From an egg to a fledgling

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Chapter 3

The influence of tourism and predation risk on the breeding success of the African Black Oystercatcher, *Haematopus moquini*, on Robben Island, South Africa

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Abstract

Breeding success of African Black Oystercatchers, *Haematopus moquini*, was monitored over three austral summers on Robben Island, South Africa from 2001 to 2004. Robben Island is a busy tourist destination which has a resident population that live and work on the island in addition to tourists that visit the island daily. The island also has potential predators of birds' eggs and chicks in the form of feral cats, *Felis catus*, Kelp Gulls, *Larus dominicanus*, mole snakes, *Pseudaspis cana*, and house rats, *Rattus rattus*. The mean number of fledglings produced per pair declined from 0.74 in the first breeding season to 0.41 and 0.35 in the subsequent breeding seasons. This fledgling success was slightly greater than the estimated threshold value necessary to maintain a stable population, and similar to fledging success observed in other oystercatcher species. Increased depredation of eggs and chicks and high tide events on 17 February 2003 and 10 February 2004 were the most likely causes of fledging success in the second and third breeding seasons compared to that of the first breeding season. Predation can be aggravated by human disturbance, and it was found that the area with greatest resident and tourist activity had the greatest egg and chick losses in all three breeding seasons. The area adjacent to the disturbed area had reduced breeding success in the second breeding season, which could have been a result of increased predation associated with the settlement. Breeding success in the area near the Kelp Gull breeding colony decreased in the third breeding season; the period during which the greatest number of Kelp Gulls were breeding. The potential success of a breeding attempt decreased if incubation of the clutch started later in the breeding season.

Introduction

Offshore islands generally have limited human disturbance to seabird and shorebird breeding populations, due to their inaccessibility and the long-term conservation and monitoring carried out by government and private bodies (Hockey 2000). Robben Island is about 10 km from Table Bay Harbour, Cape Town, South Africa. The island was used as a prison for many years until the last prisoners and warders left the island in December 1996 (Smith 1997). Since then, the prison has become a museum and the island a busy tourist destination that attracts about 300 000 visitors per year (S Davis, Robben Island Museum, in. litt.). Access to the island by tourists is strictly controlled; their visits are limited to three hours in which they are taken on a prison and a bus tour. Accordingly, tourist disturbance to wildlife on the island is restricted to the area near the harbour and the section of shore where the bus stops during the tour. The resident human population of the island is about 140 and they have access to the whole island but most activity is confined to the same section of shoreline used by the tourist buses. In addition, Robben Island is one of the few offshore islands on the South African coast that hosts a number of different predators including feral cats, *Felis catus*, Kelp Gulls, *Larus dominicanus*, mole snakes, *Pseudaspis cana*, dogs, *Canis familiaris*, and house rats, *Rattus rattus* (Calf & Underhill 2003). Therefore the island is an ideal study site to monitor the affects of disturbance on a discrete population of birds.

A number of seabird and shorebird species breed on Robben Island, including an increasing population of African Black Oystercatchers, *Haematopus moquini* (Tjørve & Underhill submitted manuscript-a). The number of African Black Oystercatchers currently resident on the island exceeds the one percent population level for the species, this being 55 birds (Wetlands International 2002).

The African Black Oystercatcher is the only representative of the family Haematopodidae that breeds in Africa (Summers & Cooper 1977, Hockey 1983a, Martin 1997). In the early 1980s the world population of African Black Oystercatchers was estimated to be 5000 individuals (Hockey 1983b) and they are classified as "near-threatened" both in South Africa and globally (Underhill 2000, BirdLife International 2004). Since the last census the oystercatcher population has increased to an unknown extent (Hockey 2001) but in 2002 the population was estimated to be between 5000 and 6000 individuals (Wetlands International 2002).

African Black Oystercatchers breed on both rocky and sandy shores of the mainland and offshore islands of southern Africa from November to March (Leseberg *et al.* 2000). Because African Black Oystercatchers breed over the busiest time of the holiday season, their eggs and chicks are vulnerable to the direct and indirect effects of human disturbance, in addition to the threat of predation (Jeffrey 1987, Hockey 1999a, Adams *et al.* 1999, Hockey 2000, Leseberg *et al.* 2000). Hockey (2000) found that in addition to egg losses, the loss of chicks was limiting to oystercatcher breeding success in unprotected, disturbed areas.

African Black Oystercatcher young are semi-precocial; they leave the nest soon after hatching but, because they are unable to catch and handle prey, adults provision them until after fledging (Hockey 1984a, Hockey 1996). Oystercatchers feed on mussels, limpets and other invertebrates found within the intertidal zone on sandy and rocky shores. Foraging time is therefore limited by access to the intertidal zone during low tide. Consequently, the direct and indirect impacts of human disturbance (Jeffrey 1987) and food availability may mean that chicks face starvation as well as the risk of predation.

Although Robben Island constitutes an important conservation area for the species (Barnes 1998, Underhill *et al.* 2001) oystercatchers on the island are subject to disturbance. Hockey (2000) found that oystercatchers breeding in protected areas and on offshore islands seem capable of fledging a greater number of young than those in unprotected areas as a result of low levels of disturbance and predation.

This study was conducted to determine the influence of disturbance from tourism and predation risk on the breeding success of African Black Oystercatchers on Robben Island. We evaluated the impact of human disturbance and predation on oystercatcher breeding success for three consecutive breeding seasons. Mortality and survival rates, hatching survival and fledging survival for all African Black Oystercatcher nests on Robben Island were compared across the breeding seasons. We determined breeding success for areas of different disturbance or predation risk around the island to see whether birds in areas of greater disturbance were less successful breeders. Birds breeding near the start or the end of the breeding season may be less successful as a result of predation (Lack 1968). The seasonal value of an egg was determined for African Black Oystercatcher nests on Robben Island. We discuss other factors that may limit breeding success of oystercatchers on Robben Island: food availability, environmental conditions and the age and experience of the breeding pair. The breeding success observed for African Black Oystercatchers was compared to that found by Hockey (1983a) and results from studies on other oystercatcher species.

Methods

Study area

Oystercatcher breeding was monitored during three consecutive austral summers, October to May, from 2001 to 2004 on Robben Island (33°47'S 18°21'E, Figure 3.1) in Table Bay about 11 km from the port of Cape Town, South Africa.

Robben Island has an area of 507 ha, and the coastline is approximately 10 km in perimeter (Figure 3.1). Most of the shoreline is rocky with varying degrees of exposure (Crawford & Dyer 2000), but there is a 400 m long section of sandy shore south of Murray's Bay Harbour, an area where sand accumulates (Figure 3.1). During this study human disturbance was greatest in the area between the start of the settlement and Boundary Road. This is the area in which buses and most tourist activity occur. Relative to recreational beaches on the mainland, disturbance caused by tourists was small. Residents had access to the whole island but most of their activity was restricted to the area between the harbour and Boundary Road.

