# The Roles of Coastal Birds in the Functioning of Marine Ecosystems in Southern Africa

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Seabirds and shorebirds are important predators in both the subtidal (marine) and intertidal ecosystems of Southern Africa. They are not distributed randomly, their distribution patterns being determined by the availability of food and nesting sites. Seabirds feed at sea and breed on land, and so are important redistributors of nutrients. Deposition of guano raises the level of nutrient in the vicinity of seabird breeding colonies and the effects of this are evident in the plant and animal communities of the intertidal and nearshore regions. Seabirds prey on species which are of commercial importance, and this, coupled with the need to conserve decreasing populations of many seabirds, has been the stimulus for much research to date. Shorebirds also consume species of importance to man, and in some areas are important determinants of the community structure of invertebrates. Current research into sea and shorebird populations is adopting an ecosystem rather than an autecological approach. Researchers are attempting to answer such questions as whether competition between seabirds and man for food really exists, what causes coastal bird populations to decrease, and what can be learnt by studying the behaviour and ecology of coastal birds that will help towards the effective management of shared resources.

## Introduction

Birds are common and important components of coastal ecosystems, being top predators both in nearshore and intertidal environments. The avian communities of nearshore and intertidal regions are largely discrete, though some birds, such as gulls, forage in both habitats. Nearshore (seabird) and intertidal (shorebird) avifaunas are treated separately in this review of the ecological roles of coastal birds in Southern Africa. The physical limits of the nearshore region extend from the low-water mark out to sea, approximately as far as the edge of the continental shelf. The intertidal environment is defined as that extending above the low-water spring mark to the limit of direct marine influence.

The Southern African coast, extending from the Cunene river in the west to the Zambezi river in the east, includes a variety of habitats such as mangrove swamps, estuaries, rocky shores and desert-backed beaches. The west coast is strongly influenced by the cold, nutrient-rich Benguela upwelling system, whereas the south and east coasts are influenced by the warmer Agulhas and Mozambique Currents. Much ecological research has been conducted on coastal birds in Southern Africa, but the effort has been concentrated in the Cape Province of South Africa, especially in the southwestern and eastern Cape. Some work has been done on the biology of coastal birds in South West Africa/Namibia[1,2] but none in southern Mozambique.

Most ecological research on seabirds in Southern Africa has been stimulated primarily by two factors: supposed competition between piscivores, such as cormorants *Phalacrocorax* spp. and the Cape gannet *Sula capensis*, and commercial fisheries[3,4], and the need for conservation-orientated research on species thought to be under some threat, for example the jackass penguin *Spheniscus demersus*, the Damara tern *Sterna balaenarum* and the roseate tern *S. dougallii*.[2,5-10] A series of articles is being published on the distribution, population size and conservation of individual seabird species in Southern Africa.[8,11-15] It is intended to produce similar papers for each of the 14 species of breeding seabirds.[16]

The intertidal avifauna has received less attention so far, and only in the last 10 years have studies considered the effect of birds on the intertidal environment, and the conservation of intertidally foraging species.[17-21]

An outcome of these research endeavours has been a number of publications on various aspects of the ecology of coastal birds in Southern Africa (for examples, see references cited in this article). The history of seabird research in the subcontinent has been briefly described[22] and a comprehensive bibliography has been published[23]. No similar review or bibliography yet exists for shorebirds. This paper outlines the current state of knowledge regarding the ecological roles of birds in the nearshore and intertidal regions of Southern Africa, identifies gaps in our knowledge and suggests the direction for future research.

