Nesting Habitat of Birds Breeding in a Coastal Dunefield, South Africa and Management Implications

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ABSTRACT


Damara terns Sterna balaenarum, African black oystercatchers Haematopus moquini and whitefronted plovers Charadrius marginatus, nest in the interdune hollows of the Alexandria Coastal Dunefield, South Africa. In order to manage effectively for dune breeding birds, nesting habitat and nest sites need to be identified. Nesting positions along the beach and in relation to the high water mark were recorded along 22 km of shoreline. In addition, physical variables were recorded at three levels: macro-habitat, nest-proximity and micro-habitat. Principal Co-ordinate Analysis identified which variables best described the nest sites of each species. Damara terns nested in two aggregations, plovers in the first section of shoreline and oystercatchers throughout the 22 km. Oystercatchers nested < 50 m above the high water mark while the terns and plovers nested > 70 m above the high water mark. The characteristic nest sites of each species differed in physical features at all three levels, but particularly in terms of substrate, proximity to vegetation and the high water mark, thereby resulting in clear partitioning of nest habitats. The potentially available nesting habitat for each of the three species is under-utilised. Since nesting success can be affected by human activity on the adjacent beach, active management is required to protect the nesting activities of those birds.

ADDITIONAL INDEX WORDS: Sterna balaenarum, Haematopus moquini, Charadrius marginatus, nesting, dunefield.

INTRODUCTION

In southern Africa, three endemic coastal breeding birds, Damara terns Sterna balaenarum, African black oystercatchers Haematopus moquini and whitefronted plovers Charadrius marginatus, nest predominantly in coastal dunefields (VAN T Eylingen et al., 1993). Damara terns are classified as rare breeding migrants with less than 120 breeding pairs in southern Africa (BROOKE, 1984). The other two species, in contrast, are relatively common throughout the southern African coastline (with the exception of oystercatchers on the East coast) (MACLEAN, 1985). All three species are vulnerable to human disturbance (EARLE, 1976; FROST and SHAUGHNESSEY, 1976; SUMMERS and COOPER, 1977; RANDALL and MCLACHLAN, 1982; HOCKEY, 1983b; JEFFREY, 1987).

In the Alexandria Coastal Dunefield in Algoa Bay, all three species nest in interdune hollows (slacks) during the austral summer (peak between November and January) (UNDERHILL, COOPER and WALTNER, 1980; RANDALL and MCLACHLAN, 1982; VAN DER MERWE, 1987; WATSON, 1995). About 40 pairs of plovers, 40 pairs of oystercatchers, and 15 pairs of terns nest throughout the dunefield (RANDALL and MCLACHLAN, 1982; WATSON and KERLEY, 1995). Since these three species have different foraging strategies and prey (MACLEAN, 1985) there is no potential interspecific food resource competition. However, they utilise the same nesting area; thus if nesting habitat is a limited resource, tern population abundance may be limited by interspecific overlap in nesting habitat.

Human activity (4 × 4 off-road vehicles) along the beach bordering the dunefield is increasing, with peaks during the austral summer. Off-road vehicles were also recorded on and above the high water mark (WATSON et al., 1996). Active management of this area has thus been restricted to control at vehicle access points and limited dune stabilisation and destabilisation. Spatial and temporal overlap of dune utilisation occurs between beach-users and dune breeding birds (WATSON et al., 1996). As part of a study to determine whether it is necessary to manage the area to protect the dunefield, South Africa and Management Implications (Figure 1), between the Sun-
days River mouth (33°44′ S; 25°51′ E) and Cape Padrone (33°46′ S; 26°28′ E). This transgressive dunefield (open sand) is 120 km² in area (50 km in length, averaging 2.1 km in width) and is managed as a reserve by Cape Nature Conservation (Briers, 1993). Vehicle and pedestrian access is via two entrances by permit only, with surf angling the most popular activity (Els and McLachlan, 1990).

