COASTAL DISPERSAL BY PRE-BREEDING AFRICAN BLACK OYSTERCATCHERS *HAEMATOPUS MOQUINI*

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SUMMARY

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African Black Oystercatcher *Haematopus moquini* high-tide roost sites were located and mapped along the Atlantic coasts of South Africa and Namibia. Nearly all roosts checked contained juvenile and/or immature, individually colour-banded birds. A series of dispersal roosts were identified along the coastline, with the largest roosts being in central Namibia. Birds forage at or near the roost sites at low tide. Of birds banded in southwestern South Africa with confirmed dispersal endpoints, 65% dispersed north of Lüderitz, Namibia (average travel distance of 1595 km from natal site), 11% dispersed to northwestern South Africa (average travel distance 548 km), 19% dispersed within southwestern South Africa (average travel distance 141 km), and 5% dispersed eastward along the south coast of South Africa (average travel distance 237 km). At least 22% of re-sighted birds departed in their first year of life, and 25% returned in their third or fourth year of life. Body condition, sex and relative hatch date were not associated with roost site distances from natal colonies. Dispersal connectivity is weak in this species, as immature birds of different ages and origins mixed at roost sites along the dispersal route.

Keywords: dispersal, juveniles, immature birds, mark-recapture, Oystercatchers, Namibia, shorebirds, South Africa

INTRODUCTION

Knowledge of species' movements, including dispersal and migration, is of critical importance in understanding population biology and ecology (Horn 1983) and in developing comprehensive conservation plans (Alderman *et al*. 2010). These considerations are especially pressing for endemic species and species at risk.

The African Black Oystercatcher *Haematopus moquini*, a "Near-Threatened" shorebird (BirdLife International 2004) endemic to South Africa and Namibia, is considered to undertake partial juvenile "migration" (Hockey *et al*. 2003). It was estimated that 36%–46% of South African-hatched juvenile African Black Oystercatchers travel in their first year of life to traditional sites in Namibia, stopping at one or more sites along the way. Hockey *et al*. (2003) hypothesized that birds returned to natal areas in their third or fourth year, stopping at one or more sites during return, and that birds travelling further distances were in better body condition. This juvenile movement pattern is similar to that of some seabird species, including African Penguins *Spheniscus demersus* (Crawford *et al*. 1995, Whittington 2002) and gannets *Sula* spp. (Wodzicki 1967, Nelson 1978).

In this study, we present data on the locations of intermediate sites used by pre-breeding African Black Oystercatchers between their natal areas in South Africa and endpoints within a dispersal range that extends into Namibia. For the purposes of this study, a dispersal endpoint roost is defined as the area surrounding the high-tide roost at the end of one direction of a bird's trajectory. A dispersal stopover roost is defined as the area surrounding a high-tide roost in the area used by birds as a resting and re-fuelling point in the course of their dispersal, i.e. a site between their departure point and their endpoint (Erni *et al*. 2002). A departure point is defined as the bird's natal site. Individual roost sites are assessed in terms of their purpose as either a stopover or endpoint. A traditional site is defined as a roost that is used repeatedly by the species, particularly by immature birds, over multiple years.

We also assess potential "triggers" for dispersal, specifically whether body condition, sex and relative hatch date differ among individuals dispersing different distances, and whether birds of different ages and origins use different sites. This dispersal pattern is compared with those of other oystercatcher species. The African Black Oystercatcher is a suitable study species for further elucidation of the pattern and triggers of post-fledging dispersal because its range is both linear and concentrated in a small geographical region.

This information will contribute to our understanding of migratory or dispersal connectivity (the movement of individuals from one population to another) and, among African Black Oystercatchers in particular, the linkages of individual populations moving from breeding to non-breeding sites (Cowen *et al*. 2000, Webster *et al*. 2002). Understanding connectivity enables a better understanding of population dynamics and potential responses to changes in habitat availability and quality at breeding and non-breeding sites (Webster *et al*. 2002, Johnson *et al*. 2010). Changes in the population, distribution and movements of African Black Oystercatchers could be linked to changes in coastal land use over time (e.g. Calf &

Underhill 2002), and changes in diet due to displacement of local mussel species by the alien *Mytilus galloprovincialis*, which is now an important prey item (Hockey & van Erkom Schurink 1992; Hockey 1996b).

Knowledge of the pattern of habitat use by non-breeding African Black Oystercatchers is important in the context of land and marine use planning, including implementation activities related to the South African National Environmental Management: Integrated Coastal Management Act (Act No. 24 of 2008), Spatial Development Frameworks for the Western Cape and Northern Cape provinces (Provincial Government 2009, Office of the Premier 2012), and protected area planning and implementation (e.g. Government of South Africa 2010, Rudd *et al*. 2011). This knowledge will also help managers and researchers understand the potential vulnerability of the species in relation to climate change effects such as sea level rise (Johnson *et al*. 2010, Rudd *et al*. 2011).

STUDY AREA AND METHODS

Study area

Research was conducted on the west coasts of South Africa and Namibia in 2004 and 2005 (Fig. 1).