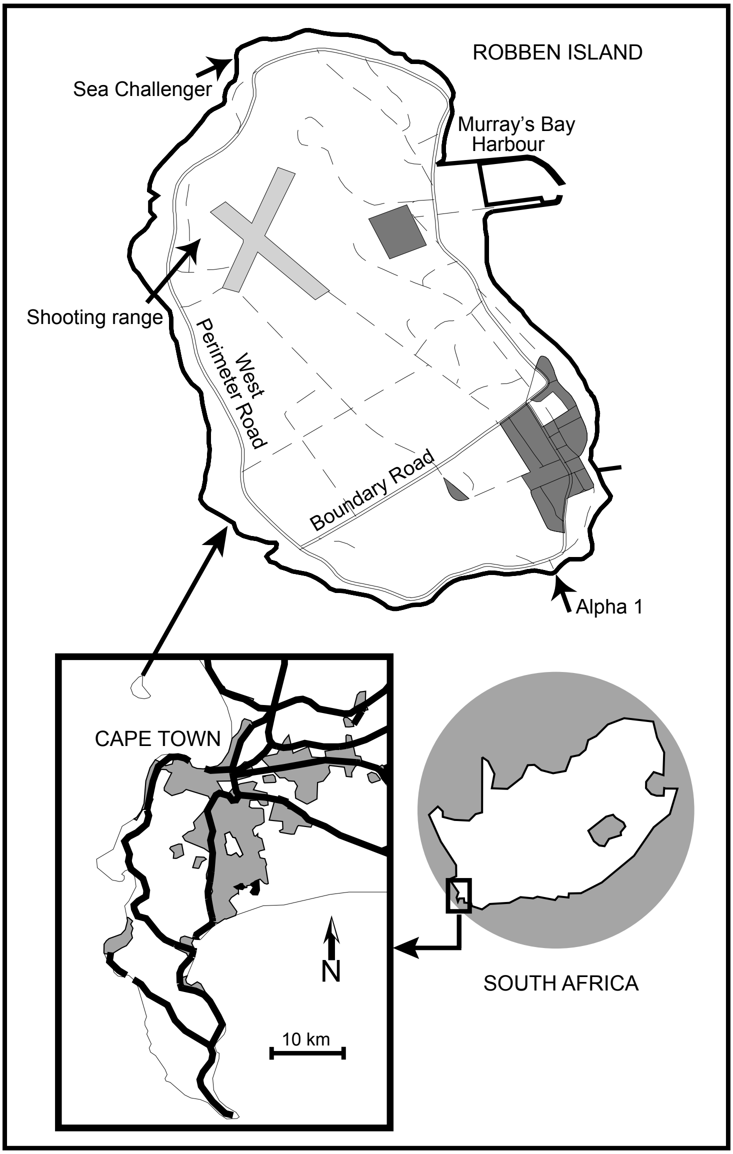

Figure 3.1. The location of Robben Island, South Africa, in Table Bay about 11 km from the port of Cape Town. African Black Oystercatchers were monitored in the 5 m to 20 m upper shore and intertidal zone along the entire shoreline of Robben Island – the narrow strip on the seaward side of the perimeter road. The dark shaded area in the south of the island is the settlement; the dark shaded area in the north is the prison, and the light shaded cross is the airstrip.

African Black Oystercatchers are found on the narrow upper shore, 5–20 m in width and the intertidal zone (limited in width by vegetation growth). Birds were not seen on the vegetated interior of the island. The African Black Oystercatchers are totally dependent on the intertidal zone for their food and most lay their clutches on the shelly and rocky areas of the upper shore.

Ringed population

From October 2001 to October 2003 111 adult oystercatchers were ringed with a stainless steel ring (SAFRING) on the right leg and a unique combination of colour rings. No birds were caught from October 2003 to April 2004 in order to eliminate the possible risk of egg predation caused by catching attempts at the nest. Oystercatchers are territorial and it was anticipated that the same pairs would nest in the same territories each year. We attempted to monitor this for colour ringed birds and determine their fledging success.

Nest positions

The GPS position of each nest was recorded. All nests were mapped with a GIS programme (ARCVIEW version 3.1 for Windows, Environmental Systems Research Institute, Inc.).

Nests, egg measurements and chicks

Nest searching occurred twice a week from the beginning of October until the end of April and breeding attempts were usually discovered during the laying or incubation stage. On finding a nest, eggs were uniquely marked, their masses were recorded to within ±0.1 g using an electronic balance (Tanita model 1479V) and length (l) measurements and two breadth measurements (b_1 and b_2) at right angles (90°) to each other over the widest part of the egg, were taken using a pair of dial callipers. Thereafter nests were revisited once a week during the first breeding season and at 3 to 4 day intervals during the subsequent breeding seasons until hatching.

Egg masses and measurements were compared between seasons, and comparisons between first, second and third clutches were made using ANOVA. Logistic regression was used to determine whether egg size influenced hatching success.

On hatching, chicks within a brood were uniquely marked. They were ringed on the right leg with a 10 mm stainless steel ring (SAFRING) when they had reached approximately 100 g. Chicks were captured every four to six days during their prefledging period and their survival monitored.

Seasonal value of an egg

The relationship between the start date of incubation (estimated using methods described in Underhill and Calf (2005) and Tjørve and Underhill (submitted manuscript-b) and the success of a breeding attempt was determined for each nest of the three breeding seasons using logistic regression. The estimated start date of incubation was used as the explanatory variable in logistic regressions, with hatching and fledging success as response variables.

Breeding success

Due to the obvious breeding behaviour of the oystercatchers and the narrow strip of coastline on which the oystercatchers bred, the chance of missing breeding attempts (nests or chicks) with frequent monitoring was small and it was assumed that all breeding attempts, eggs laid and chicks hatched were discovered during the three breeding seasons for the population of oystercatchers on Robben Island. We used the Mayfield method (Mayfield 1960, 1975) to determine mortality and survival rates (probability) of nests during the incubation stage and chicks during the prefledging period. If a nest was predated or abandoned, the date of loss or abandonment was estimated as the mid interval date between the date last observed and the date the loss or abandonment was first observed.

For nest survival the unit of exposure used was nest days: this is the number of days each nest was known to be viable. Nest mortality was calculated by dividing the total number of nests lost by the total number of nest days during the incubation stage, and nest survival was calculated as one minus the mortality rate (Mayfield 1960, 1975).

Hatching survival was calculated by dividing the number of hatchlings by the number of eggs present just before hatching. Total hatching survival was calculated by dividing the total number of hatchlings by the total number of eggs laid.

Oystercatcher chicks are semi-precocial and dates of predation or chick loss were difficult to determine; values produced from data collected are estimations. These estimations were the mid interval date between the date last observed and the date of the determination that the chick was no longer alive. Fledging survival was calculated by dividing the number of fledglings by the number of chicks hatched. Total fledging survival was calculated by dividing the number of fledglings by the total number of eggs laid. In addition, fledgling success per breeding pair and per nest were determined.

Breeding success along the shore

Breeding success of oystercatchers exposed to different predation or disturbance risks was estimated. The shore of the island was divided into four sections (Figure 3.1). The first was from Murray's Bay Harbour to the intersection of West Perimeter Road and Boundary Road which was the area most frequently disturbed by residents and tourists. The second section was from Boundary Road to the shooting range where there was little disturbance. The third section was from the shooting range to the *Sea Challenger*, where a Kelp Gull breeding colony was established in 2000 and became larger in subsequent years (Calf *et al.* 2003). The fourth section was from the *Sea Challenger* to Murray's Bay Harbour where there was the least human disturbance because the area was protected as part of an African Penguin *Sphensicus demersus* breeding colony. The number of failed breeding attempts, the number and percentage of successful breeding attempts and the number of fledglings per pair was calculated for each section of the shore.

