

BREEDING SUCCESS AND CHANGES IN NUMBERS OF AFRICAN BLACK OYSTERCATCHERS *HAEMATOPUS MOQUINI* IN RELATION TO HABITAT QUALITY AND PROTECTION STATUS

H. ANN SCOTT^{1,3}, W. RICHARD J. DEAN² & LAURENCE H. WATSON¹

¹Nelson Mandela Metropolitan University, George Campus, P Bag X6531, George 6530 South Africa

²Percy FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Private Bag X3, Rondebosch, 7701 South Africa

³Present address: PO Box 2604, Swakopmund, Namibia (ecoserve@iway.na)

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SUMMARY

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We studied populations and reproduction of African Black Oystercatchers in De Hoop Nature Reserve (DHNR), South Africa, during 1984–1998. Densities of breeding birds were slightly lower than those in other mainland areas. Rocky/mixed habitat supported a relatively higher density of breeding pairs than mixed/sandy habitat. Although there was no difference in mean annual first clutch size (1.78), replacement clutches were larger in the central and eastern sectors (1.9 eggs) than in the western sector (1.2 eggs). Mean chick-raising success (0.82 fledglings/chick) was higher than mean hatching success (0.42 chicks/egg) in all sectors. Mean fledging success/pair varied from 0.68 to 0.85 over six years, among the highest recorded anywhere. The proclamation of De Hoop Marine Reserve, including the entire coast of the nature reserve (where angling and collecting intertidal organisms are prohibited), led to a decrease both in disturbance from off-road vehicles and in direct competition from humans for marine resources. These initial benefits were not sustained in terms of breeding success, however, possibly because of increased numbers of visitors to the coast, especially after 1991. In the central sector, where human disturbance was highest, most nest failure was human-related, whereas in the less disturbed eastern sector natural factors were more important. High site fidelity is supported by the fact that 21% of all birds ringed rejoined the breeding population between eight and 14 years later, a relatively high proportion (32%) of these birds returning in their second year. Numbers of adult African Black Oystercatchers increased significantly over the study period. Although numbers of juveniles per pair appeared to benefit initially from the proclamation of the marine reserve, they showed a cyclic and overall declining tendency over the 14-year study period. This trend may be related to the increasing numbers of human visitors to the coast. DHNR is regarded as an important site for the global African Black Oystercatcher population, and this long-term study contributes to the conservation of this relatively rare species.

Key words: breeding success, disturbance, habitat, marine reserve, numbers

INTRODUCTION

Breeding success in oystercatcher populations worldwide is low (Hockey 1996b). Survival from hatching to fledging is regarded as the critical life-history period for both American Black Oystercatchers *Haematopus bachmani* (Groves 1984) and African Black Oystercatchers *H. moquini*, especially for those that breed outside protected areas (Hockey 2002, Anon. 2004) and on the mainland (Hockey 1983, Watson 1992). A survey of African Black Oystercatchers throughout South Africa in 1998 showed that, outside protected areas, their fledging success averages 0.56 (range 0.40–0.90) juveniles per pair for islands and protected mainland sites, but only 0.27 (range 0.10–0.40) juveniles per pair for unprotected mainland sites (Loewenthal 1998, Hockey 2005). African Black Oystercatchers breed during the austral summer (Summers & Cooper 1977, Hockey 1983, 2005), at a time when many people are on vacation. The birds are thus vulnerable to human disturbance at mainland sites during the holiday season (Hockey 1996a, 2000, Martin 1997, Leseberg *et al.* 2000, Jeffery & Scott 2005). Breeding failure at mainland nest sites has been attributed mainly to human disturbance (Hockey 2000). Juveniles disperse during the first year of fledging, and return to their natal sites, mainly within two to four years after hatching; as site fidelity is high, mainland populations

are unlikely to be supplemented by surplus birds from islands (Anon. 2001, 2004, Hockey *et al.* 2003).

De Hoop Nature Reserve (30°26'S 20°37'E) in the Western Cape Province of South Africa (Fig. 1) is an important mainland breeding site for African Black Oystercatchers (Scott *et al.* in press), offering good foraging and breeding habitat and a relatively protected environment. The reserve, proclaimed in 1957, is administered by the provincial agency Cape Nature Conservation (now CapeNature). Before 1986 the entire coast in that area was open to the public. The reserve area was a popular traditional venue for angling and for collecting intertidal organisms for bait and human use. In March 1986 the entire coastline was included as part of a newly proclaimed area, De Hoop Marine Reserve (which is incorporated in DHNR), where angling and collecting intertidal organisms are prohibited. In 1988 the reserve size was increased, and the coastline was extended eastwards to its present size of 43.1 km. Initially, only low numbers (< 2500 per year) of day visitors were permitted within the reserve; however, from 1990, once overnight accommodation was made available, visitor numbers increased exponentially up to 1998 (Fig. 2, DHNR records).

The long-term benefits of protected areas for African Black Oystercatchers have previously been demonstrated at Goukamma

Nature Reserve, where population size increased from 1991 to 1998 after protection was instituted (Loewenthal 1998, Hockey 2000, Leseberg *et al.* 2000, Anon. 2001). The positive effects of an increased food supply on their breeding success have also been noted (Hockey & Van Erkom Schurink 1992, Hockey 2005). The proclamation of De Hoop Marine Reserve in March 1986 improved the potential food supply for oystercatchers, through changes in prey species composition and an increase in the annual modal size class of brown mussel (Scott *et al.* in press.). Over time, these positive changes were expected to lead to an increase in the breeding success of the oystercatchers.

For this study, the coast at DHNR was divided into three sectors (see Methods), with similar habitat in two sectors, and a general gradient in habitat quality from the eastern and central to the western sector. Here, we report on the effects of habitat and of the marine reserve on the breeding success of African Black Oystercatchers during 1984/85 to 1989/90, and we detail results of a population monitoring programme carried out from 1984 to 1998. We examined (a) the proportion of pairs breeding during 1984/85 to 1989/90; (b) timing of laying periods and mean clutch sizes; (c) mean hatching success, mean chick-rearing success and the mean number of juveniles per pair; (d) causes of breeding failure; (e) proportions of oystercatchers ringed as chicks returning to their natal site, and after how long; and (f) changes in the total oystercatcher population at DHNR over 14 years.

