COMPARATIVE FORAGING ECOLOGY IN THE DARK TERN GUILD BREEDING OFF SOUTHWESTERN AUSTRALIA — INSIGHTS FROM STABLE ISOTOPE ANALYSIS

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SUMMARY


This paper uses stable isotope analysis to examine the foraging ecology of the tropical “dark” terns breeding in the subtropics off southwestern Australia and wintering at lower geographic latitudes. The δ¹³C and δ¹⁵N values of feathers and eggshell membranes indicated that Brown Noddies Anous stolidus breeding in this region were foraging in waters characterised by higher inorganic nitrogen availability and productivity than those occupied by Bridled Terns Onychoprion anaethetus. However, Bridled Terns probably foraged at a higher trophic level than Brown Noddies, and this was probably related to their habit of foraging on a range of marine organisms associated with floating rafts of macro-algae and other flotsam. The δ¹³C and δ¹⁵N values of adult primary feathers indicated that Sooty Terns Onychoprion fuscatus and Bridled Terns foraged in wintering areas close to the equator, but Sooty Terns again utilised more productive water masses. The Brown Noddies breeding off southwestern Australia appear to winter closer to the sub tropics than Bridled and Sooty Terns.

Key words: Bridled Tern, Brown Noddy, Sooty Tern, foraging habitat, stable isotopes δ¹³C δ¹⁵N, southwestern Australia

INTRODUCTION

The dark tern guild

The Bridled Tern Onychoprion anaethetus, Sooty Tern Onychoprion fuscatus, Brown Noddy Anous stolidus and Lesser Noddy Anous tenuirostris comprise an ecological guild of generally sympatric, pelagic, contact-dipping “dark” terns occupying much of the tropical Indian Ocean (Cramp 1985). In some locations, such as at the Abrolhos Islands of southwestern Australia, this guild also inhabits subtropical waters (Surman & Wooler 2003, Dunlop 2009). Since 1900 the Bridled Tern, Sooty Tern and Brown Noddy have established new “frontier” colonies on continental islands south of the Houtman Abrolhos (Fig. 1). The population dynamics of the tropical seabird populations (including the “dark” terns) undergoing distributional change off southwestern Australia were reviewed in a previous paper (Dunlop 2009). This paper presents a perspective on the foraging ecology of the “dark tern” guild enlightened by a stable isotope analysis from breeding colonies in the subtropical waters off southwestern Australia.


The diet of the Bridled Tern in the region is diverse and contains a variety of organisms with obligate or facultative associations with floating Sargassum rafts. The most frequently taken prey type is the epipelagic post-larval stage of the Black-spotted Goatfish Parupeneus signatus (Dunlop 1997).

Stable isotope analysis

Stable isotopes of carbon (δ¹³C) and nitrogen (δ¹⁵N) occur naturally in the environment. The ratios of the heavier isotopes to the common forms are changed by the physical sorting of biological processes such as photosynthesis in plants, or food digestion or metabolism in microbes and animals. These changes in the isotopic ratio are referred to as fractionation. The values given to the stable isotope ratios (δ¹³C or δ¹⁵N) are measured in parts per thousand (‰) and may be positive or negative because they represent deviations from the values of standard materials (Kelly 2000, Bond & Jones 2010, Graham et al. 2010).

Both δ¹³C and δ¹⁵N values in consumer tissues can be used to infer the sources of carbon (energy) in food chains if the producer signatures (the isotopic baselines) are known. δ¹⁵N values also show a stepwise increase with trophic level due to the tendency of animals to differentially excrete ¹⁴N during digestion and assimilate ¹⁵N during protein synthesis. The trophic position of consumers can be inferred above a known producer baseline (Bond & Jones 2010). The synthesis of different consumer tissues (e.g. blood, muscle, feathers, eggshell membranes) may involve different turnover rates (time periods) and variable fractionation patterns, which need to be considered when making inferences from stable-isotope data (Kelly 2000, Cherel et al. 2008, Bond & Jones 2010).