## The nearshore environment

The nearshore environment of Southern Africa (from low-water mark to the edge of the continental shelf) supports large numbers of both breeding and nonbreeding seabirds. Breeding seabirds are spatially restricted by the availability of safe nesting sites, such as islands and mainland cliffs, but nonbreeding species and individuals theoretically can occur throughout the region. However, seabird distribution is not random and the greatest numbers of most species probably occur within the Benguela upwelling system off the Atlantic coast[24,25]

When Rand[26-28] pioneered work on seabird distribution and diet in Southern Africa, shoaling fish, such as pilchard *Sardinops ocellata*, dominated the diets of several species of resident seabirds. After the collapse of the pilchard populations, many breeding seabirds switched to a diet consisting mainly of smaller pelagic shoaling fish, such as anchovy *Engbraulis capensis*, and there was a subsequent decrease in populations of several species of seabirds.[29] At the same time, the fishery switched from predominantly catching pilchards for canning to catching anchovy for fishmeal. Thus birds and man still exploit the same resource. The three most abundant breeding seabird species, jackass penguin, Cape cormorant *Phalacrocorax capensis* and Cape gannet, total some 577 000 breeding pairs, or 93% of the total Southern African breeding population of 14 species of seabirds.[16] Furness and Cooper[30] calculated that the populations of these three species in the Saldanha Bay fishing ground consume a total of 16 500 tonnes of fish per year, representing 30% of the mean annual commercial catch. They estimated that these three breeding species consume 11 800 t of anchovy annually, representing 23% of the anchovy biomass in the Saldanha Bay fishing ground. These figures are comparable to those calculated for other marine ecosystems.[30] Unknown numbers of nonbreeding migrant petrels, shearwaters and albatrosses, some of which are known to consume anchovies (FitzPatrick Institute, unpublished data) are also present for much of the year.[24,25,31,32] Seabirds can therefore be important predators of fish, and correlations have been obtained by comparing fluctuations in seabird numbers, guano production and fish populations.[6,29,33,34]

More recent studies of predator/prey interactions, especially those of the jackass penguin and anchovy, have suggested that seabird predators can be used in a predictive manner to make

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deductions about aspects of their prey such as distribution, behaviour and population size. It may be possible, for example, to use analyses of anchovies consumed by jackass penguins to estimate the rate of recruitment of juvenile fish to the commercially exploitable fraction of the population, since juvenile anchovies are eaten by penguins earlier in the year than they appear in commercial catches. Anchovies appear to occur in both 'open' (dispersed) and 'closed' (concentrated) shoals (R. P. Wilson, personal communication) and only the latter are commercially exploitable. It appears that, whereas Cape cormorants feed primarily on closed shoals, jackass penguins do not (R. P. Wilson, unpublished data). Thus, a simultaneous comparison of the diets of the two species may yield valuable information on the rate of recruitment of anchovies from the population as a whole to the commercially exploitable fraction, the 'stock', and act as an early warning of recruitment failure should juvenile anchovies fail to be found in the diet of jackass penguins in any year (see also Duffy and Laurenson, in press).[35]

The relationships between seabirds, especially the Cape gannet, and the pilchard ('sardine') run off Natal, South Africa, have not yet been studied, but may also yield valuable information on the dynamics of the prey population through studies similar to those described above. Research on the feeding ecology and population dynamics of the Cape gannet in the Benguela region is being undertaken by the Sea Fisheries Research Institute (A. Berruti, personal communication) and at Algoa Bay, eastern Cape, in the Agulhas Current (G.J.B. Ross, personal communication).[36] The Algoa Bay gannet population has increased in size recently,[37] whereas at least some Benguela populations have decreased.[29] An explanation for this may be that while pilchards have all but disappeared from the diet of the Benguela gannet populations,[38] they form an important part of the diet of the Algoa Bay gannet population.[36]

Geographical variation in the diet, adult size and breeding success of jackass penguins may also indicate differences in food supply and hence highlight the effects of commercial fisheries. Jackass penguin populations, as well as Cape gannets, are decreasing at most breeding sites in the Benguela but increasing in the warmer Agulhas region.[29] Research on jackass penguins by the FitzPatrick Institute in the Benguela, and by the University of Port Elizabeth in Algoa Bay,[39] may also increase understanding of prey dynamics. Much less is known about nonbreeding visitors.[11] Whereas something is known of their distribution,[24,32] little is known of their precise numbers and diet.[25,40] Studies have begun at the FitzPatrick Institute to fill this gap.