METHODS

A detailed breeding study of the African Black Oystercatcher was carried out from 1984/85 to 1989/90, over the entire reserve coastline as demarcated in August 1984 (10.7 km; Fig. 1). This was followed by an eight-year monitoring period, until 1997/98. Oystercatcher numbers were recorded over the full study period (see below).

On the basis of physical and topographical characteristics, the study area was divided into three sectors: the eastern (E, 3.1 km), central (C, 2.0 km) and western (W, 5.6 km) sectors (Scott *et al.* in press.). Three habitat types were identified in varying proportions within each sector: rocky habitat consisting of continuous stretches of rock of more than 200 m along the shore line; sandy habitat comprising continuous stretches of sand of more than 200 m along the shore line; and mixed habitat consisting of rocky and sandy stretches, interspersed over shore lengths of less than 200 m. Rocky/mixed habitat dominated in E and C sectors, where wave-cut platforms were present, whereas mixed/sandy habitat was more common in W sector.

Proportions of pairs that bred

Monthly surveys were carried out between August 1984 and July 1990, noting numbers of oystercatcher adults, numbers of pairs and details of subsequent breeding activity on a standardized form.

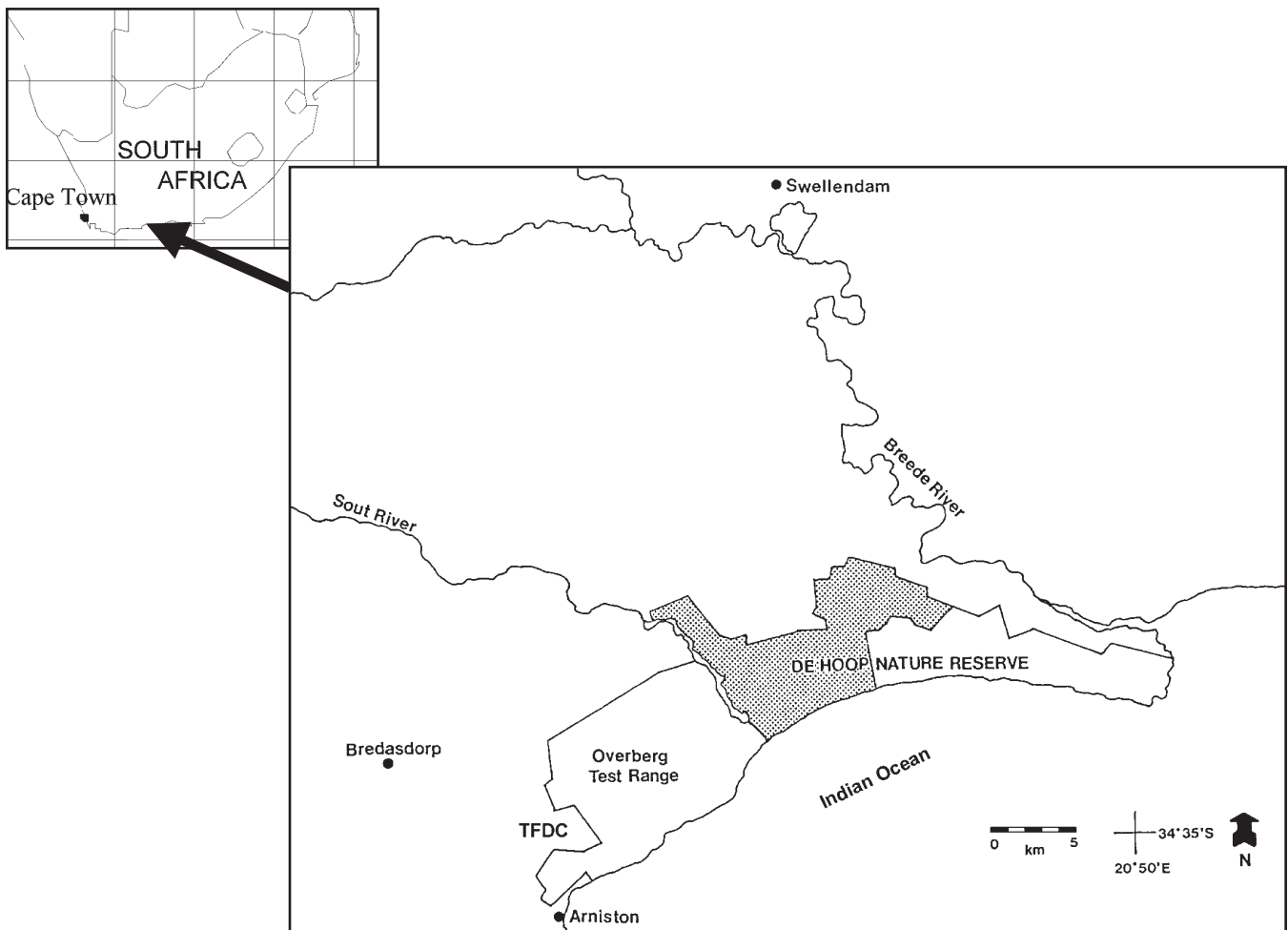


Fig. 1. The study area, De Hoop Nature Reserve, in relation to South Africa (inset). Shading indicates the size of the reserve and length of the coastline at the start of the present study (August 1984).

These regular surveys were supplemented by additional site visits and opportunistic observations when necessary (e.g. in order to confirm the hatching or fledging of chicks, or to ring chicks) during the breeding season. For statistical purposes it was assumed that the data were normally distributed (except in the obvious case where the data were proportional and were thus arcsine transformed following Zar 1999). The proportion of adults that were paired was calculated as a percentage of the total number of adults in each sector at the end of the breeding season (in March) each year. The proportion of pairs present that laid eggs was calculated as a percentage of the total number of pairs per territories occupied in each sector each year. After arcsine transformation, a one-factor ANOVA (Zar 1999) was used to test whether the mean annual proportions of pairs that bred were equal among sectors. Where the ANOVA gave rise to a significant result, Tukey's test (Zar 1999) was used *post hoc* to test for individual differences between treatments.