An artificially stabilised littoral dune occurs for about 2.5 km east of the Sundays River mouth (McLachlan et al., 1982; Avis, 1989) and a 500 m stretch of the privately owned coastline, 17 km east of the river mouth has been stabilised with vegetation. Interdune hollows are found from 2.5 km east of the river mouth, for about 30 km, and constitute 0.1% of the total dunefield area. These hollows or slacks vary from being wet and sparsely vegetated near the river in the west to dry and barren further eastwards. Slacks average 40-50 m in width, and are demarcated by steep dune slipfaces in the west, and gentle stossfaces in the east. They form about 20–50 m above the driftline and extend about 200 m inland (McLachlan et al., 1982). Overtopping (tide washing over driftline into slacks) is regarded as infrequent in the dunefield and was only recorded once during the non-breeding season.

Seventeen plant species are found in the slacks (Van der Merwe, 1987); with Arctotheca populifolia, Sporobolus virginicus, Juncus kraussii and Gazania rigens the most abundant (McLachlan et al., 1982). East of the wetter slacks, the slack floor is composed of aeolianite (cemented sand) (Bate and Dobkins, 1992), sand and pebble substrate and sparse vegetation. The foredunes become steeper 22 km east of the river mouth and the interdune hollows decrease in size and frequency. The dunefield from the river mouth to this 22 km point was used for this study (Figure 1). This shore-parallel strip incorporated a range from wet, vegetated to dry, barren slacks in which about 15 pairs of terns, 30 pairs of oystercatchers and 30 pairs of plovers nest (Watson and Kerley, 1995).

**Sampling**

The entire dunefield was searched to identify nesting areas (i.e., areas in which birds were nesting) during the 1991/1992 (austral summer) breeding season. The dunefield was then surveyed monthly to locate and monitor nests of the three species. Nest site surveys, undertaken during the 1992/1993 and 1993/1994 breeding seasons, included observations on nest position along the transect and in relation to the high water mark. Nest locations were non-intrusively flagged and nest monitoring continued on a weekly basis until nesting had been completed. A nest site was considered abandoned if no activity was observed for two weeks. Observer disturbance at the nest site was kept to a minimum as nest contents could be identified from at least 5 m. Due to the open habitat and the birds behaviour (mobbing and distraction displays) during the breeding season the number of overlooked nests can be considered negligible.

In order to determine which physical variables best described the nesting sites of each species, physical characteristics of the nesting sites were recorded at three levels: macro-habitat (slack), nest-proximity (distance to physical features, e.g., dunes, vegetation, high water mark, etc.) and micro-habitat (1 m² around the nest) levels (Hockey, 1982; Burger and Gochfeld; 1990, Flemming et al., 1992) immediately after nest abandonment. The three levels enable the identification of the most suitable landscape scale for

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Figure 1. Map of the study area, the Alexandria Coastal Dunefield on the northern shores of Algoa Bay, indicating the survey transect.
quantifying nest site characteristics and eliminates confusion caused by grouping variables.

The macro-habitat or slack features were recorded to determine, on a landscape scale, which were the most characteristic features of each species' nesting habitat. The slack substrate or plant cover was recorded using a point intercept technique (Mueller-Dombois and Ellenberg, 1974), at 10 cm intervals along a 15 m tape set out in the four cardinal directions (600 points for each site). Sand, shell, pebble (1–5 cm, 5–10 cm, 10–20 cm, > 20 cm), aeolianite (< 10 cm, > 10 cm), dicotyledons, monocotyledons and debris (flotsam, jetsam and litter) cover were recorded at each site. The state of the slack entrance (mouth) i.e., closed or open to the beach was recorded. The height of the slip and stoss faces of the west and east dunes were estimated. Slack area was estimated by measuring the width (slip to stoss base) and length (back of slack to front dune or storm high water mark) of each slack.

Nest-proximity (distance to physical features) features measured included: distances to the slipface, stossbase, back of the slack, high water mark, storm high water mark, nearest vegetation, debris, and nearest neighbour (nearest active nest).

