Corella, 1990, 14(4): 107-112

Australasian Bird Reviews - Number 2

THE BREEDING SEABIRDS OF SOUTHWESTERN AUSTRALIA: TRENDS IN SPECIES, POPULATIONS AND COLONIES

J. N. DUNLOP[1] and R. D. WOOLLER[2]

[1]School of Biology, Curtin University of Technology, Bentley, WA 6102
[2]Biological Sciences, Murdoch University, WA 6150

Received 7 December, 1989

Australia has the only continental west coast with a poleward flowing warm, low salinity boundary current. This water mass, the Leeuwin Current, masks the deeper, equatorward, cold water, Westralian Current along the continental slope for much of the year, although it flows strongly only from about April to August.

In southwestern Australia, apparently as a consequence of the Leeuwin Current, tropical seabird species breed much further south than their usual latitudinal limits and often share nesting islands with southern, cool water species in peculiar communities. On the south coast of Western Australia the cool water breeding seabird fauna is apparently depauperate, due to the intrusion of the tropical drift.

There are evidently both short and long-term cycles in the strength and dominance of the Leeuwin Current which profoundly affect the distribution and biology of the breeding seabird species. The prevalent conditions appear to influence nesting season, reproductive periodicity, and range extension or contraction. Trends may be evident at the species, population and colony level.

INTRODUCTION

The continental islands of southwestern Australia extend from the Houtman Abrolhos group, off Geraldton, on the west coast (with their northern limit at 28°20′S latitude), to the Recherche Archipelago, off Esperance, on the south coast, extending eastwards to beyond Cape Arid (33°51′S, 124°06′E). Physiographically, the seabird nesting islands and rocks can be divided into three systems, on the basis of their geology and distance from the continental shelf edge (Fig. 1).

Seabird Islands

The Houtman Abrolhos consists of an archipelago of three island groups lying between 28°20′ and 29°00′S latitude and from 60–80 km off the coast, bringing them close to the continental slope. Most of the islands are composed of low lying Pleistocene and Holocene limestone, originally formed as coralgal reefs or in back-reef lagoons (Playford *et al.* 1970). The largest ones, such as North, East Wallabi and West Wallabi islands, are overlain by extensive recent, calcareous dune sands and are well vegetated. At the other extreme, a number of the smaller islands consist only of poorly vegetated, recent accumulations of stormcast, coralline rubble and shell grit (Storr *et al.* 1986).

The second system consists of over fifty inshore islands along the west coast between Dongara and Mandurah (Fig. 1). These are composed of Pleistocene aeolianite limestone and represent the elevated parts of dunal ridges drowned by the Holocene rise in sea level. Again, the larger islands are overlain with recent calcareous sands of varying depth, whilst the smallest ones are simply limestone rocks or pinnacles. Distances from the coast vary from as little as 200 m in the case of Sandland Island, to 10 km for the Beagle Islands and about 24 km for some of the satellites of Rottnest Island (Fig. 1).

A third system of granite islands and rocks begins at Cape Naturaliste continuing around Cape Leeuwin and along the south coast to encompass the Recherche Archipelago (Fig. 1). The continental shelf in this region is steeply sloping and most of the islands are within reach of sub-littoral marine environments by seabirds.

Climate and Oceanography

Climatically, southwestern Australia is Mediterranean with hot, dry summers and rainfall in cool, winter months. Rainfall in the southwestern region is much lower at the northern and eastern extremities than it is around the Capes. Day length varies significantly with season between 28°00'S and 35°00'S, making it a potentially important factor in the proximate timing of breeding in seabirds.

Although retaining a Mediterranean climate, the oceanography of southwestern Australia differs markedly from other continental western coasts. This is brought about by the passage of warm, low salinity, tropical water from the western Pacific Ocean via the Indonesian Archipelago and Timor Sea. Arising from this water-mass a tropical drift, known as the Leeuwin Current, flows on the outer continental slope southwards along the western Australian coast and around Cape Leeuwin (Godfrey and Ridgeway 1984; Pearce and Cresswell 1985). The Leeuwin Current varies in strength seasonally, flowing most strongly from April to August (Pearce and Phillips 1988). However, the typical cold, equatorward, west coast boundary current, the Westralian Current, appears to have little influence on conditions in the waters of the continental slope (Pearce and Cresswell 1985).

