

THE ROLE OF FORAGING ECOLOGY IN THE CONTRASTING RESPONSES OF TWO DARK TERNS TO A CHANGING OCEAN CLIMATE

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SUMMARY

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The Bridled Tern *Onychoprion anaethetus* and Brown Noddy *Anous stolidus* meta-populations breeding off southwestern Australia have shown contrasting responses to changes in the regional ocean climate. Bridled Terns have expanded their distribution southward, founding 40–50 frontier colonies up to 1 400 km from the edge of their historical range (pre-1900) at the Houtman Abrolhos islands. Some of these frontier colonies are amongst the largest recorded for this species anywhere. Conversely, the Brown Noddy's response to recurrent poor breeding performance at the Houtman Abrolhos has been limited dispersal and the establishment of only one frontier colony, at Lancelin Island, 280 km south of its stronghold on Pelseart Island. Egg-laying has started progressively later at the Bridled Tern frontier colony on Penguin Island, probably tracking a shift in the seasonal peak in sea temperature. The start of egg-laying in the Brown Noddy colony on Lancelin Island is significantly correlated with the long-term trend in the Southern Oscillation Index (SOI), with earlier breeding during *La Niña* periods when the Leeuwin Current is flowing strongly. The converse was the case in the Bridled Tern, which started breeding earlier during protracted *El Niño* periods. We present long-term trends in the timing of breeding of both species in relation to the *El Niño* Southern Oscillation. We also review the foraging ecology of the two species off southwestern Australia and discuss the role that differences in foraging ecology between the two species may have in accounting for contrasting population responses to a changing ocean climate.

Key words: Bridled Tern, Brown Noddy, foraging ecology, changing ocean climate, southwestern Australia

INTRODUCTION

At least eight seabird species populations of tropical origin have undergone southward shifts in breeding distribution off southwestern Australia over the last century, but particularly over the last 4–5 decades (Dunlop 2009). The poleward movement of tropical species is in line with observations and predictions in relation to global warming (Chambers *et al.* 2011). However, individual species respond differently, and the observed shifts in distribution may have very different implications for long-term population size (Wormworth & Şekerciöglu 2011).

There have been marked oceanographic changes in shelf and oceanic waters off southwestern Australia in recent decades. These changes include a general weakening of the Leeuwin Current due to the increasing frequency and duration of *El Niño* events, a background rise in mean sea temperature of up to 0.9 °C since the 1950s and a delay in the annual peak in sea temperature of 10–20 days over a similar period (Pattiararchi & Buchan 1991, Pearce & Feng 2007, Feng *et al.* 2009, Caputi *et al.* 2010). These changes in ocean climate and associated shifts in marine productivity have been implicated in the establishment of frontier colonies of tropical seabirds south of the Houtman Abrolhos islands off southwestern Australia (Dunlop 2009); for the locations of the species discussed, see Fig. 1. Trends in the timing of breeding and in the number of breeding Noddies (Brown Noddy *Anous stolidus* and Lesser Noddy *A. tenuirostris*) and Sooty Terns *Onychoprion fuscata* at the

Abrolhos islands over the last 2 decades appear to indicate a long-term decline in marine productivity (Surman & Nicholson 2009a).

Three “dark” tern species were amongst the tropical seabirds involved in the observed southward redistribution of colonies in the region: Bridled Tern *Onychoprion anaethetus*, Sooty Tern and Brown Noddy (Dunlop 2009). The Lesser Noddy, the fourth member of the tropical pelagic tern guild in this region, has not as yet established any frontier colonies south of its stronghold in the Houtman Abrolhos islands (Surman & Wooller 1995, Surman & Wooller 2003). This may be attributable to a lack of suitable tree-nesting habitats (e.g. mangroves) on the islands further south.

Here, we synthesize various previously reported aspects of the foraging ecology of the Bridled Tern and Brown Noddy in the region, summarize previously reported changes in geographical distribution and present additional analyses on the timing of breeding in these species. We suggest that the differences in foraging ecology between the two dark tern species explain contrasting responses to changes in ocean climate off southwestern Australia.