Results

Breeding pairs

The number of breeding pairs, i.e. pairs that laid eggs, varied between the three consecutive breeding seasons: 64, 68 and 49, respectively. In the first breeding season, 2001–2002, the number of pairs observed on the island in the beginning of November was 61. Sixty-four pairs attempted to breed – 5% more than the number of pairs present at the start of the breeding season. At the start of the second breeding season, 2002–2003, there were 97 pairs on the island, and 68 (70%) pairs attempted to breed. There were 87 pairs at the start of the third breeding season, 2003–2004, and 47 (54%) of these attempted to breed.

Both individuals of five breeding pairs from the first season and 15 pairs from the second breeding season were colour-ringed. All ringed individuals remained on their territories in the following breeding seasons. Despite being on their territories in the following seasons, not all ringed pairs attempted to breed in subsequent seasons. None of the birds from colour-ringed pairs returned the following season with a different partner.

Nest positions

African Black Oystercatcher nests were found along the entire coast of Robben Island. The oystercatcher territories are linearly distributed along the shore, and the nests are found in a narrow strip of the upper shore just above the high tide water mark (limited by vegetation growth). There were no nests in the interior of the island. One pair bred on the sandy shore south of the harbour during the second breeding season, but otherwise all breeding attempts were made on the rocky shore. In all three breeding seasons nest density was low on the western side of the island. This side of the island is exposed because it faces the ocean rather than the bay.

Clutch size, egg measurements and chicks

Over the three-year study 205 nests were found on Robben Island: 16 one-egg (8%), 177 two-egg (86%) and 12 three-egg (6%) clutches. Three-egg clutches have become more common in African Black Oystercatchers breeding on the west coast islands of South Africa (PAR Hockey pers. comm.) but no significant increase in clutch size was found across the three breeding seasons (Chi squared: $\chi^2_4 = 2.29$, $P > 0.05$) on Robben Island. One hundred eggs from 68 clutches from the first breeding season, 146 eggs from 85 clutches from the second breeding season and 64 out of 103 eggs from 52 clutches laid during the third breeding season were used in the analysis.

Egg size was normally distributed. Median and mean egg measurements for all seasons for first, second and third clutches are shown in Appendix 1. We found the fresh mass of eggs to be 57.9 g (SD = ± 4.1, n = 36). No biologically significant difference was found in egg size ($l \times b_1 \times b_2$) between first, second and third clutches

(ANOVA: $F_{2, 393} = 2.80$, $P = 0.06$), and egg size did not change significantly during the breeding season (Linear regression: $R^2 = 0.001$, df = 395, $P = 0.506$). There was a significant difference in egg size (ANOVA: $F_{2, 393} = 4.02$, $P = 0.02$) and in egg mass (ANOVA: $F_{2, 359} = 3.93$, $P = 0.05$) across the three breeding seasons. Egg size was related to hatching success: eggs that hatched were larger than those that failed to hatch (Mann-Whitney U: U = 16741.0, P = 0.013).

Fifty-four chicks from 45 broods in the first breeding season, 60 chicks from 37 broods in the second breeding season and 24 chicks from 14 broods in the third breeding season fledged successfully.

Seasonal value of an egg

The date of the start of incubation of a nest was related to its hatching and fledging success. Eggs that were laid earlier in the season had a better hatching success (Logistic regression: logit (hatching success) = 6.438 + –0.033 (days after 1 July), $t = -4.71$, df = 395, $P < 0.001$) and a better fledging success (Logistic regression: logit (fledging success) = 4.467 – 0.028 (days after 1 July), $t = -4.67$, df = 395, $P < 0.001$).

Breeding success

The first nest of the first breeding season was found on 15 November 2001 and 68 nests from 57 breeding pairs were found during the season (Table 3.1). The chicks of seven pairs were found after hatching (Table 3.1). The first nest of the second breeding season was found on 14 November 2002 and 85 nests from 68 breeding pairs were found during the season (Table 3.1). The chicks of one pair were found after hatching (Table 3.1). The third breeding season started later than the previous two seasons (Tjørve & Underhill submitted manuscript-b): the first nest was found on the 29 November 2003. During the breeding season there were 49 breeding pairs and a total of 52 nests found with an additional two clutches found after hatching (Table 3.1).

Twenty-one percent of the eggs present at hatching in the first breeding season did not hatch (Table 3.3). This decreased to 12% and six percent in the second and third breeding seasons, respectively (Table 3.3).

During the first breeding season 15% of the broods were lost between hatching and fledging (Table 3.2). All but four chicks were lost within 14 days of hatching (mean = 8.4 days, SD= 6.2, n = 32). Two 19 day old chicks from the same brood, a 23 day old and a 24 day old chick, were lost after they were two weeks old. The number of broods lost between hatching and fledging was greater in the second breeding season, 22% (Table 3.1, Table 3.2). The mean age of chick loss during this breeding season was 6.3 days (SD= 6.7, n = 26). All but two chicks were lost within two weeks; one chick was lost at 20 days, and one at 32 days. The corpses of the two large chicks that were lost showed signs of cat predation; breast muscles and guts devoured leaving some bones, feathers and the rings (Calf & Underhill 2003). Forty-seven of the first clutches failed: 14 were washed away; 11 were depredated as eggs or chicks; two were trampled and two were abandoned after semi-predation (a single egg was depredated). The third oystercatcher breeding season was less successful than the previous two (Table 3.2): 72% of the number of breeding pairs in the previous season despite a similar total number of adult birds present at the start of the breeding season. Predation of eggs was greater (Table 3.2). Most chicks that were lost, disappeared on hatching day and all chick losses occurred within 12 days (mean = 3.2, SD = 3.1, n = 11). Re-lays were less successful than first clutches due to a higher rate of egg loss (Table 3.2).

The second breeding season saw the greatest number of chicks hatch from first clutches (68 compared to 59 and 31 in the first and third breeding seasons, respectively) and the first breeding season had the greatest number of chicks hatch from second clutches (9 chicks compared to 4 and none in the second and third breeding seasons, respectively). There were no third clutches in the first breeding season and the third clutch of the third breeding season did not result in fledglings but two of the five third clutches of the second breeding season hatched four chicks and three of these survived to fledging.

According to the Mayfield method, the survival rate of nests during incubation decreased across the three breeding seasons (Table 3.3). The probability of a brood surviving to fledging was greatest in the first breeding season and lowest in the second breeding season (Table 3.3). The overall survival of an egg to fledging decreased from 0.368 fledglings per egg in the first breeding season to 0.199 and 0.155 in the second and third breeding seasons, respectively (Table 3.3). A similar decreasing trend was observed in the number of fledglings per pair (Table 3.3).

Table 3.1. Number of African Black Oystercatcher nests on Robben Island, South Africa, across three consecutive breeding seasons: the first (2001–2002), second (2002–2003) and third (2003–2004).

	First	Second	Third
Number of first clutches	57	67	47
Number of second clutches	11	13	4
Number of third clutches	0	5	1
Total number of nests	68	85	52
Broods found after hatching	7	1	2
Clutches disappeared as eggs	15 (22%)	43 (51%)	26 (53%)

Table 3.2. African Black Oystercatcher hatchlings and fledglings per nest on Robben Island, South Africa, across three consecutive breeding seasons: first (2001–2002), second (2002–2003) and third (2003–2004). These values are shown in figure 3.2.

	First		Second		Third	
	Hatchlings	Fledglings	Hatchlings	Fledglings	Hatchlings	Fledglings
First clutch	1.04 (59)	0.72 (41)	1.01 (68)	0.46 (31)	0.66 (31)	0.34 (16)
Second and third clutches	1.00 (11)	0.81 (9)	0.44 (8)	0.22 (4)	0.00 (0)	0.00 (0)
Including broods found after hatching		0.78 (59)		0.41 (35)		0.35 (19)

Table 3.3. Survival and mortality of eggs during incubation, hatching survival and numbers of fledglings produced per pair and per nest for African Black Oystercatchers on Robben Island, South Africa, over three consecutive breeding seasons: the first (2001–2002), second (2002–2003) and third (2003–2004).