As top predators, which consume appreciable portions of the biomass of their prey, seabirds can have large effects on trophic dynamics in the environments in which they live. They may also be sensitive to environmental change and thus could be used as 'biological samplers' to study the dynamics of their prey, and perhaps ultimately as predictors of the resources available both to them and for commercial exploitation.

Seabirds were a food source for prehistoric man.[41] Beach patrols for dead seabirds conducted by the African Seabird Group[42] have yielded information which is being compared with this prehistoric information as well as with the fossil record,[43] to discover and explain changes in seabird communities and their food resources that have occurred over a period of seven million years.[44]

## The intertidal environment

The influence of birds on processes operating within the Southern African intertidal region is a recent subject of study. Over the past ten years, many data on the numbers and distribution of shorebirds around the coast have been gathered[45-49] and some information exists on seasonal fluctuations in shorebird abundance[50-52] and energy requirements.[17,18,21,53] While some shorebird studies were carried out as early as the 1950s,[54] it has only been since the mid-1970s that workers have tried to understand the roles of birds in intertidal predatory processes.[17-19,53,55-59] Emphasis has been placed on estimating the importance of birds in energetic pathways[17,56] and intensive study has been concentrated at Langebaan Lagoon in the southwestern Cape,[53,56] at the sandy beaches in Algoa Bay[17] and along the rocky intertidal shores of the western Cape.[58,59]

At Langebaan Lagoon, curlew sandpipers *Calidris ferruginea* alone consume approximately 12% of annual invertebrate production.[18] Shorebirds at sandy beaches of the subcontinent consume between 10% and 49% of the annual invertebrate production in various areas around the coast.[21] The importance of birds as predators and distributors of nutrients in sandy intertidal regions is therefore considerable, a fact not always appreciated by those who study sandy beaches as ecosystems.

The effect of predation by birds on the structure and dynamic changes of invertebrate communities is the subject of continuing research at the FitzPatrick Institute. Research has concentrated on the effects of predation by African black oystercatchers *Haematopus moquini* on rocky-shore invertebrates in the western Cape. Oystercatchers consume large invertebrates, such as mussels and limpets,[59,60] which are dominant elements in intertidal communities of invertebrates. Work has concentrated on trying to explain the effects (and origins) of the much higher densities of oystercatchers at islands visited by seabirds than on the mainland, mainly with regard to predation on populations of the abundant upper-shore limpet *Patella granularis*, a major component of the oystercatcher's diet.[59] The middle and upper intertidal regions of islands are characterized by large beds of macro-algae, which are noticeably absent on the mainland. Macro-algal growth is limited by limpet grazing and is thus enhanced by removal of limpets by oystercatchers. Algal growth rates are much higher at islands than on the mainland,[61] probably owing to nutrient input from seabird guano, feathers, corpses and nesting material. Limpet growth is correspondingly fast. Oystercatchers are size-selective predators on limpets, and, at islands, though not on the mainland, some limpets grow too large for oystercatchers to handle. These very large limpets at islands may provide the key to the maintenance of limpet populations. Female gamete production in limpets is proportional to size, and between 45% and 90% of the annual output of limpet gametes at islands is produced by limpets too large to be preyed upon by oystercatchers.

Rocky shores lend themselves to study because the invertebrate communities are clearly visible at low tide and appropriate sampling techniques can be devised readily. Future research will investigate whether (or how) other shorebird species regulate or influence invertebrate communities, and the importance of nutrient enrichment by deposits of seabird guano to intertidal and infratidal communities.