Micro-habitat or specific nest site variables in the immediate vicinity of the nest were recorded using a 1 m² quadrat divided at 10 cm intervals. Percentage ground cover was estimated, by point intercept (Mueller-Dombois and Ellenberg, 1974). The following variables were recorded: sand, shell, pebble (1–5 cm, 5–10 cm, 10–20 cm, > 20 cm), aeolianite (< 10 cm & > 10 cm), dicotyledons, monocotyledons and debris. The height of the nest (nest elevation) above the surrounding area was measured. An index of sand compaction at the nest was obtained using a penetrometer (Malcolm, 1964); measuring soil resistance to penetration of a 7 mm diameter staff under a force of 1.28 N.

Nest Availability

A crude estimate of the maximum number of potentially available nesting habitats were calculated with regards to the nest habitat characteristics and minimum nearest neighbour distances for each species. Surveys of the entire dunefield and 1:30,000 (1990) ortho-photographical maps were used to identify these sites throughout the 22 km shoreline, and calculate total available area. Nest area requirements were estimated from minimum nearest neighbour distances for each species to calculate minimum area needed per breeding pair.

Data Analysis

Principal Component Analysis (PCA) was used to determine which physical variables explained most of the variability amongst the nesting sites at the micro-habitat, nest-proximity and macro-habitat scales. Percentage data were arcsine transformed and highly correlated variables were excluded from the PCA. Chi-squared analysis was used to determine the randomness of nearest neighbour nesting species (Zar, 1984).

RESULTS

Nest Distribution

During the 1992/1993 breeding season (Figure 2a) 73.9% (51) and in the 1993/1994 season (Figure 2b) 74.9% (65) of the dune-breeding birds nested in the first 10 km of the transect. During the 1992/1993 breeding season (Figure 2a) Damara terns nested in two concentrations along the transect; 75% (21) at 6–10 km and 18% (5) at 14–16 km east of the Sundays River mouth. During the 1993/1994 season (Figure 2b) tern nests (n = 22) were mostly (96%, 21) located 6–10 km east of the river mouth with only one nest recorded 15–16 km from the mouth. During both breeding seasons (Figure 2a & 2b) oystercatchers nested throughout the transect, with 67% (1992/1993, 22) and 50% (1993/1994, 15) of the nests recorded in the first 10 km east of the Sundays River mouth. During the 1992/1993 season only 5 active whitefronted plover nests were recorded (Figure 2a) while during 1993/1994, 35 were recorded (Figure 2b) and of those, 66% were 2–7 km east of the Sundays River mouth. During the 1992/1993 season two oystercatcher nests were found between the river mouth and the start of the slacks but were abandoned by the birds after one week and during the 1993/1994 season one nesting attempt near the river mouth was unsuccessful.

Nest distance to the high water mark were pooled for each species over the two breeding seasons. There were no significant differences between years for each species, but differences between species were significant (F = 29.97; df = 2, 85; p = 0.000). Damara terns nested a mean distance of 114 m, oystercatchers 49 m and plovers 165 m (Table 2), from the high water mark. Seventy-three percent (46) of the oystercatchers nested < 50 m above the high water mark (Figure 3). Only one nest was found more than 100 m inland, with 90% of the nests situated closer than 70 m to the high water mark. One oystercatcher nest was recorded below the spring high water mark. However, it lasted less than two weeks before being flooded by the tide. Ninety percent (45) and 88% (38) of the terns and plovers respectively, nested further than 70 m from the high water mark (Figure 3).

Seventy-nine percent, 75% and 36% of tern, oystercatcher and plover nests, respectively were situated in slacks that were open to the beach. Conspecifics comprised 79%, 81% and 84% of nearest nesting neighbours for nesting terns, oystercatchers and plovers, respectively. This nearest neighbour selection is not random (Chi² = 11.4; df = 4; p < 0.05). Mean nearest neighbour distances were 176 m, 396 m and 219 m for terns, oystercatchers and plovers respectively (Table 2).