	Calculation	First	Second	Third
Nest incubation mortality	M = # nests lost / # nest days	0.014	0.026	0.052
Nest incubation survival	S = 1–M	0.986	0.974	0.948
Probability of nest survival during incubation	$S^{\text{days of incubation (28)}}$	0.671	0.485	0.223
Egg mortality	M = # eggs lost / # egg days	0.013	0.022	0.051
Egg survival	S = 1–M	0.987	0.978	0.949
Probability of egg survival during incubation	$S^{\text{days of incubation (28)}}$	0.686	0.530	0.232
Brood mortality during prefledging period	M = # brood lost/# brood days	0.019	0.038	0.021
Brood survival during prefledging period	S = 1–M	0.981	0.962	0.979
Probability of brood survival	$S^{\text{days of prefledging period (40)}}$	0.464	0.211	0.433
Chick mortality during prefledging period	M = # chicks lost/# chick days	0.016	0.027	0.016
Chick survival during prefledging period	S = 1–M	0.984	0.973	0.984
Probability of chick survival	$S^{\text{days of prefledging period (40)}}$	0.526	0.330	0.520
Hatching survival	# hatchlings / # eggs just before hatching	0.794	0.876	0.939
Total hatching survival	# hatchlings / # eggs laid	0.625	0.470	0.301
Fledging survival	# fledglings / # chicks hatched	0.588	0.423	0.516
Survival of an egg to fledging	# fledglings / # eggs laid	0.368	0.199	0.155
Fledglings per pair	# fledglings / # breeding pairs	0.877	0.485	0.388
Fledglings per nest	# fledglings / # nests	0.735	0.384	0.352

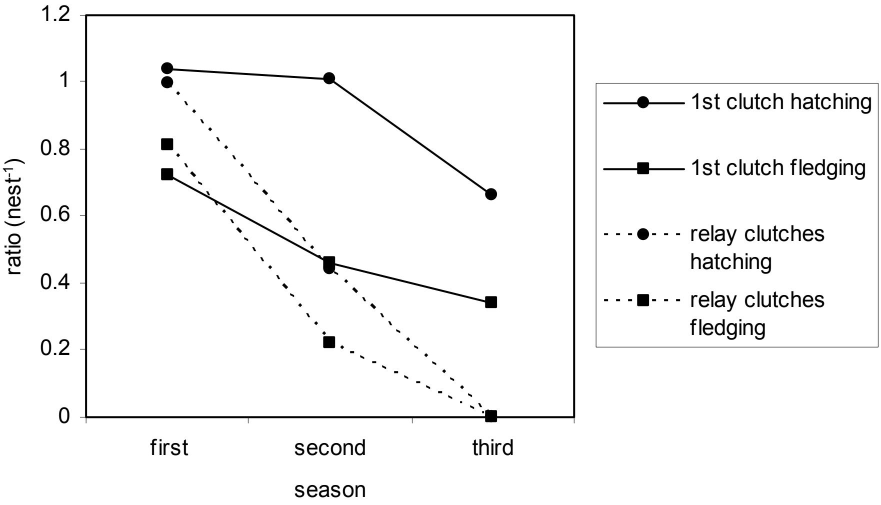

Figure 3.2. Hatching and fledging success of African Black Oystercatchers on Robben Island, South Africa, over three consecutive breeding seasons: the first (2001–2002), second (2002–2003) and third (2003–2004).

Extreme high tide events

Unusually stormy weather resulting in high seas and long intervals between waves combined with a spring high tide produced large breakers that pushed beyond the normal spring high tide limit on 17 February 2003 (Calf & Underhill 2005). By the middle of February 67 pairs had attempted breeding and 21 oystercatcher nests were still active on Robben Island on 16 February. Fourteen of these were first breeding attempts and seven were second breeding attempts after their first attempt failed. Before 17 February, 10 pairs had relaid after their first clutch or chicks were lost. Of these second clutches, three were predated before 17 February and the remaining seven were washed away in the extreme high tide event.

The eggs of one nest hatched between the nest check on 16 February and the high tide on 17 February and the chicks were able to find shelter from the waves and thus survived. The tidal event on 17 February resulted in the loss of 20 clutches. No chicks were lost during the high-tide event. Nine pairs nested after 17 February (five pairs were attempting their third clutch, three pairs their second clutch and a single pair attempted their first clutch of the season). The remaining pairs abandoned breeding activities. Five of the relaid clutches survived to hatching, and three of these successfully raised chicks to fledging. As a result of these relays, the breeding season was extended (Tjørve & Underhill submitted manuscript-b), and the chicks from these nests fledged in April.

The third oystercatcher breeding season started later and was shorter in length than the previous two (Tjørve & Underhill submitted manuscript-b). By

10 February 2004, 47 pairs had attempted to breed and one pair had attempted a second clutch. Two nests remained on the island, both first breeding attempts for the season and both were washed away in the extreme high tide event. Of the five nests laid after the high tide event in 2004 two were first clutches of the season and three were relays of pairs that had lost their clutches before the high tide event. One pair laid their third clutch of the season after 10 February 2004. All of these nesting attempts were depredated as eggs.

Breeding success along the shore

Breeding success (percentage of successful breeding attempts) was significantly different in the four sections of the shore across the three breeding seasons: (1) Murray's Bay Harbour to the intersection of West Perimeter Road and Boundary Road, (2) from Boundary Road to the shooting range, (3) from the shooting range to the *Sea Challenger* and (4) from the *Sea Challenger* to Murray's Bay Harbour ($\chi^2_{12} = 338.67$, $P < 0.01$).

In all three seasons most nests were found in the section of shore between Murray's Bay Harbour and the intersection of Western Perimeter Road and Boundary Road (1). During the three seasons 59%, 38% and 31%, respectively, of the nests found were within this area (Table 3.4). During the second breeding season the section of shore from the intersection of Western Perimeter Road and Boundary Road to the shooting range (2) had the same percentage of nests, 38%, as the section from the harbour to the Boundary Road intersection (Table 3.4).

The area of highest egg (35% of breeding attempt losses) and chick (13% of breeding attempt losses) depredation was the area most frequented by tourists and residents, between Murray's Bay Harbour and the intersection between West Perimeter Road and Boundary Road (1, Figure 3.3). Forty-eight of the first, 11 of the second and three of the third clutches were lost in this area over the three breeding seasons (Figure 3.3). The percentage of successful breeding attempts in this section of the shore was 40.8%, 12.5% and 11.8% in the three breeding seasons respectively (Table 3.4, Figure 3.3). The success of breeding attempts in this section of the shore declined between the first and the second breeding season. A similar trend was seen in the section from the intersection of West Perimeter Road and Boundary Road and the shooting range (2, Table 3.4). A decrease in the success of oystercatcher breeding attempts in the section from the shooting range to the *Sea Challenger*, the gull colony (3), was observed between the second and the third breeding seasons, 66.7% to 14.3% (Table 3.4, Figure 3.3). Fifty-seven percent of the oystercatcher breeding attempts in the section from the *Sea Challenger* to Murray's Bay Harbour (4) were successful (Table 3.4, Figure 3.3). Breeding success was relatively consistent in this section across the three breeding seasons: 61.5%, 50% and 60% respectively. Unlike the first and the second breeding season eggs and chicks were depredated along all sections of the coast during the third breeding season (Figure 3.3c).