Laying periods and clutch sizes

The number of nests and clutch sizes were recorded for each oystercatcher territory during surveys (see above). The main laying periods for first clutches were classed as "early" if laid before December, "average" if laid during December to mid-January, and "replacement clutches" if laid from mid-January/February onwards. The earliest laying dates in C sector were back-dated to estimated laying dates, based on the presence of two small broods of chicks (C_1 and C_2 classes, see below). A clutch was regarded as "missed" when a chick was present but no egg had been recorded at the appropriate time.

Clutch sizes, egg losses and clutch replacement were recorded for each territory during surveys. A one-factor ANOVA and Tukey's test (Zar 1999) was used to test whether the mean annual first clutch sizes were equal among sectors. As there was no difference, the results were pooled in the final analysis to obtain a mean first clutch size for the study area. Mean replacement clutch sizes were analysed in the same way but separately from first clutches, to avoid "pseudoreplication" (Hurlbert 1984).

Breeding success

Numbers of chicks and of fledglings were recorded for each territory during surveys (see above). Chicks were subdivided into four size categories, namely C_1 (0–10 d or < one-quarter of size at

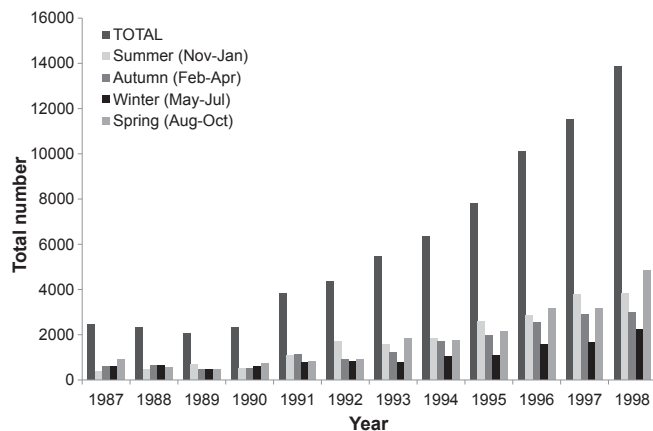


Fig. 2. Annual (November to October) and seasonal distribution of visitors to De Hoop Nature Reserve, 1987 to 1998 (DHNR records).

fledging); C_2 (11–20 d or one-quarter to one-half size); C_3 (21–30 days or one-half to three-quarter size); and C_4 (31–40 d or > three-quarter size; see also Leseberg *et al.* 2000).

Hatching success was determined by calculating the mean number of chicks per egg annually for each sector. A one-factor ANOVA and Tukey's test (Zar 1999) was used to test whether these means were equal among sectors. Eggs laid in clutches that were assumed to have been missed (see above) were added to the total for each year for the purposes of the analysis, using the mean first clutch size calculated for this study. Chick-rearing success was determined by calculating the annual mean number of fledglings per chick for each sector, and tested as above. The annual mean number of fledglings per breeding pair was also calculated for each sector. To test the hypothesis that there was no change in these annual means over time within C sector, they were compared by linear regression (Zar 1999).

Causes of breeding failure

Causes of nest failure were assigned where possible on the basis of observations and/or circumstantial physical evidence (e.g. tracks or other signs, or observations of potential predators) in the vicinity of failed nests during surveys (see above). Although sample sizes were small, percentages were assigned to the various causes of nest failure as an indicator of trends.

Post-breeding dispersal

Oystercatcher chicks within the study site were fitted opportunistically with metal rings and plastic rings with a unique annual colour combination from 1984/85 to 1989/90, in order to determine their movements after fledging. Resightings of ringed oystercatchers were recorded when present, and as part of a breeding pair, during the monthly surveys up to 1990 and annual counts up to 1998, and on an opportunistic basis from the surrounding areas. Recoveries of rings from dead birds were also noted. All ringed birds within the study site were recorded during a survey in March 1998. As the species has high site fidelity (Hockey *et al.* 2003), it was assumed that all birds observed with only a metal ring and no coloured plastic ring had hatched at the study site.

Bird counts

Total numbers of adults, pairs and juveniles were counted in each sector each month from 1984/85 to 1989/90. From 1991 to 1998 total numbers of adults and juveniles were counted once a year in March, subdivided into counts per sector from 1996 to 1998 only. Pairs were counted only during the first six years and the final three years of the study. Linear regression analysis (Zar 1999) was carried out on the total annual numbers of adults over the 14-year period, to test that there was no change in the population over time. A two-factor ANOVA and Tukey's test (Zar 1999) was used to test whether the average numbers of adults between the two periods (1985 to 1990 and 1996 to 1998) were equal among sectors. Numbers of juveniles per pair were analysed in the same way.

RESULTS

Proportions of pairs that bred

The mean proportion of pairs present that bred during 1984 to 1990 was significantly higher in C sector (65%) and E sector

(56%) than in W sector (38%; ANOVA $F = 41.320$, $P < 0.001$; Table 1). Nonbreeding birds were also present in small groups in areas adjacent to breeding territories, forming larger “roost” groups mainly from June to August.