METHODS

Timing of breeding

The timing of the first egg laid in each breeding season was determined for the Bridled Tern colony on Penguin Island for 24

of the 26 years from 1986 to 2011. First laying dates were also determined for the Brown Noddy colony on Lancelin Island over an 18-year period between 1994 and 2011. The laying date for the first egg was determined by the observation of a freshly laid egg, from weight loss (Wooller & Dunlop 1980, Dunlop & Goldberg 1999, Garavanta & Wooller 2000), from observation of first hatching or from early chick growth. When a range of methods was utilized during a season, the earliest resulting date was selected. The first laying dates for each year for both species/colonies are plotted, along with the 3-year rolling mean annual Southern Oscillation Index (SOI) in Fig. 2 for those years (from 1994 onwards) when there were complete and comparable data sets. The mean annual SOI was calculated by adding the monthly SOI values for each year (Australian Bureau of Meteorology) and then producing a rolling 3-year average of the annual sums. The data were explored for correlations with the

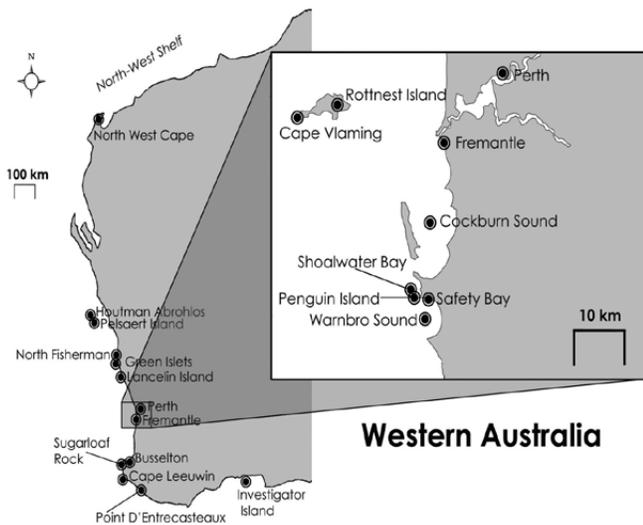


Fig. 1. Locality map for seabird islands of southwestern Australia.

mean annual SOI in the breeding year, and the rolling mean annual SOI with the previous year, previous 2 years and previous 3 years. There was no correlation with the current year, marginal significance with the 2-year rolling average, highly significant correlations after 3 years, and declining correlations after 4 years.

RESULTS

Foraging ecology

Our current knowledge of aspects of the foraging ecology of Bridled Terns and Brown Noddies breeding on islands of southwestern Australia is summarized in Table 1.

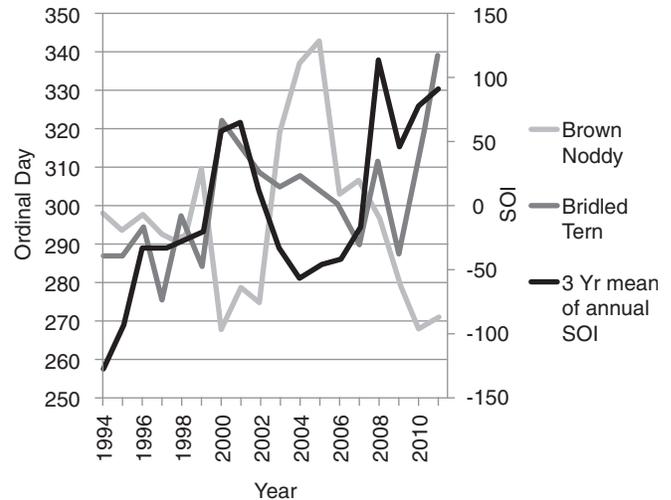


Fig. 2. First laying dates for the Bridled Tern colony on Penguin Island and the Brown Noddy colony on Lancelin Island between 1994 and 2011. Also plotted is the 3-year mean annual Southern Oscillation Index (SOI) for the same period.

TABLE 1
Comparative summary of foraging ecology in the Bridled Tern and Brown Noddy off southwestern Australia