In marine ecosystems the carbon isotopic ratio (δ¹³C) in phytoplankton is determined by the availability of CO₂ for photosynthesis. During photosynthesis all plants preferentially fix the common lighter
12C isotope within their tissues. However, where CO2 is limited, a relatively high proportion of the heavier 13C isotope is fixed, producing a larger or “enriched” δ13C value in the resulting biomass. Sea temperature, vertical mixing, the rate of CO2 fixation (i.e., productivity), and light or trace metal limitation all influence the amount of dissolved CO2 available for photosynthesis in marine waters. As a consequence, phytoplankton living in warm, highly stratified and less seasonal tropical environments, with limited aqueous CO2 levels, have relatively high δ13C values compared with those from cooler, higher latitude waters. This effect produces a broad latitudinal gradient in δ13C values across the oceanic basins (Bond & Jones 2010, Graham et al. 2010). Shallower, well-mixed and relatively productive inshore and shelf waters also tend to have more enriched δ13C values than the adjacent oceanic waters. Dominant producers in the littoral zone, including macro-algae and seagrasses, have higher δ13C values than phytoplankton. Carbon from these benthic systems may be exported into the pelagic food chains of the continental shelves. This “benthic–pelagic coupling” may also contribute to higher δ13C values in the biota of inshore and shelf environments (Graham et al. 2010) than in the biota of oceanic ones.

The δ15N values in marine producers such as phytoplankton depend on the fractionation of the nitrogen source. This is influenced by the various nitrifying and de-nitrifying transformations occurring through the nitrogen cycle. Inorganic (nitrate) nitrogen is relatively enriched in 15N, producing high δ15N values, which are also indicative of high nitrogen availability. Recycled (ammonia) nitrogen is less enriched in 15N and recently fixed (N2) nitrogen is depleted in 15N. The δ15N values therefore are a combined indicator of nitrate source, availability and uptake (Graham et al. 2010).

This paper uses carbon and nitrogen stable isotope analysis to build on existing knowledge of the foraging ecology of three dark tern species breeding in southwestern Australia and, in particular, of differences in their foraging habitats.

**METHODS**

This study uses the δ13C and δ15N signatures of feathers and eggshell membranes to investigate the foraging ecology of three dark tern species (Bridled Tern, Sooty Tern and Brown Noddy) with breeding colonies off the lower west coast of Western Australia (Fig. 1).

Feather keratin is laid down during the moult, and the δ13C and δ15N values in the protein structure capture a discrete foraging period coincident with feather growth. Once completed, feathers are inert structures that are not subject to tissue turnover (Cherel et al. 2008, Bond et al. 2009). Eggshell membranes are primarily composed of collagen (Yu Hung & Yu-Jie 2009). This protein is laid down in the oviduct during the latter stages of egg formation. It is not known whether there are any significant differences in stable isotope fractionation between keratin and collagen synthesis.

The sixth primary feather was extracted from adults to determine their stable isotope values from foraging during the nonbreeding
Early in the breeding season Bridled Terns take small coastal forage fishes, including year 1 sardines or “pilchards” *Sardinops vagas* (Dunlop 1997). Sardines captured in the local fishery in 2004 were also analysed for their stable isotope signatures, and scales were used for the analysis of these adult fish to avoid the high lipid content of the muscle tissue.

**Stable isotope analysis**

The $\delta^{13}C$ and $\delta^{15}N$ values from feather and eggshell membrane samples collected in 2006/07 were analysed by Western Australian Biochemistry Centre. Samples collected later were analysed at the Natural Isotopes Laboratory at Edith Cowan University in Perth, Western Australia. There were no significant differences in $\delta^{13}C$ and $\delta^{15}N$ values for the equivalent tissues analysed by the two laboratories.

Replicates were used to test the precision of the isotopic analysis. The $\delta^{13}C$ and $\delta^{15}N$ values for the equivalent tissues analysed by the two laboratories were interspaced with the samples for calibration.

