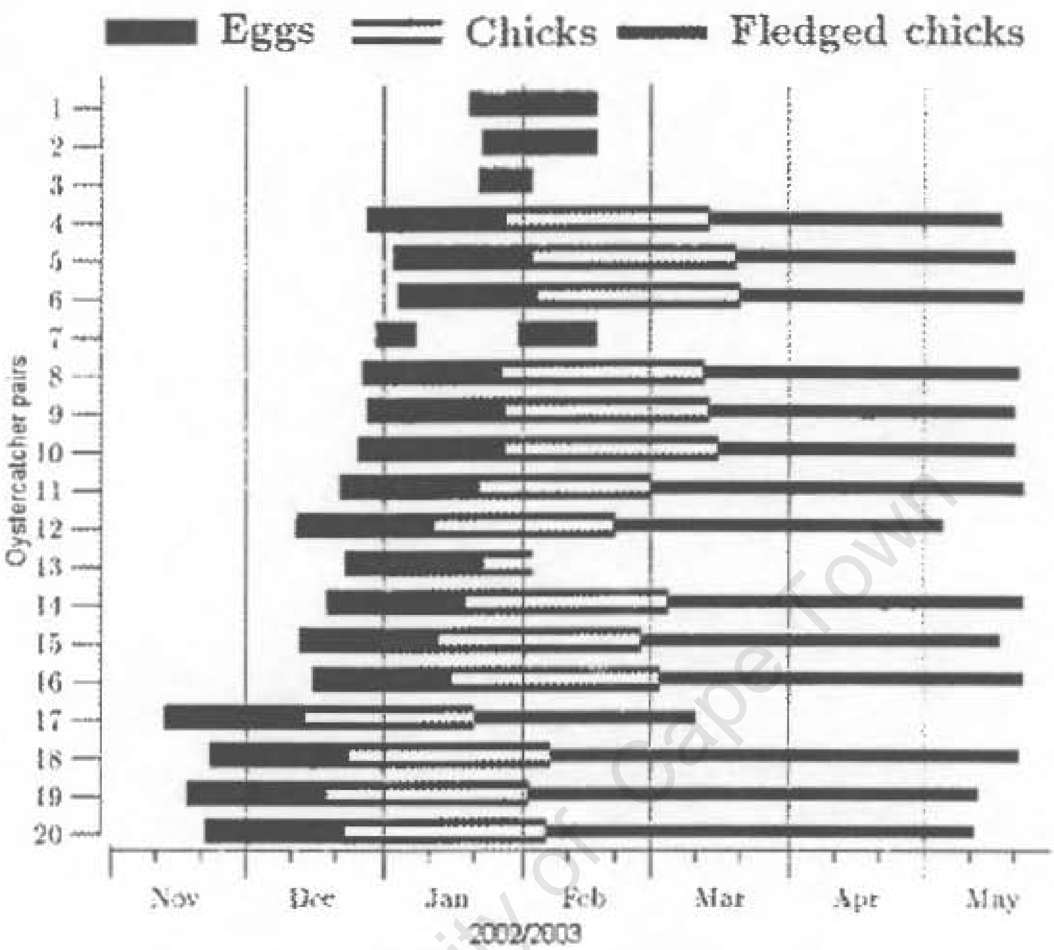


Figure 2. Graphical representation of incubation and chick-rearing of individual pairs of African Black Oystercatchers in relation to date at Dyer Island during the 2002/2003 breeding season. Time spent incubating is represented by a thick black line, time spent rearing chicks to fledging is represented by two lines and time spent chick-rearing post-fledging is represented by a thin black line.

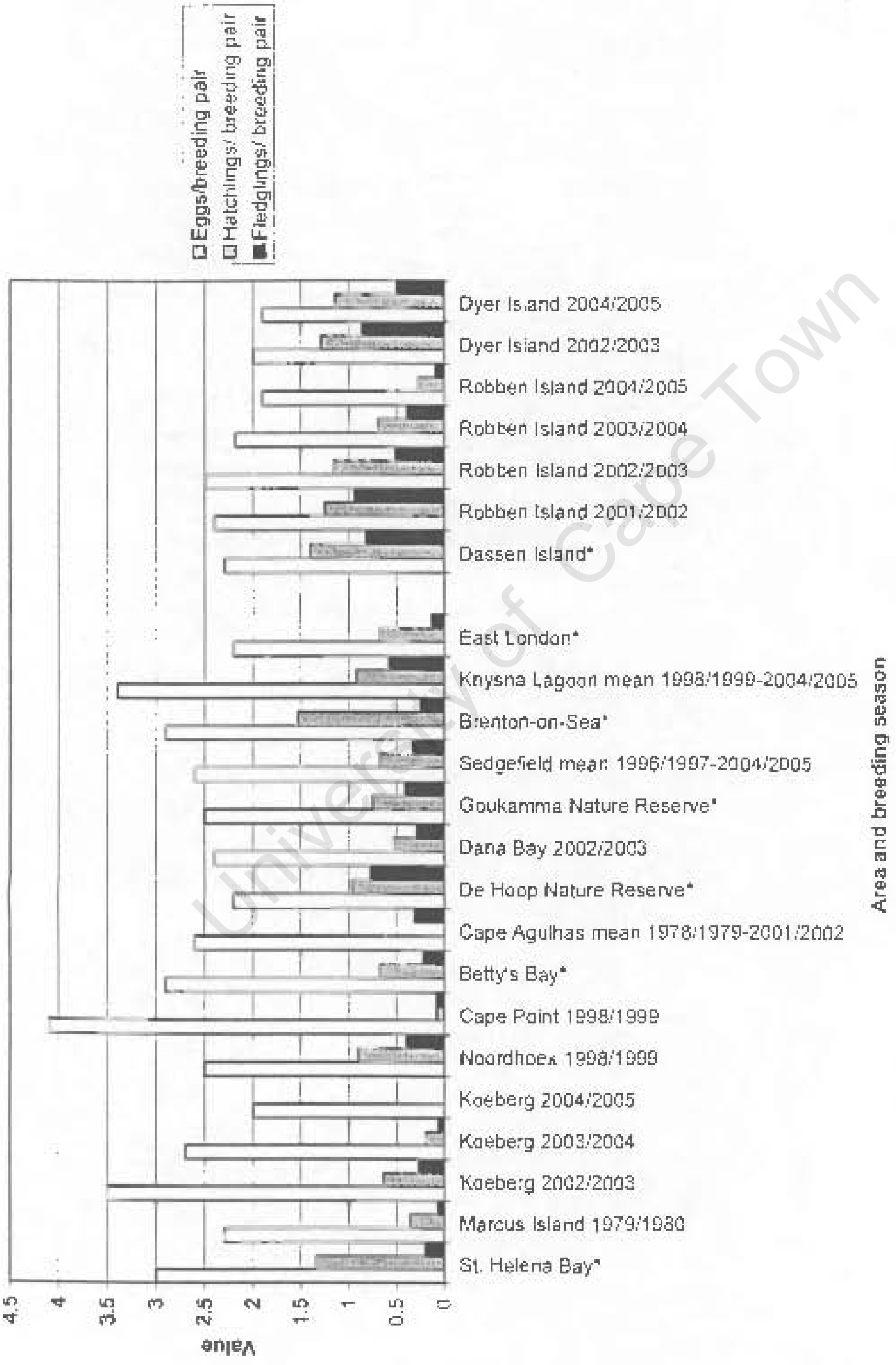


Figure 3. Histogram plot showing breeding productivity at the different areas over different breeding seasons, with mainland sites and island sites grouped together and arranged from west to east.

Chapter 4

Feeding behaviour and prey of African Black Oystercatchers *Haematopus moquini* on a sandy shore in the Western Cape

Introduction

The range of African Black Oystercatcher *Haematopus moquini* extends along the coast of South Africa and Namibia (Summers & Cooper 1977, Hockey 1983a, Martin 1997, du Toit *et al* 2003) and is classified as "near-threatened" both in South Africa and globally (Underhill 2000, BirdLife International 2004). Adults are territorial and stay on their breeding territories throughout the year (Summers & Cooper 1977, Hockey 1983a, 1984b, du Toit *et al* 2003). On the Eastern Cape mainland, sandy shores support the highest numbers of oystercatchers compared to other shore types (Hockey 1983a) and their distribution is correlated to the abundance of sand bivalves *Donax serra* and *D. sordidus* (McLachlan *et al.* 1980, Ward 1990). On the Western Cape mainland, which supports 34% of the total oystercatcher population (Hockey 1983a), mixed and rocky shores support higher densities of oystercatchers than sandy shores, although wave-cut platforms backed by beach and mixed shores are the preferred breeding habitats (Summers & Cooper 1977, Hockey 1983a). According to Hockey (1983a), 13% of the total population occur on Western Cape sandy shores.

The feeding behaviour and prey of the African Black Oystercatcher has been extensively studied on rocky shores (Hockey 1981b, 1984b, Hockey & Underhill 1984). On sandy shores, it has been studied in the Eastern Cape (McLachlan *et al.* 1980, Hockey 1981b, Ward 1990), where the available prey species are those that occur in the relatively warm seas of the Agulhas Current. However, there are no descriptions of African Black Oystercatcher feeding behaviour on sandy shores adjacent to the Benguela Upwelling System in the Western Cape, where a different set of available prey species characterize sandy shores.

In this chapter, I hope to gain insight on feeding behaviour and prey of the African Black Oystercatcher on a Western Cape sandy shore because the available prey species differ from those already described. The study is based on behaviourial observations and correlated with sampling that was done at the site. Knowledge of the oystercatchers prey may play a role in understanding conservation threats.

Methods

Observations of foraging oystercatchers were carried out from December 2004 to June 2005 at Koeberg Nuclear Power Station (33 40'S, 18 25'E), Western Cape, South Africa. For a full description of the study area, see thesis introduction. The observations took place along the beach immediately south of the power station. The section of beach included in the study area is approximately 500 m long, backed by dunes, has fine-grained sand, a wide intertidal area (gentle slope) and always has washed-up kelp (*Ecklonia maxima* and *Macrocystis angustifolia*) along the high-tide mark.

Beach zones were divided into four categories: swash zone (also known as the splash zone), wet sand, damp sand, dry sand. Zones were based on the observed saturation of the sand and therefore were not fixed. The swash zone (1–2 m wide) was defined as the area covered by water in the current wave movement, the wet sand zone extended from the water's edge to the upper limit of the current wave movement (not covered by water) (5–30 m wide depending on the height of the tide on the shore), the damp sand extended from the wet sand up the shore to the previous high-tide mark (15–100 m wide) and the dry sand extended up to the dunes and dune plants (more than 60 m wide on this gently-sloping beach).

The birds were observed from a vantage point on a dune overlooking the beach at a distance of c. 10–80 m and were not disturbed by the presence of the observer. There was infrequent human disturbance on the beach. Eight known pairs (based on territoriality and position along the coast) and unknown single adults were observed; a maximum of 14 adults in total being monitored at any time. Observations were made during daytime only, for periods up to three hours, at all stages of the tide and under all except the most extreme weather conditions, with temperatures ranging from 6.0–29.7°°C and wind speeds from 1.1-8.4 m/s. Meteorological data were obtained from the Eskom meteorological office, based at the Koeberg Nuclear Power Station. The temperature and wind measurements used were recorded 10 m above the ground. There was light rain on only one observation day; behaviour on this day seemed consistent with non-rain behaviour. Poor visibility prevented the observer from collecting data during periods of fog, strong winds and heavy rain. Tide height data were obtained from the Hydrographer, South African Navy.

Initially, focal birds were observed using a telescope (Kowa 20–60×zoom) until the various types of feeding techniques could readily be classified and possible prey caught could be identified. Prey size was estimated by comparing its size relative to the bird's bill, as described by Goss-Custard *et al.* (1987). Each feeding technique was divided into searching time (bird actively searching for prey until locating prey), handling time (retrieving prey and handling to a suitable position to open or eat), opening time (opening hard-shelled prey) and eating time (swallowing prey).

Focal birds were observed (using 8×40 binoculars) to establish the length of at least one feeding bout; this is the time each bird fed using a single feeding technique before stopping feeding or changing to another technique. When using a single feeding technique; the beach zone used, the type of prey caught, the individual searching, handling, opening and eating times and the quantity of prey consumed per minute were recorded. Instantaneous scans (Altmann 1974) were made every five minutes and all birds within vision (using 8×40 binoculars) that had identifiable feeding techniques, as well as the total number of birds present, were recorded. The number of birds feeding using a particular technique was expressed as a percentage of the total number of birds feeding at that particular time.

The spectrum of available prey present on this beach was extracted from Griffiths & Robinson (2004, 2005) who undertook bi-annual marine environmental sampling surveys in summer and in winter at Koeberg Nuclear Power Station. The sampling took place at Ou Skip (33°41'S, 18°26'E), near the southern limit of the study site (Figure 1 thesis introduction); during spring low tide. Their results for 2004 are presented in Table 1.

Calorific values and dry mass values for *Donax* were obtained from McLachlan & van der Horst (1979), calorific values for *Scololepsis, Nephtys* and average values for isopod and amphipod species, as well as a conversion ratio of wet mass to dry mass were obtained from Field *et al.* (1980). Wet mass values for *Scololepsis, Nephtys* and average values for isopod and amphipod species were obtained from C.L. Griffiths *in litt.* The energy values of the prey species were calculated from these values, energy consumed by the oystercatchers feeding on each prey species was calculated using the values obtained for quantity prey consumed per minute (Table 2) and the energy available on the beach from each prey species was calculated from the maximum density of each prey species sampled at Koeberg (Griffiths & Robinson 2004, 2005)

Results

Nine feeding activities were observed; these are listed in decreasing order of observed frequency: (1) single probing for small polychaetes, (2) multiple probing for large polychaetes, (3) kelp and dune-plant probing, (4) pecking surface prey, (5) single probing for small *Donax serra*, (6) eating washed-up mussels, (7) eating mussels and Goose Barnacles present on the kelp, (8) kleptoparasitism of *Donax serra* from Kelp Gulls and (9) multiple probing for *Donax serra*. Pecking water prey was observed once. Single probing (activities (1) and (5)) represents one feeding technique and is discussed under this heading, as is multiple probing (activities (2) and (9)). The feeding activities are summarised in Table 2. Only one feeding activity was observed in a single bout of feeding.

Single probing

When searching for small worms, this feeding technique was used on the wet and damp sand zones. The oystercatcher made a single probe into the substrate, to a depth of half the length of the bill or more. If the probe was successful, it gently tugged a small worm out and swallowed it. Small, round prey were also taken. When the birds fed on the wet sand they would walk in and out of the swash zone to avoid the waves. While feeding on small worms, the bird would occasionally use multiple probing (see description below) to feed on small worms. No kleptoparasitism by Kelp Gulls or other oystercatchers was observed while feeding in this way. All the oystercatchers observed used this technique when foraging. It was used in 47% of the total number of bird-foraging observations (Table 2).

Searching for prey took on average 6 seconds (1–60), handling and eating took on average one second each. A mean of 7.82 (0–20) prey items were consumed in a minute. Feeding bouts were observed for a mean of 32.5 (5–110) minutes (Table 2).

The main prey items were worms approximately 20 mm long; the most likely species was *Scololepsis squamata.* Griffiths & Robinson (2004, 2005) showed that this species is abundant on this shoreline (Table 1), *Orbinia angrapequensis* is longer (up to 50 mm) and is present at the site in far lower densities (Griffiths & Robinson 2005). Small round prey, approximately 5 mm long were also taken. These could be one or more of the following species, found by Griffiths & Robinson (2004, 2005) at the site: *Eurydice longicornis, Exosphaeroma pallidum, Pontogeloides latipes, Excirolana natalensis, Urothoe grimaldii* and *Gastrosaccus psammodytes* (Table 1).

Scololepsis has an energy value of 0.01 kJ per prey item, with the bird obtaining 0.08 kJ per minute feeding using this technique (Table 3). With a density of 9 500 *Scololepsis* per m^2 of beach (Table 1), the energy available to the birds from *Scololepsis* is 95 kJ/m^2 (Table 3).

A variation of this technique was used when oystercatchers were feeding on small (20–30 mm length) *Donax serra* on the damp sand. The oystercatcher walked slowly forward and made a single, deep probe into the sand. If successful, it pulled the bivalve out, carried it to a hole in the sand and wedged it there for support while the bivalve flesh was extracted and eaten. The exact technique for extracting the bivalve flesh was never visible, but undamaged empty hinged-shells were collected after the feeding bout suggesting that the bivalve had been stabbed between the valves. It was used in 0.9% of the total number of bird-foraging observations (Table 2). Only three individual oystercatchers were observed single probing for *Donax.* No kleptoparasitism by Kelp Gulls or other oystercatchers was observed.

The bird searched for the bivalve for on average 50 seconds (10–230), handling took on average 7 seconds, opening took on average two seconds and eating on average one second. A mean of 1 (0–3) bivalves were consumed in a minute. Feeding bouts were observed for a mean of 13 (5–30) minutes (Table 2).

Small *Donax* have an energy value of 1.93 kJ per prey item, with the bird obtaining 1.93 kJ per minute feeding using this technique (Table 3). With a density of 160 *Donax* per m² of beach (Table 1), the energy available to the birds from *Donax* is 308.8 kJ/m² (Table 3).

Multiple probing

When feeding on large worms, this technique was used on the wet sand and in the water in the swash zone. The oystercatcher ventured into the water up to the base of the keel; preferring to run towards the water searching and feeding on the backwash and run away from the water on the swash (half the time spent on this technique was walking). The bird probed repeatedly into the substrate with the bill slightly open, while moving slowly forward. The bill was inserted to approximately half its length, sometimes deeper. After a bout of probing (5–10 seconds), the bird lifted its head and walked a few steps forward before repeating the process. Once the large worm was caught, it was gently tugged to the surface and swallowed in several gulps. If there were other oystercatchers or Kelp Gulls in the vicinity, the bird would carry the prey farther up the beach before eating it. Kleptoparasitism by Kelp Gulls and other oystercatchers, even the bird's own mate, was observed. All the oystercatchers observed used this technique when foraging. It was used in 35% of the total number of bird-foraging observations (Table 2).

Searching for prey took on average 225 seconds (5–585), handling took on average 10 seconds and eating took on average five seconds. A mean of 0.25 (0–3) bivalves were consumed in a minute. Feeding bouts were observed for a mean of 26 (5–125) minutes (Table 2).

The most obvious prey items caught using this behaviour were marine polychaetes that were approximately the length of the oystercatchers' bill. The species identified by sampling at this site by Griffiths & Robinson (2004, 2005) were *Nephtys capensis* (65 mm) and *Glycera tridactyla* (60 mm) (Table 1). Small round prey were also caught, approximately 5 mm in length. *Eurydice longicornis, Pontogeloides latipes* and *Gastrosaccus psammodytes* were the macroflora present at the mid- to low-intertidal zone (Griffiths & Robinson 2004, 2005) (Table 1).

Nephtys has an energy value of 0.81 kJ per prey item, with the bird obtaining 0.20 kJ per minute feeding using this technique (Table 3). With a density of 50 *Nephtys* per m² of beach (Table 1), the energy available to the birds from *Nephtys* is 40.5 kJ/m² (Table 3).