Laying periods and clutch sizes

Total numbers of clutches by year, laying period and sector are shown in Table 2. The earliest estimated laying dates were 1 and

TABLE 1
Annual numbers (and % of the maximum total number of territories occupied) of pairs that bred in the eastern, central and western sectors during the period 1984/85 to 1989/90 (n = total number of territories identified)

Sector (number of territories identified)	Year; number of pairs breeding (% of territories occupied)						Mean \pm SD (range) of all years
	1984/85	1985/86	1986/87	1987/88	1988/89	1989/90	
Eastern (n = 15)	9 (60.0)	10 (66.7)	8 (53.3)	8 (53.3)	8 (53.3)	7 (46.7)	55.6 ^a \pm 6.9 (46.7–66.7)
Central (n = 11)	5 (45.5)	8 (72.7)	7 (63.6)	8 (72.7)	9 (81.8)	6 (54.6)	65.2 ^a \pm 13.4 (45.5–81.8)
Western (n = 7)	1 (14.3)	3 (42.9)	3 (42.9)	3 (42.9)	3 (42.9)	3 (42.9)	38.1 ^b \pm 11.7 (14.3–42.9)

^{a-b}Means with the same symbols do not differ significantly.

TABLE 2
Laying periods, expressed as annual number (and %) of early and of average recorded first clutches; estimated number of missed first clutches; and annual number of replacement clutches in the eastern, central and western sectors for the period 1984/85 to 1989/90 (n = total number of clutches per year)

Sector	Year	First clutches, no. (%)			Replacement clutches, no.	Total clutches, no.
		Recorded		Missed, no.		
		Early	Average			
		Oct/Nov	Dec–15 Jan			
Eastern	1984/85	3 (33.3)	6 (66.7)	0	1	10
	1985/86	4 (44.4)	5 (55.6)	1	4	14
	1986/87	3 (50.0)	3 (50.0)	2	4	12
	1987/88	3 (37.5)	5 (62.5)	0	1	9
	1988/89	3 (37.5)	5 (62.5)	0	3+1 ^a	12
	1989/90	3 (42.9)	4 (57.1)	0	3	10
	Total	19 (40.4)	28 (59.6)	3	17	67
Central	1984/85	0 (0)	4 (100)	1	1	6
	1985/86	2 (33.3)	4 (66.7)	2	4+1 ^a	13
	1986/87	2 (33.3)	4 (66.7)	1	2	9
	1987/88	3 (42.9)	4 (57.1)	1	3+1 ^a	12
	1988/89	5 (71.4)	2 (28.6)	2	2	11
	1989/90	4 (66.7)	2 (33.3)	0	1	7
	Total	16 (44.4)	20 (55.6)	7	15	58
Western	1984/85	0 (0)	1 (100)	0	0	1
	1985/86	0 (0)	3 (100)	0	0	3
	1986/87	1 (33.3)	2 (66.7)	0	1	4
	1987/88	2 (66.7)	1 (33.3)	0	0	3
	1988/89	1 (50.0)	1 (50.0)	1	2	5
	1989/90	1 (33.3)	2 (66.7)	0	1	4
	Total	5 (33.3)	10 (66.7)	1	4	20

^a Additional clutch is a third clutch.

6 October 1988, in adjacent territories in the central sector. The earliest confirmed replacement clutch was recorded on 5 December 1987, in E sector.

Mean annual sizes of first clutches over six years did not differ among sectors (E, 1.85 eggs; C, 1.88 eggs; W, 1.60 eggs; ANOVA $F = 2.625$, $P > 0.10$), and these mean sizes were therefore pooled (1.78 eggs; Table 3). However, the mean annual size of replacement clutches in both E sector (1.95 eggs) and C sector (1.93 eggs) were significantly larger than in W sector (1.17 eggs; ANOVA $F = 4.616$, $P < 0.05$), where replacement clutches were produced in only three years (Table 3).

Breeding success

There was no difference in mean hatching success among sectors (E, 0.38 chicks/egg; C, 0.40; W, 0.53; ANOVA $F = 0.562$, $P > 0.50$; Table 4). Chick-rearing success was higher, but also did not differ among sectors (E, 0.78 fledglings/chick; C, 0.80; W, 0.61; ANOVA $F = 0.859$, $P > 0.40$; Table 4). The proportions of fledglings per pair varied from 0.68 in E sector to 0.78 in C sector and 0.85 in W sector (Table 5). Within C sector, the mean number of fledglings per pair showed an increasing trend that was significant for the first five years of the study period, doubling from 0.6 to 1.2 ($R^2 = 0.865$, $F = 19.286$, $P < 0.05$), although not maintained during the sixth year (Table 5).

TABLE 3
Annual sizes of recorded first and replacement clutches per breeding pair (mean ± SD and range) in the eastern, central and western sectors for the period 1984/85 to 1989/90 (n = total number of clutches)

Sector	Year; size of clutch (first or replacement [R]); mean ± SD (n)												All years, mean ± SD (range)	
	1984/85		1985/86		1986/87		1987/88		1988/89		1989/90		First	R
	First	R	First	R	First	R	First	R	First	R	First	R		
Eastern	1.7±0.5 (6)	2.0±0 (4)	1.8±0.4 (8)	1.5±0.6 (5)	2.0±0 (5)	2.0±0 (5)	1.8±0.5 (6)	3.0±0 (3)	1.8±0.7 (5)	1.5±0.6 (7)	2.0±0.6 (7)	1.7±0.6 (3)	1.85±0.12 (1.7–2.0)	1.95±0.56 (1.5–3.0)
Central	2.0±0 (2)	2.0±0 (3)	2.2±0.4 (6)	1.6±0.6 (4+1 ^c)	1.7±0.5 (5)	2.0±0 (3)	1.7±0.5 (7)	2.0±0.8 (3+1 ^c)	1.9±0.4 (5)	2.0±0 (4)	1.8±0.4 (5)	2.0±0 (2)	1.88±0.19 (1.7–2.2)	1.93±0.16 (1.6–2.0)
Western	1.0±0 (1)	-	2.0±0 (3)	-	1.7±0.6 (3)	1.0±0 (1)	1.7±0.6 (3)	-	1.5±0.7 (2)	1.5±0.7 (2)	1.7±0.6 (2)	1.0±0 (2)	1.60±0.33 (1.0–2.0)	1.17 ^b ±0.29 (0–1.5)
Total													1.78±0.15	

^{a-b}Means with the same symbols do not differ significantly.

^c Additional clutch is a third clutch.