Aspect of foraging ecology	Bridled Tern	Brown Noddy
Prey capture	In-flight contact dipping (Dunlop 1997, Surman & Wooller 2003)	In flight-contact dipping (Surman & Wooller 2003)
Foraging range	20–80 km (Dunlop 1997)	>100 km (Surman & Wooller 2003)
Relationship with foraging predatory fish	Facultative, in the absence of competition from other dark terns, particularly Black or Lesser Noddies (Dunlop 1997, Dunlop 2011)	Near obligate with small, surface-feeding tuna (Catry <i>et al.</i> 2009, Hulsman 1988, Gaughan <i>et al.</i> 2002, Jaquemet <i>et al.</i> 2004 & 2007, Surman & Wooller 2003, Ramos <i>et al.</i> 2006)
Prey types	Post larval fish and crustaceans, as well as insects (Dunlop 1997)	Post larval fish and squid (Gaughan <i>et al.</i> 2002, Surman & Wooller 2003, Surman & Nicholson 2009 a & b)
Prey length	Multi-modal, high proportion under 10 mm (Dunlop 1997)	Mean fish 51 mm, squid 39 mm (Gaughan <i>et al.</i> 2002)
Prey diversity	Spread over 20+ taxa (Dunlop 1997)	Concentrated in 2–3 taxa (Gaughan <i>et al.</i> 2002)
Prey shifts within breeding season	In pre-laying and late chick-rearing periods (Dunlop 1997, Aurélie Labbé unpublished data)	None (Gaughan <i>et al.</i> 2002, Surman & Nicholson 2009b)
Foraging habitat	Offshore on continental shelf (Dunlop <i>et al.</i> 1988, Dunlop 1997)	Oceanic, shelf edge, canyons and beyond (Gaughan <i>et al.</i> 2002, Surman & Nicholson 2009b)
Water mass productivity	Oligotrophic (Dunlop 2011)	Higher in inorganic nitrogen (Dunlop 2011)

Bridled Terns forage offshore over oligotrophic, continental shelf waters, utilising a wide range of prey types and sizes, a proportion of which are taken from floating rafts of seaweed or associated with other flotsam. Bridled Terns switch prey types within and between seasons. Brown Noddies forage largely beyond the continental shelf in relatively productive environments probably at shelf edge upwellings or in Leeuwin Current eddies. Tuna associated with these localized productive areas are probably important in making prey available to Brown Noddies. Unlike Bridled Terns, the Brown Noddies in this region take a narrow range of prey species, and have not been observed switching prey types during the breeding season.

Changes in distribution

Bridled Tern

Bridled Terns were observed breeding at the Houtman Abrolhos islands in 1843 (Storr *et al.* 1986) but were not recorded further south (at Rottnest Island) until 1889 (Fig. 1). They were the first tropical seabird species to establish frontier colonies south of their original recorded distribution in the region. They were observed in the Safety Bay area south of Fremantle in 1901 and breeding on the smaller islands in Shoalwater Bay (32°18'S) by 1921. Bridled Terns were breeding on the islands around Cape Leeuwin (34°23'S) by 1956 (Dunlop 2009). There were unpublished reports of the species breeding along the western portion of the south coast of Western Australia near Point D'Entrecasteaux (34°50'S, 116°01'E; Fig. 1) in the late 1990s.

In January 2008 a small group of Bridled Terns was recorded on Haul-Out Rocks (34°42'S, 118°39'E) east of Albany, and in December 2007 Bridled Terns were observed on Investigator Island (34°05'S, 120°52'E; Fig. 1) on the eastern portion of the south coast, indicating that the species may have reached the western edge of the Recherche Archipelago. An expedition to Investigator Island in late January 2008 confirmed a successful breeding colony of around 400 pairs that may have been present for at least a decade (Dunlop 2009). Surman & Wooller (2000) recorded Bridled Terns in the area in December 1995. Recent unconfirmed reports suggest that there is now a colony of Bridled Terns on Termination Island, due south of Esperance in the western Recherche Archipelago. Overall, the breeding range of the Bridled Tern has shifted south and then east about 1 400 km since the late 19th century, expanding rapidly along the south coast of Western Australia over the last 2 decades.

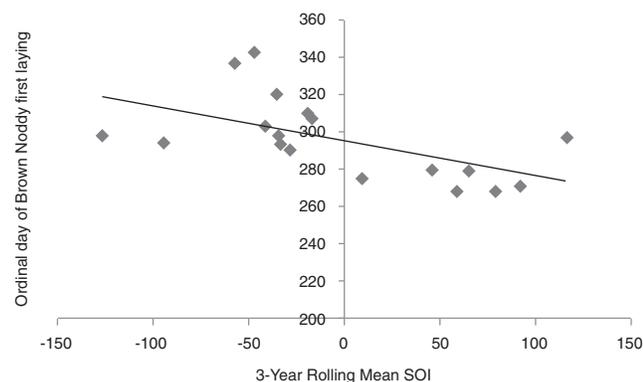


Fig. 3. Relationship between first laying dates in the Brown Noddy colony on Lancelin Island and the 3-year rolling mean annual Southern Oscillation Index (SOI) $R^2 = -0.571$, $P < 0.01$.