Macro-Habitat

Utilising data for the macro or slack habitat level, the PCA plot (Figure 4) variables accounted for 51% of the variation in nest site characteristics and indicates that plover nests were characterised by sandy substrate and vegetation (dicotyledons or monocotyledons). Oystercatcher nest sites were defined by the presence of pebbles, with pebble > 5 cm being most important. Oystercatcher sites were also characterised by larger slack area and greater debris cover. Damara tern nest sites were distinguished by shell and aeolianite ground.
Nest-Proximity

The PCA plot of proximity of features within the slack to nests (Figure 5) accounts for 73% of the variation in nesting characteristics. Nest sites of all three species were best described by distances from the high water mark, the storm water mark and vegetation. The plovers nest furthest from the high water mark (Table 2 & Figure 5), the oystercatchers closest, and the Damara terns at intermediate distances. The plovers nest closest to vegetation (Table 2), with the terns furthest. This results in greater overlap between terns and oystercatchers than between terns and plovers on the PCA plot. Distances to vegetation, debris, the high water mark, the storm berm, the back of the slack and to the dunes differed significantly for all three species (Table 2). The only feature that did not differ significantly was dis-

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Figure 2. a. Nest position along the survey transect (Alexandria Coastal Dunefield) for Damara terns, African black oystercatchers and whitefronted plovers during the 1992/1993 breeding season. b. Nest position along the survey transect (Alexandria Coastal Dunefield) for Damara terns, African black oystercatchers and whitefronted plovers during the 1993/1994 breeding season. Legend for 2b follows 2a viz. tern (N = 22), oystercatcher (N = 30), plovers (N = 35).
Distance to nearest neighbour ($F = 1.27; df = 2, 85; p = 0.2859$), (Table 2).

**Micro-Habitat**

The first two components of the specific nest site PCA plot are responsible for 48% of the variability in nesting characteristics (Figure 6). Damara tern nests were associated with aeolianite, especially small aeolianite fragments < 10 cm. Tern nests were also characterised by low debris cover and high sand compaction. However, these vectors are shorter, indicating less importance. Oystercatcher nest sites were associated with pebble cover, particularly pebble sizes 5–10 and 10–20 cm, which conformed with the mean pebble diameter in the slacks of 10.35 ± 4.19 cm ($n = 500$). Plover nests were associated with sand and vegetation cover and nest elevation. Vector length indicates that sand and dicotyledonous cover are more important with respect to plover nests. Presence of aeolianite, debris, sand, pebble, vegetation and nest elevation differed significantly between species (Table 3), but shell cover and sand compaction did not ($F = 1.67; df = 2, 85; p = 0.1938$ and $F = 1.45; df = 2, 85; p = 0.2417$, respectively) (Table 3).

**Nest Site Availability**

The mean aerial extent of the 15 slacks with Damara terns was 5,200 m$^2$. Ninety slacks with characteristics similar to those with nesting birds were recorded along the 22 km of coastline. Considering minimum nearest neighbour distances, one pair requires 4,500 m$^2$ for nesting. The total potentially available nesting area (468,000 m$^2$) suggests that 104 pairs could nest in this area. However only one nest per slack was recorded and if slack number rather than area is limiting the ninety potentially available slacks could therefore support 90 pairs of terns. Thus 17% of the available nesting habitat is being utilised.

Oystercatchers nested between interdune hollows near the high water mark with a minimum nearest neighbour distance of 50 m and a single nest per slack. One hundred potentially available nesting sites were recorded although only 30 pairs occur. Thus 30% of the potentially available oystercatcher nesting habitat is utilised.

Whitefronted plovers nested in slacks which averaged 6,000 m$^2$ in extent. The minimum nearest neighbour distance of 50 m ($r = 25$) gives an estimated 1,963 m$^2$ required per nest. The 44 wet or vegetated slacks recorded provide a total of 264,000 m$^2$ potentially available for nesting, suggesting that 134 pairs could be supported in this area. However, the average slack size in which nests were found was larger than the predicted nesting area, although it appears that one pair per slack is the norm irrespective of slack size. Certain slacks supported more than one pair and birds were recorded nesting in unvegetated areas. These factors and the estimated nesting territory suggest that the dunefield could support a larger number of plovers.