When using this technique, oystercatchers occasionally found and ate large (approximately 40–50 mm length) *Donax serra* and Plough Shells (*Bullia* spp.). One bird was observed to specifically search for *Donax serra* in the swash zone. The bird ran out as the water drained, probing deeply (the whole bill was submerged in the substrate) for bouts of 5−10 seconds. Once successful, the bivalve was carried to the edge of the wet sand by one bill being inserted between the valves. The bill was inserted and the valves were pushed apart, the flesh was scissored away from the shell, and carried farther up the shore (away from other oystercatchers and Kelp Gulls), shaken and eaten in smaller pieces. When eating *Bullia*, the foot of the prey was held between the bill and scissored away from the shell. The flesh was then shaken loose before swallowing. Kleptoparasitism was observed by Kelp Gulls (described by Hockey 1980) and other oystercatchers. Four individuals were observed eating *Donax* or *Bullia* that had been caught when feeding on large polychaetes although only one bird was seen specifically feeding on large *Donax* (it was used in 0.3% of the total number of bird-foraging observations (Table 2)). Some birds caught *Donax* when feeding on worms but left them on the sand.

Searching took one minute, handling and carrying one minute, opening one minute and eating took two minutes. This technique was observed once, the bird ate one bivalve in 20 minutes observed (Table 2).

Large *Donax* have an energy value of 9.11 kJ per prey item, with the bird obtaining 1.82 kJ per minute feeding using this technique (Table 3). The large *Donax* were not sampled from the beach as they always occurred below the water level.

Kelp probing

This technique was used wherever the kelp lay, generally in the dry sand zone above the high tide mark and was therefore available at all states of the tide. There was always kelp on the beach, but more was present after rough sea conditions. The oystercatcher picked up and shook the kelp and then pecked up the prey that were exposed, or scattered. The bird would also probe deeply under the kelp (the whole bill was submerged in the sand), with the bill at an angle to the vertical to catch prey. It probed repeatedly before lifting its head approximately every five seconds. Birds would move from one piece of kelp to the next. Two birds in a pair would often feed together, with the one bird shaking the kelp and both catching the prey that scattered. It seemed to the observer that the one bird used the technique and the other bird took advantage of the available prey. This was noted regularly in a banded pair in which the same individual always shook the kelp. All observed birds used this technique. It was used in 12.5% of the total number of bird-foraging observations (Table 2). This technique was never used during strong winds as the birds generally escaped the wind-blown sand by sleeping or moving into the protected dune area.

Searching for prey took on average six seconds (0.5–59) ; this was made up of the time it took to move from one piece of kelp to the next and to lift and shake the kelp. The bird then pecked the prey up in quick succession; handling taking on average 0.5 seconds and eating on average 0.5 seconds. A mean of 8.35 (0–34) prey items were consumed in a minute. Feeding bouts were observed for a mean of 25.2 (5−170) minutes (Table 2).

Prey taken were approximately 10 mm long. The macrofauna identified at the mid- to high-intertidal zone by Griffiths & Robinson (2004, 2005) were *Euyridice longicornis, Exosphaeroma pallidum, Pontogeloides latipes, Excirolana natalensis, Talorchestia quadrispinosa* and *Urothoe grimaldii* (Table 1). *Tylos granulatus* and coleopteran and dipteran larvae are also associated with kelp (Bally 1981) and are also possible prey items.

On average the isopod and amphipod species have an energy value of 0.04 kJ per prey item, with the bird obtaining 0.33 kJ per minute feeding using this technique (Table 3). With a density of approximately 250 isopods per m^2 of beach (Table 1), the energy available to the birds from the isopod and amphipod species is 10.0 kJ/m^2 (Table 3).

A variation of this technique was seen when the birds probed under the plants at the base of the dunes. This was difficult to observe because the birds were often out of field of vision because the observer was also sitting in the dunes. It was difficult to see when the birds swallowed and the size of the prey caught. This technique was seen in strong south-easterly winds when the dunes provided some protection from the wind. There was regular evidence of this technique being used by the footprints and peck-holes around these plants; these signs were more common than expected from the number of observations and the possibility exists that the birds regularly used this technique at night. Possible prey items could be terrestrial species (beetles, terrestrial isopods) as well as *Tylos granulatus* and *Talorchestia quadrispinosa* occuring at this level (Bally 1981).

Other feeding techniques

Oystercatchers pecked small prey from the surface of the wet or damp sand. The prey items were too small to see with the telescope but the birds walked slowly along the beach and pecked regularly from the surface of the sand before swallowing. Searching took on average 4 seconds (0.5–29), handling on average 0.5 seconds and eating on average 0.5 seconds. A mean of 11.17 (2–32) prey items were consumed per minute (Table 2). This was observed as a separate foraging technique used for a mean of 10 (5–35) minutes, but also seen between bouts of other feeding techniques, or before beginning feeding using one of the more common techniques. It was used in 2.6% of the total number of bird-foraging observations (Table 2). Possible prey items include the amphipods and isopods listed above.

Birds were observed eating unidentified mussels that had been washed up in rough seas (0.8% of the total number of bird-foraging observations) and eating unidentified mussels and Goose Barnacles (*Lepas* sp.) on recently washed-up kelp (0.5% of the total number of bird-foraging observations) (Table 2). The mussels were picked up from the sand or off the kelp and carried to the damp sand, wedged in the sand for support, opened by pushing the valves apart, scissoring the flesh out and eating it. The Goose Barnacles were eaten directly off the kelp, but the technique used to extract the flesh was not directly observed.

One bird was seen stealing large *Donax serra* from Kelp Gulls after the bivalves were dropped onto the wet sand to open the shell, as described by Siegfried (1977) and

McLachlan *et al.* (1980). This behaviour was observed once (February 2005 at low tide); the bird actively used this as a foraging technique and ate two bivalves in this way, in a 30 minute time span. The bird stood on the beach watching the Kelp Gulls feeding, once the bivalve was dropped, it rushed in to grab the bivalve before the gull could swoop down to reach it. It then chased the gull away, took the bivalve and ate it. This is the first record of kleptoparasitism by African Black Oystercatchers of Kelp Gulls, although kleptoparasitism in the opposite direction is well-known (Hockey 1980).

One bird was observed feeding on prey on the surface of the water, although the prey were too small to see in the telescope. The bird walked in the water around some rocks, often submerged up to the keel, and pecking up prey from the water. The intake rate was 1–5 prey per minute and the bird fed for 90 minutes. The most likely prey is *Gastrosaccus psammodytes* present at the water's edge (Griffiths & Robinson 2004, 2005) (Table 1).

Discussion

Feeding techniques

Single probing

Hockey (1981b) described single probing when African Black Oystercatchers were feeding on *Donax serra* on sandy shores in the Eastern Cape. Hulscher (1976) termed this behaviour "single peck" for the Eurasian Oystercatcher *Haematopus ostralegus* feeding on cockles *Cardium edule* on intertidal flats on Schiermonnikoog in the Dutch Waddensee. He also stated that in general, the Eurasian Oystercatcher uses single pecking when foraging on superficial prey as well as on terrestrial prey such as earthworms (*Lumbricidae*), leatherjackets (Crane Fly *Tipula* spp. larvae) and caterpillars (Hulscher 1996). Lauro & Nol (1995) described "slow pecking" of Pied *H. longirostris* and Sooty *H. fuliginosus* Oystercatchers feeding on polychaetes on intertidal mudflats in Tasmania, Australia. All refer to the oystercatchers locating the prey visually before pecking or probing (Hulscher 1976, 1996, Hockey 1981b, Lauro & Nol 1995).

The African Black Oystercatcher at Koeberg beach used single probing when feeding on small polychaetes (*Scololepsis*) which were abundant. *Scololepsis* is a semi-sedentary species that migrates vertically in the sand but remains in the zone of retention (Bally 1981). In the March 2005 sampling (Griffiths & Robinson 2005), *Scololepsis* occurred at a level that was available to the birds at spring high tide. This prey item is therefore available throughout the tide. Single probing was also used when feeding on *Donax serra* measuring 20–30 mm length (juveniles) in the damp sand. On the west coast of South Africa, juvenile *Donax serra* migrate to stay in the shallow water while the adults remain sub-tidally (Bally 1981, Branch & Branch 1981). Single probing appeared to be using sight-location of the prey, as the probes generally resulted in obtaining prey although no visual cues of either main prey were apparent to the observer.

Multiple probing

Hulscher (1976, 1996) referred to this technique as "sewing" or multiple pecking, where it was used by the Eurasian Oystercatcher to locate deeper buried prey on intertidal flats on Schiermonnikoog in the Dutch Waddensee. Hockey (1981b) referred to this technique as "stitching" and the African Black Oystercatcher used it to locate the bivalve *Donax sordidus* on sandy shores in the Eastern Cape. Lauro & Nol (1995) described "fast pecking" of Pied and Sooty Oystercatchers feeding on crabs, snails and bivalves on intertidal mudflats in Tasmania, Australia. This technique is used at low prey densities as well as to touch-locate prey (Hulscher 1976, 1996, Hockey 1981b, Lauro & Nol 1995).

The African Black Oystercatcher at Koeberg beach used multiple probing when feeding on large polychaetes (*Nephtys* and *Glycera*), found in low densities in the wet sand (Griffiths & Robinson 2004, 2005). These polychaetes burrow in saturated fine-grained sand and migrate with the tidal movement (Bally 1981). Adult *Donax serra* of 40–50 mm length were also taken; these large bivalves have limited horizontal migration up and down the shore and generally remain subtidally (Bally 1981, Branch & Branch 1981). *Donax serra* occurs at low densities at this site (Griffiths & Robinson 2004, 2005). Plough Shells *Bullia* spp. were also taken but were absent in the sampling in both 2004 and 2005, although present in previous years (Griffiths & Robinson 2004, 2005). Multiple probing appeared to be using touch-location, as the bill probed repeatedly through the sand before obtaining prey. It was performed with the bill slightly open, possibly to increase the area available to locate prey.

Other feeding techniques

Kelp probing was used by all observed birds, although a degree of skill seemed to be needed in lifting and shaking the kelp. In a individually marked pair, only one bird performed this function, while both birds ate the scattered prey. Not all birds attempted searching for and eating bivalves (*Donax serra* and unidentified mussels on kelp). These suggest some specialization is needed for these techniques. Unfortunately, not enough data was collected to differentiate individually marked birds specialising on different techniques. Other techniques seemed opportunistic (surface pecking, eating washed-up mussels and stealing bivalves from Kelp Gulls).

Feeding specialization

There are currently 10 species of oystercatcher globally. There is little morphological divergence within the genus, but consistent differences in bill morphology between hard and soft diet specialists (Hockey 1996a, b). Birds having longer, thinner bills with pointed tips usually forage on soft prey, such as polychaetes; in contrast, birds having shorter, thicker bills with blunt tips usually forage on hard-shelled prey, such as mussels (Hockey & Underhill 1984, Hulscher 1985, Hulscher & Ens 1992, Durell *et al.* 1993, Lauro & Nol 1995, Ens *et al.* 1996a, Hockey 1996a, b, Sutherland *et al.* 1996). The dominant dietary components vary little between all oystercatchers in that those species which feed on rocky shores feed primarily on molluscs (mussels, limpets, gastropods and chitons) and those that feed on soft substrata feed primarily on bivalve molluscs and polychaetes (Hockey 1996b). There is considerable specialization on an individual level, although this is not absolute (Sutherland *et al.* 1996, Durell 2000, Sitters 2000).

The factors that have been reported to influence specialization of feeding behaviour in individual oystercatchers of all species are bill morphology, search speed, available prey, dominance of the bird, ease of learning the technique and the profitability versus risk trade-off. Birds in a particular habitat should, in theory, adopt the technique and take prey that gives a good trade-off between profitability of the prey and the risks involved in that particular prey species (Hulscher 1996, Sutherland *et al.* 1996, Zwarts *et al.* 1996a, b, Durell 2000). These factors are discussed below in relation to the African Black Oystercatcher on a Western Cape sandy shore.

Bill morphology

Bill morphology plays a major role in the feeding technique adopted (Hockey & Underhill 1984, Hulscher 1985, Hulscher & Ens 1992, Durell *et al.* 1993, Lauro & Nol 1995, Hulscher 1996, Sutherland *et al.* 1996, Durell 2000) especially on a long-term time frame. There is extensive literature on bill morphology (species and sexual dimorphism) affecting and being effected by feeding technique and hard or soft prey. The mean bill lengths of all oystercatcher species feeding on soft prey are 82 mm for males (SD 9 mm) and 88mm (SD 6 mm) for females and feeding on hard prey are 71 mm (SD 6 mm) for males and 78 mm (SD 4 mm) for females (Hockey 1996a, b). The African Black Oystercatcher male has the shortest average bill length, 63 mm (Hockey 1981a) of all the oystercatcher species (Hockey 1996a, b). Hockey & Underhill (1984) reported that male and female African Black Oystercatchers (on rocky shores) remove prey in differing proportions (both eat mussels but males take more limpets and whelks and females take more polychaetes and small unshelled items) based on differing bill morphology.

On the sandy beach at Koeberg, all observed birds, both males and females, foraged extensively on polychaetes and small crustaceans. Of the 10 adult oystercatchers caught on the sandy shore and measured, four had culmen lengths under 70 mm (Appendix 7 in Chapter 2), one of these birds was known to be male and two are likely to be males based on their weights (634 g and 621 g) (male birds mass range: 582–757 g, female birds mass range: 646–800 (Hockey 1981a)). These bill lengths are below the averages reported above (for birds feeding on soft prey) and are an intriguing result especially considering that in the Western Cape, 39% of all African Black Oystercatchers occur on sandy shores (Hockey 1983a). The birds with shorter bills are likely to be the birds which were proficient at foraging on *Donax serra,* although these techniques were rarely observed. The birds having longer bills are likely to be the birds that located large *Donax serra* but did not attempt to open them. It is also possible that some oystercatchers spend some time foraging away from their territories on rocky shores, which may account for the relatively short bills. It is unlikely however, that they spend large quantities of time away from their territories, as pairs were generally observed foraging together. More detailed observations are required to verify this hypothesis.

Search speed

Search speed has been found to influence the type of prey caught, while excluding other available prey from the diet (Ens *et al.* 1996a, Hulscher 1996, Sutherland *et al.* 1996). Search speed depends on conspicuousness of cues and prey density (Hulscher 1996). Sutherland *et al.* (1996) discusses the concept of an optimal search rate to maximise the intake rate, where the search rate for a cryptic species will be lower than for a conspicuous species. Birds can only search at one speed at a time; therefore some prey are effectively ignored. This was noted by Ens *et al.* (1996a): Eurasian Oystercatchers either searched slowly for *Macoma balthica* (a bivalve) or fast for *Nereis diversicolor* (a polychaete). The absence of visual cues or visibility influences search speed in that birds move more slowly when using touch location compared to visual location (Hulscher 1976, 1996, Sitters 2000). Density of available prey affects the type of locating technique used and therefore the search speed (Hulscher 1976, Zwarts *et al.* 1996a).

In the African Black Oystercatcher, a fast search speed was seen in single probing (based on visual location) for *Scololepsis* (present in high densities), while a slow search speed was seen in multiple probing (based on touch location) for *Nepthys* and *Glycera* (present in low densities). Both techniques were never observed in the same feeding bout. The difference in search speed and technique was also used when the oystercatchers were foraging for *Donax serra.* The smaller bivalves were located in the damp zone and therefore visual cues were present and visual location and a fast search rate were seen, however when the large bivalves were in the submerged sand and no visual cues were present, touch location and a slow search rate were seen. Hockey (1981b) also reported single probing of *Donax serra* as it occurred in higher densities than *Donax sordidus,* which was located through touch location and "stitching".

Available prey

The prey caught depends on the available prey in the birds' habitat (for example: prey activity at different times of tide, day or season, dominant prey species) (Hulscher 1976, 1996, Hockey & Underhill 1984, Bunshoeke *et al.* 1996, de Vlas *et al.* 1996, Ens *et al.* 1996a, Zwarts *et al.* 1996a, Sitters 2000).

This coastline supports low densities of *Donax serra* (Griffiths & Robinson 2004, 2005) and the oystercatchers therefore fed on the other prey species present in high numbers (compared to African Black Oystercatchers feeding mainly on *Donax* spp. on sandy shores in the Eastern Cape (McLachlan *et al.* 1980, Ward 1990)). The main available prey item at Koeberg was the polychaete *Scololepsis,* which is a sedentary species and accessible to the birds throughout the tide. There are numerous isopod, amphipod and terrestrial species available above the high-tide mark, especially associated with kelp. At low tide, larger polychaetes are also available (*Nephtys* and *Glycera*), as are *Donax serra* and numerous isopod and amphipod species. The oystercatchers can therefore feed throughout the tidal cycle and are not restricted by the tide height (Chapter 5) as reported extensively in the Eurasian Oystercatcher, as well as the African Black Oystercatcher feeding on rocky shores (Hockey & Underhill 1984, Hockey 1984b).

No observations were conducted at night-time, although there was evidence that birds had probably been feeding around the dune plants at night. Hockey (1984b) reported the period of time spent on foraging activity at night (by African Black Oystercatchers on a rocky shore) as 59% of the time spent on foraging activity during the day and birds were more likely to form communal roosts at night-time than during the day. This behaviour is attributed to a higher predation risk during the night than during the day. There are many nocturnal mammalian predators present at the study site (Chapters 2) that can take cover in the dune vegetation (also mentioned in Hockey 1984b), so this presumably plays a role and birds may prefer to spend the night on the exposed beach. At night-time, the feeding techniques used may differ due to lower visibility and although intake rates can still be high, touch-location of prey may be more energy costly than sight-location (for example Hulscher 1976, Sitters 2000). More detailed observations are required to establish the behaviour patterns of oystercatchers on sandy shores at night as well as the feeding techniques and prey caught during this time.

There was little variation between the prey species richness and abundance sampled between the summer and winter sampling periods (Griffiths & Robinson 2004) and therefore prey seem to be uniformly available throughout the year. There has been little change in the species and densities sampled during the 20 years of sampling at this site (Griffiths & Robinson 2004, 2005). There are no real climatic extremes at the site (temperatures ranged from 6.0–29.7°°C) and therefore little variation in prey species activity is expected.

<u>Dominance of the bird</u>

The habitat (and therefore the prey available) used by the bird may be influenced by the dominance of that individual (Sutherland *et al.* 1996, Durell 2000, 2003, Sitters 2000, Hockey 2001). Goss-Custard & Durell (1983, 1987) and Goss-Custard *et al.* (1982) referred to immature (subdominant) Eurasian Oystercatchers being displaced from preferred feeding territories by adult birds and Sitters (2000) observed subdominant Eurasian Oystercatchers either enduring high levels of interference at preferred feeding areas or feeding at less-profitable sites. Juvenile African Black Oystercatchers partially migrate to "nursery areas" which lie beyond the breeding range (Hockey *et al.* 2003) in order to avoid competition with adult oystercatchers on feeding territories because they are inefficient foragers (Hockey 2001).