Bird banding

From November 1998 through April 2005, a total of 988 oystercatcher chicks were captured near nest sites and banded on the right leg with a short plastic coloured band, denoting year, and on the left leg with a long plastic coloured band, denoting banding region within the species' breeding range in South Africa (Table 1 and Fig. 1) and engraved with a unique three-character code. Data collected from 1999 to 2005 by other researchers (Leseberg 2001, Hockey *et al.* 2003, Oystercatcher Conservation Programme [OCP]

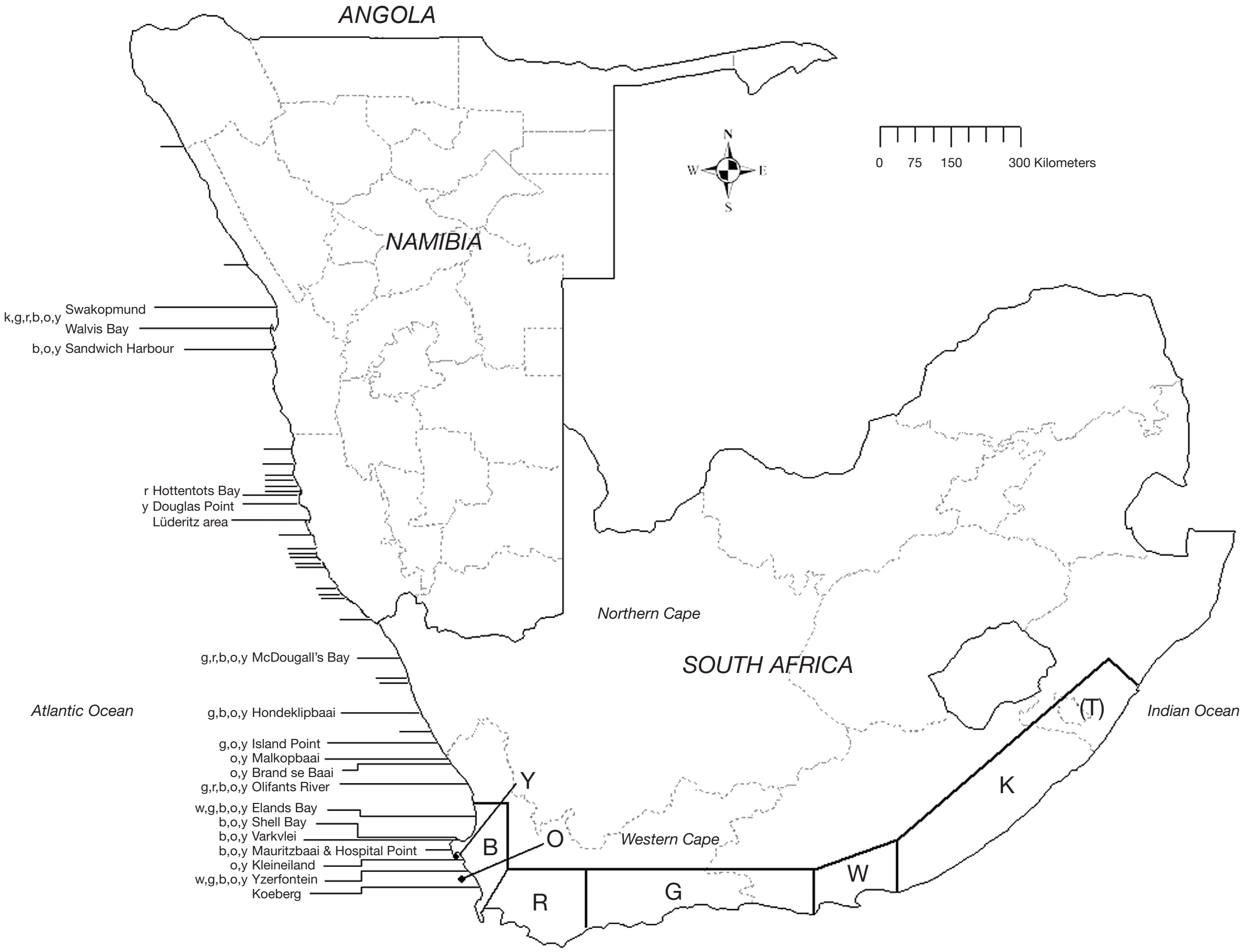

Fig. 1. Map of southern Africa showing African Black Oystercatcher banding regions and Atlantic coast roost locations. Banding regions (from Table 1) are marked with capital letters; lower-case letters indicate origins of birds observed at each roost site. Roost sites are indicated by horizontal lines. Only those location names referred to in the text are labelled on the map. The names of all roost site locations indicated by horizontal lines are, from north to south: Hoanibmond, Cape Cross Bay, Swakopmund, Walvis Bay, Sandwich Harbour, Easter Point, north of Arkona, Clara Hill, (no name), Gibraltar, Black Rock, Hottentots Bay, Douglas Point, Lüderitz area, Elizabeth Bay area, Pomona Island area, (no name), south of Possession Island, Bogenfels Arch, Driemasterbaai, Panther Head, (no name), (no name), (no name), McDougall's Bay, Kleinsee, north of Witstrandjie, Hondeklipbaai, Uilspieëlduin, Island Point, Malkopbaai, Brand se Baai, Olifants River, Elands Bay, Shell Bay, Varkvlei, Mauritzbaai & Hospital Point, Kleineiland, Yzerfontein and Koeberg.

unpublished data) were also used for analyses. Culmen, tarsus, wing and mass measurements were recorded in situ for all chicks, and blood samples were collected from some banding areas for sex determination. Following data collection, chicks were replaced in the hiding spots in which they had been found. Of birds banded, 75% were in the three northwestern banding regions: Lambert's Bay to Cape Point (395 km shoreline length), Saldanha Bay islands and Dassen Island (presented as regions B, Y and O, respectively, in Fig. 1).