**DISCUSSION**

PCA proved to be a valuable heuristic tool in identifying the most appropriate scale at which nesting characteristics could be quantified and physical variables which most correlated to nest site selection.

As in Namibia (Frost and Shaughnessy, 1976; Culling, 1978) Damara terns exhibited semi-colonial behaviour by nesting in aggregations in the dunefield. These were far
from the high water mark in slacks with bare aeolianite substrate surrounded by high transverse dunes.

Oystercatchers nested throughout the dune field amongst pebbles and debris where nest contents were camouflaged. These sites were near or on the high water mark, adjacent to their feeding sites on the beach. African black oystercatchers and other Haematopus species characteristically nest near feeding sites (SUMMERS and COOPER, 1977; HOCKEY, 1982; ENS et al., 1992) and the spatial distribution of H. moquini in the Alexandria Coastal Dunefield could be due to their feeding territories (HALL, 1959; HOCKEY, 1983a) as a result of the availability of their intertidal food source, Donax serrus (WARD, 1991). HALL (1959) and HOCKEY (1982) observed oystercatcher nests to be well camouflaged and near physical objects. Oystercatchers may have been selecting nest sites near small pebbles (5–10 cm) of a similar size to the eggs (6.07 × 4.01 cm), thereby enhancing camouflagge (HOCKEY, 1983a).

Whitefronted plover nests were concentrated within a few kilometres of the western end of the dune field. This area is

Table 1. Comparison of mean values (± S.D.) of environmental variables measured at the macro-habitat scale between the nests of Damara terns, African black oystercatchers and whitefronted plovers. ANOVA and Tukey range test results are given.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Damara Tern (n = 25)</th>
<th>Oystercatcher (n = 32)</th>
<th>Plover (n = 25)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand cover (%)</td>
<td>65.4 ± 10.9*</td>
<td>75.6 ± 10.2*</td>
<td>85.6 ± 5.4*</td>
<td>**</td>
</tr>
<tr>
<td>Shell cover (%)</td>
<td>7.3 ± 11.1*</td>
<td>4.2 ± 6.5*</td>
<td>30.4 ± 4.1*</td>
<td>*</td>
</tr>
<tr>
<td>Pebble (1–5 cm) cover (%)</td>
<td>0.0 ± 0.1*</td>
<td>2.9 ± 6.8*</td>
<td>0.0 ± 0.1*</td>
<td>*</td>
</tr>
<tr>
<td>Pebble (5–10 cm) cover (%)</td>
<td>0.6 ± 1.7*</td>
<td>4.6 ± 3.2*</td>
<td>0.1 ± 0.1*</td>
<td>**</td>
</tr>
<tr>
<td>Pebble (10–20 cm) cover (%)</td>
<td>0.8 ± 1.9*</td>
<td>6.4 ± 2.5*</td>
<td>0.2 ± 0.7*</td>
<td>**</td>
</tr>
<tr>
<td>Pebble (&gt;20 cm) cover (%)</td>
<td>0.4 ± 0.9*</td>
<td>3.2 ± 2.5*</td>
<td>0.3 ± 1.2*</td>
<td>**</td>
</tr>
<tr>
<td>Aeolianite (&lt;10 cm) cover (%)</td>
<td>17.1 ± 10.7*</td>
<td>1.1 ± 2.1*</td>
<td>3.4 ± 6.1*</td>
<td>**</td>
</tr>
<tr>
<td>Aeolianite (&gt;10 cm) cover (%)</td>
<td>8.0 ± 8.1*</td>
<td>0.3 ± 1.1*</td>
<td>0.1 ± 0.2*</td>
<td>**</td>
</tr>
<tr>
<td>Dicotyledon cover (%)</td>
<td>0.0 ± 0.1*</td>
<td>0.1 ± 0.6*</td>
<td>4.8 ± 3.1*</td>
<td>**</td>
</tr>
<tr>
<td>Monocotyledon cover (%)</td>
<td>0.0 ± 0.0*</td>
<td>0.0 ± 0.0*</td>
<td>2.1 ± 2.6*</td>
<td>**</td>
</tr>
<tr>
<td>Debris cover (%)</td>
<td>0.4 ± 0.6*</td>
<td>1.6 ± 1.4*</td>
<td>0.5 ± 0.7*</td>
<td>**</td>
</tr>
<tr>
<td>Slipface height (m)</td>
<td>9.8 ± 4.7*</td>
<td>6.7 ± 5.4*</td>
<td>5.2 ± 1.7*</td>
<td>**</td>
</tr>
<tr>
<td>Stossface height (m)</td>
<td>9.6 ± 3.8*</td>
<td>5.5 ± 3.6*</td>
<td>5.2 ± 0.9*</td>
<td>**</td>
</tr>
<tr>
<td>Slack area (m²)</td>
<td>5,255 ± 5,262*</td>
<td>88,904 ± 179,669*</td>
<td>6,004 ± 5,266*</td>
<td>**</td>
</tr>
</tbody>
</table>