At this site, only adult African Black Oystercatchers were observed feeding and no dominance or interference was seen to influence feeding. The birds were territorial and fed on their breeding territories throughout the year, so that there is no effect of feeding in flocks of birds where bird density comes into play (as in the Eurasian Oystercatcher during the non-breeding season). Aggression relating to territoriality as a behaviour type was seen as 0.2% occurrence (compared to feeding as 22.8% occurrence) from birds observed on the sandy shore (Chapter 5).

Ease of learning the technique

Some shorebird specializations are related to individual skills (Durell 2000). Safriel (1985) proposed that probing in soft surfaces for soft-bodied prey is a "primitive" feeding mode suggesting a lack of feeding specialization, hence the diversity of techniques and prey species caught. Hard-shelled prey items, however, are difficult to open and oystercatchers must use skill and force to extract the flesh (Hulscher 1996). Sutherland *et al.* (1996) stated that although some diets and feeding techniques may be intrinsically more difficult to learn than others, this is an insufficient explanation for specialization. African Black Oystercatchers attack only gaping mussels (on rocky shores) and therefore do not use the variety of feeding techniques used by other oystercatcher species (Hockey 1981b). This is attributed to the availability of large mussels, the small tidal range in southern Africa, mussel activity (gaping for most of the low tide) and high mussel density rather than to a difficulty in learning techniques (Hockey 1981b). Hockey (1981b) also referred to "specialist" birds that depredate whelks and winkles. The hardening of the bill as the birds mature may influence the way in which feeding develops in the first few years of an oystercatcher's life (Sutherland *et al.* 1996) and it may be a combination of this change, as well as learning behaviour, that results in the different feeding techniques (Durell 2003). Hockey (2001) noted that juveniles are inefficient foragers and migrate to areas with abundant, easily handled food and little competition from adults. Juveniles are less proficient in foraging ability compared to adult birds, but it is difficult to differentiate age-related feeding differences caused by learning, morphology and dominance (Wunderle 1991).

African Black Oystercatchers feeding on sandy shores did show differences in ability or willingness to attempt certain techniques and prey items. Some birds caught and discarded large *Donax serra*. This could possibly be a profitability versus risk trade-off decision, or it could be a lack of ability in not having learnt the technique for opening mussels. In one pair of oystercatchers, it was one bird which always shook the kelp and the mate fed on the scattered prey, this second bird may not have learnt this technique, or it may have been purely opportunistic.

The profitability versus risk trade-off

Feeding specialization can be seen as an individual strategy which is dependent on specific priorities and constraints (Durell 2000). Two risks associated with feeding are eating parasitized prey and damaging the bill (even resulting in death) (Hulscher 1996, Sutherland *et al.* 1996, Sitters 2000). Risks involved in certain feeding techniques may also include kleptoparasitism by other birds (Hockey 1980). Profitability of prey depends on the biomass consumed relative to the time spent handling the prey (Zwarts *et al.* 1996a, b). Prey that is large, soft-bodied, swallowed whole and superficial are therefore more profitable than prey that is small, hard-shelled, that must be opened before feeding and deeply buried (Zwarts *et al.* 1996a, b). Intake rates depend on search time and profitability of the prey (Zwarts *et al.* 1996a, b). The birds should, in theory, adopt the technique and take prey that gives a good trade-off between profitability of the prey and the risks involved in that particular prey species (Hulscher 1996, Sutherland *et al.* 1996, Zwarts *et al.* 1996a, b, Durell 2000).

African Black Oystercatchers feeding on sandy shores did seem to conform to the principles outlined above; there was a large prevalence of shallowly-buried polychaetes and superficial small crustaceans in the diet and an unwillingness to eat the deeply-buried hard-shelled *Donax serra,* although the large *Donax* had a high energy value. It is not clear why so few birds were seen foraging on the small *Donax,* because it has a high energy value and a high density on the beach. Zwarts *et al.* (1996a) reported that large prey can be profitable even when 80% of the feeding time is spent in searching. The high profitability of larger sized prey, even when there is a slow search speed, explained why many birds foraged on large polychaetes (*Nephtys* and *Glycera*) even at a low feeding rate. This is seen in the high energy value of these polychaetes compared to the *Scololepsis.* The dominance of *Scololepsis* in the diet, although a small prey item with a low energy value, can be explained by the fact that it is profitable (being soft-bodied and shallowly-buried), has no risks attached to it (soft-bodied, unknown levels of parasitism, no kleptoparasitism was observed) and occurs at a high density enabling a high search speed. It is also available throughout the tide and year, although nocturnal feeding is unknown.

Conclusion

African Black Oystercatchers foraging on sandy shores of the Western Cape, where there is a low density of the main prey item previously reported (*Donax* species), feed mainly on polychaetes (*Scololepsis, Nephtys* and *Glycera*) during the daytime. They also feed on small crustaceans (especially associated with the drift-line kelp) and *Donax serra.* Bill morphology did not seem to play as important a role as reported extensively although probably did influence some individual feeding specialization. The sandy shore offers a diverse array of possible prey items throughout the tidal cycle and although specialization was present (particularly for an individual bout of feeding), the adaptable oystercatchers used a variety of techniques and opportunistic behaviours to utilise the available prey.

Further studies are needed to fully elucidate and quantify the feeding behaviour and prey items of African Black Oystercatchers on the Western Cape sandy shores. The studies needed are (1) night-time observations to quantify time spent feeding at night as well as different techniques used and prey caught, (2) continuous observations of individually marked birds in pairs to better describe male and female time budgets, feeding techniques and prey caught and (3) energy budgets of oystercatchers feeding on sandy shores to quantify the relative amount of prey species caught compared to energy requirements.

Acknowledgements

Eskom Koeberg Nuclear Power Station provided access to the study site; we especially acknowledge the helpfulness of Gert Greeff and Hilton Westman, nature conservators at the site. The Meteorological office at Eskom's Koeberg Nuclear Power Station provided meteorological data and the hydrographer at the South African Navy provided tidal data. Charles Griffiths and Tamara Robinson of the Marine Biology Research Institute at the University of Cape Town provided access to the sampling results done at Koeberg, as well as much help and information. Charles Griffiths and Humphrey Sitters commented on drafts. The project was supported by the National Research Foundation, the Earthwatch Institute, and the University of Cape Town Research Committee.

Table 1. Summary of macrofaunal prey species sampled at Koeberg Nuclear Power Station beach in 2004 (Griffiths & Robinson 2004) and feeding technique used when depredated by African Black Oystercatchers. Prey species information from Bally (1981), Branch & Branch (1981) and Branch *et al.* (1994).

Species	Max length (mm)	Max densities per m²	Position on transect line above low tide (0 m). August 2004	Prey behaviour	Swash zone	Wet sand	Damp sand	Dry sand	Feeding technique
Polychaetes									
Scololepsis squamata	20	9 584	5–50m	Semi-sedentary, migrates vertically		✓	✓		Single probing
Nephtys capensis	65	53	0–10m	Migrate horizontally and vertically	✓	✓			Multiple probing
Glycera tridactyla	60	16	5–10m	Migrate horizontally and vertically	✓	✓			Multiple probing
Isopods									
Eurydice longicornis	9	256	0–55m	Migrates horizontally, forage in water	✓	✓	✓		Single probing, multiple probing, kelp probing
Exosphaeroma pallidum	10	21	65–70m	Migrates horizontally, forage in water			✓		Single probing, kelp probing
Pontogeloides latipes	9	48	25–80m	Migrates horizontally, forage in water		✓	✓	✓	Single probing, multiple probing, kelp probing
Excirolana natalensis	9	21	40–80m	Migrates horizontally, forage in water			✓	✓	Single probing, kelp probing
Amphipods									
Talorchestia quadrispinosa	20	176	45–80m	Air-breathing scavenger, burrows dry sand, feeds on kelp at night			✓	✓	Kelp probing
Urothoe grimaldii	6	176	60–80m	Burrows and feeds in sand			✓	✓	Single probing, kelp probing

Mysids									
Gastrosaccus psammodytes	12	5	0m (January 2004)	Surf zone: highly mobile in sand and water	✓	✓			Single probing, multiple probing
Bivalve molluscs									
Donax serra	>40	165	15–25m	Adults sub-tidally, limited movement	✓				Multiple probing
	<40			Juveniles migrate horizontally		✓	✓		Single probing

Table 2. Feeding techniques used by African Black Oystercatchers when feeding on a South African West coast sandy beach at the Koeberg Nuclear Power Station.

	Single probing	**Multiple probing**	**Kelp probing**	**Surface pecking**	**Single probing**	**Washed up mussels**	**Kelp mussels**	**Stealing bivalves**	**Multiple probing**
Prey	Small polychaete	Large polychaete	Various	Various	Small *Donax serra*	Unidentified mussels	Unidentified mussels, *Lepas.* sp.	Large *Donax serra*	Large *Donax serra*
Zone	Wet sand, damp sand	Swash, wet sand	Dry sand	Wet sand, damp sand	Damp sand	Wet sand	Damp sand	Wet sand	Swash
Searching time (seconds)	6 (1–60)	225 (5–285)	1 (0.5–59)	4 (0.5–29)	50 (10–230)	60	30	510 (60–660)	60
Handling time (seconds)	1	10	0.5	0.5	7	60	60	60	60
Opening time (seconds)	-	-	-	-	2	60	90	60	60
Eating time (seconds)	1	5	0.5	0.5	1	120	120	120	120
Total time (seconds)	8 (3–62)	240 (20–600)	2 (1.5–60)	5 (1.5–30)	60 (20–240)	300	300	750 (300–900)	300
Quantity prey consumed per minute	7.82 (0–20) n=132	0.25 (0–3) n=203	8.35 (0–34) n=51	11.17 (2–32) n=6	1.00 (0–3) n=11	0.20 (0–1) n=8	0.20 (0–1) n=15	0.08 (0–1) n=10	0.20 (0–1) n=5
Length feeding bout observed (minutes)	32.5 (5–110) n=46	26.0 (5–125) n=45	25.2 (5–170) n=21	10.0 (5–35) n=15	13.0 (5–30) n=5	10.0 (5–20) n=4	7.5 (5–10) n=4	7.5 (5–15) n=4	20 n=1
Percentage of total number of birds observed foraging in 5 minute periods (n=1413)	47.0%	35.0%	12.5%	2.6%	0.9%	0.8%	0.5%	0.4%	0.3%

Table 3. Relative profitability of prey species on a West coast sandy beach at the Koeberg Nuclear Power Station. Calorific values and dry mass values for *Donax* were obtained from McLachlan & van der Horst (1979), calorific values for *Scololepsis, Nephtys* and average values for isopod and amphipod species, as well as a conversion ratio of wet mass to dry mass were obtained from Field *et al.* (1980). Wet mass values for *Scololepsis, Nephtys* and average values for isopod and amphipod species were obtained from C.L. Griffiths *in litt*.

Prey species	**Calorific value (kJ/g)**	**Dry mass (g)**	**Prey Energy value (kJ)**	**Quantity prey consumed per minute**	**Energy consumed per minute**	**Maximum density of prey per m² of beach**	**Energy available on beach (kJ/m²)**
Donax (25 mm)	18.84	0.1025	1.93	1.00	1.93	160	308.8
Donax (45 mm)	18.84	0.4836	9.11	0.20	1.82	No data	
Scololepsis	19.68	0.0006	0.01	7.82	0.08	9 500	95.0
Nephtys	19.68	0.0411	0.81	0.25	0.20	50	40.5
Isopod and amphipod species	9.98	0.0043	0.04	8.35	0.33	250	10.0

Chapter 5

Activity Patterns of African Black Oystercatchers *Haematopus moquini* on sandy and rocky shores at Koeberg Nuclear Power Station

Introduction

The range of African Black Oystercatcher *Haematopus moquini* extends along the coast of South Africa and Namibia (Summers & Cooper 1977, Hockey 1983a, Martin 1997, du Toit *et al* 2003) and the species is classified as "near-threatened" both in South Africa and globally (Underhill 2000, BirdLife International 2004). Adults are territorial and stay on their breeding territories throughout the year (Summers & Cooper 1977, Hockey 1983a, 1984b, du Toit *et al* 2003). The behaviour of the African Black Oystercatcher has been studied on rocky shores in the Western Cape (Hockey 1984b) and on sandy shores in the Eastern Cape (Ward 1990), where feeding, and therefore other behavioural activities, are strongly tide dependent. The main prey species on the Koeberg sandy shore, are available to the birds throughout the tide (Chapter 4), indicating that oystercatcher behavioural activities may be different to those recorded elsewhere. Koeberg Nuclear Power Station and Nature Reserve has the advantage that rocky and sandy shores are in close proximity and behavioural data can be collected at both shore types in similar conditions, enabling comparison between the two areas.

In this chapter, the diurnal activity patterns and behaviour of African Black Oystercatchers on a sheltered rocky shore and on an exposed sandy beach are evaluated throughout the annual cycle and the full tidal regime. Previous studies on African Black Oystercatchers have used time budgets in relation to tide variables (Hockey 1984b, Ward 1990). Ghosh *et al.* (2003) studied the effects of tide and weather on behavioural activities on the Eurasian Oystercatcher *H. ostralegus* while Kersten (1996) studied time and energy budgets of the Eurasian Oystercatcher during the breeding cycle. None of these studies provided a continuous prediction of activity patterns with an extended set of explanatory variables. We describe, in considerable detail, a statistical approach to the analysis of behavioural data in relation to observed explanatory variables. This study is, in part, therefore, methodological.

In this chapter, we aim to model activity patterns of the African Black Oystercatcher using various tide and weather variables and comparing the birds behaviour on sandy and rocky shores. Intensive behavioural observations were collected and analysed using a generalized linear model.

Methods

Fieldwork methods

Observations were carried out from June 2003 until June 2005 at two sites at Koeberg Nuclear Power Station (33° 40'S, 18° 25'E), Western Cape, South Africa. Chapter 2 contains a full description of this study area. One site was a section of artificial rocky shore within the harbour area. Birds were observed at a distance of c. 10–40 m from inside a car and were not disturbed by its presence. Constant, but generally low-intensity, human disturbance was caused by harbour personnel at the site but the birds seemed conditioned to it (Chapter 3). Observations continued at these times unless the disturbance caused most of the birds to leave the area. The second site was a section of sandy shore; observations were made from a vantage point on a dune overlooking the beach at a distance of c. 10–80 m and the birds were not disturbed by the presence of the observer. There was infrequent human disturbance on this beach. These two sites were used for the study period and the same birds observed. During the observations 2–12 birds were present. The two study sites were less than 1 km apart.

Instantaneous scans (Altmann 1974) were made every two minutes and the behavioural activities of all birds within vision (using 8×40 binoculars) were noted. The total number of times each activity was performed by the birds during 10 scans at two-minute intervals was recorded, so that each observation period lasted 20 minutes. Observations were continued for time periods of up to 3 hours, or nine observation periods. Activities of individual birds were recorded for all the birds visible, not on specific focal birds, so that birds departing, arriving or moving out of sight did not impact the observations except to alter the total number of observations in that period of time.

Behavioural activities were classified as foraging (including searching, handling and swallowing), standing (standing on one or two legs with head in normal position and alert), sleeping (standing on one or two legs with the head tucked between the wings), lying down (lying down with legs folded beneath body and head either upright or tucked between wings), incubating (lying down on eggs and head either upright or tucked between wings), preening (all preening movements, scratching of head with feet, shaking movements, including short breaks of 1-2 seconds between preening activities and bathing, ie flapping wings in water and covering back with water), walking (not while foraging), flying, piping (generally pairs with head down and beaks open, walking along-side each other and calling), aggression towards other oystercatchers (where aggression was seen as a charge to chase the other bird away, either walking or flying), aggression towards birds of other species and other behaviour activities, such as mating and investigating objects. Aggression towards other oystercatchers generally revolved around territorial disputes where birds initially stood alert, then approached each other, accompanied by a large amount of piping from one or more pairs, head-bobbing, pseudosleeping (described by Makkink (1942)), picking-up stones (described as "throwing straws" by Makkink (1942) and "object toss" by Schmechel (2001)) and chasing. Both pseudo-sleeping and "throwing straws" were explained by Tinbergen (1952) as displacement activities.

No observations were conducted at night-time and therefore activity patterns for the whole day-night cycle cannot be evaluated. Observations were conducted throughout the year but there was little breeding activity and insufficient data accumulation in both the 2003/2004 and 2004/2005 breeding seasons (Chapter 2) to compare activity budgets between the breeding and non-breeding periods. The records of incubating birds and adults rearing chicks were therefore not representative samples and apart from a mention in Table 1 are not analysed further.

Description of rarely documented behaviour in the African Black Oystercatcher is also included in this chapter. For example, studying the process resulting in divorce is time-consuming and difficult (Bruinzeel 2004) and therefore we took the opportunity of documenting this behaviour observed while conducting other observations.

Statistical Methods

The data for each behaviour during a 20-minute observation period were regarded as having binomial distribution (the count of the number of times a particular behaviour occurred while a total number of behaviours was observed). It is therefore appropriate to analyse them using a generalized linear model with a binomial distribution and logistic link function (McCullagh & Nelder 1983, Crawley 1993 and see Underhill *et al.* 1992 for a similar application of generalized linear models). A suite of explanatory variables were considered as candidates to model each particular behaviour. These models were fitted using GenStat 8 (GenStat Committee 2005).

The height of the tide at the central time of each observation period was determined in two ways. Firstly, by linear interpolation from the standard tide tables which provide predicted hourly heights above chart datum (South African Navy 2003, 2004, 2005). Secondly, we assumed that the line of tide heights from the high (or low) tide preceding the observation period to the low (or high) tide following it could be described by a trigonometric sine curve. Suppose the high tide had predicted height H above chart datum and the low tide had predicted height L above chart datum, and the time between the high tide and low tide was T hours; these values were obtained from the standard tide tables (South African Navy 2003, 2004, 2005). There are two situations: the observation time follows high tide or it follows low tide. The first step is to convert time from (or to) high tide to an angle θ, in such a way that at high tide the angle is 0° and at low tide it is 180°. If the preceding tide was a high tide and the prediction of tide height is to be made at time t hours after high tide, then $\theta = 180 \times t/T$, and the predicted height at this time is given by $h = 0.5 \times (H-L) \times \cos(\theta) + L + 0.5 \times (H-L)$, with analogous formulae for the height t hours before high tide. The rate r at which the tide is rising or falling is given by the derivative of h with respect to t, $r = -0.5 \times (H-L) \times \sin(\theta)$. We used the height h, the rate r, and the interaction rh between them as explanatory variables. If the rate of change term is significant in a model, it means that the behaviour being investigated depends not only on the absolute height of the tide, but also on how close the height is to high tide; ie it allows behaviour to be modelled differently on spring tides and neap tides. If the interaction term is significant in a model, it means that the behaviour being investigated does not occur symmetrically on outgoing and incoming tides. We used the second method to predict tide heights, largely because this approach enabled the rate and interaction variables to be defined more precisely than would be possible by linear interpretation of the hourly tide heights. These trigonometrically predicted heights did not differ from the interpolated heights from the tide tables by more than 4 cm, which is far less than the deviation in the level of the sea caused by fluctuations in atmospheric pressure (c. 1 cm per millibar; South African Navy 2004).