TABLE 4
Mean annual proportions of chicks per egg and of fledglings per chick in the eastern, central and western sectors for the period 1984/85 to 1989/90 (n¹ = total number of eggs; n² = total number of chicks)

Sector	Year						Mean + SD (range)
	1984/85	1985/86	1986/87	1987/88	1988/89	1989/90	
Chicks per egg							
Eastern (n ¹ = 120)	0.4	0.2	0.3	0.7	0.3	0.4	0.38 ± 0.17 (0.2–0.7)
Central (n ¹ = 108)	0.3	0.2	0.5	0.3	0.7	0.4	0.40 ± 0.18 (0.2–0.7)
Western (n ¹ = 32)	0	0.8	0.8	1.0	0.4	0.2	0.53 ± 0.39 (0–1.0)
Total (n ¹ = 260)	0.4	0.3	0.4	0.6	0.5	0.3	0.42 ± 0.12 (0–1.0)
Fledglings per chick							
Eastern (n ² = 42)	1.0	0.5	1.0	0.7	0.8	0.7	0.78 ± 0.19 (0.5–1.0)
Central (n ² = 44)	0.8	0.8	0.6	1.0	0.8	0.8	0.80 ± 0.13 (0.6–1.0)
Western (n ² = 19)	0	0.6	0.8	1.0	0.3	1.0	0.61 ± 0.40 (0–1.0)
Total (n ² = 105)	0.91	0.80	0.79	0.83	0.74	0.77	0.81 ± 0.1 (0–1.0)

Causes of breeding failure

Likely causes of egg loss in C and E sectors are indicated in Table 6. No causes of egg loss were observed in W sector. Causes of chick loss could not be determined. In E sector, 50% of egg losses were ascribed to natural causes, whereas in C sector, only 29% of losses were considered natural (Table 6). Twenty-five percent of all losses in E sector were related to tidal washaways, compared with only 14% in C sector. Abnormalities were observed in single chicks in three different broods: a beak deformity (chick observed for three months), beak deformity plus growths and injuries on one leg; and blindness in one eye. One fledgling exhibited white feathers in its wing plumage.

Post-breeding dispersal

In total, 87 chicks were ringed during the study period (Table 7). After dispersal, two ringed subadults were first resighted in 1988, at age two and three years respectively. Among 28 birds ringed as chicks that were resighted, nine were seen at age two (32%) and 22 up to age five (79%). Two ringed birds breeding in 1992 were 2–7 years old (according to their colour combinations), while four ringed birds breeding in 1994 could have been 4–9 years old. The 18 birds with a metal ring recorded in 1998 represented 21% of the total number ringed during the study period. Seven birds were resighted and two found dead in the area between the western boundary of De Hoop up to 45 km westwards, outside the protected area (Table 7).

Bird counts

The total number of adults counted in March within the study area increased significantly from 1985 to 1998 ($R^2 = 0.6477$, $F = 22.060$, $P < 0.001$; Fig. 3). Within E and C sectors there were highly significant increases in numbers of adults between March 1985–1990 and March 1996–1998, whereas in W sector numbers of adults remained stable (ANOVA sector: $F = 114.442$, $P < 0.001$; period: $F = 36.628$, $P < 0.001$; interaction sector/period: $F = 24.220$, $P < 0.001$; Fig. 3). Total numbers of juveniles per pair of adult oystercatchers were higher in March 1985–1990 than in March 1996–1998 (Fig. 4); no differences were apparent among sectors (ANOVA sector: $F = 0.656$, $P > 0.50$; period: $F = 3.373$, $P > 0.05$; interaction sector/period: $F = 0.621$, $P > 0.50$; Fig. 4).

TABLE 5

Mean annual proportions of fledglings per pair in the eastern, central and western sectors for the period 1984/85 to 1989/90 (n = total number of pairs that bred)

Sector and number of pairs	Year; mean proportion of fledglings per pair						Mean \pm SD (range)
	1984/1985	1985/1986	1986/1987	1987/1988	1988/1989	1989/1990	
Eastern (n = 50)	0.8	0.2	0.8	1.0	0.6	0.7	0.68 \pm 0.3 (0.2–1.0)
Central (n = 43)	0.6 ^a	0.6 ^a	0.7 ^a	0.9 ^a	1.2 ^a	0.7	0.78 \pm 0.2 (0.6–1.2)
Western (n = 16)	0	1.5	1.3	1.7	0.3	0.3	0.85 \pm 0.7 (0–1.7)

^a Significant increase from 1984/85 to 1988/89.

DISCUSSION

Proportions of pairs that bred

The proportions of pairs of African Black Oystercatchers that bred within the De Hoop study site appear to be slightly lower than those in other mainland areas (75%; Loewenthal 1998; Jeffery & Scott 2005), although the densities of adults were relatively high for a mainland population (Scott *et al.* in press.). This trend could be related in part to density-dependent effects on fitness (Begon *et al.* 1990, Goss-Custard & Durell 1990, Hockey 1996a, Heg *et al.* 2000). In addition to increased competition for limited resources, individual birds would also interact directly with one another and prevent others from occupying and exploiting such resources. However, this trend could also be associated with increasing numbers of human visitors to the coast (see below). Within the study area, the positive association of the oystercatchers with rocky/mixed habitat (Scott *et al.* in press.) is further supported by significantly higher mean proportions of pairs that bred in C sector (65%) and E sector (56%) during the first six years, compared with W sector (38%).