Recent decades have also seen remarkable growth in the size of some colonies south of the Houtman Abrolhos islands (e.g. North Fishermen [Johnstone 1978], Lancelin [pers. obs.], Penguin [Dunlop & Jenkins 1994] and Rottnest Islands) and a general infilling of the southern breeding areas with the occupation of additional breeding sites (Dunlop & Wooller 1990, Dunlop & Jenkins 1994). There are now 40–50 colonies (occupied islands) south of the Houtman Abrolhos islands. Some of these islands support several thousand pairs (e.g. Penguin Island [Dunlop & Jenkins 1994], Lancelin Island, North Fisherman Island [Burbidge *et al.* 1996]). These are large colonies compared with most of those reported from other Indian Ocean regions (Cramp 1985, Diamond 1976, Nature Seychelles 2003) or from the Houtman Abrolhos islands (typically in the tens to a few hundred pairs per island; Fuller *et al.* 1994). Large colonies of several thousand pairs do occur in the Pilbara region off northwestern Western Australia (e.g. at Bridled Island in the Lowendal Group 20°38'S, 115°23'E; Dunlop 1996). Bridled Terns breeding off southwestern Australia are present at their colonies between September and April and winter in the northwest Sulawesi Sea (between 4°N and 7°N between June and August; Dunlop & Johnstone 1994).

Brown Noddy

Brown Noddies had not been recorded breeding south of Pelsaert Island in the Houtman Abrolhos islands (28°54'S) before 1991/92 (Fig. 1). In that year, five pairs were discovered nesting on Lancelin Island (31°00'S; Fig. 1), a southward extension of breeding range of approximately 280 km.

The Lancelin colony grew exponentially between 1994/95 and 1997/98 and had reached about 900 pairs in 1998/99 (Dunlop & Mitchell 2001). It was estimated that net immigration ceased around 2002, but the colony continued to grow gradually through natal recruitment (Dunlop 2005, 2009). It was estimated at about 1 300 pairs in 2010 (Dunlop pers. obs.). In the 2003/04 season, Brown Noddies began prospecting Penguin Island (32°S, approximately 450 km south of Pelsaert Island) and continued to do so during late December and January in 2004/05, 2005/06 and 2006/07 (Dunlop pers. obs.). None was recorded there in 2007/08, but the pattern of visitation resumed between 2008/09 and 2011/12.

Brown Noddies breeding off southwestern Australia are migratory, being present at or around their colonies from September to April and absent from May to August. These birds are thought to winter in the subtropical Indian Ocean (Dunlop 2011).

Changes in the timing of breeding

The first laying dates of the Brown Noddies at Lancelin Island were not strongly correlated with the annual monthly Southern Oscillation Index (SOI). However, a relationship was evident with the longer-term SOI trend (Fig. 2) with egg-laying occurring earlier in *La Niña* (+ SOI) years and later under prolonged *El Niño* conditions. A significant negative correlation was found between the first laying date and the 3-year rolling mean annual SOI (Fig. 3, $R^2 = -0.571$, $P < 0.01$).

There was a positive correlation between first laying date and the 3-year rolling mean annual SOI in the Bridled Tern (Fig. 4, $R^2 = 0.643$, $P < 0.025$) over the same period (1994–2011). Bridled Terns therefore tended to lay later in *La Niña*-dominated periods

versus *El Niño* periods, the opposite pattern to that observed in the Brown Noddy. The longer-term Bridled Tern data contains a *La Niña* period from 1986–88 that appears to be an exception to this trend. There is, therefore, more uncertainty in the relationship between timing of breeding and the *El Niño*–Southern Oscillation (ENSO) for the Bridled Tern than for the Brown Noddy.

First laying dates in Bridled Terns have become significantly later over the last 25 years (Fig. 5, $R^2 = 0.645$, $P < 0.005$). No long-term chronological pattern is evident in the laying dates of the Brown Noddies at Lancelin Island.

DISCUSSION

The Bridled Tern and Brown Noddy, along with the Lesser Noddy and Sooty Tern, are members of a “contact-dipping” guild of dark-plumaged tropical terns. This paper documents the marked contrast in the observed responses of the Brown Noddy and Bridled Tern to a changing ocean climate off southwestern Australia in relation to our current understanding of their foraging ecology (Table 1). Changes in geographical distribution and timing of breeding have also been observed in the Sooty Tern in the region (Dunlop 2009, Surman & Nicholson 2009 a & b).