More subtle effects of tide were modelled using a Fourier analysis approach, as used for example to model daily rainfall probabilities (Zucchini & Adamson 1984) and to model seasonality of occurrence (Underhill *et al.* 1992, Harrison *et al.* 1997). Besides the first "harmonic", which describes tide height with a cosine curve, we used the second and third harmonics to enable the model to fit subtle departures from the cosine curve. Fuller details of the approach are contained in Underhill *et al.* (1992).

We also considered daylength D as an explanatory variable. At the latitude of Koeberg, the equation $D=12.1031 - 0.3681\times\sin(\alpha) + 2.1919\times\cos(\alpha)$, where α is the day of the year, starting with 1 January as day 1 and 31 December as day 365, expressed as an angle, $\alpha=360\times(\text{day of the year})/365$, provides an estimate of daylength correct to within five minutes throughout the year. This equation was derived by regression from local tables of times of sunrise and sunset (South African Navy 2003, 2004, 2005). The derivative of this expression with respect to α provides an estimate of the rate of change of daylength: $dD/d\alpha= 0.3681\times\cos(\alpha) - 2.1919\times\sin(\alpha)$. If $dD/d\alpha$ is a significant explanatory variable, it means that the way the behaviour is related to daylength is different when daylength is increasing (spring) compared with when it is decreasing (autumn).

Meteorological variables were obtained from the Meteorological Office at Eskom's Koeberg Nuclear Power Station. We used wind speed w, temperature t, their squares w^2 and t^2, and their interaction wt as explanatory variables, along with variables such as time of day and time of day squared (where midday was defined as time 0), so that the time of day variable was negative in the morning and positive in the afternoon. Observations were not made during rain, so the impact of rain on behaviour was not quantified. Other potential weather variables, which incorporated wind direction, and components of wind speed by direction were also considered, but were not statistically significant, and are not described further.

In the generalized linear models, explanatory variables were entered successively into the model. For a variable to be accepted into the model, it needed both to be statistically significant using the conventional model selection approaches, and it needed to reduce the value of the Akaike Information Criterion (AIC). An exception was that the "harmonics", the pairs of sine and cosine terms were entered in pairs, as recommended by Zucchini and Adamson (1984). With the variables windspeed, temperature and time, if the squared variable was significant, we also automatically included the variable itself. We express the fit of the model using the concept "percentage of deviance explained", as calculated by Genstat 8 (Genstat Committee 2005). For each of the behaviours, we provide the percentage deviance explained when tide height is the only explanatory variable, when the model contains all significant explanatory variables related to tide, and the best model we found with all significant explanatory variables and the minimum (AIC). We tabulate the detailed results for this model.

Tide activity plots were generated from the predicted proportion of birds on each behaviour activity during spring, average and neap tides, with other explanatory variables taken at average values (Figures 1 and 2). For ease of interpretation, the behaviours are shown over two full tide cycles. The typical spring tide had mean high and low tide sea levels of 1.74 m and 0.25 m; a typical neap tide had mean high and low tide sea levels of 1.26 m and 0.70 m; the average tide had mean high and low tide sea levels of 1.50 m and 0.47 m (South African Navy 2005). The effects of the tide can be visualised for each behaviour on the rocky (Figure 1) and the sandy (Figure 2) shores.

Contour plots were generated to visualise the effects of both windspeed and temperature on the proportions of each behaviour, with all other explanatory variables set at average values. Figures 3a and 4a show all the observed combinations of windspeed and temperature on the rocky and sandy shores respectively, contained within a convex hull (Green & Silverman 1979). Both figures show a range in windspeed values of 0−10 m/s and temperature values of 3−27 °C. There were gaps in the data around the periphery of the convex hull; in particular the combination of cool temperatures and high windspeeds never occurred. Contour plots portray the modelled interaction between windspeed and temperature on the behavioural activity. Figures 3b−f and 4b−f provide diagrammatic contour plots of the relationship between temperature and windspeed; the darker shades represent combinations of temperature and windspeed which lead to increases in the behaviour activity. The scale of the plots is in units of probability; ie the logistic values in which the generalised linear modelling took place were back-transformed to probabilities. The contours are at equal intervals; however these intervals are relative, rather than absolute. This causes no loss of generality, because interactions between wind and temperature and the other explanatory variables were not included in the models. These plots should not be interpreted beyond the limits of the convex hull, because this involves extrapolation beyond the combinations of temperature and windspeed that were actually observed.

Results

A total of 265 hours of observations were undertaken (795 observation periods) of which 383 observation periods were on the rocky shore and 412 on the sandy shore. These spanned the full range of tidal conditions, and were evenly spread throughout the year. The numbers of separate behaviours (on individual birds) which were observed were 25 365 and 30 483 on the rocky and sandy shores, respectively (Table 1). On both rocky and sandy shores, the most frequently observed behaviours were feeding (24% and 23%, respectively), standing (18% and 13%), sleeping (18% and 26%), lying (16% and 19%) and preening (18% and 13%); these five behaviours accounted for more than 90% of all observations on both shore types (Table 1). The results from the generalized linear modelling focus mainly on these behaviours. For the other behaviours observed, the results of the modelling are tabulated and discussed briefly.

Generalised linear model

Feeding

More time was devoted to feeding than to any of the other behaviours; on rocky shores, 24% of all the behavioural observations were of birds feeding; on sandy shores it was 23% (Table 1).

In the best models we found for feeding behaviour, the explanatory variables in the final model accounted for 58% of the deviance on the rocky shore, and for 30% on the sandy shore (Table 2). On the rocky shore, tide height alone was the key explanatory variable, accounting for 55.2% of the deviance (95% of the deviance accounted for), whereas on the sandy shore, it accounted for 9.2% of the deviance (31% of the deviance accounted for) (Table 2). The inclusion of the two further tide-related explanatory variables increased the percentage of deviance explained to 57.4% and 17.0% on rocky and sandy shores, respectively (Table 2). This result implies that the tides are the main factor controlling the feeding patterns of African Black Oystercatcher on this section of rocky shore, whereas this is not the case for the sandy shore, where the tides play a relatively small role, and where our explanatory variables account for less than a third of the total deviance.

The impact of the tidal explanatory variables, with the remaining explanatory variables set at average values, on the percentages of each behaviour type on the rocky shore is represented in Figure 1. On the rocky shore, at low tide at spring tide, the model predicted that 60% of birds were feeding, whereas 35% fed at low tide at neap tide. At high tide, the estimated proportions feeding were 1.5% at spring tide, and 8% at neap tide. At spring tide, feeding almost ceased for the four hour period centred on high tide. The interaction between the tide height and the change in tide height causes a slight asymmetry in the pattern of feeding relative to low tide. The model suggested that on rocky shores, more feeding occurred on the falling tide and peaked an hour before low tide.

On rocky shores, the explanatory effects of all the other variables were relatively small with a modest increase in the percentage of deviance explained from 57.4% to 58.4% (Table 2). Both daylength and the change in daylength were statistically significant explanatory variables (Table 2). The coefficient for daylength had a negative sign, indicating that a larger proportion of birds were feeding when the daylength was short, i.e. during winter. The coefficient for change in daylength had a negative sign, indicating that more birds were feeding when daylength was decreasing, i.e. during autumn. Temperature, windspeed, their squares and their interaction were also significant contributing factors (Table 2). The quadratic nature of the significant terms involving windspeed and temperature suggested that, with all other explanatory variables held constant, there is an optimal temperate and windspeed at which there is a peak proportion of birds feeding (Figure 3b); the peak lies at 20°C and a windspeed of 4.4 m/s. The diagrammatic contour plot of the relationship between temperature and windspeed suggested a generally inverse relationship between these two variables, and that the "summit" of the "hill" showing this relationship was more of a "plateau" than a "pinnacle" (Figure 3b). This contour plot needs to be interpreted in relation to the convex hull of observed combinations of temperature and windspeed (Figure 3a); extrapolation beyond the convex hull is likely to be misleading. However, the model did also suggest that less birds were feeding in hot and windy as well as cool and calm conditions (Figure 3b).

Time of day and its square were also significant variables (Table 2). The quadratic showed that, keeping all other explanatory variables constant, feeding on rocky shores peaked in the early morning and late afternoon and estimated the minimum at 11h50; this follows from the property that the minimum or maximum value of the quadratic equation ax^2+bx+c is at $-b/2a$, in this case at $-0.00716/2\times0.02022=-0.18$, ie 0.18 of an hour (about 10 minutes) before noon.

The impact of the tidal explanatory variables, with the remaining explanatory variables now set at their average values, on the percentages of each behaviour type on the sandy shore is represented in Figure 2. On the sandy shore, and especially at neap tide, the tide height had less influence on the proportion of birds feeding than on the rocky shore. Through the tide cycle at neap tide, the proportion feeding ranged from a minimum of 15% to a maximum of 40% of the birds feeding. At spring tide, there was a greater range, from a minimum of 7% to a maximum of 55% of the birds feeding. Feeding activity peaked an hour before low tide and reached a minimum two hours after high tide with more birds feeding on the falling tide but a proportion of birds continued to feed during the rising tide.

On the sandy shore, the pattern was different to that on the rocky shore. The non-tidal variables increased the percentage of deviance explained from 17.0% to 29.6% (Table 2). As on the rocky shore, both daylength and the change in daylength had negative coefficients (Table 2) indicating that birds were feeding more intensively during autumn and winter. The striking difference between the rocky and sandy shores was the effect of the two weather variables, temperature and windspeed. The interaction between the two variables had a negative coefficient in the regression model (Table 2), indicating that when it was both hot and windy the proportion of time devoted to feeding decreased disproportionately. Figure 4b shows the diagrammatic contour plot of the relationship between the proportion of birds feeding in relation to the fitted temperature and windspeed variables. The general pattern is similar to that on the rocky shore (Figure 3b) in that there is also an inverse relation between the variables, with a larger proportion of birds feeding in warm temperatures in relatively calm wind conditions, and *vice versa*. The overall summit of the hill depicting the relationship lay outside the convex hull of observed temperatures and windspeeds, at 9°C and 9.2 m/sec. For a selection of combinations of these two explanatory variables within the convex hull, the model suggests that at a temperature of

25°C, the windspeed at which the largest proportion of birds were feeding was 3.2 m/s; at 20°C, it was 5.2 m/s; and at 15°C, it was 6.8 m/s (Figure 4b).

Time of day and its square were also significant variables (Table 2). The quadratic showed that, keeping all other explanatory variables constant, feeding on sandy shores peaked at an estimated 14h40.

Standing

On rocky shores, 18% of behavioural observations were of birds standing; on sandy shores it was 13% (Table 1). The explanatory variables in the model for standing accounted for 20% of the deviance on the rocky shore and 7% of the deviance on the sandy shore (Table 3). Thus, on the sandy shore, although some of the explanatory variables (tide, time of day and weather) were formally statistically significant (Table 3), they were not good predictors of the proportion of birds standing.

On the rocky shore, the tidal variables together accounted for 1.9% of the deviance and the remaining variables increased the percentage of the deviance accounted for to 20.0% (Table 3). More birds were standing at low tide and with a falling tide (Table 3, Figure 1). More birds were standing with long days and decreasing daylength, i.e. in summer and autumn (Table 3). Temperature and windspeed variables interacted together so that more birds were found to stand in conditions when it was both cool and calm and hot and windy (Figure 3c). Time of day and its square were also significant variables (Table 3). The quadratic showed that, keeping all other explanatory variables constant, standing on rocky shores peaked at an estimated 10h30.

Sleeping

On rocky shores, 18% of behavioural observations were of birds sleeping, on sandy shores it was 26% (Table 1). The explanatory variables accounted for 45% of the deviance on the rocky shore, and for 39% on the sandy shore (Table 4).

On the rocky shore, tide height alone accounted for 33.1% of the deviance, the other tidal variables increased this to 35.4% and the remaining explanatory variables increased the proportion of the deviance accounted for to 44.6% (Table 4). More birds were sleeping at high tide and a falling tide (Table 4). At spring tide, there were few birds sleeping during the four-hour period centred on low tide but 50% of birds were sleeping an hour after high tide (Figure 1c). At the neap tide, this effect was less extreme with 30% sleeping an hour after high tide (Figure 1a). More birds were sleeping when the days were short and when the daylength was increasing, i.e. in winter and spring (Table 4). More birds were sleeping in conditions of both low temperatures and in high winds (Table 4, Figure 3d). Time of day and its square were also significant variables (Table 4); the quadratic showed that, keeping all other explanatory variables constant, more birds were sleeping in the morning with an estimated minimum at 16h00.

On the sandy shore, tide height accounted for 13.2% of the deviance, the other tidal variables increased this to 16.9% and the remaining variables increased the proportion of the deviance accounted for to 39.1% (Table 4). More birds were sleeping at high tide and when the tide was rising (Table 4). The proportion of birds sleeping at a sping tide was at a maximum between four hours before and three hours after high tide (Figure 2c). More birds were sleeping at low temperatures and low windspeed (Table 4, Figure 4d). Time of day and its square were also significant variables (Table 4); the quadratic showed that, keeping all other explanatory variables constant, more birds were sleeping in the early morning and late afternoon, with an estimated minimum at 13h00.

Lying

On rocky shores, 16% of behavioural observations were of birds lying; on sandy shores it was 19% (Table 1). The explanatory variables accounted for 33% of the deviance on the rocky shore, and for 40% on the sandy shore (Table 5).

On the rocky shore, tide height accounted for 17.5% of the deviance, the other tidal variables increased this to 24.3% and the remaining variables increased the proportion of the deviance accounted for to 33.2% (Table 5). A larger percentage of birds were lying over the high tide period than during low tide (Table 5). At a spring tide, 33% of birds were lying an hour before high tide, and more birds were lying on the rising tide (Figure 1c). The model suggested that more birds were lying when the days were short and also when daylength was increasing, i.e. in winter and spring (Table 5). At all windspeeds, the proportion of birds lying was a maximum when the temperature was about 21°C; at this temperature the model suggested that fewest birds were lying when the windspeed was about 5 m/s and increased for both lower and higher windspeeds (Figure 3e). Time of day and its square were also significant variables (Table 5); the quadratic showed that, keeping all other explanatory variables constant, lying on rocky shores peaked at an estimated 13h00.

On the sandy shore, tide height accounted for 8.6% of the deviance, the other tidal variables increased this to 17.5% and the remaining variables increased the proportion of the deviance accounted for to 39.5% (Table 5). More birds were lying when the tide was high and on a falling tide (Table 5). There was a maximum of 50% and 40% of the birds lying two hours after a spring and a neap high tide respectively (Figure 2). More birds were lying in warm and calm conditions (Figure 4e). More birds were lying when the days were long and with an increasing daylength, i.e. in summer and spring (Table 5). Time of day and its square were also significant variables (Table 5); the quadratic showed that, keeping all other explanatory variables constant, lying on sandy shores peaked at an estimated 13h00.

Preening

On the rocky shore, 18% of behavioural observations were of birds preening; on sandy shores it was 13% (Table 1). The explanatory variables accounted for 21% of the deviance on the rocky shore, and for 19% on the sandy shore (Table 6).

On the rocky shore, tide height accounted for 1.9% of the deviance, the other tidal variables increased this to 3.7% and the remaining variables increased the proportion of the deviance accounted for to 21.3% (Table 6). More birds were preening when the tide was high and when the tide was rising (Table 6, Figure 1). The model suggested that more birds were preening in winter and in autumn (Table 6). More birds were preening at low temperatures and low windspeed (Figure 3f). Time of day was also a significant variable. Time was entered into the model linearly with a positive sign (Table 6), suggesting that preening behaviour increased through the day.

On the sandy shore, tide height accounted for 5.5% of the deviance, the other tidal variables increased this to 8.1% and the remaining variables increased the proportion of the deviance accounted for to 18.8% (Table 6). Birds preened more when the tide was low and when the tide was rising (Table 6, Figure 2). The model suggested that more birds were preening in winter and in autumn (Table 6). The interaction between temperature and windspeed and their effect on the amount of birds preening is represented in Figure 4f. As on rocky shores, birds preened more at low temperatures and at lower windspeeds.

Other behaviour activities

There was striking difference in the frequency with which birds were observed walking on rocky shores (420 observations, 1.7%) and sandy shores (1161 observations, 3.8%) (Table 1). (This behaviour excluded walking while searching for food; see Methods). The explanatory variables accounted for 3.2% of the deviance on the rocky shore with the only variable having statistical significance being tide height (Table 7). More birds were walking at low tide. The explanatory variables accounted for 6% of the deviance on the sandy shore (Table 7). Tide height and other tide variables, temperature and wind were all significant factors (Table 7). On both types of shore the given variables played a small role in determining the conditions under which the birds were walking.

Flying accounted for 1.7% and 2.0% of the behavioural observations on the rocky and sandy shores respectively (Table 1). The explanatory variables accounted for 18% of the deviance on the rocky shore, and for 19% on the sandy shore (Table 8). On the rocky shore, the tidal variables accounted for 5% of the deviance; more birds were flying when the tide was low and was falling (Table 8). This model also suggested that more birds were flying in summer and spring. Temperature, windspeed and time of day were all significant variables (Table 8). On the sandy shore, the explanatory variables other than tide height accounted for most of the deviance accounted for in the fitted model (Table 8). The model suggests that more birds were flying when the days were long i.e. in summer (Table 8). Temperature, windspeed and time of day variables were significant (Table 8).

Piping was recorded infrequently, but more on the sandy shore (334 observations, 1.1%) than on the rocky shore (126 observations, 0.5%) (Table 1). The available explanatory variables accounted for 10% of the deviance on the rocky shore, and for 9% on the sandy shore (Table 9) and therefore played a small role in determining the conditions under which birds were piping.

Aggressive behaviour towards other oystercatchers was observed rarely: on the rocky shore there were 34 observations (0.1%) and on the sandy shore 52 observations (0.2%) (Table 1). The explanatory variables accounted for 12% of the deviance on the rocky shore, and for 8% on the sandy shore (Table 10) and therefore played a small role in determining the conditions under which birds were aggressive. The negative coefficients for tide height in the models for both sandy and rocky shores suggested that most aggression towards other oystercatchers took place at low tide (Table 10).

Aggressive behaviour towards other seabirds was also a rarely observed behaviour: on the rocky shore there were 29 observations (0.1%) and on the sandy shore 30 observations, 0.1% (Table 1). The explanatory variables accounted for 11% of the deviance on the rocky shore, and for 4% on the sandy shore (Table 11). On the rocky shore, variables related to daylength and temperature, were included in the model (Table 11). On the sandy shores, the only significant explanatory variable was tide height; the negative coefficient for this variable suggests that more oystercatchers tended to be aggressive to other species at low tide rather than at high tide (Table 11).

Tide activity plot

This model is a generalization and it must be remembered that only feeding, sleeping and lying were closely correlated with the tide cycle on both the rocky and sandy shore.

On the rocky shore, all behaviours were markedly tide related (Figure 1). Feeding occurred mainly at low tide (a symmetrical pattern peaking one hour before low tide), preening occurred mainly at high tide and on a rising tide, standing occurred mainly on a falling tide, sleeping and lying occurred mainly at high tide. During spring tides this pattern was exaggerated with few birds feeding two hours before and after the high tide, although at neap tide there was a small proportion of birds feeding at high tide. Other behaviours (preening and standing) occurred together with feeding at low tide but sleeping and lying filled most of the "gap" left at high tide.