Laying periods and mean clutch sizes

The egg-laying period for the De Hoop study site was mainly from December to mid-January (59% of clutches; Table 2), as reported previously (Summers & Cooper 1977, Hockey 1983, 1996a, Jeffery 1987, Ward 1990, Watson 1992, Vernon 2004, Jeffery & Scott 2005). The earliest estimated laying dates during the present study (1 and 6 October 1988) are slightly earlier than previous observations (10 October–1 May, Summers & Cooper 1977), but not as early as two September clutches from the west coast (Hockey 2005). Clutch replacement for African Black Oystercatchers has been recorded

TABLE 6
Egg losses from natural and human-related causes in the eastern and central sectors for the period 1984/85 to 1989/90 (n = number of egg losses for which suspected causes could be recorded)

Possible cause	Sector; number (%) of egg losses		
	Eastern sector	Central sector	Total
Natural			
Tidal washaway	2 (25.0)	2 (14.3)	4 (18.2)
Egg rotten, infertile	1 (12.5)	–	1 (4.6)
Egg rotten, fertile	–	2 (14.3)	2 (9.1)
Hole pecked in egg (by gulls?)	1 (12.5)	–	1 (4.6)
Subtotal	4 (50.0)	4 (28.6)	8 (36.4)
Human-related			
Suspected disturbance by anglers	2 (25.0)	4 (28.6)	6 (27.2)
Other suspected human disturbance	2 (25.0)	6 (42.8)	8 (36.4)
Subtotal	4 (50.0)	10 (71.4)	14 (63.6)
Total	8	14	22

from 24 December onwards (Jeffery 1987) but usually starts at the beginning of February (Hockey 1983). At De Hoop one replacement clutch was as early as 5 December, but most replacement clutches were recorded from mid-January to March.

The mean first clutch size at De Hoop (1.78 eggs, range 1.00–2.21; Table 3) is slightly greater than that recorded at Cape Agulhas (1.68 eggs), to the west of the reserve and outside the protected area (Jeffery & Scott 2005), and slightly above the average clutch sizes for the species on the south coast of the Western Cape (Hockey 2005). In other oystercatcher species, including Eurasian Oystercatchers, replacement clutches are usually smaller than first clutches (Harris 1967, Heppleston 1972). Although no similar evidence has been documented for the African Black Oystercatcher (Hockey 1983), the mean replacement clutch size in W sector (1.17 eggs; Table 3) was significantly smaller than in E (1.85 eggs) and C sectors (1.88 eggs). This finding could be related to differences in habitat (and food) quality.

Breeding success

Breeding success in oystercatcher populations worldwide is low (Hockey 1996b), which is to be expected in a bird that is long-

lived, with a small population and low adult mortality (Begon *et al.* 1990, Newman 1992, Loewenthal 1998). Hatching success (percentage chicks/egg) is variable among species, ranging from 14–25% in the American Oystercatcher *H. palliatus* (Nol, 1989) to 30% in the Australian Pied Oystercatcher *H. longirostris* (Newman 1992), 25–46% in the American Black Oystercatcher *H. bachmani* (Hartwick 1974) and 44–82% in the Eurasian Oystercatcher *H. ostralegus* (Harris 1967). For the African Black Oystercatcher, hatching success varies from 12–46% within individual pairs, populations and years (Hockey 1983, Ward 1990, Watson 1992, Elwell 1998). Mean hatching success at De Hoop (0.42 chicks/egg) lies at the upper end of this range, with no increase over the first six years, and no differences among sectors (0.38 in E sector, 0.40 in C sector and 0.53 in W sector; Table 4).

Survival from hatching to first flight is regarded as the critical life-history period for species such as the American Black Oystercatcher (Groves 1984) and African Black Oystercatcher, especially for those species that breed outside protected areas where mortality is caused by dogs, off-road vehicles and other forms of human disturbance (Hockey 2002, Anon. 2004). More than 60% of Eurasian Oystercatchers and 85% of African Black Oystercatcher chicks die within their first 1–2 weeks (Hockey 1996a, 2006). Mean

TABLE 7
Numbers of oystercatchers ringed as juveniles in the De Hoop study area (1984/85 to 1989/90) and age at which they were recorded as present, part of a breeding pair or dead, 1984/85 to 1997/98 (n = 87 ringed birds)

Year	No. of birds ringed	Age (years)										
		<1	1	2	3	4	5	6	7	8	Unknown age	
1984/85	6											
1985/86	10											
1986/87	17											
1987/88	20			1	1							1
1988/89	22	2		4								
1989/90	12				1							
1990/91				1 ^a								
1991/92				3	2	3	2					4
					1 ^b							1 ^b
1992/93						2	1					6
1993/94								1				4
												4 ^b
1994/95											1 ^a	6
1995/96										2 ^b		4 ^b
1996/97												1
												3 ^b
1997/98												3
												15 ^b
Total no.	87	2	0	9	5	5	3	1	2	1		18
												(maximum)
% of known-age birds		7.1	0	32.1	17.9	17.9	10.7	3.6	7.1	3.6		20.7

^a Dead.

^b Recorded as one of a breeding pair.

chick-raising success (0.82 fledglings/chick) at De Hoop was thus high. The fact that it was higher than mean hatching success (0.42 chicks/egg, see above) appears to indicate that, within the study site, the incubation period may be more sensitive than the period from hatching to first flight. However, some very small chicks that did not survive may have been missed in counts.

Fledging success ranges from 0.57–0.61 per pair for the Eurasian Oystercatcher (Heppleston 1972) to 0–0.50 per pair for the American Oystercatcher (Nol 1989) and 0.19–1.10 per pair for the American Black Oystercatcher (Hartwick 1974); this ratio is generally less than one fledged young per pair per year (Hockey 1996a). For African Black Oystercatchers, the ratio of fledglings per pair is regarded as the critical reproductive parameter; a stable population needs to rear 0.35 fledglings per pair per year (Hockey 2002, 2005). A national survey of the species in 1998 showed that, outside protected areas, the ratio of juveniles (chicks and fledglings) per pair is 0.56 (range 0.40–0.90) for islands and protected mainland sites, but 0.27 (range 0.10–0.40) for unprotected mainland sites (Loewenthal 1998, Hockey 2005). At Cape Agulhas, an unprotected area to the west of De Hoop, fledging success over 24 years was 0.32 ($n = 10\text{--}37$ pairs/year; Jeffery & Scott 2005). At De Hoop, mean fledging success per pair for the first six years of the study period was thus higher than in other mainland areas, and (with a range of 0.68–0.85 fledglings per breeding pair) among the highest recorded at any other mainland or island site, well above the “critical” benchmark figure of 0.35 fledglings per pair per year.