Aerial surveys

To locate oystercatcher high-tide roosts north of Elands Bay, South Africa (Fig. 1), aerial surveys were conducted in May 2004 from Elands Bay to Lüderitz, Namibia, and in August 2004 from Lüderitz along the Skeleton Coast to the Cunene River on the border between Namibia and Angola (Fig. 1). Roosts south of Elands Bay were considered to be well known, so the area was not surveyed from the air. Aerial surveys were preferable to ground surveys due to the distances involved and the inaccessibility of much of the terrain. Aerial surveys could be conducted only during a three-hour high-tide window during a spring tide cycle, at a time when the weather was clear. A Cessna-172 four-seater high-wing plane was used for both surveys.

In addition to the pilot, one or two observers were aboard the plane. Each observer carried a set of 1:50 000 topographical maps of the coast. Data recorded included the location of the roosts (through the use of the maps and a portable geographical positioning system [GPS] unit), a count of the birds in the roost and indicators of disturbance or human land use.

The plane averaged an altitude of 61 m above ground, at a speed of 180 km/h. A slightly faster speed was maintained over open, sandy areas. The pilot followed the coastline, flying slightly offshore. The pilot avoided islands, due to the presence of breeding seals and birds, and because African Black Oystercatchers do not generally form large roosts on islands. A flight altitude of at least 305 m was required at the Orange River mouth and the Atlas and Wolf Bays area in Namibia because of the presence of flamingos and seal colonies, respectively. No oystercatcher roost exists at the Orange River mouth. Any roost at the bays would have been missed.

TABLE 1
Colour codes for banding regions and relative numbers of birds banded in each region

Region (South Africa)	Band colour (letter code)	Number of birds banded as of June 2005	% total birds banded as of June 2005
Lambert's Bay to Cape Point	Blue (B)	109	11
Saldanha Bay islands	Yellow (Y)	352	36
Dassen Island	Orange (O)	279	28
Cape Point to Breede River	Red (R)	46	5
Breede River to Cape St. Francis	Green (G)	149	15
Cape St. Francis to Cape Padrone	White (W)	34	3
East of Cape Padrone	Black (K)	10	1
East coast	Turquoise (T)	9	1

Ground-truthing roost sites

At each roost, the number of birds was counted, and banded birds were identified with 20–60× zoom lenses at roosts between Koeberg in the south and Port Nolloth in the north of South Africa using telescopes from February to July 2004 and February to June 2005. Roosts were prioritized for ground-truthing based on the number of birds estimated from the air and the accessibility of the area. Ground-truthing took place at the following roosts in South Africa: Koeberg, Yzerfontein, Kleineiland, Mauritzbaai/Hospital Point, Varkvlei, Shell Bay, Elands Bay, Olifants River, Brand se Baai, Malkopbaai, Island Point, Hondeklipbaai and McDougall's Bay. These roosts were checked one to three times in both 2004 and 2005. The roost at Walvis Bay, Namibia, was checked once in 2004. Roosts were checked at spring high tides to ensure that the maximum number of birds would be present. Data collected since 1999 by other researchers at Namibian roosts (Douglas Point, Hottentots Bay, Sandwich Harbour, Walvis Bay, Swakopmund) were also used for analyses (Leseberg 2001, OCP unpublished data).

Data collected included total number of birds, band colours and band numbers. Unbanded first- and second-year birds can be identified by reddish-brown eyes with a narrow, burnt-orange eye ring, greyish-pink legs and brownish bills (Hockey 1986); these were also recorded. The areas around the roost sites were checked for foraging banded birds at low tide. The numbers of banded birds will always be underestimates, because in some roosts it was not always possible to see the legs of all birds, and with time the engraved rings become increasingly worn and difficult to read.

The ages, hatch years, origins, previous movements and individual characteristics of individually identified birds recorded at the different roosts were determined from existing databases of banded and re-sighted birds, and compared among roosts. Only bird ages and general origins could be determined if the three-digit code on the long plastic band was unreadable.

Data analysis

Databases on all banded and re-sighted birds had previously been set up and were maintained throughout the study. As of June 2005, 340 of the 988 banded birds had been re-sighted at least once.

To determine the timing of the birds' movements, only those birds that could be identified to individual level (i.e., those on whose long plastic bands the number could be read) were included in the analysis. The decision to do this was initially made to avoid counting the same bird twice, then maintained for consistency.

Hockey *et al.* (2003) assumed that birds that had been seen at local dispersal roosts (in that case less than 150 km from natal sites) between six months and two years from hatching did not undertake longer-distance movements. Following observations that some birds left the vicinity of their natal sites for Namibia in their second year or later, a more conservative method was chosen: only those birds that were seen in at least two consecutive years at a particular endpoint roost were included in the analysis. This was interpreted as an indication that the birds did not continue further north. All birds seen at Namibian roosts were used in the analysis, as they are among the northernmost known roosts in the birds' range. This more conservative method reduced the sample size (*n* = 106); however, the results allowed for more rigorous confirmation of a bird's dispersal endpoint and the method reduces the chance of Type II error.