* p < 0.05; ** p < 0.001; N.S. not significant at p < 0.05.

Different letter superscripts (a–c) denote significant difference between features for the nesting habitat of each species according to Tukey's multiple range test (p < 0.05).
characterised by vegetated slacks and nests were far from the high water mark and near vegetation, elevated above the slack floor. MACLEAN and MORAN (1965) suggest that nesting on sand near physical objects renders eggs less conspicuous. Flooding of the slacks may occur during storms and high spring tides and by nesting on an elevated platform nest destruction can be avoided. Alternatively, since dicotyledonous vegetation in the slacks is associated with small hummock dunes (McLACHLAN et al., 1982; McLACHLAN et al., 1987) which provide naturally elevated platforms, the use of elevated nest sites could be a function of nesting close to vegetation.

These dune breeding birds are clearly nesting nearer to conspecifics than other species. FASOLA and CANOVA (1992) observed a number of ground-breeding shorebird species nesting in the same habitat with reduced interspecific interactions due to conspecific nesting associations. HALL (1959) recorded a nearest neighbour distance of 112–540 m between oystercatcher nests, similar to that in this study. FROST and SHAUGHNESSY (1976) recorded Damara terns nesting 100–150 m from each other, while CLINNING (1978) recorded them about 57 m apart. In this study Damara terns nested further apart than in Namibia. The slacks of the Alexandria Coastal Dunefield are considerably smaller than the interdune plains of Namibia, possibly excluding a second nest within a slack. Also, with one nesting pair per slack, the birds may be less conspicuous to predators (FROST and SHAUGHNESSY, 1976). The selection for nesting nearer conspecifics could, however,

Table 2. Comparison of mean distances (± S.D.) from nests of Damara terns, African black oystercatchers and whitefronted plovers and features of the habitat. ANOVA and Tukey range test results are given.

<table>
<thead>
<tr>
<th>Distance to: (m)</th>
<th>Damara Tern (n = 28)</th>
<th>Oystercatcher (n = 32)</th>
<th>Plover (n = 25)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation</td>
<td>9.2 ± 20.6*</td>
<td>7.5 ± 8.7*</td>
<td>1.6 ± 2.8*</td>
<td>**</td>
</tr>
<tr>
<td>Nearest neighbour</td>
<td>175.8 ± 133.9*</td>
<td>396.3 ± 854.0*</td>
<td>219.2 ± 329.3*</td>
<td>**</td>
</tr>
<tr>
<td>Debris</td>
<td>166.9 ± 229.3*</td>
<td>20.5 ± 86.3*</td>
<td>361.5 ± 222.2*</td>
<td>**</td>
</tr>
<tr>
<td>High water mark</td>
<td>114.8 ± 45.3*</td>
<td>49.9 ± 25.3*</td>
<td>165.1 ± 82.4*</td>
<td>**</td>
</tr>
<tr>
<td>Storm berm</td>
<td>96.4 ± 47.0*</td>
<td>29.7 ± 24.5*</td>
<td>147.6 ± 79.4*</td>
<td>**</td>
</tr>
<tr>
<td>Back of slack</td>
<td>39.6 ± 45.8*</td>
<td>72.5 ± 85.3*</td>
<td>46.8 ± 39.2*</td>
<td>**</td>
</tr>
<tr>
<td>Slipface</td>
<td>23.7 ± 16.9*</td>
<td>26.7 ± 26.0*</td>
<td>21.5 ± 18.4*</td>
<td>**</td>
</tr>
<tr>
<td>Stossedune</td>
<td>20.5 ± 18.2*</td>
<td>15.2 ± 17.8*</td>
<td>28.4 ± 19.3*</td>
<td>*</td>
</tr>
</tbody>
</table>