Elsewhere in Southern Africa, little is known about the ecology of shorebirds on rocky shores. The diet of the African black oystercatcher has been studied at various rocky localities between Lüderitz and East London[59,62] but knowledge of the food and behaviour of other species on rocky shores is very limited. A major handicap is the lack of a description of invertebrate faunas of sandy beaches in Namibia. Recent surveys of shorebirds there have shown that beaches in the north support unusually large numbers of some bird species, but the reasons for this are not known.[21] On the sandy beaches of the east coast of Southern Africa, densities of shorebirds are low.[21] Nutrient input to such beaches is probably erratic, occurring mostly during cyclones and seasonal flooding of rivers. Where these beaches support large populations of ghost crabs *Ocypode* spp. they have small populations of scavenging isopods.[63,64] Isopods are eaten by shorebirds (FitzPatrick Institute, unpublished data) and thus, by diverting energy away from these species, ghost crabs may effectively compete with shorebirds for food.

Several studies on shorebirds have emanated from the Western Cape Wader Study Group, an amateur organization based in Cape Town,[48] dealing primarily with numbers, distribution, migration, biometrics and moult of waders (Charadrii). These data provide valuable baseline information on which further studies can be

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built.[19,21]

Despite the wealth of numerical and distributional data on shorebirds that exists from the coast, islands and estuaries of Namibia and South Africa, little more than anecdotal accounts and local checklists exist for coastal birds in Mozambique.[65-67] Much information is available on the intertidal invertebrate communities of Inhaca Island, southern Mozambique,[66] which is known to be an important wintering locality for several species of migratory shorebirds (J. C. Sinclair, *in litt.*).[67] Considerable potential exists for further research at Inhaca Island.

Although the majority of birds that feed intertidally eat invertebrates, some species, such as kingfisher *Ceryle* and *Alcedo* spp., are primarily piscivorous, and others such as the little egret *Egretta garzetta* eat both fish and invertebrates.[68] These species are relatively sparsely distributed around the coast,[48] and almost nothing is known of their impact on intertidal faunas. One seabird, the crowned cormorant *Phalacrocorax coronatus*, which preys mainly on klipfish *Clinus* spp. (FitzPatrick Institute, unpublished data), can forage intertidally during the high tide period.

## Interrelations between the nearshore and intertidal environments

Although the nearshore and intertidal environments have been treated separately in this review for the purpose of clarity, they are closely linked and neither should be viewed in isolation. The most important avian elements transferring nutrients within and between the two regions are the breeding seabirds. Although seabirds derive their energy requirements from the nearshore environment, they breed on land. The presence of breeding colonies and roosting aggregations results not only in the deposition of guano, feathers and corpses on land, but also the transport of marine macro-algae from the sea to the land as nesting material by some cormorants. Nutrient enrichment from seabird colonies has been shown to lead to an 'upgrading' of nutrient status and phytoplankton and zooplankton production in waters near seabird breeding colonies,[69] and current research at the FitzPatrick Institute suggests that the intertidal area of rocky shores is enriched in terms of algal and invertebrate production, in turn supporting high densities of invertebrate-eating shorebirds. In many parts of Southern Africa, such as northern Namibia, Transkei and Natal, there are no offshore islands. Species such a cormorants nest and roost on the mainland, on cliffs, headlands or on open beaches. The consequences of local nutrient enrichment for the intertidal and subtidal environments by roosting birds on the mainland coast have never been investigated, but seabird guano has been shown to affect terrestrial vegetation on islands off the subcontinent.[70] Many species, such as terns *Sterna* spp., use traditional roost sites, and deposit guano locally over long periods. Whether this has an effect in increasing invertebrate production is not known, but results from seabird breeding islands in Saldanha Bay suggest that this may be the case.[58,61]

Intertidal ecologists normally study intertidal biology at low tide. However, the intertidal environment is submerged twice a day at high tide, effectively increasing the size and diversity of the nearshore region. Birds such as gulls, terns and cormorants, which forage close inshore during high tide, exploit both the intertidal and nearshore environments simultaneously. Additionally, predators such as fish have access to, and forage on, intertidal invertebrates at high tide.[71]

The greatest rate of transport of nutrients from the land, through the intertidal region, to the nearshore environment is likely to occur during heavy rain, which is irregular on the west coast, and during conditions of heavy swell, when beds of guano that have accumulated above the high-water mark during calm weather are washed into the sea. The effect of such intermittent nutrient input is not known. Cormorants, especially Cape cormorants, may roost intertidally at low tide on both sandy and rocky shores, thus providing nutrients directly to the intertidal environment.