Based on the date of banding and on the dates and locations of re-sighting, year of dispersal, year of return and year of return to natal site were calculated for those birds recorded travelling to endpoints north of Elands Bay. Elands Bay is within the birds' main South African breeding range and is therefore considered the northernmost "local dispersal roost." "Year of return" is defined as the year in which a bird that had been re-sighted at a dispersal endpoint was later re-sighted further south. "Year of return to natal site" is defined as the year in which a bird that had been re-sighted at a dispersal endpoint was later re-sighted at its natal site. "Natal site" is defined as the actual area at which the bird hatched. A bird year was set as starting on 1 December of any given year for calculation purposes and because a new season of bird banding generally begins in December.

In most cases, it was not possible to determine the exact year of dispersal or return because many birds were not re-sighted in consecutive years; however, a range of years within which the dispersal or return took place could be determined. If birds had not been seen to return following dispersal, we did not assume that the bird returned or would return from dispersal. The number of birds dispersing in each year or range of years was counted. Year 1 refers to a hatch-year bird.

An index of body condition was measured as the ratio of mass (g) to tarsal length (mm) of chicks at the time of banding. Hatch date was calculated by estimating the age in days of a chick at the time of banding based on the relationship between tarsal length (mm, the most conservative growth parameter) and age documented by Hockey (1984). Relative hatch date of an individual was calculated as the number of days by which its hatch date followed the hatch date of the earliest-banded bird in any given breeding season. The use of relative hatch date, rather than actual hatch date, provided a means of comparing within years and among years. Linear regression analysis was used to compare each variable against distance travelled and dispersal endpoint. Distance travelled was calculated in kilometres from a bird's natal site to its dispersal endpoint using an existing database of relative shoreline positions of points around the coast, with a scale based on alongshore distance in kilometres from a common reference point. Relative shoreline position was also used as a measure of the dispersal endpoint to determine whether the use of a certain destination, rather than travelling distance, was determined by body condition or relative hatch date.

Age (bird years), hatch years and origin were also compared for birds seen at different roosts. Data from observations at both high tide and low tide were included. Chi-squared analysis was used to determine whether observed proportions of re-sighted birds from different origins at confirmed endpoints reflected the proportions of birds banded at each origin, or indicated disproportionate representation. Only presence/absence information is presented rather than numbers of birds of different ages and origins because it was not possible to account for all birds present at all roosts.

RESULTS

Destinations

Oystercatcher roost sites, including previously known roosts, were identified along the entire South African and Namibian west coasts (Fig. 1). Because there are no records of successful breeding between Lüderitz and Möwe Bay in Namibia, it can be safely assumed that the birds at roosts north of Lüderitz are all non-breeding juveniles, immatures and subadults (Braine 1987, OCP unpublished data).

Of the total number of individually marked birds (N = 106) for which dispersal endpoints were confirmed, 65% dispersed north of Lüderitz, Namibia (with an average travel distance of 1 595 km from their natal site), 11% dispersed to northwestern South Africa from the Olifants River to the Namibian border (average travel distance 548 km), 19% dispersed within southwestern South Africa from the Cape Peninsula to Elands Bay (average travel distance 141 km), and 5% dispersed eastward along the south coast of South Africa (average travel distance 237 km) (Fig. 2). It is unknown how many dispersed to southern Namibia, due to the inaccessibility of the area.

Timing

The results do not fully support the conclusion by Hockey *et al.* (2003) that all African Black Oystercatchers travel away from the vicinity of their natal areas in their first year of life and return in their third or fourth year of life. Of those birds travelling north of Elands Bay, 22% definitely dispersed in their hatch year and 4% definitely dispersed later than their hatch year; 25% definitely returned in their third or fourth year, whereas 9% definitely returned in their second year (Table 2). It can be concluded that the birds disperse when they are immature, but not necessarily while they are juveniles.

Uncertainties arose because not every bird was re-sighted in every year. Therefore, in many cases it was only possible to determine the range of years within which a bird moved in a particular direction. For example, bird A36, banded in 1999, was re-sighted in its first year at Walvis Bay. It was not re-sighted again until its third year,

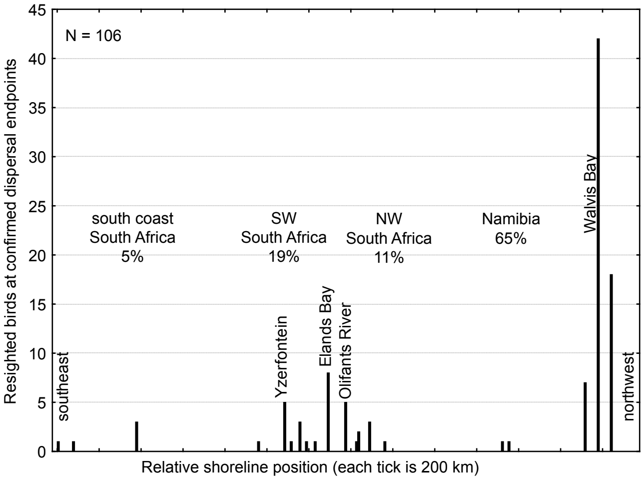

Fig. 2. Number of re-sighted birds moving from natal colony to each confirmed dispersal endpoint.

in the vicinity of its natal site; then it was re-sighted in its fourth year at its natal site. It can only be concluded that it returned to the vicinity of its natal site between its first and third years and to the natal site itself between its first and fourth years. Given these uncertainties, of 139 birds observed to have travelled north of Elands Bay and 32 returning birds re-sighted, 73%–99% dispersed in their first or second year and 9%–87% returned between their second and fourth year.