Bridled Terns forage over the continental shelf for a diversity of mainly small prey items, including post-larval fishes and crab megalopae associated with floating rafts of *Sargassum* and other flotsam (Dunlop 1997). Their preferred prey types are associated with the oligotrophic waters typical of the mid-shelf conditions over much of the region (Dunlop 2011). The spectacular southward expansion in the distribution of the Bridled Tern, spanning about 6° of latitude or 1 400 km of coastline, is probably attributable to a shift in suitable prey resources in response to rising background sea temperature. Many marine species, including their larval and post-larval stages, occur and persist further south when sea temperatures in this region are elevated (Pearce & Hutchins 2007, Caputi *et al.* 2011). The changing temperature regime may effectively lengthen the period when suitable (mostly tropical) prey species are available, with the peak in abundance occurring later. Weak Leeuwin Current conditions reduce cross-shelf mixing and productivity (Feng *et al.* 2009), potentially increasing the foraging area for a species adapted to clear-water oligotrophic conditions and the avoidance of competitors.

The Bridled Tern’s adaptable foraging ecology (Table 1) may contribute to its ability to exploit new opportunities and geographical

areas. The inability of the other dark terns to follow may have also released the Bridled Tern from competition within its guild, particularly with the similarly sized Lesser Noddy, with which it probably has the highest degree of niche overlap (Surman & Wooller 2003). This competitive release provides a explanation for the relatively large population sizes now observed at the frontier colonies south of the Houtman Abrolhos islands.

Devney *et al.* 2009 report greater sensitivity to *El Niño* events in pelagic (oceanic) species than inshore foraging species. The same trend is clearly evident off southwestern Australia (Surman *et al.* 2012), particularly when these species are also migratory. Although not strictly an inshore forager, the Bridled Tern’s foraging grounds over the continental shelf may be relatively buffered against ENSO-induced changes in oceanic productivity due to the availability of resources supplied by benthic food chains. Flotsam foraging represents a form of benthic–pelagic coupling.

It is unclear why Bridled Terns breed earlier during *El Niño* periods. The observed delay in Bridled Tern laying dates may be tracking the receding peak in sea temperature observed in the region (Pearce & Feng 2007), indicating that this tern is adapting its timing of reproduction to the changes in ocean climate. Breeding success is very difficult to estimate in Bridled Terns on Penguin Island because the chicks are mobile and difficult to trace consistently under the dense vegetation cover. However, in years when laying is extremely late, few fledglings are produced (Dunlop pers. obs.).

The large (130 000 pair) Brown Noddy colony on Pelsaert Island in the Houtman Abrolhos islands has frequently suffered low breeding performance, or complete failure, over at least the last 2 decades as a result of low prey availability (Surman & Nicholson 2009a & b). Historically, these poor breeding seasons were generally associated with *El Niño* events, although in recent years they have become decoupled from the ENSO cycle (Surman & Nicholson 2009a & b).

Breeding failure at core colonies in the region is thought to have driven dispersal in pre-breeders and the initiation of frontier colonies south of the former breeding range (Dunlop 2009). However, the Brown Noddy has at this stage established only one frontier colony, at Lancelin Island 280 km south of Pelsaert Island. Prospecting Brown Noddies have been recorded at Penguin Island (400 km south of Pelsaert Island) during late December and January in most years since 2003, but breeding has not been initiated there. Information from stable isotope analyses indicates that the dominant

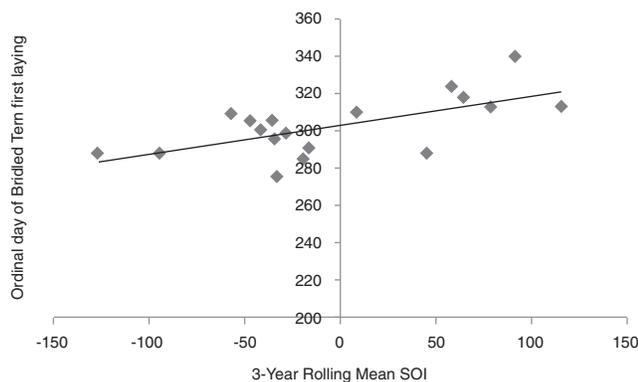


Fig. 4. Relationship between first laying dates in the Bridled Tern colony on Penguin Island and the 3-year mean annual Southern Oscillation Index (SOI) $R^2 = 0.643$, $P < 0.025$.