The number of breeding pairs compared to pairs present on the shore between Alpha 1 and Boundary Road decreased significantly from the first to the third breeding season ($\chi^2_3 = 170.63$, $P < 0.01$). There were 17 pairs with territories between

Alpha 1 and Boundary Road in the first breeding season (Figure 3.3a); 14 (82%) of these attempted breeding. The analogous figures in the second breeding season were 24 pairs of which 14 (58%) attempted to breed (Figure 3.3b), and in the third breeding season, 7 pairs out of 26 (27%) in this area attempted to breed (Figure 3.3c).

Table 3.4. Breeding success of African Black Oystercatchers in four different areas of the shore of Robben Island, South Africa, over three consecutive breeding seasons: the first (2001–2002), second (2002–2003) and third (2003–2004).

Breeding season	Harbour to Boundary Road	Boundary Road to Shooting Range	Shooting Range to *Sea Challenger*	*Sea Challenger* to Harbour
Number of breeding attempts				
First	40	14	10	13
Second	32	32	9	14
Third	17	15	7	15
Failed				
First	20	4	4	5
Second	28	26	3	7
Third	15	12	6	6
Succeeded				
First	20	10	6	8
Second	4	6	6	7
Third	2	3	1	9
Percentage of successful breeding attempts				
First	50.0	71.4	60.0	61.5
Second	12.5	18.8	66.7	50.0
Third	11.8	20.0	14.3	60.0
Number of fledglings per pair				
First	0.45	0.79	0.80	0.69
Second	0.13	0.28	1.11	0.86
Third	0.18	0.27	0.14	0.80

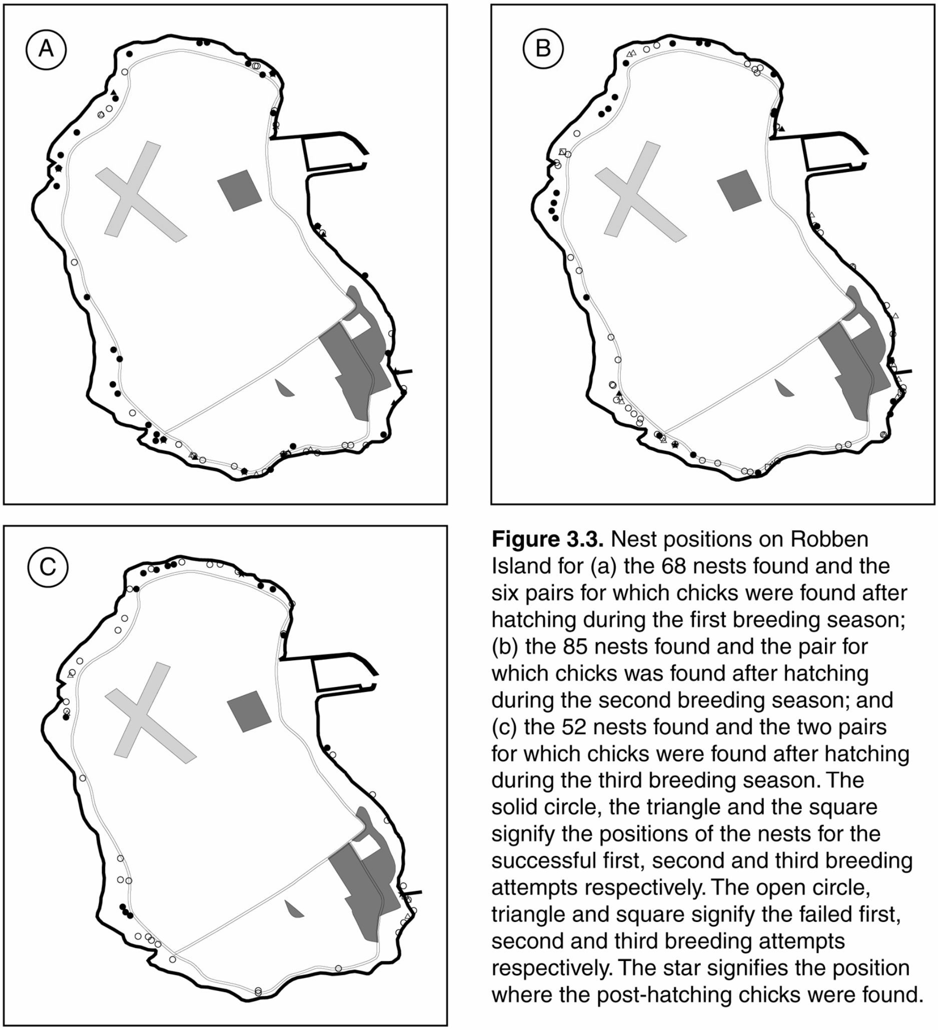

Figure 3.3. Nest positions on Robben Island for (a) the 68 nests found and the six pairs for which chicks were found after hatching during the first breeding season; (b) the 85 nests found and the pair for which chicks was found after hatching during the second breeding season; and (c) the 52 nests found and the two pairs for which chicks were found after hatching during the third breeding season. The solid circle, the triangle and the square signify the positions of the nests for the successful first, second and third breeding attempts respectively. The open circle, triangle and square signify the failed first, second and third breeding attempts respectively. The star signifies the position where the post-hatching chicks were found.

From eggs to fledglings

Fifty-seven (84%) of all the clutches found during the first breeding season consisted of two eggs; 27 of these hatched two chicks and nine hatched one chick successfully. Ten (37%) of the clutches that hatched two chicks raised both chicks to fledging. Seventy-four (87%) of the clutches found during the second breeding season consisted of two eggs; 28 of these hatched two chicks and nine hatched a single chick. Twelve (43%) of the two-egg clutches that hatched raised both chicks to fledging. During the third breeding season, 47 (90%) nests were two-egg clutches; 14 hatched both chicks and one hatched a single chick. Three (21%) two-egg clutches that hatched both chicks fledged both chicks. When looking at fledging success in relation to clutch size one can argue that fledging success is greater for one-egg clutches than for two or three-egg clutches ($\chi^2_2 = 63.8$, $P < 0.001$). The small number of one-egg clutches, 16, and three-egg clutches, 12, compared to the large number of two-egg clutches, 177, means that there was a greater chance for two-egg clutches to lose one egg or one chick to predation than for one-egg or three-egg clutches.

Most chicks were lost within two weeks of hatching. It was presumed that the majority of chick losses were due to predation rather than starvation or any other environmental impacts because no sickly or starving chicks were found and the corpses of two large chicks were found consumed in the characteristic manner of a cat predation (Calf & Underhill 2003). The 17 February 2003 tidal event resulted in a loss of all nests present at the time (the second breeding season) in all areas along the coast.

Discussion

Breeding pairs

African Black Oystercatchers are sedentary; their food availability varies little during the year and they do not migrate large distances after the breeding season, but remain on or near their territories for most or all of the year (Summers & Cooper 1977, Hockey & Underhill 1983, Underhill *et al.* 1999). During this study it was not possible to determine whether oystercatchers on Robben Island remained on their territories because an insufficient number of birds were colour-ringed. All breeding birds that were ringed were found in the same territories in following breeding seasons. Pairs were present in areas where breeding attempts had been unproductive the previous breeding season, and some of these pairs did not attempt to breed; note, for example, the declining number of breeding birds between Alpha 1 and Boundary Road (Table 3.4).