Multi-purpose sites

Sites were assessed for their dispersal function for individual birds. We had hypothesized that roosts north of Elands Bay and south of the Orange River were located in stopover areas for young birds travelling to or from dispersal endpoints in Namibia. However, 10 individual birds were re-sighted in both 2004 and 2005 at Olifants River, Brand se Baai, Malkopbaai, Island Point and Hondeklipbaai, showing that these sites were dispersal endpoints for those birds. Five birds re-sighted between 2000 and 2003 at Namibian roosts were re-sighted at Brand se Baai, Olifants River and Malkopbaai roosts in 2004 and 2005, suggesting that these are also stopover sites for birds travelling south.

These results indicate that a single roost site marks an area used by some immature oystercatchers as a northward or southward stopover site and by others as a dispersal endpoint. More importantly, they show that there are a series of dispersal endpoints along the entire South African west coast. The proximity of these multi-purpose sites to the regions where most birds were banded (Saldanha Bay islands and Dassen Island) may be relevant to energetics considerations.

Furthermore, 50%–100% of banded birds seen at high-tide roosts were observed foraging in the immediate vicinity of the roost site at low tide at Elands Bay, Olifants River, Brand se Baai, Malkopbaai, Island Point and McDougall's Bay. This indicates the function of the sites both as high-tide roosts and as low-tide foraging areas.

Traditional sites

Regardless of their purpose, sites were assessed for their repeated use by the species, particularly by immature birds, over multiple years. Roost sites at Elands Bay, Olifants River, Brand se Baai, Malkopbaai, Island Point, Hondeklipbaai and McDougall's Bay were used by oystercatchers in both 2004 and 2005. Local residents had seen oystercatchers in these areas, plus Kleinsee, in previous years, further confirming that they are traditional sites used year after year by the species. Individual birds may use multiple roosts, however. Movement of banded birds has been recorded between Malkopbaai and Island Point, between Swakopmund and Walvis Bay, and between Walvis Bay and Sandwich Harbour.

TABLE 2
Consistency of re-sighting observations with hypotheses (percentages in parentheses)

Hypothesis	No. (%) consistent	No. (%) maybe consistent	No. (%) inconsistent	Total
Year of dispersal = 1	30 (21.6)	103 (74.1)	6 (4.3)	139 (100)
Year of return = 3 or 4	8 (25.0)	21 (65.6)	3 (9.4)	32 (100)

Which birds travel farther?

This study demonstrated that immature oystercatchers can disperse a range of distances along the southern African coastline; therefore, it is more appropriate to consider distance travelled as a continuous variable rather than developing distance categories. To determine what triggered birds to travel different distances, distance travelled (km) and dispersal endpoint (relative shoreline position) were compared relative to body condition (the ratio of mass [g] to tarsal length [mm] at the time of banding), relative hatch date within a given year, hatch year, age, sex and region of origin.

Linear regression analyses showed no significant relationship between maximum distance travelled (km) and body condition ($F_{1,98}$ = 0.06, P = 0.802) or relative hatch date ($F_{1,99}$ = 0.16, p = 0.690); or between dispersal endpoint and body condition ($F_{1,98}$ = 0.41, P = 0.523) or relative hatch date ($F_{1,99}$ = 0.94, P = 0.334). Nor is there any evidence that sex was a factor determining maximum distance travelled: blood sample analysis showed that three males and two females from South African natal sites travelled to roosts in Namibia.

Furthermore, immature birds of different ages, hatched in different years and from different origins exhibited low dispersal connectivity and did not use different roosts but rather mixed along the dispersal route. Birds of more than one age class were recorded at all roosts visited, with the exception of Douglas Point and Hottentots Bay, which were only visited on one occasion, and Koeberg, at which no birds colour-banded through the OCP had ever been seen (N. Parsons, pers. comm.). To avoid the same bird being counted twice (i.e. if the same bird was at a roost site in two successive years), hatch years of birds at each site were also compared. Birds hatched in different years were observed to roost together.

Birds from more than one origin were seen at all roosts ground-truthed more than once (Fig. 1). Banded birds from all origins were not seen at all ground-truthed roost sites. Birds from banding regions "Y" and "O", representing offshore islands, were seen at 15 and 14 of 17 sites, respectively. This could be because the banding effort is highest at these two areas (36% and 28% of all banded birds, respectively). In order from northwest to southeast: birds from region "B" were seen at 10 of 17 roost sites; from region "R" at four of 17 sites; from region "G" at seven of 17 sites; from region "W" at two of 17 sites; and from region "K" at one of 17 sites. This does not suggest a clear pattern regarding bird origin and distance travelled; birds from six of seven origins, including one from the easternmost banding region, were seen at Walvis Bay/Swakopmund.