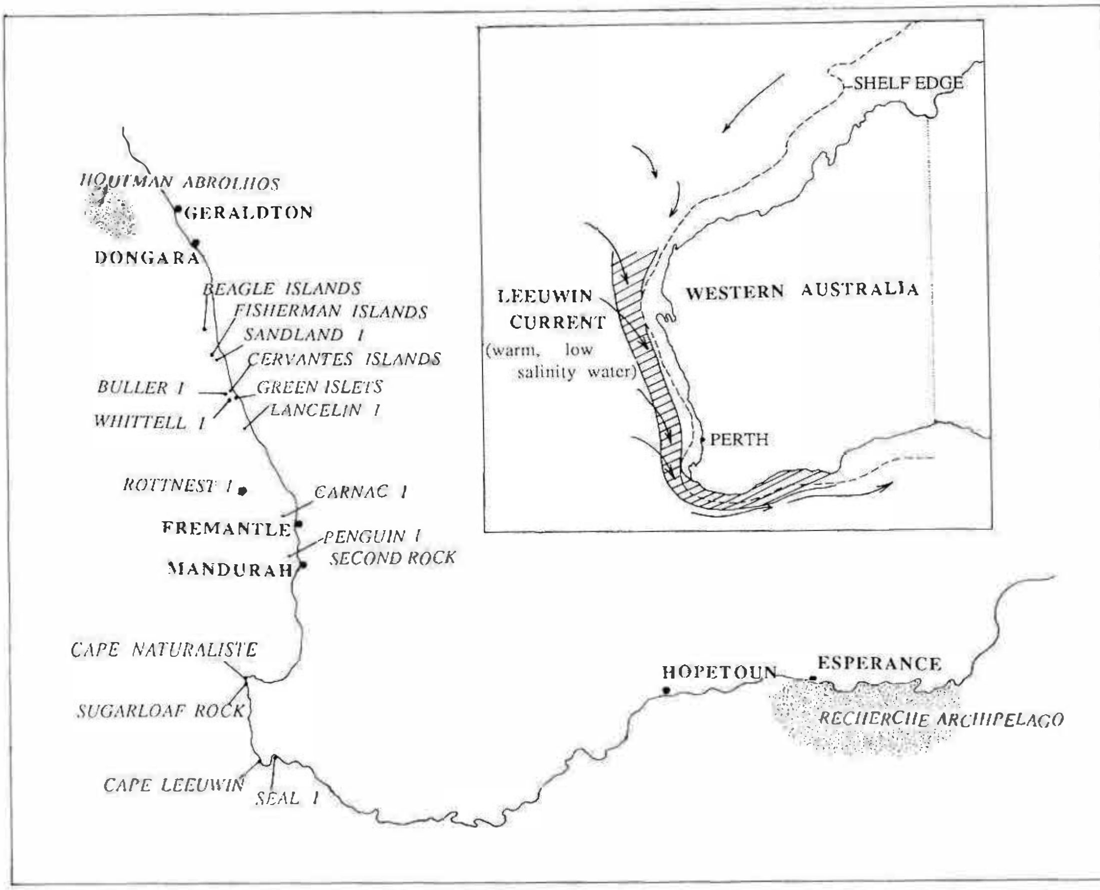

Figure 1. *Location map showing the area of influence of the Leeuwin Current off southwestern Australia (insert) and the position of breeding islands, archipelagos and other localities mentioned in the text.*

It has now been demonstrated that the strength of the Leeuwin Current shows considerable inter-annual variation and that in El Niño-Southern Oscillation (ENSO) years the influence of the Current is reduced (Pearce and Phillips 1988). The strength of the Leeuwin Current appears to be a factor in the recruitment of puerulus (actively swimming larvae) of the Western Rock-lobster *Panulirus cygnus* (Pearce and Phillips 1988). The Current has also been generally implicated in the extreme southward penetration of a wide range of tropical marine organisms into southwestern Australian waters (Wilson and Allen 1987). It is perhaps not surprising, therefore, that this unique oceanographic feature has also been implicated in the anomalous distribution and breeding biology of marine bird populations in the region (Dunlop and Wooller 1985).