* p < 0.05; ** p < 0.001; N.S. not significant at p < 0.05.
Different letter superscripts (*) denote significant difference between features for the nesting habitat of each species according to Tukey's multiple range test (p < 0.05).
be a function of the clumped availability of suitable nesting habitat.

Different foraging strategies of the three species limit competition for food. Whitefronted plovers and African black oystercatchers are resident species, feeding and nesting in the Alexandria Coastal Dunefield, exhibiting intraspecific territorial behaviour over their food and nesting resources (Hall, 1959; Blaker, 1966; Hockey, 1983a; van der Merwe, 1987). In contrast, the terns feed in the surf zone and estuary (Frost and Shaughnessy, 1976; Clinning, 1978) and although they nested in individual slacks, they exhibited semicolonial behaviour (Frost and Shaughnessy, 1976; Clinning, 1978) by 'group mobbing' intruders and in group foraging. This social behaviour may influence the potential selection of nest sites in the dunefield.

There are clear differences in the physical features (particularly substrate, vegetation and distance to high water mark) characterising the nesting habitats of each species. There is thus limited potential for interspecific nesting habitat competition and, if food is not a limiting resource, the numbers

Table 3. Comparison of mean values (± S.D.) of environmental variables measured at the micro-habitat scale (1 m²) between the nests of Damara terns, African black oystercatchers and whitefronted plovers. ANOVA and Tukey range test results are given.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Damara Tern (n = 28)</th>
<th>Oystercatcher (n = 32)</th>
<th>Plover (n = 25)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shell cover (%)</td>
<td>6.9 ± 10.9°</td>
<td>8.7 ± 7.9°</td>
<td>9.4 ± 14.0°</td>
<td>N.S.</td>
</tr>
<tr>
<td>Sand cover (%)</td>
<td>60.6 ± 12.9°</td>
<td>63.5 ± 8.9°</td>
<td>74.9 ± 13.3°</td>
<td>**</td>
</tr>
<tr>
<td>Pebble (1-5 cm) cover (%)</td>
<td>1.7 ± 8.7°</td>
<td>3.4 ± 6.7°</td>
<td>0.0 ± 0.0°</td>
<td>**</td>
</tr>
<tr>
<td>Pebble (5-10 cm) cover (%)</td>
<td>1.4 ± 4.9°</td>
<td>7.7 ± 4.3°</td>
<td>0.1 ± 0.2°</td>
<td>**</td>
</tr>
<tr>
<td>Pebble (10-20 cm) cover (%)</td>
<td>0.9 ± 2.9°</td>
<td>9.8 ± 5.3°</td>
<td>0.1 ± 0.4°</td>
<td>**</td>
</tr>
<tr>
<td>Pebble (&gt;20 cm) cover (%)</td>
<td>0.4 ± 1.52°</td>
<td>2.6 ± 2.9°</td>
<td>0.0 ± 0.0°</td>
<td>**</td>
</tr>
<tr>
<td>Aeolianite (&lt;10 cm) cover (%)</td>
<td>19.8 ± 10.8°</td>
<td>1.1 ± 3.3°</td>
<td>4.2 ± 7.6°</td>
<td>**</td>
</tr>
<tr>
<td>Aeolianite (&gt;10 cm) cover (%)</td>
<td>8.3 ± 10.5°</td>
<td>0.0 ± 0.0°</td>
<td>0.0 ± 0.0°</td>
<td>**</td>
</tr>
<tr>
<td>Dicotyledon cover (%)</td>
<td>0.0 ± 0.0°</td>
<td>0.1 ± 0.5°</td>
<td>8.8 ± 9.9°</td>
<td>**</td>
</tr>
<tr>
<td>Monocotyledon cover (%)</td>
<td>0.0 ± 0.0°</td>
<td>0.0 ± 0.0°</td>
<td>1.7 ± 3.0°</td>
<td>**</td>
</tr>
<tr>
<td>Debris cover (%)</td>
<td>0.01 ± 0.03°</td>
<td>0.2 ± 0.2°</td>
<td>0.1 ± 0.1°</td>
<td>**</td>
</tr>
<tr>
<td>Sand compaction (index)</td>
<td>0.9 ± 0.7°</td>
<td>1.4 ± 1.1°</td>
<td>1.3 ± 0.7°</td>
<td>N.S.</td>
</tr>
<tr>
<td>Nest elevation (cm)</td>
<td>0.2 ± 0.9°</td>
<td>0.5 ± 2.6°</td>
<td>3.3 ± 6.6°</td>
<td>*</td>
</tr>
</tbody>
</table>