There were no significant differences between the observed proportions of re-sighted birds of different origins (Table 1) at confirmed endpoints (divided into four regions; Fig. 2), taking into account the proportions of birds banded at each origin (Table 1; Namibia: χ^2 = 11.96, df = 1,7, P = 0.10; northwest South Africa: χ^2 = 2.63, df = 1,7, P = 0.92; southwest South Africa: χ^2 = 3.00, df = 1,7, p = 0.89; south coast South Africa: χ^2 = 3.36, df = 1,7, P = 0.85). In other words, the number of birds from western banding regions seen at different endpoints reflects the relative numbers banded in each region. Given that a portion of birds breeding on the south and east coasts are known to disperse eastward (Hockey *et al.* 2003), these figures also suggest that a disproportionately high number of south and east coast-bred birds travel west.

DISCUSSION

The results provide a more complete explanation of the dispersal pattern of young African Black Oystercatchers, building on those of Hockey *et al.* (2003). Our findings suggest that the dispersal pattern is not dichotomous (movement to Namibia or Angola versus local dispersal) as originally hypothesized (Hockey *et al.* 2003) for birds breeding on the west coast of southern Africa. Instead, the pattern is indicative of dispersal to a range of distances, from a few to more than 2 000 km from natal sites, along the South African or Namibian coasts. Most birds re-sighted thus far (65%) moved to endpoints in Namibia north of Lüderitz, but some (11%) remained at endpoints along the South African northwest coast (Figs. 1, 2). These numbers may be skewed by the more intense re-sighting efforts in Namibia; however, the results do not show a gradual decrease in numbers of birds travelling to areas further north, highlighting the significance of the Namibian endpoints.

These roost sites are traditional, with immature birds recorded roosting there in two or more years. In the case of Walvis Bay, the roost is known to have been used more than 100 years ago (Gurney 1872). A single site can be used by some individuals as a staging site and by others as a dispersal endpoint. The sites are used by birds on both departure from and return to natal sites. Furthermore, the immediate vicinity of the roost sites serves as a foraging area at low tide.

The results also suggest that the timing of the birds' dispersal is more complex than was originally hypothesized. Not all birds depart in their first year, nor do all birds return to the vicinity of their natal areas in their third or fourth year. The uncertainty and data gaps in determining age at departure and return is a common obstacle in capture-mark-recapture studies (Pollock *et al.* 1990, Lebreton *et al.* 1992). With additional years' data collection, this dispersal pattern could be described in more detail.

Birds hatched in different years mixed at roost sites along the dispersal route. Birds of different origins also mixed at roost sites along the dispersal route, with numbers re-sighted proportional to numbers banded in each region. Therefore, the loss or alteration of any particular dispersal endpoint would not likely have any more effect on one breeding population than on another. Dispersal connectivity among African Black Oystercatchers is therefore weak, a resilience strategy that could enable response to large-scale climate and other environmental changes (Webster *et al.* 2002). Black Oystercatchers in British Columbia and Alaska also demonstrate weak connectivity between breeding and non-breeding sites (Johnson *et al.* 2010).

There was no indication why certain birds travelled further than others. Body condition, relative hatch date and sex did not differ significantly for immature African Black Oystercatchers dispersing different distances. This begs the question of whether travelling distance in immature African Black Oystercatchers is inherited: some siblings have been recorded at the same endpoint, even as far north as central Namibia. The oystercatchers' dispersal pattern may reflect existing ecological conditions, including intra-specific competition related to population density and changes in food availability. Its similarity to the movements of other oystercatchers provides some insight.

Migration among oystercatcher species is rare. Only two oystercatchers worldwide, the Eurasian Oystercatcher *H. ostralegus* and the Black Oystercatcher *H. bachmani*, are significantly migratory, in response to cold winters (Andres & Falxa 1995, Hulscher *et al.* 1996). Mesic climatic conditions allow adult African Black Oystercatchers to remain in their breeding areas throughout the year. Black Oystercatchers may also undergo natal dispersal (Johnson *et al.* 2010).

The behaviour of many immature African Black Oystercatchers of remaining at a "wintering" site or dispersal endpoint for a few years prior to returning to their natal/breeding area is similar to the pattern shown by the Eurasian Oystercatcher. Reasons for this behaviour include the lack of advantage for young birds to migrate long distances back to the breeding region before they reach sexual maturity, and the opportunity provided on the non-breeding grounds to forage without adult competition (Ericksson 1987). Oystercatchers and other waders require some time to develop efficient foraging skills; therefore, they can forage more successfully in their inefficient years if they do not need to compete with more proficient adults (Cadman 1980, Goss-Custard & Dit Durell 1987, Hulscher *et al.* 1996, Hockey *et al.* 1998, Leseberg 2001). Furthermore, because oystercatchers have deferred sexual maturity (Hockey 1996a), if they are not experiencing energy stress on their non-breeding grounds (Leseberg 2001), there may be no benefit to them in returning to their breeding grounds before reaching breeding age. It is not known how a juvenile Eurasian Oystercatcher chooses a destination, although it has been hypothesized to be an inherited trait (Hulscher *et al.* 1996).