**Statistical analysis**

Tables 1 and 2 summarize the collecting localities, tissue types, sample sizes and $\delta^{13}C$ and $\delta^{15}N$ values for the three tern species (Table 1) and four fish species (Table 2) sampled for stable isotope analysis. Mean $\delta^{13}C$ and $\delta^{15}N$ values between samples were compared using Student’s *t*-test.
RESULTS

There were no significant differences in the δ\textsuperscript{13}C and δ\textsuperscript{15}N values for samples of the same feathers collected in 2006/07 and 2008/09, so these results have been combined in the analysis (Fig. 2).

Similarly, there were no significant differences in either the δ\textsuperscript{13}C or δ\textsuperscript{15}N values in the eggshell membranes or chick feathers from Bridled Terns and Brown Noddies. However, the δ\textsuperscript{13}C of adult primary feathers of both species differed significantly from the feathers produced during the breeding season (Bridled Tern chick to adult \( t = 3.42, P < 0.01 \); Brown Noddy chick to adult \( t = 3.0, P < 0.01 \)), by being relatively enriched in 13C.

Both the δ\textsuperscript{13}C and δ\textsuperscript{15}N values from adult Sooty Tern primary feathers were significantly higher than those of the Bridled Tern (Bridled Tern — Sooty Tern primaries \( \delta^{13}C \ t = 3.91, P < 0.01; \delta^{15}N \ t = 3.77, P < 0.01 \)) and Brown Noddy (Brown Noddy — Sooty Tern \( \delta^{13}C \ t = 5.75, P < 0.001; \delta^{15}N \ t = 2.60, P < 0.01 \)).

The δ\textsuperscript{13}C or δ\textsuperscript{15}N values did not differ between the post-larval Gnorhynchus and Engraulis from Brown Noddy regurgitates. These were, however, significantly more enriched in both 13C and 15N than the undigested fragments of Parupeneus post-larvae collected from the Bridled Terns (\( \delta^{13}C \ t = 3.39, P < 0.01; \delta^{15}N \ t = 2.37, P < 0.05 \)). The scale samples from coastal foraging sardines were enriched in 13C with respect to all the post-larval prey types and significantly depleted in 15N with respect to Gnorhynchus/Engraulis consumed by the Brown Noddies (\( \delta^{15}N \ combined \ Gnorhynchus/Engraulis \ t = 8.642, P < 0.001 \)).

DISCUSSION

Dark tern foraging ecology

The foraging ranges, and consequently marine habitats, of the dark terns are related to body size. The larger Sooty Terns and Brown Noddies forage at greater distances and in more oceanic environments than the smaller “outer shelf” foraging Bridled Terns and Lesser Noddies (Dunlop 1997, Surman & Wooller 2003, Jaquemet et al. 2004, Ramos et al. 2006, Catry et al. 2009). Indeed, it could be argued that the guild subdivides into large and small dark terns.

Another related factor reducing potential competition within the guild is the strength of the commensal association with foraging sub-surface predators. Sooty Terns have an obligate relationship with epipelagic tuna Tunnus spp. (Jaquemet et al. 2004, 2007, Cherel et al. 2008), and Brown Noddies may also largely depend on the foraging opportunities these fish provide in the oceanic environment (Ramos et al. 2006). Lesser Noddies crowd the surface over foraging tuna (Hulsman 1988, Surman & Wooller 2003, Jaquemet et al. 2004) but also forage over less aggregated predators such as Dolphinfish Coryphaena equiselis (Jaquemet et al. 2004, 2007), Queenfish Seriphus politus, Spanish Mackerel Scomberomorus maculatus and Wahoo Acanthocybium solandri (pers. obs.).