On the sandy shore, behaviour was tide related but it was not as marked as on the rocky shore (Figure 2). Feeding occurred mainly at low tide (the pattern is asymmetrical; peaking an hour before low tide but with a gradual decrease to two hours after high tide), preening occurred mainly at low tide and on a rising tide, standing occurred mainly at low tide and on a rising tide, sleeping and lying occurred mainly at high tide with sleeping on a rising tide and lying on a falling tide. Feeding occurred throughout the tide, even during spring high tide. Other behaviours (preening and standing) occurred together with feeding at low tide but sleeping and lying filled most of the "gap" left at high tide.

Behavioural observations

Death and divorce

One breeding pair (both adults colour banded) laid three clutches in the 2002/2003 breeding season with six eggs in total and two chicks that hatched but did not survive for longer than 17 days. In the 2003/2004 breeding season, one nest was initiated on 22–23 December 2003, and contained two eggs. One egg disappeared on 4 January 2004. One of the adults was found dead by a member of the public, in the week 7–14 January 2004. The adult that died was assumed to be the female based on mass and measurements (breeding season mass 778 g and culmen length 75.6 mm) compared to the surviving mate (breeding season mass 673 g and culmen length 67.5 mm) (see Hockey 1981a). The second egg disappeared on 18 January 2004. The remaining adult was observed alone during this period but was seen together with one member of the neighbouring pair (both unbanded birds) from 4 February 2004. This new "pair" was observed feeding together, piping and chasing other birds away although no attempt at breeding was made. The neighbouring pair had not attempted breeding in either the 2002/2003 or 2003/2004 breeding seasons and was present on their territory for 93% and 78% of the weekly bird counts over the two breeding seasons respectively (Chapter 2). One of the unbanded adults moved between the banded and unbanded birds and occasionally all three were seen feeding and piping together. This situation remained unchanged until the end of the study and no eggs were laid by either "pair" in the 2004/2005 breeding season.

Discussion

The fieldwork protocol used in this study enabled in-depth statistical analyses of behaviour patterns in relation to a large suite of explanatory variables. The 20-minute observation periods proved both short enough that changes in explanatory variables during the periods were small, yet sufficiently long to provide adequate sample sizes of behaviour activity for the generalized linear models.

Through this study, we were able to compare and contrast the activity patterns and behaviour of African Black Oystercatchers at a sheltered rocky shore and at a nearby exposed sandy shore.

Tide variables

The results obtained on the rocky shore largely conformed to the overall pattern described by Hockey (1984b) at Marcus Island (33° 03'S, 17° 58'E), Western Cape, South Africa. He divided behaviour into five main activities: feeding, roosting, sitting, preening and bathing and alarming and displaying. On the Marcus Island rocky shore, Hockey also found that tide height was the key explanatory variable for describing the proportion of birds feeding. His graph of the observed average proportion of birds feeding at different tide heights produces results comparable to those of the generalized linear model described here (i.e. most feeding occurs on the falling tide and peaks just before low tide). Most of the shore of Marcus Island is far more exposed than the extremely sheltered shore within the harbour at Koeberg Nuclear Power Station. It is therefore tempting to generalize, and anticipate that the pattern of feeding behaviour observed at these two rocky shore study sites are comparable to feeding at all rocky shores.

This generalization appears self-evident, because on rocky shores, oystercatchers predate mussels, limpets and other intertidal invertebrates which are only exposed and available to the birds at low tide, it therefore follows that tidal height will be the most important factor determining when they are feeding. Because the rocky shore study site at Koeberg was largely protected from wave action, it has the advantage of it being possible to exclude the impact of this variable on behaviour, but has the disadvantage that it was not possible to study the effect of storms and swells on behaviour. On Marcus Island, under storm conditions, feeding activity was greatly reduced (Hockey 1984b). This generalization could be confirmed by using the approach in this study at sites with a range of exposure levels. Hockey (1984b) notes that the nocturnal/diurnal feeding ratio of oystercatchers at Marcus Island is 0.59, this occurs more on a rising tide. Lower feeding activity at night has been attributed to higher predation risk at night as well as a temporal variation in diet (Hockey 1984b, Hockey & Underhill 1984). No nocturnal observations were done at Koeberg to collaborate these findings.

Ward (1990) studied oystercatcher behaviour patterns on a sandy shore in the Eastern Cape. He found that oystercatcher behaviour was tide dependent; the birds fed at mid-tide, predominantly 2–4 hours before and after low tide, with reduced feeding activity at both high tide and low tide. On this Eastern Cape beach, this was the time that the main prey species (*Donax serra*) was active and available to the birds. This is explained by the occurrence of adult *Donax serra* mid-tidally in the Eastern Cape (Branch *et al.* 1994). However, on Western Cape sandy shores, the adult *Donax serra* occur sub-tidally (Branch *et al.* 1994), they were found in low densities at Koeberg during this period (Griffiths & Robinson 2004, 2005) and did not constitute the main prey species of the oystercatchers (Chapter 4). There is also great diversity of macrofaunal species present on the sandy shores of the Western Cape (Bally 1981, Branch & Branch 1981, Chapter 4).

This is the first quantitative study of African Black Oystercatcher behaviour on a sandy shore in the Western Cape. It was therefore unexpected that tide height would play a far smaller role in explaining feeding behaviour than it did on rocky shores or on sandy shores of the Eastern Cape. This result becomes less surprising once the nature of the two shores are considered. The intertidal zones on sandy shores are mobile, defined by levels of water saturation on the unstable sand substrate, the macrofauna that inhabit these zones are also mobile which is in contrast to the hard substrate on rocky shores with more defined intertidal macrofaunal zonation (Bally 1981, Branch & Branch 1981). This enabled the birds to search for food on sandy beaches throughout the tide (Chapter 4).

On the tide activity plots (only tide variables are considered and other variables are given average values); the general pattern shows that more birds are feeding at low tide, along with preening and standing, and more birds are sleeping and lying at high tide on both the rocky and sandy shores at Koeberg. The main difference between rocky and sandy shores is that feeding occurs throughout the tide on the sandy shore even during a spring high tide whereas it almost ceases for the four hour period centred on the spring high tide on the rocky shore.

Other variables

The harbour is sheltered and variables other than tide were less important than the tide height. Weather conditions (windspeed and temperature) accounted for some of the variance for each behaviour type and played a substantial role in explaining feeding activity on the exposed sandy shore. On sandy shores, wind makes feeding more difficult, both by increasing wave action and by sand particles being blown across the beach. High temperatures lead to dessication of the surface sand layer, and potential prey either migrate horizontally or burrow deeper into the substrate. It is therefore not surprising that the proportions of birds feeding on the sandy shore correlated more with the weather conditions and were less tide dependent than the birds feeding on the rocky shore. It must be remembered that the model (time and windspeed interaction) is programmed on available data and the predictions for cool and windy conditions are not supported by actual data as these conditions were rarely encountered.

Daylength was also a contributing variable in many behaviour types although a pattern is hard to establish. Daylength could be associated with the oystercatchers annual cycle in behaviours such as preening and flying. On both rocky and sandy shores, daylength and the change in daylength were significant explanatory variables and more birds were preening in autumn and winter months. This corresponds with the moulting behaviour of the African Black Oystercatcher as the birds moult from March until November (Summers & Cooper 1977). On both rocky and sandy shores, daylength was a significant explanatory variable and more birds were flying in the summer months. This could relate to more territorial disputes occurring during the breeding season, when more birds are present on their territory (Chapter 2, Hockey 1983b).

Other behaviours

There were proportionately more birds walking on the sandy shore than on the rocky shore, this can be explained by larger territories on the sandy shore (6.8 breeding pairs/km and 11 breeding pairs/km on sandy and rocky shores respectively) (Chapter 2). More walking, flying and aggression occurred during low tide (along with feeding), this corresponds to the birds being more active and alert and having more territorial disputes during feeding.

Divorce is well documented in the Eurasian Oystercatcher *Haematopus ostralegus*; divorce rates of 8% in a population have been noted on Skokholm Island, Wales (Harris 1987) and Schiermonnikoog, The Netherlands (Bruinzeel 2004). Divorce occurs through either desertion or usurption (Ens *et al.* 1993). Desertion follows the better option hypothesis where the deserter (most often a female) increases future fitness (ie. survival and future reproduction) by moving to another mate (Ens *et al.* 1993, Bruinzeel 2004). The new mate is generally available through the death of it's previous mate (Ens *et al.* 1993). Hockey (1996b) states that divorce occurs at a lower rate in the African Black Oystercatcher than the 8% mentioned above, although it has not been studied in the same detail. In the Koeberg oystercatchers studied over three breeding seasons (Chapter 2), only one pair was speculated to have divorced but this study is limited by a lack of individually-marked birds, and the possibility exists that this occurs on a larger scale. It appears that the unbanded (unconfirmed) female deserted her mate and paired up with the widowed banded (confirmed) male on the neighbouring territory. The unbanded bird moved between unbanded and banded birds for the rest of the study (another breeding season), which also happens in the Eurasian Oystercatcher (Bruinzeel 2004), and neither "pair" bred. Divorce results in intermittent breeding in the Eurasian Oystercatcher with a median pause of 2.4 years (Bruinzeel 2004). Polygynous pairbonds have also been observed in the Eurasian Oystercatcher *Haematopus ostralegus* (Briggs 1984, Heg & van Treuren 1998, Heg 1999) and American Black Oystercatcher *Haematopus bachmani* (Morse 2005). The polygynous pair consists of a male that has pair bonds with two females. This is unlikely in the pair being discussed as the bird that died was female. However, further studies are needed to establish the gender of the unbanded birds and to establish the long-term behaviour and consequences.

Conclusion

The result of this research has been to quantify the effect of several explanatory variables on the different behavioural activities of the African Black Oystercatcher on rocky and sandy shores on a Western Cape mainland site. The main difference seen is the dependence of the rocky shore birds on the tide height, especially feeding, sleeping and lying and the relative importance of all the variables (tide, weather conditions, daylength and time of day) on most behaviour activities on the sandy shore birds. Feeding on the sandy shore occurs throughout the tidal cycle but was more dependent on weather variables.

Acknowledgements

Eskom Koeberg Nuclear Power Station provided access to the study site; we especially acknowledge the helpfulness of Gert Greeff and Hilton Westman, nature conservators at the site. The Meteorological Office at Eskom's Koeberg Nuclear Power Station provided meteorological data and the hydrographer at the South African Navy provided tidal data. The project was supported by the National Research Foundation, the Earthwatch Institute, and the University of Cape Town Research Committee.

Table 1. Number of observations made and percentage occurrence for each behaviour type for the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005.

Behaviour type	**Rocky shore**		**Sandy shore**	
	Total number of observations	**% occurrence of each behaviour**	**Total number of observations**	**% occurrence of each behaviour**
Feeding	6095	24.0%	6936	22.8%
Standing	4433	17.5%	3817	12.5%
Sleeping	4625	18.2%	7779	25.5%
Lying	3964	15.6%	5628	18.5%
Incubating	643	2.5%	185	0.6%
Preening	4484	17.7%	3935	12.9%
Walking	420	1.7%	1161	3.8%
Flying	394	1.6%	620	2.0%
Piping	126	0.5%	334	1.1%
Aggression to oystercatchers	34	0.1%	52	0.2%
Aggression to other seabirds	29	0.1%	30	0.1%
Other	118	0.5%	6	0%
Total	**25365**	**100%**	**30483**	**100%**

Table 2. Results of the generalised linear models for feeding of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	55.2	57.4	58.4	9.2	17.0	29.6
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	1.128	0.263	4.29	–2.868	0.323	–8.89
Tide height	–3.301	0.0704	–46.89	–1.2315	0.0498	–24.74
Δ Tide height	1.140	0.145	7.87	0.446	0.146	3.06
Tide height × Δ Tide height	–0.882	0.154	–5.72	–0.568	0.144	–3.95
Sin 2θ	0.3138	0.0501	6.26	–0.1047	0.0487	–2.15
Cos 2θ	–0.1721	0.0295	–5.83	0.3157	0.0265	11.93
Sin 3θ				0.1328	0.0226	5.87
Cos 3θ				0.1331	0.0244	5.45
Daylength	–0.0814	0.0160	–5.08	–0.1274	0.0127	–10.05
Δ Daylength	–0.0636	0.0131	–4.85	–0.1105	0.0117	–9.41
Temperature	0.0997	0.0295	3.37	0.3091	0.0368	8.40
Temperature^2	–0.00186	0.000931	–2.00	–0.00580	0.000956	–6.07
Wind	0.2507	0.0496	5.05	0.7441	0.0465	15.99
Wind^2	–0.01642	0.00361	–4.55	–0.02959	0.00361	–8.20
Wind × Temperature	–0.00533	0.00266	–2.00	–0.02223	0.00215	–10.32
Time	0.00716	0.00990	0.72	0.1651	0.0102	16.20
Time^2	0.02022	0.00267	7.59	–0.03039	0.00291	–10.45

Table 3. Results of the generalised linear models for standing of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	1.8	1.9	20.0	3.6	4.0	7.4
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	−3.720	0.236	−15.75	−4.808	0.381	−12.64
Tide height	−0.2997	0.0526	−5.69	−0.5418	0.0535	−10.12
Δ Tide height	−0.757	0.161	−4.69	0.155	0.166	0.93
Tide height × Δ Tide height	0.736	0.168	4.37	−0.276	0.160	−1.72
Sin 2θ	−0.1569	0.0514	−3.05	−0.0871	0.0573	−1.52
Cos 2θ	−0.0595	0.0256	−2.32	0.1949	0.0292	6.68
Sin 3θ	0.0816	0.0256	3.19			
Cos 3θ	0.0463	0.0259	1.79			
Daylength	0.2547	0.0167	15.25			
Δ Daylength	−0.1565	0.0136	−11.54			
Temperature	−0.0351	0.0120	−2.93	0.2840	0.0398	7.14
Temperature^2				−0.00479	0.00104	−4.59
Wind	−0.1877	0.0434	−4.33	0.1593	0.0507	3.14
Wind^2				0.01506	0.00374	4.03
Wind × Temperature	0.00847	0.00213	3.97	−0.01600	0.00238	−6.74
Time	−0.0337	0.0101	−3.33	−0.05304	0.00989	−5.36
Time^2	−0.01203	0.00269	−4.47	0.00923	0.00300	3.08

Table 4. Results of the generalised linear models for sleeping of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	33.1	35.4	44.6	13.2	16.9	39.1
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	−3.278	0.303	−10.83	1.152	0.159	7.23
Tide height	2.7152	0.0660	41.13	1.3296	0.0392	33.90
Δ Tide height	−1.775	0.167	−10.63	0.2555	0.0215	11.88
Tide height × Δ Tide height	1.878	0.171	10.95			
Sin 2θ	−0.3640	0.0545	−6.68	0.0393	0.0218	1.80
Cos 2θ	−0.0656	0.0283	−2.32	−0.0990	0.0222	−4.47
Sin 3θ	0.2096	0.0274	7.64	0.0893	0.0206	4.33
Cos 3θ	−0.0689	0.0276	−2.49	0.1164	0.0207	5.61
Daylength	−0.1311	0.0170	−7.73			
Δ Daylength	0.0820	0.0148	5.52			
Temperature	−0.1004	0.0361	−2.78	−0.21417	0.00955	−22.44
Temperature^2	0.00481	0.00121	3.98			
Wind	0.6092	0.0529	11.52	−0.4504	0.0382	−11.80
Wind^2	0.00832	0.00399	2.09	0.01190	0.00312	3.81
Wind × Temperature	−0.02713	0.00334	−8.11	0.02080	0.00214	9.72
Time	−0.0902	0.0120	−7.54	−0.08888	0.00739	−12.03
Time^2	0.01134	0.00284	3.99	0.04449	0.00228	19.51

Table 5. Results of the generalised linear models for lying of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	17.5	24.3	33.2	8.6	17.5	39.5
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	−6.347	0.437	−14.54	−9.201	0.413	−22.26
Tide height	1.4584	0.0633	23.04	1.5761	0.0572	27.56
Δ Tide height	−0.1374	0.0264	−5.20	−2.299	0.164	−14.00
Tide height × Δ Tide height				2.076	0.157	13.18
Sin 2θ	0.1479	0.0320	4.63	−0.1474	0.0525	−2.81
Cos 2θ	−0.4660	0.0288	−16.20	−0.4606	0.0267	−17.23
Sin 3θ	−0.1777	0.0288	−6.16	−0.1169	0.0234	−4.99
Cos 3θ	−0.1579	0.0278	−5.69	−0.1786	0.0244	−7.33
Daylength	−0.0939	0.0179	−5.24	0.3270	0.0151	21.64
Δ Daylength	0.2268	0.0156	14.56	0.1323	0.0128	10.32
Temperature	0.4951	0.0503	9.83	0.3033	0.0489	6.20
Temperature^2	−0.01196	0.00133	−9.01	−0.00757	0.00133	−5.71
Wind	−0.2349	0.0360	−6.53	−0.4350	0.0519	−8.37
Wind^2	0.02177	0.00338	6.44			
Wind × Temperature				0.01529	0.00261	5.85
Time	0.0828	0.0134	6.18	0.1743	0.0110	15.86
Time^2	−0.04381	0.00368	−11.91	−0.07782	0.00350	−22.24

Table 6. Results of the generalised linear models for preening of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	1.9	3.7	21.3	5.5	8.1	18.8
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	1.212	0.214	5.66	2.456	0.278	8.82
Tide height	0.1843	0.0509	3.62	–0.6396	0.0559	–11.44
Δ Tide height	0.3162	0.0773	4.09	0.475	0.170	2.80
Tide height × Δ Tide height	–0.4646	0.0783	–5.93	–0.505	0.169	–3.00
Sin 2θ				0.2761	0.0563	4.90
Cos 2θ				–0.2336	0.0296	–7.89
Sin 3θ				–0.0923	0.0264	–3.50
Cos 3θ				0.1092	0.0278	3.93
Daylength	–0.1274	0.0156	–8.19	–0.0646	0.0141	–4.58
Δ Daylength	–0.0407	0.0135	–3.01	–0.0480	0.0136	–3.54
Temperature	–0.0730	0.0115	–6.32	–0.3150	0.0330	–9.55
Temperature^2				0.00743	0.000916	8.11
Wind	–0.1968	0.0426	–4.62	0.0078	0.0502	0.16
Wind^2	–0.02629	0.00408	–6.44	–0.03483	0.00444	–7.85
Wind × Temperature	0.01696	0.00253	6.69	0.01083	0.00250	4.33
Time	0.0271	0.0101	2.67			

Table 7. Results of the generalised linear models for walking of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			Sandy shore		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	3.2			4.2	4.8	6.2
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	–3.500	0.118	–29.72	–4.537	0.603	–7.53
Tide height	–0.652	0.127	–5.12	–0.7093	0.0850	–8.35
Δ Tide height				0.651	0.272	2.39
Tide height × Δ Tide height				–0.732	0.266	–2.75
Sin 2θ				0.1271	0.0935	1.36
Cos 2θ				0.1761	0.0488	3.61
Temperature				0.2108	0.0664	3.17
Temperature^2				–0.00469	0.00175	–2.69
Wind				–0.1635	0.0567	–2.88
Wind^2				0.01755	0.00604	2.91

Table 8. Results of the generalised linear models for flying of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	0.8	4.9	18.4		2.6	18.8
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	–8.514	0.869	–9.80	–12.19	1.15	–10.58
Tide height	–0.702	0.199	–3.52	–0.458	0.126	–3.65
Δ Tide height	–0.938	0.485	–1.93	1.086	0.190	5.73
Tide height × Δ Tide height	1.09	0.501	2.19	–1.369	0.186	–7.35
Sin 2θ	–0.013	0.157	–0.08			
Cos 2θ	–0.6517	0.0866	–7.52			
Daylength	0.3646	0.0590	6.18	0.2540	0.0404	6.29
Δ Daylength	0.0827	0.0419	1.97			
Temperature	0.153	0.107	1.43	0.524	0.134	3.91
Temperature^2	–0.00869	0.00335	–2.59	–0.01058	0.00352	–3.00
Wind	–0.432	0.153	–2.82	–0.003	0.130	–0.02
Wind^2				0.02530	0.00802	3.15
Wind × Temperature	0.02402	0.00791	3.04	–0.01440	0.00611	–2.36
Time	–0.1172	0.0279	–4.20	–0.1460	0.0259	–5.63
Time^2	0.03581	0.00677	5.29			

Table 9. Results of the generalised linear models for piping of the African Black Oystercatcher at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	0.3		9.5	1.9	4.4	8.7
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	–8.961	0.952	–9.41	–10.33	1.37	–7.55
Tide height	0.541	0.259	2.09	–0.625	0.163	–3.83
Δ Tide height				1.136	0.523	2.17
Tide height × Δ Tide height				–1.389	0.509	–2.73
Sin 2θ				0.137	0.184	0.75
Cos 2θ				0.4362	0.0983	4.44
Daylength	0.3175	0.0784	4.05	–0.0102	0.0507	
Δ Daylength				–0.0065	0.0426	
Temperature				0.673	0.169	3.99
Temperature^2				–0.01745	0.00444	–3.93
Wind	–0.529	0.153	–3.46			
Wind^2	0.0508	0.0132	3.86			
Time	–0.1463	0.0543	–2.69	–0.2022	0.0385	–5.25

Table 10. Results of the generalised linear models for aggression of the African Black Oystercatcher towards other oystercatchers at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	5.7	9.8	11.9	5.2		8.0
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	–5.937	0.508	–11.68	-5.562	0.338	–16.47
Tide height	–1.253	0.547	–2.29	–1.203	0.380	-3.16
Δ Tide height	–1.442	0.754	–1.91			
Tide height × Δ Tide height	2.327	0.917	2.54			
Time	–0.224	0.111	–2.02	–0.2304	0.0817	–2.82

Table 11. Results of the generalised linear models for aggression of the African Black Oystercatcher towards birds of other species at Koeberg Nuclear Power Station from June 2003 until June 2005. See text for further details.