Spreading or expansion of resident bird populations usually occurs because of an increase in population size; increased densities may lead to increased competition, pushing juveniles to distant areas to avoid this competition (Rappole 1995). In the early 1980s, the world population of *H. moquini* was about 4 800 birds. Since then, numbers have increased to ca 6 700 birds (OCP unpublished data), with concomitant increase in the densities of territorial adults around the coast. Although the roost of immature oystercatchers at Walvis Bay has existed since the 19th century (Gurney 1872), the number of birds that disperse further distances may be increasing as the species' population increases. It is unknown, however, whether the current increase represents a return to previous levels or a new expansion of the population, as the population's trajectory prior to the 1980s is unknown. Population genetics research is currently planned by the OCP.

Our results show a proportionally higher number of re-sighted birds at dispersal endpoints in Namibia, compared with endpoints closer to their natal sites. Choice of dispersal endpoint is therefore not driven by minimizing energy expenditure. Non-breeding distributions of other oystercatcher species are predicted by variation in prey availability (Goss-Custard *et al.* 1996, Johnson *et al.* 2010). Increased frequency of dispersal of *H. moquini* to further distances is similarly predicted to be correlated with increases in prey availability; for example, increased abundance of the alien mussel *Mytilus galloprovincialis*. Increases of such alien species have led to increased overall intertidal mussel abundance and biomass along the South African and Namibian coasts (Branch & Steffani 2004; Robinson *et al.* 2005; E. Wieters, pers. comm.). Increased food availability may be leading to increased breeding success (Hockey & van Erkom Schurink 1992), followed by higher density, forcing young birds to disperse further to avoid competition with adults.

CONCLUSIONS

Sites along the entire west coast of South Africa, and presumably Namibia, are traditionally used by young African Black Oystercatchers as both dispersal stopover sites and dispersal endpoints. Birds leave their natal areas while they are immature, but not necessarily juvenile. Access to sites outside of the species' primary breeding areas, and therefore away from competition with adults for space and food, provides an advantage to immature oystercatchers, which are inefficient feeders. These findings emphasize the importance of these sites to oystercatcher life cycles, although no individual breeding population appears to be dependent on a single site.

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REFERENCES

ALDERMAN, R., GALES, R., HOBDAY, A. J. & CANDY, S.G. 2010. Post-fledging survival and dispersal of shy albatross from three breeding colonies in Tasmania. *Marine Ecology Progress Series* 405: 271–285.

ANDRES, B.A. & FALXA, G.A. 1995. Black Oystercatcher: *Haematopus bachmani*. In: Poole, A. & Gill, F. (Eds.). The birds of North America, no. 155. Philadephia: The Academy of Natural Sciences.

BIRDLIFE INTERNATIONAL. 2004. Threatened birds of the world [CD-ROM]. Cambridge: Birdlife International.

BRAINE, S. 1987. Extension of the breeding range of the African Black Oystercatcher *Haematopus moquini*. *Madoqua* 15: 87–88.

BRANCH, G.M. & STEFFANI, C.N. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *Journal of Experimental Marine Biology and Ecology* 300: 189–215.

CADMAN, M.D. 1980. Age-related foraging efficiency of the American Oystercatcher (*Haematopus palliatus*). M.Sc. thesis. Toronto: University of Toronto.

CALF, K.M. & UNDERHILL, L.G. 2002. Productivity of African black oystercatchers *Haematopus moquini* on Robben Island, South Africa, in the 2001-2002 breeding season. *Wader Study Group Bulletin* 99: 45–49.

COWEN, R.K., LWIZA, K.M.M., SPONAUGLE, S., PARIS, C.B. & OLSON, D.B. 2000. Connectivity of marine populations: open or closed? *Science* 287: 857–859.

CRAWFORD, R.J.M., BOONSTRA, H.G.v.D., DYER, B.M., & UPFOLD, L. 1995. Recolonization of Robben Island by African Penguins, 1983-1992. In: Dann, P., Norman, I., & Reilly, P. (Eds.). The penguins: ecology and management. Chipping Norton, New South Wales, Australia: Surrey Beatty and Sons. pp. 333–363.

ERICKSSON, M.O.G. (Ed.). 1987. Proceedings of the Fifth Nordic Ornithological Congress, 1985. Onsala, Sweden, 5–9 August 1985.

ERNI, B., LIECHTI, F., & BRUDERER, B. 2002. Stopover strategies in passerine bird migration: a simulation study. *Journal of Theoretical Biology* 219: 479–493.

GOSS-CUSTARD, J.D. & DIT DURELL, S.E.A. le V. 1987. Age-related effects in oystercatchers *Haematopus ostralegus,* feeding on mussels, *Mytilus edulis*: foraging efficiency and interference. *Journal of Animal Ecology* 56: 521–536.

GOSS-CUSTARD, J. D., DIT DURELL, S.E. le V., GOATER, C.P., HULSCHER, J.B., LAMBECK, R.H.D., MEININGER, P.L. & URFI, J. 1996. How oystercatchers survive the winter. In Goss-Custard, J.D. (Ed.). The oystercatcher: from individuals to populations. Oxford: Oxford University Press. pp. 133–154.

GOVERNMENT OF SOUTH AFRICA. 2010. National protected area expansion strategy for South Africa 2008. Pretoria: Government of South Africa.

GURNEY, J.H. 1872. Notes on the birds of Damaraland and the adjacent countries of South-West Africa. London: John van Voorst.