*p < 0.05; **p < 0.001; N.S. not significant at p < 0.05.
Different letter superscripts (°°°) denote significant difference between features for the nesting habitat of each species according to Tukey's multiple range test (p < 0.05).
of potential nesting birds supported in this area would be much greater. At present, less than 20% and 30% of the potentially available tern and oystercatcher nesting habitat respectively is utilised. Damara tern nesting habitat is thus not limiting and the low tern population may be due to the fact that the Alexandria Coastal Dunefield is at the eastern extremity of their range (Fearn and Bourne, 1978; Williams and Myer, 1986). Food may be limiting or the birds nesting here may be an isolated group returning each year. A comparison of resource availability for this population and that on the West coast of southern Africa is required to explain the small size of the Alexandria Coastal Dunefield population.

No unimpacted areas (Watson and Kerley, 1995) which would allow a human interference comparison on habitat selection were available during the study. Long term studies may reveal shifts in habitat use due to human interference and population changes.

Management

Approximately 3 km (14%) of the potentially available nesting habitat for these three species in the Alexandria Coastal Dunefield has been artificially stabilised through the establishment of vegetation. As the birds nest in predominately barren, unvegetated or low vegetated areas the stabilised areas are unsuitable for nesting and further stabilisation of these nesting and potential nesting areas should be discouraged.

Management of dune breeding birds includes the protection of nesting habitat as well as specific nest sites. In the Alexandria Coastal Dunefield these include a range from wet, vegetated to dry, barren slacks. Off-road vehicles need to be kept away from these areas and therefore below the high water mark. Oystercatchers nest along the entire coastline near the high water mark and their nests are the most susceptible to off-road vehicles. The areas 6–10 km and 14–16 km east of the Sundays River mouth are important nesting habitats for Damara terns while the plovers are concentrated in the slacks close to the river mouth. Fencing nesting sites and patrolling the coastline to discourage nest disturbance should reduce the impact of off-road vehicles on the nesting birds. However, vehicle mortalities of young are prevalent after the nesting stage when the fledglings of all three species move to, and are fed on the beach (Watson, 1995). Fledgling mortality due to off-road vehicles could be reduced by restricting vehicles to the first three kilometres east of the Sundays River mouth during the breeding season (October to February). Alternative management strategies could include educating beach-users, enforcing speed limits or limiting the number of vehicles on the beach during the breeding season. Beach-users are currently generally unaware of the dune breeding birds and the threats that vehicles pose to these species (Watson, 1995). Thus educating beach-users regarding these problems may significantly reduce their impact on these bird populations. The success of these management strategies needs to be carefully monitored. Closure of the dunefield and beach to vehicular traffic during the breeding season may, however, be the only long term option to ensure the breeding success of these birds.

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