SEABIRD BIOGEOGRAPHY

When viewed as a static assemblage of species, the seabird fauna of southwestern Australia is a biogeographical paradox. On many of the west-coastal islands where seabirds breed, species from southern cool waters and tropical species nest sympatrically. For example, at the Houtman Abrolhos (Storr *et al.* 1986), tropical Sooty Terns *Sterna fuscata*, Common Noddies *Anous stolidus* and Lesser Noddies *A. tenuirostris* nest on islands which are also utilized by cool-water species such as Little Shearwaters *Puffinus assimilis*, White-faced Storm-petrels *Pelagodroma marina* and Pacific Gulls *Larus pacificus*. In the Fremantle area, tropical Bridled Terns *Sterna anaethetus* and Roseate Terns *Sterna dougallii* nest on islands which are also breeding stations for the Little Penguin *Eudyptula minor*, a southern cool-water species (Dunlop and Wooller 1986). In the extreme south-west, around the Capes, tropical seabirds such as the Bridled Tern and Red-tailed Tropicbird *Phaethon rubricauda* come in contact with the Fleshy-footed Shearwater *Puffinus carneipes*, which typically breeds adjacent to the southern cool waters (Serventy *et al.* 1971).

The explanation for this assemblage lies primarily in the southward penetration of tropical species along the west coast, such that a number of these species breed there at a much higher latitude than on the east coast of Australia or, in some cases, elsewhere in the world (Serventy *et al.* 1971; Harrison 1983). Thus, the Sooty Tern and the two noddies have large breeding populations at the Houtman Abrolhos, well beyond their normal latitudinal limits. Roseate Terns now breed as far south as Warnbro Sound (32°20′S), the most southerly nesting station in the southern hemisphere, and the Bridled Tern's distribution extends to breeding colonies off Cape Leeuwin (34°25′S). The Red-tailed Tropicbird colony at Sugarloaf Rock at Cape Naturaliste (33°34′S) is an extreme outlier, as the nearest extant, although unstable, colony is on the Houtman Abrolhos at Pelsaert Island (28°57′S). The only large, stable population of this species in the eastern Indian Ocean is on Christmas Island at 10°30′S.

Much of the southward penetration of tropical seabirds into the region probably occurred over hundreds, possibly thousands, of years prior to European settlement. However, observations during ornithological history indicate that the process is continuing, with recent marked range extensions in the Bridled, Roseate and Sooty Terns and the Red-tailed Tropicbird (Dunlop and Wooller 1986; R. E. Johnstone, pers. comm.). The distributions of these tropical species are almost certainly related to short and long-term fluctuations in the strength and influence of the Leeuwin Current (Dunlop and Wooller 1986; Dunlop *et al.* 1988).

In the long term, the influence of the Leeuwin Current may also have determined the composition of the seabird assemblages on the islands along the south coast, east of Cape Leeuwin. Here the fauna is comprised, more typically, of southern, cool-water species such as the Little Penguin, Fleshy-footed Shearwater, Short-tailed Shearwater *Puffinus tenuirostris*, Little Shearwater, Great-winged Petrel *Pterodroma macroptera*, White-faced Storm-petrel and Black-faced Cormorant *Phalacrocorax fuscescens* (Serventy *et al.* 1971; Storr 1987). However, for the region's latitude and position, the seabird fauna is rather depauperate in cool water species by comparison with southeastern Australia and New Zealand (Storr 1987; Harrison 1983). Seabirds which are conspicuously absent might include the Fairy Prion *Pachyptila turtur*, Common Diving Petrel *Pelecanoides urinatrix*, Sooty Shearwater *Puffinus griseus*, Australasian Gannet *Morus serrator*, White-fronted Tern *Sterna striata* and possibly one or two additional Gadfly Petrels *Pterodroma* spp. In contrast to its role in expanding the distribution of tropical seabirds, the influence of the warm, low salinity water mass of the Leeuwin Current may eliminate marine habitats for some cool-water species.