A considerable number of bird species are specialist intertidal foragers. Many of them migrate and consequently their impact varies seasonally.[21,50,52] Invertebrate communities should reflect these seasonally varying energy demands by the avifauna. It is the study of such processes that will assist us in understanding how equilibria are maintained at different trophic levels and consequently allow proposals to be made for the conservations and exploitation of both intertidal and nearshore resources.

## Gaps in our knowledge

To date, research on coastal birds in Southern Africa has concentrated in the cold, nutrient-rich Benguela upwelling system off the western Cape coast, and in Algoa Bay in the eastern Cape. Although some research has been carried out in Namibia, this region and the extreme southern Cape and warmer regions of the Indian Ocean are areas where further investigation is required.

Compared with the breeding species, little is known of the numbers, distribution and dietary requirements of nonbreeding seabirds in the nearshore environment: of significance here are albatrosses, petrels, shearwaters and terns.[24,25,32] The migrant common and Arctic terns *Sterna hirundo/paradisaea* have a summer population of *c.* 150 000 in South Africa alone[72] but nothing is known of their diets or trophic importance in the subcontinent. Kelp gulls *Larus dominicanus* steal prey from cormorants feeding near the shore[73] and on land, but the ecological significance of this behaviour is unknown. Berry[1] has related the breeding season of the Cape cormorant to abiotic factors such as seasonal variation in upwelling. Practically nothing is known of why other Southern African coastal birds breed when they do: for example, why do the sympatric kelp and Hartlaub's gulls *L. hartlaubii* breed at different times of the year?

While studies, motivated primarily for conservation reasons, have been undertaken on rare species of seabirds such as the Damara and roseate terns, less is known about more general threats such as pesticides and other forms of pollution. A preliminary study of pesticide levels in some seabird eggs in Southern Africa (National Institute for Water Research, unpublished data) needs to be extended to other species of seabirds and to other regions. Plastic pellets have been found in the stomachs of great shearwaters *Puffinus gravis* collected in local waters.[74] Practically no data exist on pesticide levels or other pollutants in Southern African shorebirds.

In the intertidal region, gulls, primarily the kelp gull, constitute a major proportion of shorebird biomass in much of Southern Africa.[21] Although some work has been done on the breeding biology of the species (FitzPatrick Institute, unpublished data), little is known of its foraging ecology in the intertidal region.[75,76] Even less is known about the smaller Hartlaub's gull, a common resident of the southwestern Cape.

Apart from the African black oystercatcher, which has been studied in detail,[62,77] very little is known of the foraging ecology of waders on rocky shores in Southern Africa.

## The direction of future research

Frost[78] has comprehensively reviewed the present directions in and future prospects for Southern African ornithology. Implicit in his discussion is that future ornithological research in this region should move away from classical autecological studies, concentrating rather on the functional roles played by birds in ecosystems. Such research will require higher levels of sophistication than has been attained previously. For example, there will be an increasing need for experimental work to test hypotheses generated from field observations. Some experimental work has already been undertaken on seabirds in Southern Africa[35,79-83] and is now beginning on birds of the intertidal region.

The examples we have cited make it clear that coastal birds are essential components in the functioning of marine ecosystems. Research in Southern Africa will continue to focus on coastal birds in relation to their environment rather than in isolation.

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## Syntheses

*The following summaries of the various sessions are prepared by the respective conveners.*

## Open Ocean

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The convener's introduction dealt with the two revolutions which have affected the earth sciences during the past 20 years. The domain which lies below the deep sea covers two-thirds of the terrestrial surface and an impartial orbiting observer, newly arrived from outer space, would surely name our planet 'Ocean'. In spite of their importance in area, almost nothing was known about the rocks below the deep sea until the 1950s. Since then scientists on ships from Columbia University and the Scripps Institution of Oceanography have brought in revolutionary gains concerning these rocks: (i) they are usually covered by a thin veneer of sediment, which can be penetrated by a vessel with a drill rig; (ii) below the sediment there is always basalt, a rock of volcanic origin; (iii) the basalts are *always* very young by geological standards. The oldest is ~ 180 million years old — about one twentieth of the age of the oldest rocks on the continents.