	Rocky shore			**Sandy shore**		
Percentage mean deviance accounted for	**Tide height**	**Tide variables**	**All variables**	**Tide height**	**Tide variables**	**All variables**
	2.2	5.0	11.0	4.1		
Explanatory variable	**estimate**	**s.e.**	**t**	**estimate**	**s.e.**	**t**
Constant	–3.88	1.95	–1.99	–5.835	0.402	–14.50
Tide height				–1.292	0.479	-2.70
Daylength	0.261	0.183	1.43			
Δ Daylength	–0.493	0.161	-3.05			
Temperature	–0.697	0.191	-3.65			
Temperature^2	0.01803	0.00519	3.47			

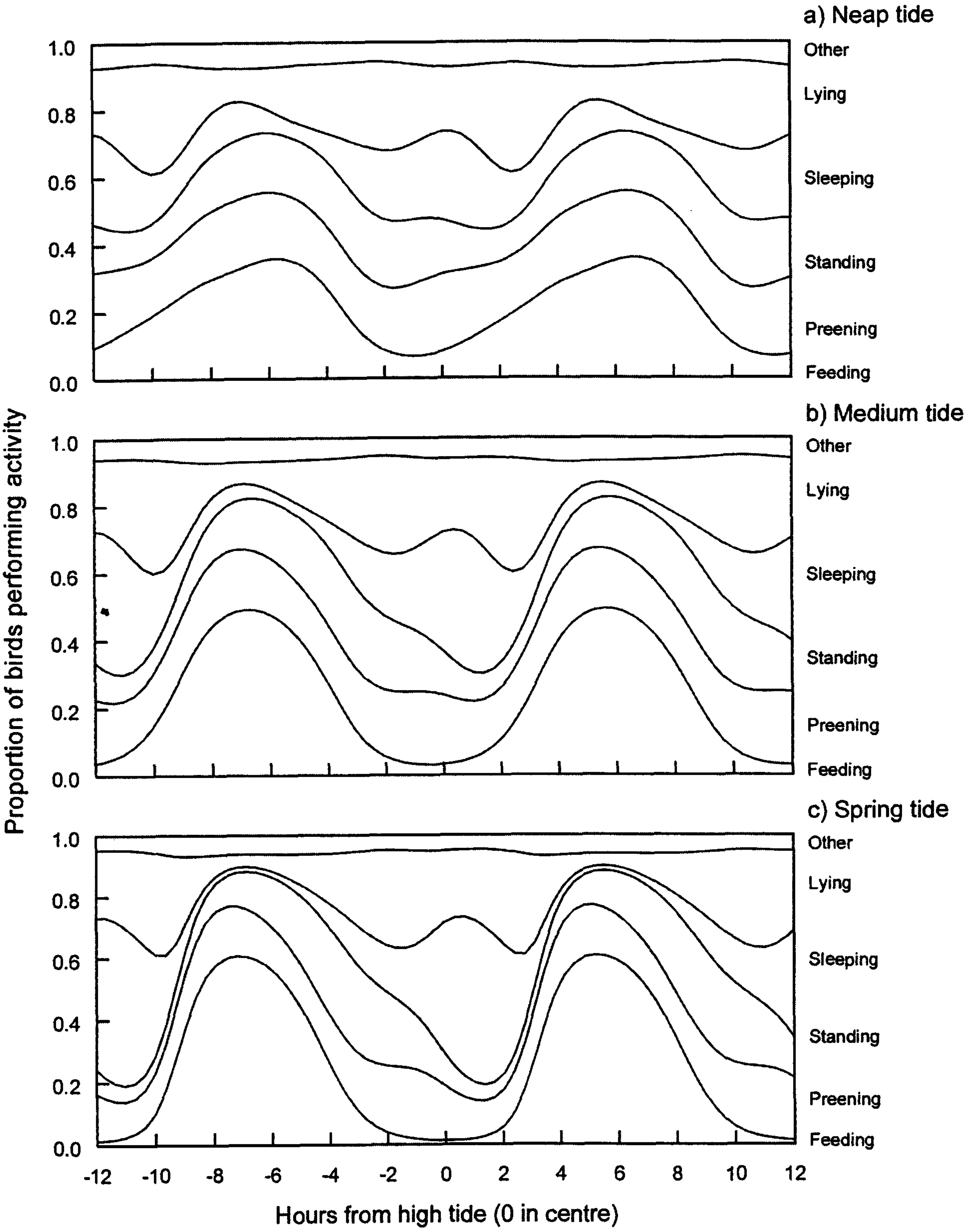


Figure 1. Tide activity plot of African Black Oystercatcher behaviour activities on the rocky shore at Koeberg during spring, average and neap tides, with other explanatory variables set at average values. Two full tide cycles are shown with high tide in the centre of each figure.

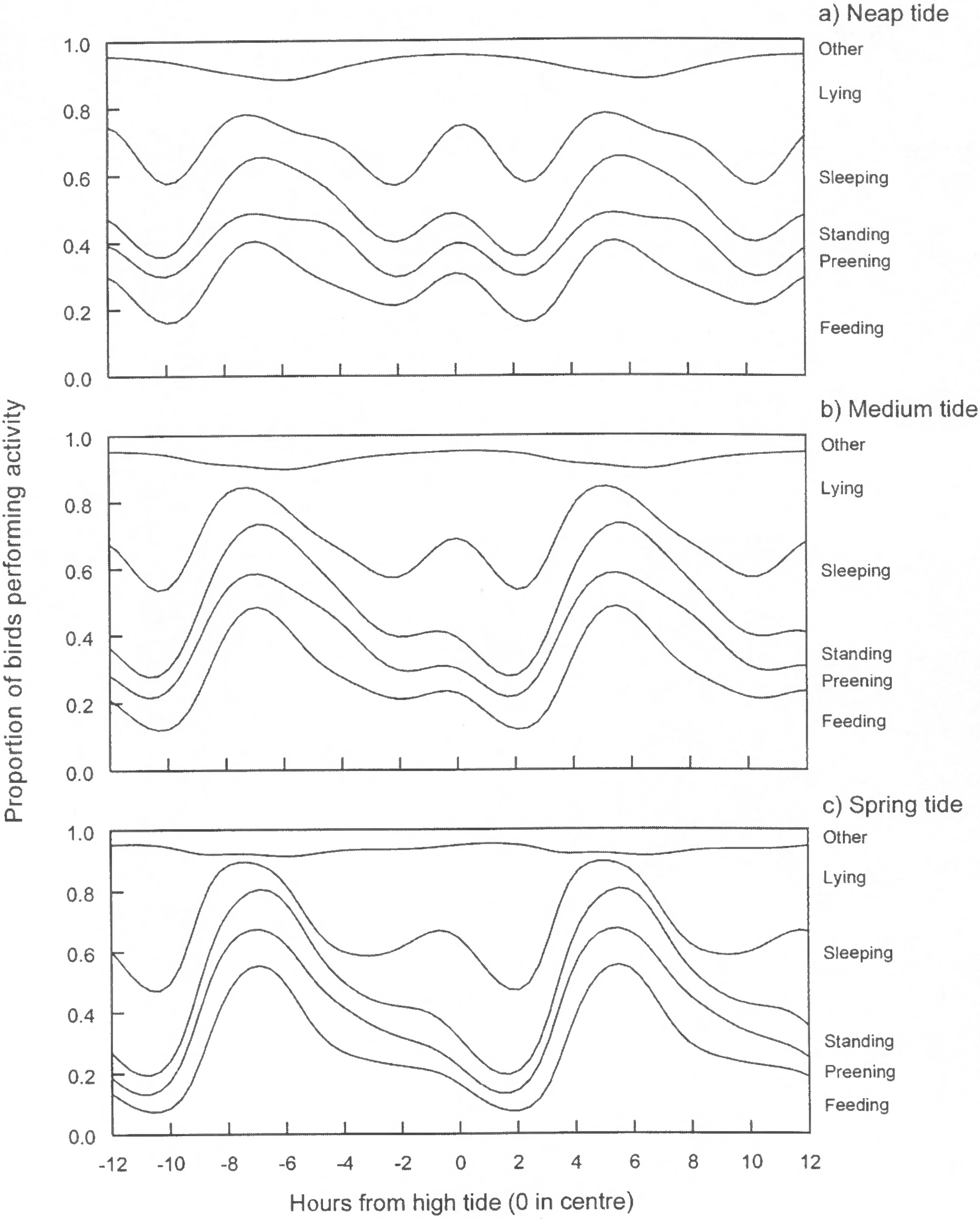
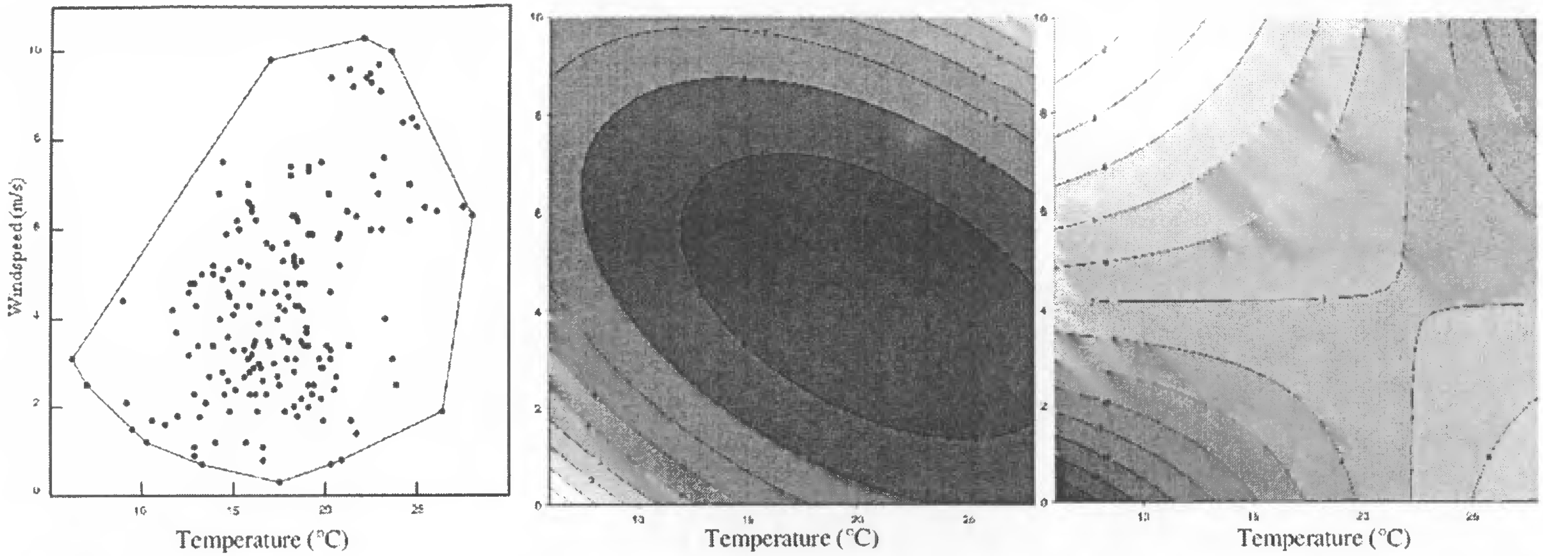


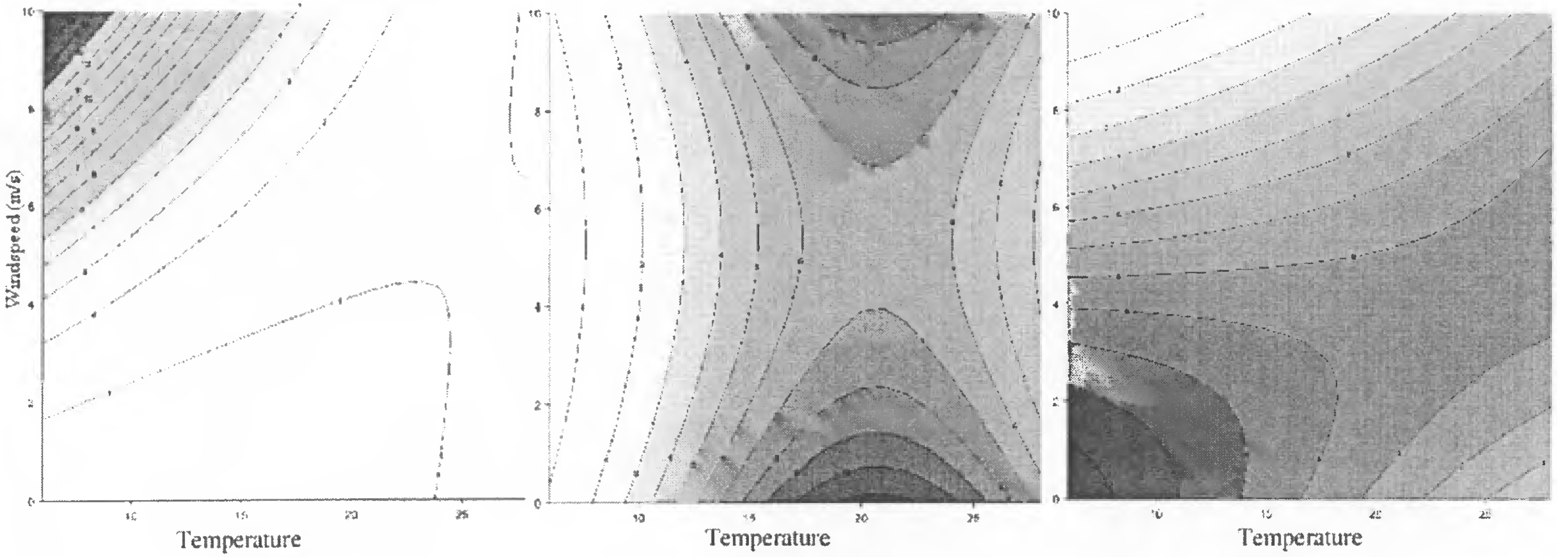
Figure 2. Tide activity plot of African Black Oystercatcher behaviour activities on the sandy shore at Koeberg during spring, average and neap tides, with other explanatory variables set at average values. Two full tide cycles are shown with high tide in the centre of each figure.