Breeding success for populations of African Black Oystercatchers on the Saldanha Bay islands on the west coast of South Africa increased by up to 156% between the early 1980s and 2003, and this has been ascribed to the increased food supply resulting from the introduction of alien invasive mussels *Mytilus galloprovincialis* (Hockey & Van Erkom Schurink 1992, Hockey 2005). African Black Oystercatchers show a positive association with mixed/rocky habitat in E and C sectors of the De Hoop study site, which corresponds with the dominance of brown mussel *Perna perna* in the chick diet, supplemented by a high diversity of 25 other prey items (Scott *et al.* in press). The alien mussel was not recorded at De Hoop during the study period. Before the proclamation of De Hoop

Marine Reserve in March 1986, human disturbance was highest in C sector and included the large-scale collection of intertidal species, in particular *P. perna*, the dominant oystercatcher prey item in E and C sectors. Large sections of these mussel beds were chopped out and disturbed by bait collectors. After proclamation this harvesting ceased. Although proportions of *P. perna* in the chick diet remained unchanged immediately after proclamation of the reserve, an increase in *P. perna* annual modal size classes was recorded in E and C sectors (Scott *et al.* in press.), which could indicate a recovery after human exploitation. This increase corresponds with an increase in the ratios of fledglings per pair in C sector for the first three years after proclamation. Although not sustained, the increase appears to support the relationship between breeding success and food in terms of habitat and time.

Causes of breeding failure

The main causes of breeding failure cited for the African Black Oystercatcher are storms during the egg stage and predation of chicks (Hockey 1996a). Clutch losses for the species are generally higher on the mainland than on islands, as demonstrated in an exceptional case when Marcus Island (on the West Coast of South Africa) was joined to the mainland by a causeway, resulting in the introduction of mammalian predators (Hockey 1983). Further causes of failure include burial of nests by sand and failure to hatch; however, the main cause is human development and disturbance: crushing of eggs or chicks by off-road vehicles, horses or people; predation of chicks (mainly by dogs), exacerbated by disturbance that forces parents away from guarding chicks; and drowning of chicks by incoming tides when hiding from disturbances in the intertidal zone (Hockey 1996a, 2006). Secondary effects of human disturbance may include the starvation of chicks (Groves 1984, Leseberg *et al.* 2000), although this factor is now regarded as being less significant than originally proposed (Anon. 2004, Hockey 2006). This view is supported by the fact that chick mortality normally occurs when chicks are very young (Hockey 1996a) and their energetic requirements are correspondingly low.

Like many other species, oystercatchers are likely to face potential negative effects from rapidly changing climatic factors

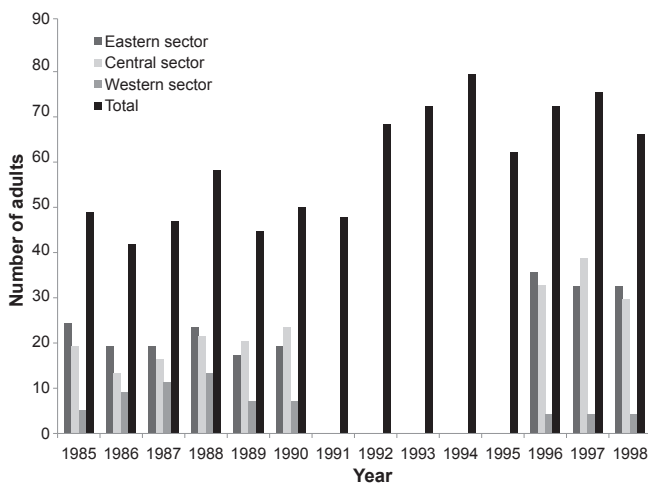


Fig. 3. Numbers of adult oystercatchers counted in March in the eastern, central and western sectors (1985–1990 and 1996–1998), and total numbers for the study area (1985–1998).

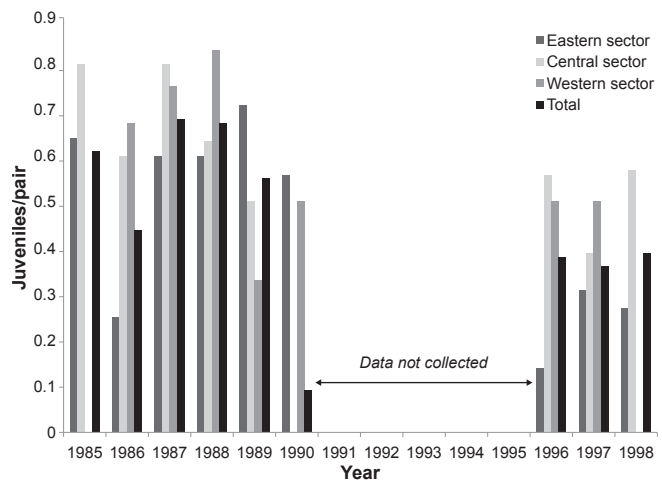


Fig. 4. Numbers of juveniles (chicks or fledglings) per pair of adult oystercatchers counted in March in the eastern, central and western sectors, and total numbers for the study area (1985–1990 and 1996–1998).

(Intergovernmental Panel on Climate Change 2001, Midgley *et al.* 2001, Simmons *et al.* 2004). Since climate change models predict greater storm frequency, elevation of mean sea level and an increase in storm surges, the negative effects of tidal and wave wash-outs on oystercatcher nests, observed in our study and elsewhere (Hockey 1983, Calf & Underhill 2005), are likely to increase.