The process of 'sea-floor spreading' explains these facts. Let the reader focus attention on the long mid-ocean ridges, such as the ridge mid-way between South Africa and Antarctica. New hot material is continually rising to the surface at the ridge crest. The colder sea floor on the north side moves away northwards from the ridge and Africa is carried passively northwards, as if it were firmly fixed to a conveyor belt. Similarly, the sea floor on the south side moves southwards and the Antarctic continent is carried passively southwards, in conveyor-belt style. Most of the rock of the deep ocean floor was initially formed by volcanism at the ridge, and is termed MORB (mid-ocean ridge basalt). Elsewhere on the planet there are subduction zones, where the ocean floor plunges steeply down towards the earth's interior. The rate of destruction of sea floor, in these zones, equals the rate of creation of new sea floor at the ridges. Figure 1 illustrates a mid-ocean ridge.

The volcanic rocks which form the bedrock below the sea are all very young because the global rate of turnover (in the continued rifting, passive translation and plunging just described) is fast. The lower-density continents carry rocks which are 10 to 20 times older, because they always float passively on the conveyor belt, and never plunge downward in a subduction zone. It was also found that the global pattern of conveyor-belt motions could be simplified into the cap-like movements of about 20 rigid plates. This finding has made it possible to reconstruct the vectorial movements of the continents over the past 200 million years with considerable precision. Between 400 million years ago and 200 million years ago, studies of the orientation of the remanent magnetism possessed by rock strata permit continued analysis of the movement of the continents. Professor Nicolaysen showed a film of the movements of the continent during the past 400 million years, computed by scientists of the Shell Development Co., in cooperation with academics from Chicago, Ann Arbor (Michigan) and Oxford.

As the initial findings moved to the status of firmly established facts, a great effort was devoted to understanding why the sea floor undergoes a rapid turnover. Once again, a data base of deep-sea measurements turned out to be of crucial importance: this time measurements of the heat flow through the rocks at the bottom of the sea. An exceptionally high heat flow at the mid-ocean rifts was demonstrated as well as a simple law describing the gradual reduction in heat loss as the observer moves away from the ridge crest. Synthesis of these findings showed that most of the heat of the earth's interior is pouring out of the oceanic regions. The turnover of the sea floor is ultimately a convective process. Sea-floor spreading and plate motions represent *the* most important method whereby the heat (stored and accumulating) in the earth's interior gets dissipated. Two smaller-scale convecting systems provide useful analogues: the behaviour of solid basalt overlying a pool of molten magma in a Hawaiian volcano, and the behaviour of solid candle-wax overlying a pool of molten candle-wax in a laboratory cooking pot. Films were shown of these phenomena; they gave the participants in the session an insight as to why a significant component of South Africa's current deep-ocean geoscience is focused at the mid-ocean ridge crest. The asthenosphere — the partially molten mantle whose energy 'drives' sea-floor spreading and yields frozen basalts — comes very close to scientists at the ridge crest. Here it lies perhaps a kilometre below the sea bottom, and magma chambers may be even closer; below the South African highveld,

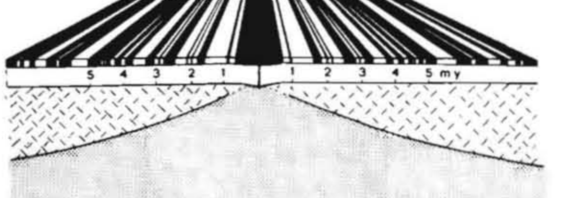


Fig. 1. Schematic section across a modern mid-ocean ridge. Proceeding downwards, there is magnetically striped ocean floor covering oceanic crust (white), oceanic lithosphere (hachured) and asthenosphere (grey).

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