a) Convex hull

b) Feeding

c) Standing

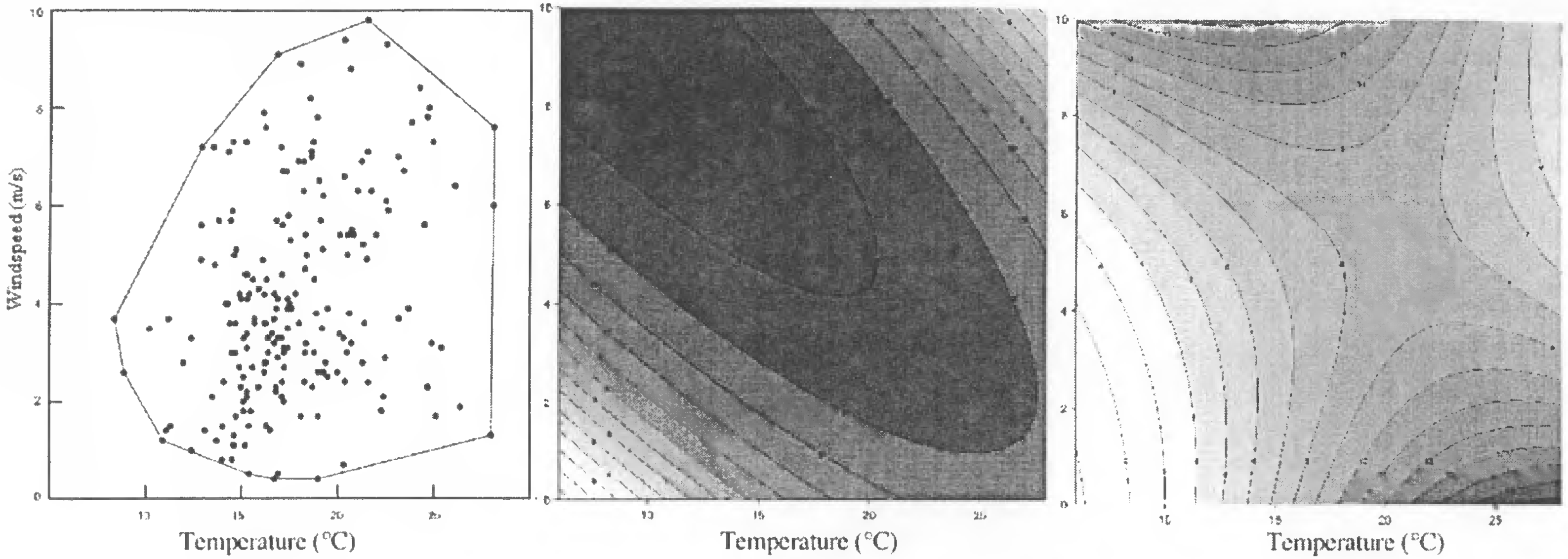


d) Sleeping

e) Lying

f) Preening

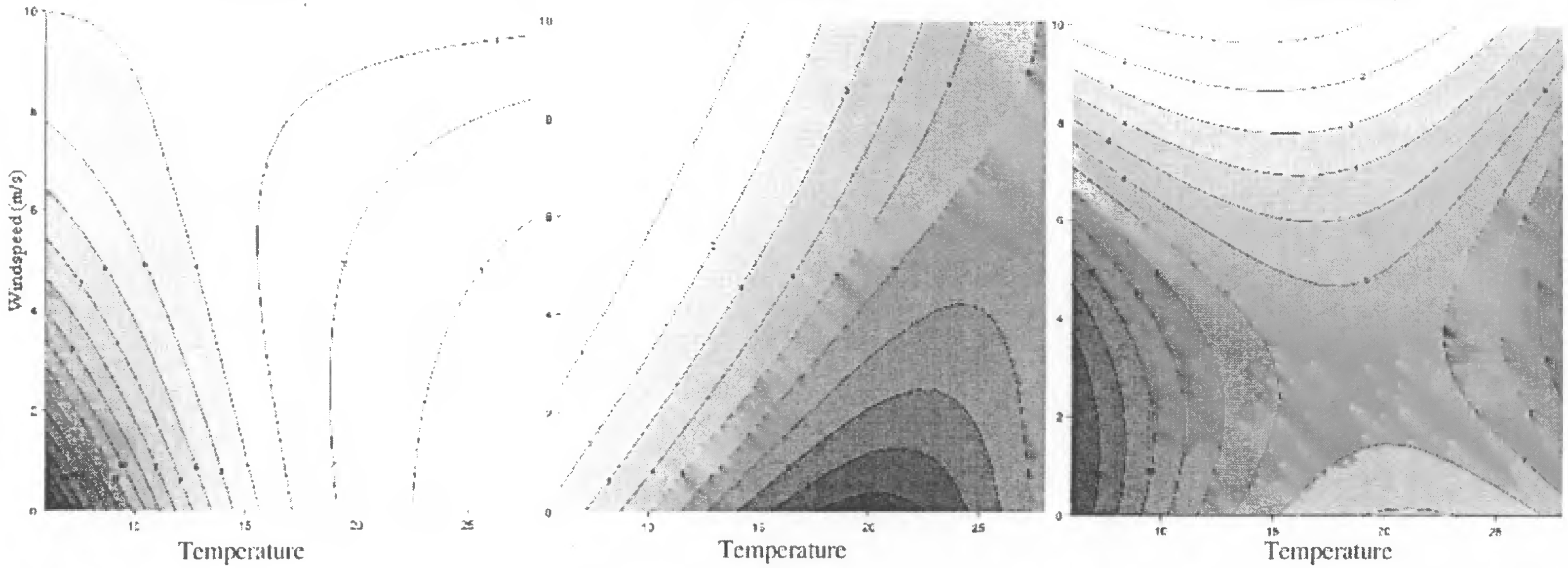
Figure 3. Diagrammatic contour plots showing the effects of windspeed and temperature on African Black Oystercatcher behaviour activities on the rocky shore at Koeberg in the generalised linear models. In a) the convex hull figure shows the actual behaviour data observation points. In b) to f) the darker shades represent combinations of temperature and windspeed which lead to increases in the activity. See text for detail.



a) Convex hull

b) Feeding

c) Standing



d) Sleeping

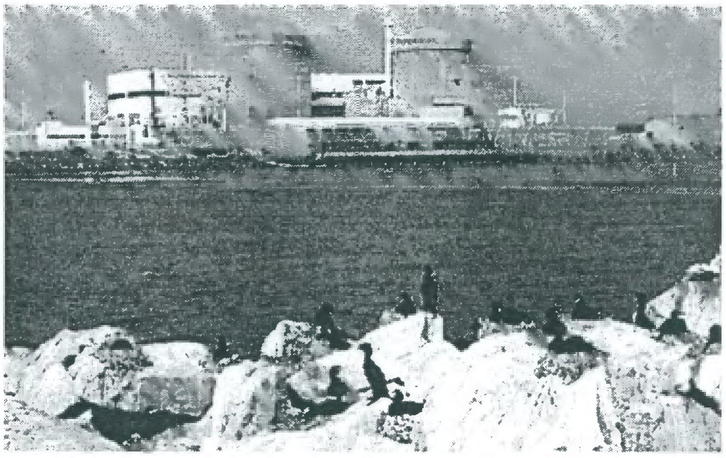
e) Lying

f) Preening

Figure 4. Diagrammatic contour plots showing the effects of windspeed and temperature on African Black Oystercatcher behaviour activities on the sandy shore at Koeberg in the generalised linear models. In a) the convex hull figure shows the actual behaviour data observation points. In b) to f) the darker shades represent combinations of temperature and windspeed which lead to increases in the activity. See text for detail.

Chapter 6

The importance of Koeberg Nuclear Power Station and Nature Reserve for seabirds and shorebirds: conservation implications and recommendations



Introduction

Power stations, and particularly nuclear power stations, seem unlikely candidate sites for Wetlands of International Importance in terms of the Ramsar Convention, or for Important Bird Areas, as defined by BirdLife International. However, in this chapter, we argue that the nature reserve adjacent to the Koeberg Nuclear Power Station is of considerable conservation significance, and that it does meet the criteria both for a Ramsar wetland and for an Important Bird Area. We also discuss specific recommendations that Eskom, the national power generator in South Africa, could implement to improve the conservation status of seabirds and shorebirds at this site.

The African Black Oystercatcher *Haematopus moquini* was studied at the Koeberg Nuclear Power Station and Nature Reserve from November 2002 to June 2005. During this time, incidental observations of seabird and shorebird species breeding in the area were recorded and the general operation of the harbour and beaches were observed. This study site provides an area of low human disturbance suitable for the breeding of several endemic seabirds and shorebirds, and the sheltered harbour provides ideal feeding habitat for oystercatchers. The site has the potential to play a valuable role in the conservation management of this species, as well as several other seabirds in the Western Cape

In this chapter, the aim was to summarise the most important conservation issues affecting seabirds and shorebirds breeding at Koeberg and to provide some practical recommendations.

Koeberg Nuclear Power Station and Nature Reserve

Koeberg Nuclear Power Station (33 40'S, 18 25'E) lies 30 km north of Cape Town and is surrounded by a 3 000 ha nature reserve. On the shore side of the high-security area is a harbour, which consists of a northern and southern breakwater, and a water outflow channel (Figures 1 and 2 thesis introduction). On either side of the harbour, the coastline consists of sandy shore. Koeberg Nuclear Power Station is a National Key Point site (Act 102 of 1980 under South African Legislation) and imposes heavy penalty for illegal entry. See the thesis introduction for more detail of the study site.

The harbour area provides a sheltered rocky shoreline and potentially little disturbance by humans and predation by terrestrial mammals. It thus provides similar opportunities for the breeding of several species of seabirds as occur on the offshore islands where these species breed most successfully. Human disturbance in the harbour is limited to routine harbour maintenance and operation and maintenance of the dredging machine (which is not present in all years). The north beach is exposed, isolated and inaccessible while the south beach is more sheltered, has finer sand and a wider intertidal area than the north beach. The beach areas are part of a nature reserve, with a large diversity of predators. There is some human disturbance on the south beach.

Seabirds and shorebirds breeding at Koeberg

There have been 174 bird species recorded at the Koeberg Nature Reserve (Johnson 1995). These include terrestrial birds, waterbirds and seabirds. In this chapter we only consider the seabird and shorebird species.

The gently sloping intertidal area, on the inside of the harbour (Figure 3 thesis introduction), provides excellent habitat for the African Black Oystercatcher. The oystercatcher also occurs on the sandy beaches north and south of the harbour. This species is discussed in more detail below. The oystercatcher is endemic to southern Africa and is classified as "near-threatened" in South Africa and globally (Underhill 2000, BirdLife International 2004).

The only other shorebird recorded breeding on the beaches north and south of the harbour was the White-fronted Plover *Charadrius marginatus*. This species occurred in unexpectedly low numbers, with fewer than 10 birds being present. This is far less than the density of 11.2 birds/km recorded in this area three decades ago on 29 December 1975 (Summers *et al.* 1976). The reasons for this are unclear. It would be worth investigating if this pattern of decline of this species is replicated at other sites; if so, it would be indicate a need for a conservation investigation of the status of the White-fronted Plover.

Other wader bird species present breeding within the Koeberg Nature Reserve included the Crowned Lapwing *Vanellus coronatus*, Blacksmith Lapwing *V. armatus* and

Spotted Thick-knee *Burhinus capensis.* These species bred mainly on flat areas covered with dune vegetation.

All four species of marine cormorants (Cape Cormorant *Phalacrocorax capensis,* Crowned Cormorant *P. coronatus*, Bank Cormorant *P. neglectus* and White-breasted Cormorant *P. carbo*) have been recorded breeding in the harbour area (Table 1.) (du Toit *et al.* 2003, Crawford *et al.* 1999, Marine and Coastal Management unpubl. data). The four species are endemic to southern Africa. The Bank Cormorant is classified as "Endangered" and the Crowned Cormorant and Cape Cormorant are classified as "Near-threatened" respectively in the global IUCN red data list (Crawford 2000a, b, c; BirdLife International 2004). Cape Cormorants and White-breasted Cormorants were observed to breed mainly from October to January on both the northern and southern harbour breakwaters, Crowned Cormorants bred mainly from December to March on the walls of the pump house and Bank Cormorants have an extended breeding season (March to November) breeding on the breakwaters.

The nominate subspecies of Swift Tern *Sterna bergii bergii* bred between February and July in the water outflow area in 2002, 2003 and 2005, and a few bred on the roofs of the nearby buildings in 2004. This subspecies is endemic to southern Africa and has a relatively small population estimated at c. 20 000 birds (Cooper *et al.* 1990, du Toit *et al.* 2003). In 2002, approximately 500 chicks fledged at Koeberg (J.R. le Roux pers. comm.). The subsequent two breeding attempts were unsuccessful because of predation; up to 700 nests were deserted as a result of predation by a Yellow Mongoose *Cynictis penicillata* in March 2003 and up to 400 nests were depredated by a feral cat *Felis catus* in May 2005.

Hartlaub's Gulls *Larus hartlaubii* bred from March until September in the water outflow area and, on occasions, have bred on the roofs of buildings within the security area. Of the c. 50 species of gull in the world, there are only nine species which are less abundant, with a total population estimated at c. 30 000 birds (Wetlands International 2002, du Toit *et al.* 2003). This species is endemic to southern Africa.

The value of the Koeberg Nuclear Power Station to African Black Oystercatchers

Density

The breakwaters of the harbour area (c. 1 km of artificially-created rocky shoreline within the harbour and at right angles to the original coastline) support 23 pairs of African Black Oystercatchers (46 birds/km) while the south beach area (c. 500 m of shoreline) supports eight pairs (32 birds/km) and the north beach area (c. 2 km of shoreline) supports another eight pairs (8 birds/km) (Chapter 2). Summers *et al.* (1976) reported no African Black Oystercatchers on this section of shoreline (Melkbostrand to Robbesteen) in summer 1975/1976. Hockey (1983a) recorded an overall density of 3.2 birds/km for the mainland shore (all habitat types) between Slipper Bay (St Helena Bay) and Bloubergstrand, of which the site forms part. The oystercatcher density on this mainland area has therefore increased over 30 years.

The fenced-in harbour and water outflow area covers c. 500 m of what was originally a sandy shore. Assuming the same density of 32 birds/km (south beach density), it would have supported eight pairs of oystercatchers. This area, which now includes 1 km of artificial rocky shoreline in the harbour, supports 46 birds, a 44% increase as a result of the habitat transformation (Chapter 2). There was a higher density of breeding oystercatchers in the harbour area compared to the adjacent beaches and a similar number of breeding pairs in the harbour area as in the whole beach area. The harbour has a similar productivity to an adjacent area of shoreline five times the original shore-length.

Levels of human disturbance and predation

Human disturbance in the harbour is generally limited to routine harbour maintenance and operation and maintenance of a dredging machine (which is not present in all years). There was a high level of human disturbance over the 2004/2005 breeding season due to the removal of the dredging machine in 2004 and the renovation of the south breakwater in 2004 and 2005. This is the first time that the breakwater has been renovated since construction (completed in 1984) and therefore does not represent a permanent disturbance. The fences surrounding the harbour area (and power station) and the presence of people help to deter terrestrial predators from this area. The fences have been improved over the course of the three-year study period (2002–2005). However, a Yellow Mongoose and a feral cat have been seen inside the harbour area.

The oystercatchers in the southern side of the harbour closest to the jetty, which is the busiest area of the harbour, seemed habituated to human disturbance. Tolerance of people has also been recorded by Underhill (1991) at Pringle Bay and Pond (1999) at Noordhoek beach. In the 2002/2003 breeding season, the four pairs produced nine nests and five fledglings, with two pairs laying nests after their fledglings had left the area. In January 2003, one pair successfully incubated and hatched one chick (from a two egg clutch) within 2 m of an informal braai (barbecue) area.

The beach areas are part of a nature reserve, mostly protected from human disturbance but with a large diversity of predators. There is some human disturbance (mainly walkers and dogs) on the south beach. Predators implicated in seabird and shorebird mortality include the Yellow Mongoose, Kelp Gull *Larus dominicanus*, Sacred Ibis *Threskiornis aethiopicus*, Pied Crow *Corvus albus*, various snakes, domestic dogs (south beach) and feral cats (harbour area).

Breeding productivity

Over the three-year study period, the breeding productivity of oystercatchers at Koeberg remained below that estimated to maintain a stable population. Hockey *et al.* (2005) estimated this value to be 0.35 fledglings per pair per year, however 0.27, 0.06 and 0 fledglings per pair were recorded at Koeberg in 2002/2003, 2003/2004 and 2004/2005 respectively (Chapter 2). The poor productivity at Koeberg is mainly attributed to a high level of egg and chick loss as a result of predation (Chapter 2).

Practical considerations and recommendations

1. Maintain monitoring

The African Black Oystercatcher is a long-lived bird with a low breeding rate (Hockey *et al.* 2005) and it is therefore impossible to detect trends in population growth or breeding success in a three-year study period. It is recommended that long-term detailed monitoring, as achieved for this study, be continued. This would help to evaluate the causes of poor breeding productivity at this site and help to monitor the effects of conservation management such as predator control. It would also help to establish whether this mainland site is a population sink for the African Black Oystercatcher (as surmised by Underhill (2000)) where the breeding productivity is too low to sustain the population. This is an important factor when considering application for formal conservation status as listed below.

2. Predator control

It is entirely contrary to the principles of nature reserve management to control the indigenous predators on the beach sections of the Koeberg Nature Reserve. However, dogs represent unnatural predators, and should be excluded from the south beach. Elsewhere in the Western Cape (for example at Bettys Bay (S. Starke pers. comm.)), dogs have been demonstrated to be the single most important cause of chick loss (du Toit *et al* 2003). Signposts were erected on the south beach at Koeberg during 2003 and this has helped reduce numbers of people and their dogs walking on this section. These need to be maintained and security contractors should be instructed to enforce the regulations vigorously.

In contrast, the reduction of terrestrial predators in the harbour area is a realistic target. Although the harbour is an entirely artificial habitat, the sheltered rocky shore provides excellent breeding habitat for African Black Oystercatchers, the breakwaters provide good breeding habitat for three species of marine cormorants and the flat area alongside the water outflow channel provides good breeding habitat for Swift Terns and Hartlaub's Gulls. The configuration of the power station complex near the shore, and the perimeter security installations, already provide a substantial obstacle to the movement of terrestrial predators into the harbour area. However, a feral cat and Yellow Mongoose have been spotted inside the harbour and it is recommended that these animals be removed.

3. Conservation awareness of staff and contractors

After communication with the regular harbour personnel, they took an interest in the birds breeding in the harbour; marking nests so that they did not damage them if they were working nearby. However, there is a high turnover of contract workers in the harbour area that did cause some disturbance. We recommend that these workers are made aware of the birds breeding in the harbour and how to limit their disturbance. For example, if people are continuously walking up and down the harbour, the oystercatchers constantly alarm and do not incubate or attend to their chicks but if people walk together in a group it limits the length of the time of disturbance.

Inside the harbour, the oystercatcher is subject to the most disturbance especially during the peak breeding time over the summer months. The Cape Cormorant and White-breasted Cormorant also breed during summer on the dolosse towards the ends of the breakwaters. The Crowned Cormorant breeds during summer on the walls of the pump-house. Over the winter months, the Bank Cormorant breeds on the dolosse and the Swift Tern and Hartlaub's Gull breed alongside the water outflow channel.

4. Scheduling of maintenance work

There was a high level of human disturbance over the 2004/2005 season due to the removal of the dredging machine in 2004 and the renovation of the south breakwater in 2004 and 2005. The dredging machine is not present in all years and therefore needs to be installed and removed which causes considerable disturbance. This is the first time that the breakwater has been renovated since construction (completed in 1984) and therefore does not represent a permanent disturbance.

It is appreciated that much of the maintenance work inside the harbour needs to be done during the summer when the weather is fine. However, if at all possible this should not be scheduled for the period between December and March. This is the period when disturbance to the oystercatchers in the harbour causes egg and chick mortalities. If possible, removal or installation of the dredging machine should be scheduled for June–October, where it does not impact either the African Black Oystercatcher or Swift Tern breeding seasons. The dredging machine is placed near the jetty where oystercatchers breed and pipes are stored alongside the water outflow channel where terns breed (Figure 2 thesis introduction).

5. Provision of artificial nests for oystercatchers

Nests were made in two of the tyres fixed to the arm of the jetty in the south harbour (Figure 2 thesis introduction), and eggs were laid in them in the 2003/2004 breeding season. This experiment was therefore deemed successful and it is recommended that they be maintained for future use. The disadvantages with the present design are that the chicks have nowhere to hide from predators or people and that it is difficult for the chicks to climb out of the tyre to follow the adults when foraging. Placing some boulders nearby the tyres may solve this problem. One tyre was washed away in winter 2004, potentially causing a problem as objects in the harbour water may cause obstruction in the filter to the inlet of the pump house (Figure 2 thesis introduction). Artificial nests therefore need to be thoroughly fixed to the surface to withstand the winter storms.

6. Public awareness of birds breeding at Koeberg

The construction of the harbour at Koeberg has created suitable habitat for seabirds and shore birds to breed, including several threatened species. The power station could promote its success with the oystercatchers both in the harbour area and along the beaches. This could be done by a display in the Visitors Centre, and also on the website. This display and the website could be kept up to date by the person doing the monitoring. A selection of interesting pictures could be used as well. The display and the website could promote awareness of the conservation needs of the oystercatcher throughout its range. This display could also be expanded to include the cormorant, tern and gull species breeding within the harbour.