Disturbance by humans, including researchers, may create opportunities for predation by gulls and crows (see below; Hockey 1983, Ens *et al.* 2004). Kelp Gulls *Larus dominicanus* are becoming increasingly abundant on the coast of the southwestern parts of the Western Cape, possible because of the enhanced food supply available at fishing harbours and rubbish dumps (Hockey *et al.* 1989). Half of the likely causes of egg loss in E sector were natural and half were related to human activities including disturbance, compared with primarily human-related causes in C sector (estimated at 71%; Table 6). Conversely, tidal washaways accounted for 25% of losses in E sector and 14% in C sector, which may be related to differences in habitat. We think that, although oystercatcher eggs and chicks are subject to natural predation particularly by Kelp Gulls and White-necked Ravens *Corvus albicollis*, it is likely significant only when associated with human disturbance. A large breeding colony of Kelp Gulls became established on the beach in W sector soon after the coast was closed to vehicles (e.g. 80 birds were counted there on 27 January 1987), perhaps because activities by fishing boats at Skipskop, just west of the DHNR boundary, were curtailed because of the establishment of the Overberg Test Range. This resulted in a local shortage of food for Kelp Gulls. The causes of egg loss at oystercatcher nests (including the effects of predation by Kelp Gulls) within the study area require further research.

The proclamation of De Hoop Marine Reserve led to a decrease in disturbance from off-road vehicles and to less direct competition from humans for marine resources, but these initial benefits were not sustained in terms of breeding success. This decrease in success could be associated with exponentially increasing numbers of visitors to the coast, especially after 1991.

Post-breeding dispersal

Some 36% to 46% of African Black Oystercatchers originating from South Africa travel in their first year of life to traditional nursery areas as far north as in Namibia, and return to their natal areas in the third or fourth year (Leseberg 2001, Hockey *et al.* 2003). Some birds may leave their natal areas only in their second year or later. Oystercatchers ringed in the De Hoop area (Cape Point to Breede River) have been recorded in Namibia (Anon. 2001, Hockey *et al.* 2003). The results of the current study indicate a slightly earlier return date than those recorded by Hockey *et al.* (2003).

All oystercatchers have deferred sexual maturity (Hockey 1996a). Some female Eurasian and African Black Oystercatchers first breed at three years and some males at four years, although most probably do not breed until they are older than this; one Eurasian Oystercatcher male first bred at the age of 14 years (Ens *et al.* 1996, Hockey 1996a). For African Black Oystercatchers, age at first breeding is regarded as three years for females and four years for males (Hockey & Douie 1995), but the modal age at first breeding is likely to be 5–7 years on the mainland and 8–10 years on islands (Hockey 1996a, 1996b, 2005). Although precise data for De Hoop are limited, the estimations of 2–7 or 4–9 years for age at first breeding, obtained from ring resighting data, are within these ranges.

The total of 18 ringed, breeding birds recorded in 1998 (8–14 years after fledging) represents 21% of all birds ringed in the study site and suggests high breeding site fidelity, as seen elsewhere (Anon. 2004, Hockey 1996a, Hockey *et al.* 2003).

Bird counts

The benefits of protected areas for African Black Oystercatchers were demonstrated in a national survey of the species in March 1997 (Loewenthal 1998). Since a comparable initial survey in 1980, numbers have increased substantially in the Cape of Good Hope Nature Reserve which, like De Hoop, has received protection in recent years, and in other protected areas including Cape Hangklip Sea Farm (a private nature reserve; Loewenthal 1998). A significant increase (57%) in numbers of African Black Oystercatchers from 1991 to 1998 has also been recorded at Goukamma Nature Reserve, after bait collecting and the use of off-road vehicles for commercial oyster harvesting were stopped and patrols were introduced to prevent night-time shore angling (Leseberg *et al.* 2000). Waders have responded quickly and positively to the banning of off-road vehicles from beaches in South Africa, with five species, including African Black Oystercatchers, increasing in population, in numbers of breeding pairs and/or in breeding productivity on the west and south coast (Anon. 1999, 2001, 2004, Williams *et al.* 2004). Although no comparable figures for counts of individual adults are available for the Cape Agulhas area, the annual mean number of pairs showed a highly significant increase over 24 years (Jeffery & Scott 2005). The above period included an increase from 10 pairs in 1984/85 to 22 in 1997/98, when the total population in the De Hoop study area likewise increased (Fig. 3), which appears to discount the hypothesis of local movements. The increase at De Hoop was significant within E and C sectors, whereas numbers of adults in W sector remained stable. Numbers of adults did not increase immediately after proclamation, but only after a time lag of about six years. Long-lived species, such as oystercatchers, are slow to recover from impacts such as disturbance, and it would take a number of years for small cohorts to enter the adult breeding population and therefore for population numbers to show an increase (Begon *et al.* 1990).

Ratios of fledglings to pairs at Cape Agulhas showed a cyclic trend over 24 years, peaking in 1978/79, then dropping to very low levels from 1982/83 to 1993/94 (Jeffery & Scott 2005). Thereafter, these ratios began increasing again in 1991/92, peaking in 1994/95 and in 1995/96. There was no correlation between these ratios and the increase in the numbers of adult pairs. At De Hoop, numbers of juveniles per pair appeared to benefit initially from the proclamation of the marine reserve, but showed a similar cyclic and overall declining tendency over the 14-year study period. There were no significant differences in these numbers among sectors.

Although the increase in numbers of adults at De Hoop appears to demonstrate the benefits of protection, the possibility of immigration cannot be discounted. An increase in breeding success for populations of African Black Oystercatchers on the Saldanha Bay islands on the west coast by up to 156% between the early 1980s and 2003 has been ascribed to the increased food supply resulting from the introduction of alien invasive mussels (Hockey & Van Erkom Schurink 1992, Hockey 2005). Similar mainland population increases are mentioned by Underhill (2000) and by Vernon (2004), who suggested immigration. The long-term increases in numbers of pairs at Agulhas (Jeffery & Scott 2005) and

in numbers of adults at De Hoop, both of which are associated with low breeding success, appear to confirm this scenario.

The DHNR population, at 66 birds, comprises 1% of the world population, now currently estimated at 6700 oystercatchers (Hockey 2005). According to the Ramsar Convention, a wetland is considered of international importance if it regularly supports at least 1% of the flyway or biogeographical population of at least one waterfowl species (Smart 1976). Hence, DHNR is an important site for the African Black Oystercatcher.

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