The overall view of seabird biogeography in southwestern Australia is one of increasing tropical influence due to a strengthening phase in the ebb and flow of the Leeuwin Current. Long-term trends can be inferred from the breeding distribution of species but the short-term changes are more evident at the population level.

BREEDING SEASONS AND SEABIRD POPULATIONS

Serventy *et al.* (1971) described the double-nesting phenomenon along the mid-western and southwestern coasts of Australia, in which a variety of seabird species (excluding Procellariiformes) breed, or have peaks of breeding activity, both in autumn (March to June) and spring (August to November). Nesting between March and June is normal in tropical northwestern and northern Australia, and spring/summer is typical in south-eastern Australia (Serventy *et al.* 1971). This suggests that the occurrence of autumn nesting in southwestern Australia again reflects the influence of the Leeuwin Current, which reaches its peak flow between April and August. However, autumn-nesting is not confined to tropical seabird species which indicates that more complex interactions between water masses, food availability and seabird populations are involved. The response of various species/populations to the prevalent conditions has been shown to be related to their biogeographical origins (Dunlop and Wooller 1986).

In southwestern Australia the number of seabird species showing 'double', 'bimodal' or greatly protracted breeding seasons is smaller than in mid-western Australia. However, at least the Crested Tern, Bridled Tern, Roseate Tern, Pied Cormorant *Phalacrocorax varius*, Silver Gull *Larus novaehollandiae* and Little Penguin show one or other of these patterns.

Roseate Tern colonies have been recorded, on the islands from the Houtman Abrolhos to the Fremantle area, in two quite distinct seasonal periods; the peak months for laying appearing to be April and November (Dunlop and Wooller 1986). Within this region, autumn and spring breeding groups of Roseate Terns are interspersed amongst the islands and are sometimes sympatric. Both autumn and spring colonies occur at the Houtman Abrolhos (Storr *et al.* 1986), North Fisherman Island (Johnstone 1978a), Green Islets, Whittell Island and the Beagle Islands (Ford 1965, pers. obs.). Autumn-breeding alone is recorded from Cervantes Island (Ford 1965, pers. obs.), Middle and South Cervantes Island (Ford 1965), South Fisherman Island (Johnstone 1978b) and the Fremantle Islands (Dunlop and Wooller 1986). On Buller Island (Ford 1965) and Lancelin Island (Dunlop 1979), only spring-breeding colonies have been observed.

The Roseate Terns breeding at two recently established stations on Lancelin Island and Second Rock (Dunlop 1979; Dunlop and Wooller 1986) are drawn from spring and autumn groups respectively. In effect, they represent distinct, seasonally isolated populations of the Roseate Tern, both of which are extending their breeding ranges southwards in the region.

In southwestern Australia, most Crested Terns breed from late August to December, possibly somewhat later on the south coast. However, exceptions to this general trend are at least three stations with autumn colonies, at the Houtman Abrolhos (Storr *et al.* 1986), in the Fremantle area (Dunlop and Wooller 1986), and at Rocky Island east of Hopetoun (Serventy *et al.* 1971). In the Fremantle area, between 1979 and 1984, laying by Crested Terns was markedly bimodal, with peaks in April and late August/early September; little nesting was initiated in July and none between December and February. In 1982 detailed observations showed that the autumn and spring peaks involved similar numbers of breeding pairs (Dunlop 1985a). Colour-banding demonstrated that individual breeding adults had broadly circannual (although potentially slightly subannual) reproductive cycles and tended to lay in the same sub-season in successive years. In effect there were two incompletely divided subpopulations (Dunlop 1985a, b).

The historical evidence from Rottnest Island indicated that the autumn-breeding component, nesting from April to July, was not present in the past (Dunlop and Wooller 1986), the observations suggesting that it may not have become established until 1977 or 1978. There are, therefore, parallels with the Roseate Tern situation, in that there appears to have been a sudden invasion of terns from a population with an autumn-breeding schedule, presumably from a more tropical population further north. Such populations are known from Bedout, Bluebell and Frazer Islands off the Pilbara coast (Storr 1984) and from the Houtman Abrolhos (Storr *et al.* 1986). Thus, range extension may not only be progressing at the species level but also at the population level in seabirds broadly adapted to the tropics and sub-tropics.