The declining number of breeding pairs compared to pairs present at the beginning of the breeding season may be a consequence of increasing predation and pairs choosing not to attempt breeding as a result.

Clutch size and egg measurements

The modal clutch size for this study was determined to be two eggs, the same as determined by Summers and Cooper (1977) and Hockey (1983a). This is the same clutch size recorded for American Black Oystercatchers *H. bachmani* (Hartwick 1974), Blackish Oystercatchers *H. ater* (del Hoyo *et al.* 1996) and some other oystercatcher species (Hockey 1996). These species have a range in clutch size from one to three eggs. A modal clutch size of three eggs has been recorded for American Oystercatchers *H. paliatus* (Baker & Cadman 1980), Eurasian Oystercatchers (Vermeer *et al.* 1992, Ens *et al.* 1996, Hockey 1996) and the Variable Oystercatcher *H. unicolor* (del Hoyo *et al.* 1996), and the variability in clutch size can be from two to five eggs (Hockey 1996).

Clutch size has been recorded to decrease during the breeding season for Eurasian Oystercatchers (Ens *et al.* 1996) and replacement clutches were smaller than first clutches in American Oystercatchers (Nol *et al.* 1984). This was assumed to enable faster incubation, which could enable successful chick rearing before weather conditions deteriorated in autumn (Ens *et al.* 1996, Hockey 1996). Less variation in the number of eggs in a clutch and no reduction in clutch size was found in African Black Oystercatchers during this study. This may be attributable to the mild climatic conditions and long breeding season in South Africa resulting in females being able to accrue sufficient energy to lay eggs the same size throughout the breeding season without the rush to complete incubation or chick rearing. Eggs laid later in the breeding season are, however, at greater risk of being washed away by early autumn storms. Clutch size of African Black Oystercatchers is already small, two eggs, therefore a reduction in brood size would decrease the chances of breeding success in relaid clutches.

Food resources might limit clutch and egg size of African Black Oystercatchers. Since the 1980s the Palearctic mussel *Mytilus galloprovincialis* has invaded the South African coast, where it has displaced the indigenous mussel *Aulacomya ater* (Robinson & Griffiths 2002). The birds breeding on west coast islands where *M. galloprovincialis* has invaded are laying three-egg clutches more frequently than before the mussel invasion (P. A. R. Hockey pers. comm.). By October 2003, *M. galloprovincialis* had invaded from 10% to 70% of the lower shore of Robben Island, which is less than on the adjacent mainland (KMCT unpubl. data). Since the invasion has occurred on the lower shores only, this food supply is exposed for short periods and has not greatly influenced food availability for African Black Oystercatchers. Therefore the invasion of this mussel has not reached levels observed on other offshore islands or on the mainland, and it is does not seem to have impacted oystercatcher clutch size on Robben Island.

The eggs of African Black Oystercatchers are large relative to those of other oystercatcher species (Hartwick 1974, Baker & Cadman 1980, Vermeer *et al.* 1992). Mass of modal clutch as a percentage of female mass is 15.5% for African Black Oystercatchers (Hockey 1996), which is less than that of the Eurasian Oystercatcher, 23.3%, the American Oystercatcher, 23.3%, and the American Black Oystercatcher, 21.9%. Therefore despite being large eggs, egg mass is small compared to female size –possibly a consequence of food availability. Summers and Cooper (1977) found the fresh mass of eggs to be 59.7 g (n = 27), and Hockey (1983a) found the mass of fresh eggs to be 55.8 g (n = 105), which was not significantly different to the 57.9 g determined in this study ($t = 1.72$, $P > 0.05$ and $t = -0.38$, $P > 0.05$). Egg size was consistent through the breeding season and across the breeding seasons; therefore energy resources may have been consistent.

Seasonal value of an egg

Oystercatchers are usually single-brooded and repeat clutches are produced when the eggs or chicks are lost (Ens *et al.* 1996). Eurasian Oystercatchers breed over a relatively short period, three to four months, and during this period clutch size, hatching success, hatchlings fledged and fledglings per clutch all decrease (Ens *et al.* 1996). African Black Oystercatchers have a longer breeding season, laying over a period of up to six months (Tjørve & Underhill submitted manuscript-b). Clutch size in African Black Oystercatchers does not vary during the breeding season but it was found that hatching and fledging success are dependent on the date upon which clutch incubation started.

Breeding success

Hockey (2001) estimated the threshold level for African Black Oystercatchers to maintain a stable population as 0.33 fledglings per pair during a single breeding season. The oystercatchers breeding on Robben Island exceeded this value in all three breeding seasons of this study despite the decreasing fledging success. Fledging success in the third breeding season on Robben Island was close to, but slightly above, the threshold for replacement. The declining success rate of the oystercatchers on Robben Island may be a result of several factors; predation, disturbance, food availability, environmental conditions and the age and experience of the breeding pairs. The influence of these factors will be further discussed.

Sampling methods for the second and third breeding seasons of oystercatchers on Robben Island, South Africa, included nest checks twice a week and in some cases checking on the day of hatching. As a result the number of hatchlings observed for this and the following breeding season were more accurate than that of the first season.

Predation

Oystercatchers breeding on Robben Island were exposed to similar predation risks as birds breeding on mainland shores, namely land-based predators such as cats, snakes and rats. These predators can greatly reduce the breeding success of oystercatchers, especially when exposed to disturbance. For example, oystercatchers breeding on the mainland in unprotected areas produced 0.25 fledglings per pair compared to 0.70 fledglings per pair in protected areas where fewer predators and less disturbance could impact breeding success (Leseberg *et al.* 2000, Hockey 2001).

Oystercatcher egg losses have been attributed to gull predation (Hartwick 1974, Nysewander 1977). In 2000, Kelp Gulls bred on Robben Island for the first time; 15 pairs bred in 2001, 68 pairs nested on the island in 2002 (Calf *et al.* 2003), and 87 pairs nested in 2003 (KMCT unpubl. data). The Kelp Gull breeding season coincides with that of the oystercatchers, and Kelp Gulls are known predators of

African Black Oystercatcher eggs (Summers & Cooper 1977). Ten eggs with characteristic gull predation marks were found in both 2002 and 2003 (KMCT pers obs). The oystercatchers breeding in the areas surrounding the gull colony, the quarry and associated beaches, were at the highest risk of losing eggs or chicks to Kelp Gulls. During the third oystercatcher breeding season the Kelp Gull breeding colony was at its largest and during this season a large decrease in oystercatcher breeding success was observed in the area. Prop and Quinn (2003) and Quinn *et al.* (2002) discuss the trade-off relationship between Red-Breasted Geese, *Branta ruficollis*, and birds of prey. They argue that Red Breasted Geese choose to nest near birds of prey for the protection against other predators despite the potential threat of the bird of prey to their breeding attempt (Quinn *et al.* 2002). Hartwick (1974), Nysewander (1977) and Vermeer *et al.* (1992) report a similar relationship between American Black Oystercatchers and gulls – oystercatchers benefiting from reduced predation from mammals or crows. African Black Oystercatchers may also benefit from reduced predation by other potential predators through a nesting close to Kelp Gulls. However, the nesting density of oystercatchers did not increase and fledgling success decreased in this area during the study – the decrease in fledging success in this area may not have been associated directly with increasing numbers of breeding Kelp Gulls but with the general increase in predation.