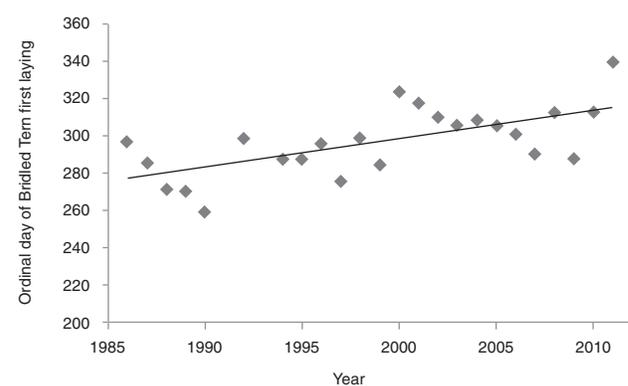


Fig. 5. Relationship between first laying dates in the Bridled Tern colony on Penguin Island and year over a 26-year period $R^2 = 0.645$, $P < 0.005$.

prey species taken by Brown Noddies in the region grow in relatively productive water masses with elevated levels of inorganic nitrogen (Dunlop 2011). Such water masses would also attract tuna (Jaquemet *et al.* 2007), which are probably important in forcing the prey species to surface, where they become available to foraging Brown Noddies. Given the Noddy's foraging range, these relatively productive areas with a higher probability of tuna aggregation are likely to be over or beyond the shelf edge. *La Niña* conditions are associated with a stronger eddy structure in the Leeuwin Current, increased mixing and higher productivity (chlorophyll *a*) at the shelf edge and beyond (Feng *et al.* 2009). Brown Noddies would therefore be expected to have higher reproductive output during *La Niña* periods.

The timing of laying in the frontier Brown Noddy colony on Lancelin tracks the long-term ENSO cycle, with earlier, and potentially more successful, breeding occurring under *La Niña* or neutral conditions. Historically, there was also higher Brown Noddy breeding success during *La Niña* years at the Abrolhos islands (Surman & Nicholson 2009 a & b, Surman *et al.* 2012), and this was associated with a proportionally high intake of the preferred fish prey (*Gonorrhynchus greyii*). However, this relationship has been breaking down over recent years (Surman *et al.* 2012). Early breeding has been associated with higher breeding success at the Abrolhos islands (Surman & Nicholson 2009 a & b). There has been a significant trend towards Brown Noddies laying later at the Abrolhos islands over the last 20 years (Surman & Nichollson 2009a) associated with reduced reproductive performance.

Interestingly, the cost to the adults of previous breeding seasons apparently influences subsequent laying dates for up to 3 years. The stress of attempting to breed during periods of low food availability can be considerable in seabirds (Kitaysky *et al.* 2007) and may influence recovery times preceding subsequent breeding attempts. It would appear that at Lancelin Island, in contrast to the recent situation at the Abrolhos islands, the ENSO cycle continues to control marine productivity in the foraging area.

Brown Noddy, Lesser Noddy and Sooty Tern populations are all showing evidence of decline at the Abrolhos islands (Surman & Nicholson 2009 a & b, Surman unpublished data). Unlike the Bridled Tern, the Brown Noddy's diet is dominated by a few prey species and shows little capacity for prey switching, within or between breeding seasons (Dunlop 1997, Surman & Nicholson 2009b). This concentration on two or three prey species and on particular, small-scale, oceanographic features with relatively enhanced productivity may explain the comparatively conservative re-distribution observed in the Brown Noddy population. Extensive areas of Brown Noddy breeding habitat (Nitre Bush *Nitraria billardieri*) remain available on Lancelin Island but potential breeding islands, with suitable foraging areas within reach, may be few and far between south of the Abrolhos islands. This may also explain the inability of prospecting Brown Noddies and Sooty Terns to establish colonies at Penguin Island over the last 8 years.

Overall, we predict that species-specific responses to changes in ocean climate will result in a significant decline in Brown Noddy, and probably Lesser Noddy and Sooty Tern populations, in the region. However, the re-distribution of the Bridled Tern has already resulted in an increase in abundance such that southwestern Australia, south of the former breeding range, is now a global stronghold for this species.

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