7. Harbour design

There are other harbours within the range of the African Black Oystercatcher which could emulate the Koeberg design (Figure 3 thesis introduction) and be modified to provide sheltered rocky shore as oystercatcher breeding habitat. One example is just outside the Victoria Basin of Cape Town Harbour, on the breakwater side. The steep artificial shore where helicopters land and take off could be made into a more gentle shelf. Oystercatchers are frequently observed here (LGU pers. obs), and it would not take much effort to provide breeding opportunities. Two or three pairs of oystercatchers would make a negligible additional hazard to helicopters, given the large numbers of cormorants, gulls, terns and pigeons which already make use of this area.

8. Koeberg Nature Reserve as an "Important Bird Area"

The African Black Oystercatcher, Crowned Cormorant and Cape Cormorant are species classified in the global IUCN red data list as "Near-threatened" and the Bank Cormorant is classified as "Endangered" (BirdLife International 2004). The Crowned Cormorant and Cape Cormorant were deemed "Least concern" by du Toit *et al* (2003). These are species of global conservation concern and therefore Koeberg qualifies in terms of Category A1 as an Important Bird Area in that a regular presence of these birds occurs (Fishpool & Evans 2001). For Category A4 for an Important Bird Area, a 1% threshold of the population of a congregatory waterbird needs to be present (Fishpool & Evans 2001). The harbour and adjoining beaches within the study area hold 70-90 African Black Oystercatchers (Chapter 2). The Koeberg harbour area holds approximately 100 Crowned Cormorants (Table 1 and NJP pers. obs.) and more than 1 000 Swift Terns have bred or attempted breeding in 2002, 2003 and 2005 (Table 1 and J.R. le Roux and NJP pers. obs.). The 1% threshold (of the global population) used in Africa for the designation of Important Bird Areas for the African Black Oystercatcher was 48 birds, for the Crowned Cormorant was 53 birds and for the Swift Tern was 500 birds (Fishpool & Evans 2001). These threshold values are exceeded, making this site an internationally significant site for these species. The Koeberg Nuclear Power Station and Nature Reserve thus qualify in terms of the criteria laid out by Fishpool & Evans (2001) as an Important Bird Area. In addition, the terrestrial component of the avifauna, in the Koeberg Nature Reserve (3000 ha), is one of the few conserved areas of West Coast strandveld relatively close to the city of Cape Town (Johnson 1995). ESKOM could approach BirdLife South Africa, and request that this area, both the coastline and the reserve, be declared an Important Bird Area.

9. Koeberg Nature Reserve as a "Wetland of International Importance"

Criterion 6 of the Ramsar Convention on Wetlands states that a Wetland of International Importance should regularly support 1% of individuals in a population of one species or subspecies of waterbird (Ramsar Convention Bureau 2006). The 1% thresholds used by the Ramsar Convention have been updated slightly from those used for Important Bird Area selection; for the African Black Oystercatcher it is 55 birds, 85 birds for the Crowned Cormorant and 200 birds for the Swift Tern (Table 1, Wetlands International 2002). Koeberg Nuclear Power Station and Nature Reserve qualify as a Ramsar Wetland of International Importance based on this criterion and possibly on other criteria related to conserving biological diversity.

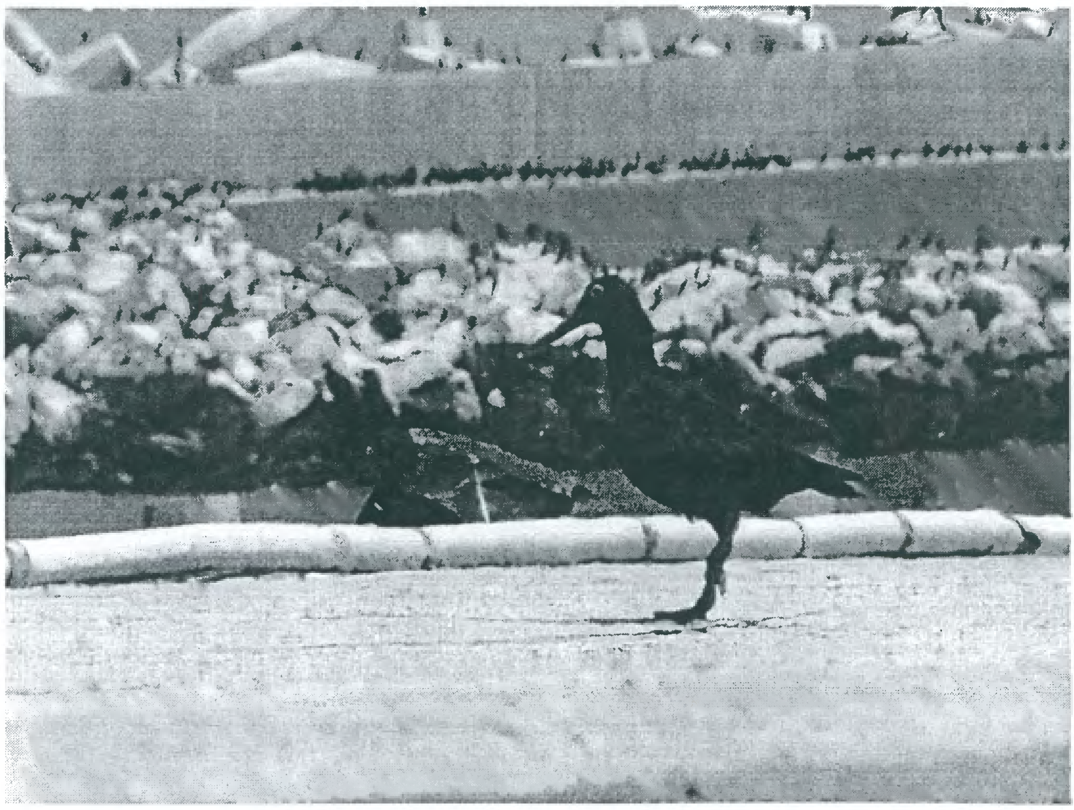
Conclusion

The Koeberg Nuclear Power Station and Nature Reserve meets the criteria for an Important Bird Area and a Ramsar Wetland of International Importance in that at least four species of global conservation concern are present and that the 1% threshold is exceeded for at least four species of waterbirds. The nuclear power station is a National Key Point having strict security for entry and therefore low human disturbance particularly within the harbour area and also on the adjoining beaches, which fall within a nature reserve. Recommendations include registration of the site for formal conservation status as listed above. In addition practical conservation measures should be implemented, such as regular monitoring, predator control, scheduling of maintenance work and conservation awareness of staff, contractors and public. Providing artificial nests and a gently-sloping harbour design could be used, where appropriate, at other harbour areas to provide breeding opportunities for oystercatchers.

Table 1. Maximum numbers of occupied nest sites and conservation status of seabirds and shorebirds recorded in the harbour area of Koeberg Nuclear Power Station. The IUCN threat category is from BirdLife International (2004) and Ramsar 1% threshold (number of birds) and population trend is from Wetlands International (2002). Number of breeding pairs is listed for the African Black Oystercatcher instead of number of nest sites due to the high levels of replacement clutches laid (Chapter 2).

Species	**IUCN threat category**	**Ramsar 1% threshold**	**Population trend**	**Number of nest sites**	**Number of birds**	**Date counted**	**Source of information**
Crowned Cormorant *Phalacrocorax coronatus*	Near threatened	85	Stable	52	104	Nov 1996	Marine and Coastal Management *in litt.*
Cape Cormorant *Phalacrocorax capensis*	Near threatened	2 200	Decreasing	562	1 124	Nov 1996	Marine and Coastal Management *in litt.*
Bank Cormorant *Phalacrocorax neglectus*	Endangered	100	Decreasing	10	20	Nov 1996	Marine and Coastal Management *in litt.*
White-breasted Cormorant *Phalacrocorax lucidus*	Least concern	120	Stable	3	6	Nov 1996	Marine and Coastal Management *in litt.*
African Black Oystercatcher *Haematopus moquini*	Near threatened	55	Increasing	46 breeding pairs	92	Jan 2003	Chapter 2
Hartlaub's Gull *Larus hartlaubii*	Least concern	300	Increasing	200	400	May 2005	NJP pers obs.
Swift Tern *Sterna bergii*	Least concern	200	Stable	600–700	1 300	Mar 2003	NJP pers obs.

Synthesis



Introduction

The African Black Oystercatcher *Haematopus moquini* is classified as "near-threatened" in South Africa and globally (Underhill 2000, BirdLife International 2004). Although no complete population count has been done since 1981, numbers are estimated to have risen from c. 4 800 to more than 6 000 (Hockey 1983a, Hockey *et al.* 2005). The oystercatcher remains on this classification because of the small population size and low reproductive rate (Hockey *et al.* 2005). A breeding success of 0.35 fledglings produced per pair per year is estimated as the level necessary for the population to remain stable (Hockey *et al.* 2005). Offshore islands support c. 30% of the world population and are important for the conservation of the species (Hockey 1983a, Underhill 2000, Hockey *et al.* 2005).

Underhill (2000) suggested that mainland sites are likely to be population sinks for the oystercatcher with low breeding productivity unable to sustain the population at these sites. This is due to human disturbance and terrestrial predators (Underhill 2000, Hockey *et al.* 2005). A 24-year study of oystercatchers breeding at Cape Agulhas, Western Cape showed a mean production of 0.30 fledglings per pair per year (Jeffery & Scott 2005), which is slightly lower than that estimated as needed to maintain a population. This study was conducted before the closure of the coast to off-road vehicles (Jeffery & Scott 2005), and numbers may increase due to a positive reaction of wader species to the vehicle ban (Williams *et al.* 2004).

The feeding behaviour and prey of the African Black Oystercatcher have been extensively studied on rocky shores (Hockey 1981b, 1984b, Hockey & Underhill 1984). On sandy shores, it has been studied in the Eastern Cape (McLachlan *et al.* 1980, Hockey 1981b, Ward 1990), where the available prey species are those that occur on shores adjacent to the relatively warm seas of the Agulhas Current. However, there are no descriptions of African Black Oystercatcher feeding behaviour on sandy shores adjacent to the Benguela Upwelling System in the Western Cape, where a different set of available prey species characterize sandy shores.

Previous studies on African Black Oystercatchers have used time budgets in relation to tide variables (Hockey 1984b, Ward 1990). Ghosh *et al.* (2003) studied the effects of tide and weather on behavioural activities on the Eurasian Oystercatcher *H. ostralegus* while Kersten (1996) studied time and energy budgets of the Eurasian Oystercatcher during the breeding cycle. None of these studies provided a continuous prediction of activity patterns with an extended set of explanatory variables.

Methods

Detailed observations of breeding productivity were done over three breeding seasons in order to examine the threats of the oystercatcher at Koeberg Nuclear Power Station and Nature Reserve. The most important conservation issues affecting seabirds and shorebirds breeding at Koeberg were identified and practical recommendations given. The investment into reproduction was measured and related to the breeding success of individual birds as well as the breeding success of the site, due to the observed differences in investment into breeding and breeding success between mainland and island sites. Breeding productivity was compared at sites around the South African coast that differed with respect to access by land-based mammals (island versus mainland sites) and by their management status (protected versus unprotected sites), in order to establish factors that have a real impact on breeding levels. A generalised linear model was used to statistically evaluate the data.

Feeding behaviour and prey of the African Black Oystercatcher on a Western Cape sandy shore were studied because the available prey species differ from those described on rocky shores and Eastern Cape sandy shores. The study was based on behaviourial observations and correlated with macrofaunal sampling that was done at the site. Intensive behavioural observations were collected on the rocky and sandy shores and analysed using a generalized linear model.

Results and discussion

Breeding productivity of a long-lived bird with high annual survival (96%) (Hockey *et al.* 2005) should ideally be studied for longer than three years. Evaluating lifetime reproductive success needs a long-term study, in which the progeny's survival and success can also be evaluated, in order to draw strong conclusions. This study's shortcoming is therefore a lack of a long-term dataset, however it does identify this site as suitable for a long-term study of the African Black Oystercatcher. A method to evaluate the investment into breeding is also introduced with the aim of using it to help evaluate lifetime reproductive success.

The breeding productivity at Koeberg over the three years of this study were well below that needed to maintain a stable population, with the main constraint of breeding productivity coming during the incubation period due to high egg predation. Comparing different oystercatcher breeding sites showed that island sites and those with low predation levels were the most successful. These were also the only factors considered that were statistically significant. These results highlight where conservation measures should be aimed. The main problem in the comparison between sites was that variables such as relative levels of disturbance and predation were not easily quantified and could only be assigned to two or three categories; this weakens the statistical comparisons.

The main prey item taken by oystercatchers on this Western Cape sandy shore was identified as the polychaete *Scololepsis* although it has a low relative energy content. A diverse range of macrafaunal prey were identified and available throughout the tide, and relative profitability compared. Feeding behaviour was described. Activity patterns of the oystercatcher were modelled using various tide and weather variables and comparing the behaviour of the birds on sandy and rocky shores. Oystercatcher behaviour on the rocky shores was strictly tide-related while weather and daylength factors played more of a role in explaining the behaviour of the birds on the sandy shore. The fieldwork protocol used in this study enabled in-depth statistical analyses of behaviour patterns in relation to a large suite of explanatory variables.

Further research

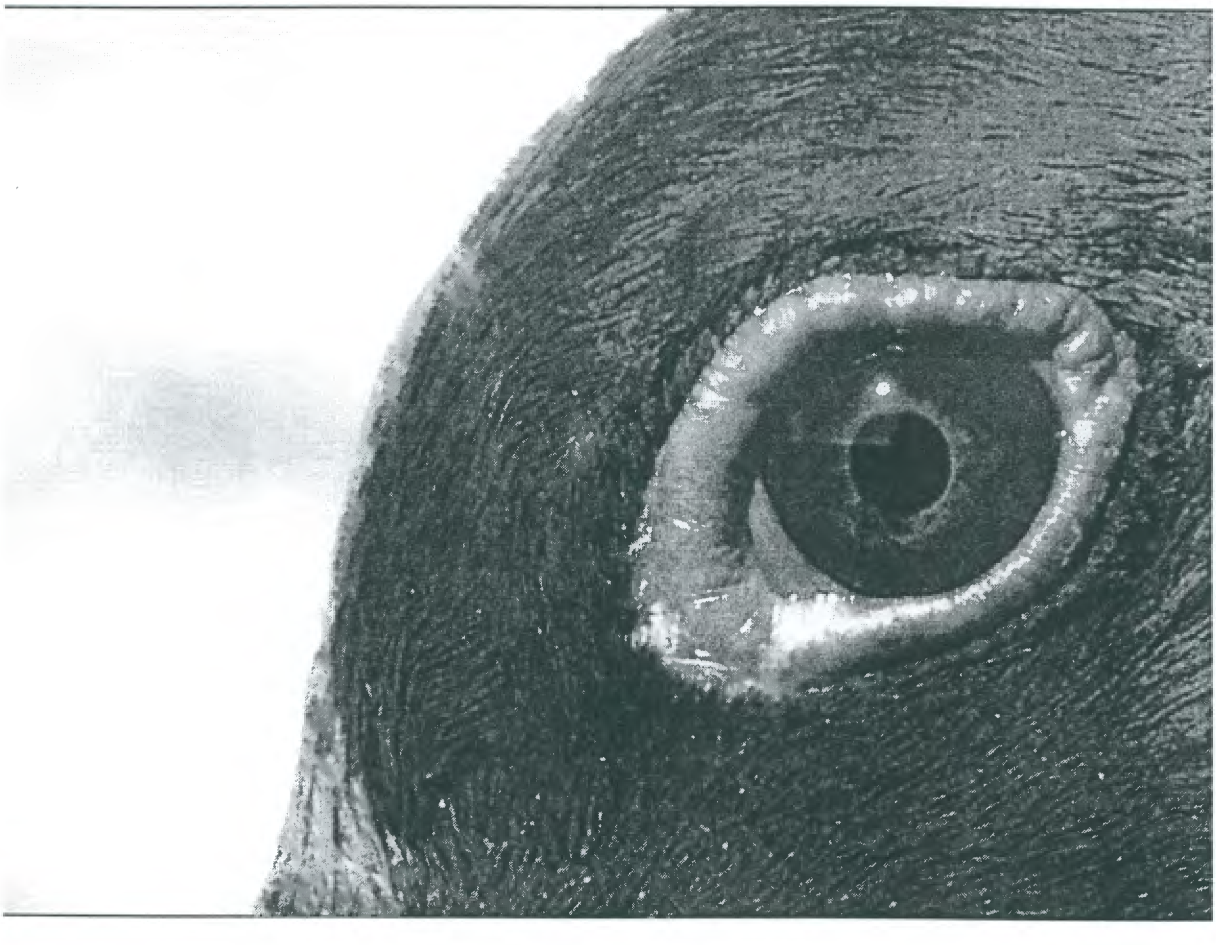
It is recommended that monitoring of oystercatchers be continued at Koeberg for several reasons: it is a mainland site with low breeding productivity and long-term data will give evidence of whether this is in fact a population sink, the effects of conservation measures (such as controlling predators in the harbour, providing artificial nest sites, limiting human disturbance in the harbour and people and dog access on the south beach) can be evaluated and lifetime reproductive success of individual birds can be studied. The Koeberg site is ideal for studying the oystercatcher because, although it is easily accessible, it has little human disturbance, researchers will not disturb sensitive island seabird colonies and it is easy to follow the progress of individual pairs as territories are well delineated. In addition, the artificial rocky shore provides ideal sheltered feeding habitat. The site architecture is such that birds can be kept in view almost continuously, which facilitates behavioural observations.

Detailed breeding productivity results of oystercatchers at various sites around the coast needs to be compiled and collated so that a more thorough investigation into the differences between areas and relative importance of conservation factors can be evaluated. It is hoped that this study will stimulate other researchers with such data to publish their information and more detailed management strategies be drawn up. Another population census of the oystercatcher should be undertaken to compare the relative percentages of the population occurring at the different sites compared to those reported by Hockey (1983a).

This is the first study on the diet of the oystercatcher on a Western Cape sandy shore. Further work needed to fully elucidate the feeding ecology of this species are (1) night-time observations to quantify time spent feeding at night as well as different techniques used and prey caught, (2) continuous observations of individually marked birds in pairs to better describe male and female time budgets, feeding techniques and prey caught, (3) energy budgets of oystercatchers feeding on sandy shores to quantify the relative amount of prey species caught compared to energy requirements and (4) relative energy values of the diets of birds feeding on sandy shores in the Eastern Cape and Western Cape and those feeding on rocky shores can be evaluated and compared, together with the birds' energy budgets.

Conclusion

Although diverse subjects have been discussed in this thesis, it is hoped that together they build a more thorough knowledge of the African Black Oystercatcher, especially on the Western Cape mainland. The most significant findings have been the identification of the main prey items of the oystercatcher on the Western Cape sandy shore, the establishment of different behaviour patterns between birds on rocky and sandy shores, due to the availability of the sandy shore macrofaunal prey throughout the tide, the identification of the incubation period as being the limiting factor in breeding productivity and the importance of island sites and those with low levels of predation in the conservation of the species.



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