Feral cats can have devastating effects on small mammal and bird populations (Hatley & Ankersen 2003, Nogales *et al.* 2004). The number of feral cats observed on the shoreline increased during this study (KMCT unpubl. data). Egg and chick losses also increased. Cat eradication on the island should increase oystercatcher breeding success.

In addition to increases in the number of feral cats and gulls, the number of mole snakes on the shore of the island has also increased during the study period (Calf 2004). Predation of oystercatcher eggs by a mole snake was observed (Calf 2004) and mole snakes were also observed to predate Kelp Gull eggs and chicks in November and December 2003 (Calf 2004).

Ens *et al.* 1996 suggested that it may be wrongly concluded that Eurasian Oystercatchers, *H. ostralegus*, refrained from breeding in a particular season if the clutch was depredated during or shortly after laying. Even though methods for searching for nests were the same in the second and third breeding seasons, predation of eggs was greater in the third season and the chance of not finding a nest before predation was greater. Breeding success may therefore be lower than calculated for the third breeding season and the impact of predation would then be more dramatic than stated. Thus the total breeding success may have been lower than the 0.33 fledglings per pair necessary to maintain a stable population.

Direct and indirect impacts of disturbance

Because of its status as a World Heritage Site, Robben Island is a tourist attraction and the number of visitors has increased in recent years. Although tourist movement on the island is strictly controlled, a minimum of two bus tours per hour disturb the section of coast from the harbour to Boundary Road from 11:00 to 19:00 hours during the summer. The road in most of this area is very close to the high water mark and as a result oystercatchers nest close to the road. Each bus tour thus results in disturbance of incubating birds, causing the birds to possibly leave their nests and expose their eggs to potential predators. This may explain the large number of egg predations in the area from Murray's Harbour to the intersection of West Perimeter Road and Boundary Road. Disturbance and the indirect effects of disturbance could also cause birds to abandon attempting to nest in these areas: note, for example, the reduction in breeding pairs between Murray's Bay Harbour and Boundary Road.

None of the 12 three-egg clutches found on Robben Island over the three seasons successfully raised three chicks to fledging. In some cases the third egg was abandoned while it was hatching or it was assumed infertile because the egg did not start to hatch. Abandonment of the third egg during hatching is possibly a consequence of human disturbance; the adults moving two of their hatchlings to safer environs within the territory as quickly as possible, thus sacrificing their last chick. Human disturbance may also cause adults to leave their chicks upon hatching, the third chick possibly being incapable of surviving due to the energetic cost of thermoregulation and hatching.

The section of shoreline between Murray's Bay Harbour and Boundary Road had the lowest percentage of successful breeding attempts in all three breeding seasons. This is most likely a result of the combined effect of disturbance and predation in this area. Increased predation occurred in all areas of the island over the study period, but the affects were most obvious in the areas from the harbour to Boundary Road and from Boundary Road to the shooting range. Success of breeding attempts in these areas decreased in the second breeding season and remained at a similar low level in the third breeding season. The area between the *Sea Challenger* and the harbour was the only area where oystercatchers successfully bred in all three breeding seasons. This is also the only area that had minimal human disturbance and there were few Kelp Gulls.

Food availability

African Black Oystercatchers, like other oystercatcher species, prey on invertebrates in the intertidal zone, and this food source shows little seasonality (Hockey 1981, L'Hyver & Miller 1991). As a result, food supplies should be limiting to breeding birds on Robben Island only if there is not enough space for sufficiently sized territories. The oystercatcher population on Robben Island has been increasing (Tjørve & Underhill submitted manuscript-a), therefore competition for food is not likely to be limiting to breeding success unless territory sizes become marginal in their ability to support breeding attempts.

Environmental conditions

The mild South African climate provides African Black Oystercatchers with long summers in which to breed (Hockey 1996). The weather in the Western Cape is driven by frontal systems, so oystercatchers nest during the summer months to prevent their eggs from being washed away by winter storms. Nesting should be completed well before the return of winter storms in the autumn, but unusual weather can have catastrophic consequences, such as that which occurred on 17 February 2003. Although extreme high tide events occurred during the last two seasons of this study, the fledging success was above the replacement level to maintain a stable population. Fledging success did, however, decrease during this three-year study, and this reduction is more likely to be attributable to predation than environmental conditions.

Age and experience of breeding pairs

Breeding success of ground-nesting birds has been attributed to breeding experience – the more experienced breeders are often more successful than younger birds because they lay larger eggs in larger clutches earlier in the breeding season (Coulson & White 1958, Nysewander 1977, Bunce *et al.* 2005, Sarsvari & Hegyi 2005, Sæther 2005). The ages of the oystercatchers in this study were unknown. The population of African Black Oystercatchers on Robben Island is increasing (Tjørve & Underhill submitted manuscript-a) therefore there may be more young and inexperienced breeders than in a stable population. Consequently, breeding success of birds on Robben Island could be lower than that of an older breeding population.

Adaptive strategies to maximise fitness

Raising three-egg clutches to fledge three chicks is unusual in African Black Oystercatchers (Hockey 1999b, PAR Hockey pers comm.), and birds on Robben Island were not able to achieve this. Incubation and hatching survival in African Black Oystercatchers was greater than fledging survival. Therefore the prefledging period was the period that influenced breeding success the most.

Ens *et al.* (1992) and Kersten (1997) hypothesised that Eurasian Oystercatcher adults may be unable or unwilling to expend their own energy in rearing two or three chicks, thereby sacrificing their longevity and lifetime reproductive success. On the basis of the fledging success of the first breeding season, 0.877 fledglings produced per pair, it was proposed that oystercatchers on Robben Island operated a brood reduction strategy (Calf & Underhill 2002): adults preferentially feeding one chick (O'Conner 1984), because most pairs reared one chick to fledging despite 93% of nests containing two or three eggs. This did not take predation into account.

It is difficult to determine the cause of chick loss if one does not observe predation events but it should have been possible to observe chicks starving, because it is not an immediate event and chicks were monitored frequently. One would assume that the adaptive value of starving a chick would only occur when the adults become time stressed feeding two or more chicks. There would be little adaptive benefit of starving a small chick if this could reduce the possibility of successfully raising at least one chick to fledging. If brood reduction was occurring in oystercatchers on Robben Island, one would therefore expect chick losses to occur during the period of maximum food requirements of the brood, close to fledging when the chicks' requirements are at their largest. This was not observed during this study. Most chicks that disappeared did so during the first two weeks after hatching, a period when they are small, not particularly agile and most vulnerable to predation. The corpses of two large chicks were found showing evidence of cat predation. The loss of eggs and small chicks suggests that chick loss is more likely a result of predation rather than brood reduction.

Hockey (1983a) found that 87.5% chick mortality in African Black Oystercatchers occurs in the first week after hatching and thereafter chick mortality reduced to less than 30%. Similarly, 61–62% of Eurasian Oystercatcher chick mortality occurred during the first week after hatching (Hartwick 1974). Predation has been identified as a major cause of chick deaths in oystercatchers (Hockey 1996). Therefore chick mortality observed in this study is more likely a result of predation than brood reduction.