The long-term stability of the sympatric, seasonal sub-populations of Crested Terns in the Fremantle area is uncertain. Since the reproductive periodicity of breeding aduls is potentially less than annual, and because the timing of colony establishment can be advanced by the presence of incubating conspecifics (Dunlop 1987), one might predict that some breeding adults would gradually move, over several seasons, from spring- to autumn-breeding. Recent observations of colour-banded terns suggest that this slow transformation may, indeed, be taking place. It is now known from banding that young reared in spring, as well as autumn, bred first aged three or four in an autumn-breeding colony. This effectively removes one of the possible barriers to an eventual merging of the sub-populations to form a single, autumn-breeding one. General observations do indicate that the spring-breeding colonies have declined in size and this trend is likely to continue as long as oceanographic and feeding conditions are most favourable from March to July.

Bridled Terns breeding on islands in southwestern Australia follow a strict migratory and breeding timetable. The birds typically arrive on their breeding grounds in early October, begin laying in late October or early November, and vacate both their breeding islands and the adjacent seas by mid-April (Storr *et al.* 1986; Dunlop *et al.* 1988b). Remarkably, there is one known exception at Newman Island in the Houtman Abrolhos. In this small population, laying is thought to occur between April and June or July (Storr *et al.* 1986; R. Johnstone pers comm.; C. Surman pers. comm.), at a time when no other Bridled Terns are present in southwestern Australia. The source of these terns is, at present, unknown.

In the Silver Gull and Little Penguin, breeding is considerably protracted and, in the latter species, the annual onset of laying can be extremely variable in response to oceanographic conditions. Both seabirds are potentially double-brooded and may replace lost clutches over several months (Wooller and Dunlop 1979; Dunlop and Storr 1981; Dunlop *et al.* 1988b). In contrast to the terns, this protracted season (which may be bi- or multi-modal) results from repeated, successful and unsuccessful, breeding attempts by members of a single population.

DYNAMICS OF RANGE EXTENSION

Much remains to be discovered about the oceanographic, trophic and biological factors underlying the range extension of tropical species and populations into southwestern Australia. Since a range of species-populations are involved, it is unlikely that intrinsic, genetic changes, influencing niche breadth are involved. It is known that invasions southwards, by tropical species are often irruptive or episodic, as was apparently the case with autumn-nesting Crested Terns at Rottnest Island. Another example was an irruption of Roseate Terns reported in the Fremantle area around 1958 (Serventy and Whittell 1976). Although there were no records of breeding from that time, the species did become established there around 1982 (Dunlop and Wooller 1986).

A short-lived breeding episode by the Red-tailed Tropicbird was recorded from Rottnest Island between 1957 and 1959. This is now known to have coincided with a period of particularly low sea-surface salinity in the area, possibly caused by a greater than usual intrusion of the Leeuwin Current onto the shelf (Dunlop *et al.* 1988c). It seems probable that oceanographic events, such as this, precipitate population irruptions and, ultimately, the occupation of new breeding stations.

In the case of the Red-tailed Tropicbird on Rottnest Island a permanent colony was not established. If the required oceanographic conditions do not persist, or fail to recur at sufficient frequency, then many of these extra-limital colonies will tend to be transient. For example, the tropicbird colony at Sugarloaf Rock now appears to be in decline. Other colonies of tropical species have, however, persisted, or continued to expand.

The population biology of a Bridled Tern colony, which has become established near Fremantle, within the last 40 years, is currently under investigation. It is hoped this will add further to our understanding of the dynamics of tropical seabird populations near the edges of breeding ranges.

ACKNOWLEDGMENTS

Over the course of more than a decade of seabird research in southwestern Australia numerous people have assisted in the field or provided observations. The banding projects were initially co-ordinated by the CSIRO and later by the ANPWS Bird Banding Schemes and their assistance has been greatly appreciated. The Western Australian Department of Conservation and Land Management has allowed us to study seabirds on the Island Reserves and continues to provide us with research accommodation on Penguin Island.

One should not allow a review paper to pass without acknowledging the important contributions made to the study of seabirds in this region by the late D. L. Serventy, J. R. Ford, and G. M. Storr.

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