HOCKEY, P.A.R. 1984. Growth and energetics of the African Black Oystercatcher *Haematopus moquini*. *Ardea* 72: 111–117.

HOCKEY, P.A.R. 1986. Family Haematopodidae. In Urban, E.K., Fry, C.H., & Keith, S. (Eds.). The birds of Africa, Vol. II. London: Academic Press. pp 190–193.

HOCKEY, P.A.R. 1996a. Family Haematopodidae (Oystercatchers). In del Hoyo, J., Elliott, A., & Sargatal, J. (Eds.). Handbook of the birds of the world, Vol. 3 – Hoatzin to Auks. Barcelona: Lynx Edicion. pp. 308–325.

HOCKEY, P.A.R. 1996b. *Haematopus ostralegus* in perspective: comparisons with other oystercatchers. In Goss-Custard, J.D. (Ed.). The oystercatcher: from individuals to populations. Oxford: Oxford University Press. pp. 251–285.

HOCKEY, P.A.R., LESEBERG, A., & LOEWENTHAL, D. 2003. Dispersal and migration of juvenile African Black Oystercatchers *Haematopus moquini*. *Ibis* 145: E114–E123.

HOCKEY, P.A.R., TURPIE, J.K., & VELÁSQUEZ, C.R. 1998. What selective pressures have driven the evolution of deferred northward migration by juvenile waders? *Journal of Avian Biology* 29: 325–330.

HOCKEY, P.A.R. & VAN ERKOM SCHURINK, C. 1992. The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. *Transactions of the Royal Society of South Africa* 48: 123–139.

HORN, H.S. 1983. Some theories about dispersal. In: Swingland, I.R. & Greenwood, P.J. (Eds.). The ecology of animal movement. Oxford: Clarendon Press. pp. 54–62.

HULSCHER, J.B., EXO, K-M., & CLARK, N.A. 1996. Why do oystercatchers migrate? In: Goss-Custard, J.D. (Ed.). The oystercatcher: from individuals to populations. Oxford: Oxford University Press. pp. 155–185.

JOHNSON, M., CLARKSON, P., GOLDSTEIN, M.I., HAIG, S.M., LANCTOT, R.B., TESSLER, D.F., & ZWIEFELHOFER, D. 2010. Seasonal movements, winter range use, and migratory connectivity of the Black Oystercatcher. *Condor* 112: 731-743.

LEBRETON, J.-D., BURNHAM, K.P., CLOBERT, J., & ANDERSON, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.

LESEBERG, A. 2001. The foraging ecology, demographics and conservation of African Black Oystercatchers *Haematopus moquini* in Namibian nursery areas. MSc thesis. Cape Town: University of Cape Town.

NELSON, B. 1978a. The gannet. Vermillion, SD: Buteo Books.

OFFICE OF THE PREMIER OF THE NORTHERN CAPE. 2012. Northern Cape Provincial Development and Resource Management Plan / Provincial Spatial Development Framework. Kimberley, South Africa: National Department of Rural Development and Land Reform. [Available online at: www.northerncapepsdf.co.za; accessed 24 July 2014].

POLLOCK, K.H., NICHOLS, J.D., BROWNIE, C. & HINES, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 100: 1–87.

PROVINCIAL GOVERNMENT OF THE WESTERN CAPE. 2009. Western Cape Provincial Spatial Development Framework. Cape Town: Western Cape Government. [Available online at: http://www.westerncape.gov.za/eng/pubs/public_information/W/186589; accessed 24 July 2014].

RAPPOLE, J.H. 1995. The ecology of migrant birds: a neotropical perspective. Washington: Smithsonian Institution Press.

ROBINSON, T.B., GRIFFITHS, C.L., MCQUAID, C.D., & RIUS M. 2005. Marine alien species of South Africa – status and impacts. *African Journal of Marine Science* 27: 297–306.

RUDD, M.A., BEAZLEY K.F., COOKE, S.J., FLEISHMAN, E., LANE, D.E., MASCIA, M.B., ROTH, R., TABOR, G., BAKKER, J.A., BELLEFONTAINE, T., BERTEAUX, D., CANTIN, B., CHAULK, K.G., CUNNINGHAM, K., DOBELL, R., FAST, E., FERRARA, N., FINDLAY, C.S., HALLSTROM, L.K., HAMMOND, T., HERMANUTZ, L., HUTCHINGS, J.A., LINDSAY, K.E., MARTA, T.J., NGUYEN, V.M., NORTHEY, G., PRIOR, K., RAMIREZ-SANCHEZ, S., RICE, J., SLEEP, D.J., SZABO, N.D., TROTTIER, G., TOUSSAINT, J.P. & VEILLEUX, J.P. 2011. Generation of priority research questions to inform conservation policy and management at a national level. *Conservation Biology* 25: 476–484.

WEBSTER, M.S., MARRA, P.P., HAIG, S.M., BENSCH, S. & HOLMES, R.T. 2002. Links between worlds: unravelling migratory connectivity. *Trends in Ecology and Evolution* 17:76–82.

WHITTINGTON, P.A. 2002. Survival and movements of African Penguins, especially after oiling. Ph.D. Thesis. Cape Town: University of Cape Town.

WODZICKI, K.A. 1967. The gannets at Cape Kidnappers. *Transactions of the Royal Society of New Zealand* 8: 149–162.