Comparison of breeding success with other oystercatcher species

Low breeding success has been seen in oystercatchers worldwide (Hartwick 1974, Baker & Cadman 1980, Nol *et al.* 1984, Hazlitt & Butler 2001, Vermeer *et al.* 1992). This low success rate has been attributed to loss of eggs rather than the mortality of dependant chicks (Hockey 1996). For example, in Virginia, 14% of 229 nests of American Oystercatchers hatched, and of the nests that produced hatchlings, 69% fledged at least one chick (Nol 1989). Blackish Oystercatchers in Argentina hatched only one out of 20 nests, and only one chick fledged (Nol 1984). Hockey (1996) reported that the causes of egg loss in most oystercatcher species are predators and storms, and because these factors vary locally, fledging success can vary in different areas within the same species. For example, the fledging success of the American Black Oystercatcher varied from 0.19 to 1.1 fledglings per pair (Hartwick 1974). Fledging success can also vary between years; for example, American Oystercatchers produced 0 to 0.5 young per pair over four years (Nol 1989). The results found in this study are not unusual for oystercatchers and the differences in breeding success between the three seasons can be attributed to the same causes as found in other studies, namely predators and storms in addition to the direct and indirect influences of disturbance.

Conclusion

Robben Island supports a large population of African Black Oystercatchers, but also supports a busy tourist attraction and a resident human population. Although the population of oystercatchers is subject to disturbance, fledging success during this study was above the estimated threshold level to maintain population levels. Oystercatcher numbers on Robben Island have increased in recent years (Tjørve & Underhill submitted manuscript-a) and may be a result of successful breeding on the island. Breeding success during this study did, however, decrease over the three years. This decrease could be attributable to several factors, but the most likely is increasing predation of eggs and chicks and storms unusually early in autumn washing eggs away.

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Appendix 3.1. Egg measurements of African Black Oystercatchers on Robben Island, South Africa, for three different breeding seasons: first (2001–2002), second (2002–2003) and third (2003–2004). Data were separated according to breeding season and clutch number within that season. Egg masses were those taken on finding the nest. Equality of means was tested for mass, length, breadth 1 and breadth 2 within and between the three breeding seasons using ANOVA, but none of these differences were statistically different. Eggs of the first, second and third clutches were significantly different in the breadth 1 (ANOVA: $F_{2,393} = 6.50$, $P = 0.002$) and breadth 2 (ANOVA: $F_{2,393} = 6.74$, $P = 0.001$) measurements.

Clutch	Mass (g)			Length (mm)			Breadth 1 (mm)			Breadth 2 (mm)			*n*
	mean	median	SD	mean	median	SD	mean	median	SD	mean	median	SD	
First season first clutch	55.4	55.5	4.38	61.6	61.3	2.43	42.2	42.3	0.95	42.2	42.3	0.97	112
First season second clutch	53.6	54.0	5.15	61.2	60.4	3.03	42.2	42.4	1.50	42.3	42.4	1.49	22
Second season first clutch	56.0	55.5	3.87	61.1	61.0	2.18	41.8	41.9	1.10	41.8	41.8	1.12	127
Second season second clutch	56.8	56.4	4.43	60.7	60.8	2.48	42.4	42.4	1.29	42.5	42.5	1.31	45
Second season third clutch	56.8	57.0	3.94	60.9	61.2	3.08	43.3	42.5	1.65	43.3	42.5	1.61	9
Third season first clutch	56.4	56.4	4.01	61.0	61.0	2.60	41.9	41.8	1.03	41.9	41.8	1.03	91
Third season second clutch	53.9	53.7	2.19	61.8	62.0	0.87	41.0	41.0	0.51	41.0	41.0	0.54	5
Third season third clutch	57.3	57.3	0.35	61.0	61.0	0.21	42.1	42.1	0.14	42.1	42.1	0.14	2
Totals													
First clutch	55.9	55.7	4.09	61.3	61.1	2.40	42.0	42.0	1.05	42.0	42.0	1.06	330
Second clutch	55.2	55.7	4.80	61.0	60.8	2.62	42.2	42.4	1.39	42.2	42.2	1.38	52
Third clutch	56.8	57.0	3.54	60.9	61.1	2.76	43.1	42.3	1.55	43.1	42.5	1.53	11

Appendix 3.2. Breeding parameters of African Black Oystercatchers on Robben Island, South Africa, for three consecutive breeding seasons: the first, (second) and **third** breeding seasons.

	Total nests	Nests in which at least one chick hatched	Total chicks hatched	Chicks hatched per nest	Nests producing at least one fledgling	Total fledglings produced	Fledglings per nest	Fledglings per egg
First clutches								
1-egg	5 (6) **3**	3 (1) **0**	3 (1) **0**	0.60 (0.17) **0.00**	3 (1) **0**	3 (1) **0**	0.60 (0.17) **0.00**	0.6 (0.17) **0.00**
2-egg	48 (57) **42**	30 (33) **15**	51 (57) **29**	1.06 (1.00) **0.69**	30 (18) **12**	36 (28) **15**	0.75 (0.49) **0.36**	0.38 (0.24) **0.18**
3-egg	4 (4) **2**	2 (4) **1**	5 (10) **2**	1.25 (2.50) **1.00**	2 (2) **1**	2 (2) **1**	0.50 (0.50) **0.50**	0.17 (0.17) **0.17**
Totals	57 (67) **47**	35 (38) **16**	59 (68) **31**	1.04 (1.01) **0.66**	35 (21) **13**	41 (31) **16**	0.72 (0.46) **0.34**	0.36 (0.23) **0.17**
Second clutches								
1-egg	0 (1) **0**	0 (0) **0**	0 (0) **0**	0.00 (0.00) **0.00**	0 (0) **0**	0 (0) **0**	0.00 (0.00) **0.00**	0.00 (0.00) **0.00**
2-egg	9 (12) **4**	6 (2) **0**	6 (4) **0**	0.67 (0.33) **0.00**	6 (1) **0**	7 (1) **0**	0.78 (0.08) **0.00**	0.39 (0.04) **0.00**
3-egg	2 (0) **0**	2 (0) **0**	3 (0) **0**	1.50 (0.00) **0.00**	1 (0) **0**	2 (0) **0**	1.00 (0) **0.00**	0.33 (0.00) **0.00**
Totals	11 (13) **4**	8 (2) **0**	11 (4) **0**	1.00 (0.31) **0.00**	8 (1) **0**	9 (1) **0**	0.81 (0.08) **0.00**	0.41 (0.04) **0.00**
Third clutches								
1-egg	0 (1) **0**	0 (0) **0**	0 (0) **0**	0.00 (0.00) **0.00**	0 (0) **0**	0 (0) **0**	0.00 (0.00) **0.00**	0.00 (0.00) **0.00**
2-egg	0 (4) **1**	0 (2) **0**	0 (4) **0**	0.00 (1.0) **0.00**	0 (2) **0**	0 (3) **0**	0.00 (0.75) **0.00**	0.00 (0.38) **0.00**
3-egg	0 (0) **0**	0 (0) **0**	0 (0) **0**	0.00 (0.00) **0.00**	0 (0) **0**	0 (0) **0**	0.00 (0.00) **0.00**	0.00 (0.00) **0.00**
Totals	0 (5) **1**	0 (2) **0**	0 (4) **0**	0.00 (0.80) **0.00**	0 (2) **0**	0 (3) **0**	0.00 (0.60) **0.00**	0.00 (0.33) **0.00**
Nest total	68 (85) **52**	43 (42) **16**	70 (76) **31**	1.03 (0.89) **0.60**	43 (24) **13**	50 (35) **16**	0.74 (0.41) **0.31**	0.37 (0.21) **0.16**
Broods	7 (1) **2**	7 (1) **2**			5 (0) **2**	9 (0) **3**	0.92 (0.21) **1.50**	
Grand total	75 (86) **54**	50 (43) **18**			48 (24) **15**	59 (35) **19**	0.57 (0.41) **0.35**	