The Bridled Tern has not been observed concentrating over predatory fish in large numbers, although small groups may gather fleetingly over “bait boils,” often in association with Wedge-tailed Puffinus pacificus and Little P. assimilis shearwaters (Dunlop 1997). The Bridled Tern appears to have a facultative association with predatory fish, utilising foraging schools of predatory fish in the absence of interference competition from seabirds that can monopolise the water surface (Hulsman 1988, Dunlop 1997).

Briddled Terns take a diverse range of larval, post-larval and immature fish and crustacean prey species associated with rafts of floating Sargassum, which are common on the Western Australian continental shelf during most of the breeding season. Typically the “windrows” of macro-algae, and the associated Sargasso-fauna communities, are concentrated in the down-welling zones created by persistent wind stress (Langmuir cells) or by tidal or temperature fronts (Dunlop 1997).

Analysis of stable isotope values

Beaked Salmon post-larvae make up 78% by volume of the dietary intake of Brown Noddies in the region during successful breeding seasons (Surman & Nicholson 2009). The δ\textsuperscript{15}N values for both the Brown Noddy eggshell membranes and chick feathers are one trophic level (2.59‰, Bond et al. 2009) above those of

<table>
<thead>
<tr>
<th>Species (collecting locality)</th>
<th>Tissue (and no. sampled)</th>
<th>δ\textsuperscript{13}C values</th>
<th>δ\textsuperscript{15}N values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parupeneus signatus post-larvae (Penguin Island)</td>
<td>Entire larvae (6)</td>
<td>-20.8 (0.578)</td>
<td>-19.81</td>
</tr>
<tr>
<td>Gnorhynchus greyi post-larvae (Lancelin Island)</td>
<td>Entire larvae (6)</td>
<td>-19.73 (0.099)</td>
<td>-19.87</td>
</tr>
<tr>
<td>Engraulis australis post-larvae (Lancelin Island)</td>
<td>Entire larvae (6)</td>
<td>-19.64 (0.285)</td>
<td>-19.29</td>
</tr>
<tr>
<td>Sardinops vagax (Fremantle purse-seine fishery)</td>
<td>Scales (6)</td>
<td>-17.82 (0.12)</td>
<td>-17.70</td>
</tr>
</tbody>
</table>

TABLE 2 Collecting localities, tissue types, sample sizes and values for δ\textsuperscript{13}C and δ\textsuperscript{15}N for the four prey fish species sampled for stable isotope analysis.
their dominant prey species (Fig. 2). This is expected, given the dominance of this prey type in the Brown Noddy’s diet.

While the $\delta^{13}C$ and $\delta^{15}N$ values from the Bridled Tern eggshell membranes and chick feathers appear to indicate a foraging environment similar to that of the Brown Noddy, there is a major discrepancy between the isotopic values in the tissues of *Parupeneus* post-larvae and the expected fractionation in the tissues of its predator (Fig. 2). *Parupeneus* post-larvae were found in 31.4% of Bridled Tern regurgitate samples examined by Dunlop (1997); however, estimation of volume was not feasible because most samples were highly digested. The Bridled Tern’s diet is much more diverse than that of the Brown Noddy in this region and is known to include a range of small predatory fish and crustaceans associated with the *Sargassum* rafts (Dunlop 1997). The mean trophic level of the Bridled Tern’s diet during the breeding season is therefore likely higher than that indicated by the tissues of the Black-spotted Goatfish post-larvae.

The Black-spotted Goatfish/Anchovy post-larvae consumed by the Brown Noddies were significantly enriched in both $^{13}C$ and $^{15}N$ compared with *Parupeneus*. This indicates that the Brown Noddies are foraging in areas with relatively elevated levels of inorganic nitrogen and productivity in comparison with foraging areas of Bridled Terns. Given the foraging range of the Brown Noddy, these areas could be small, currently unidentified, shelf-edge upwellings or warm core eddies in the Leeuwin Current. Published $\delta^{13}C$ values for particulate organic matter (Hanson *et al.* 2005) and larval fish (Waite *et al.* 2007) in Leeuwin Current structures of the adjacent deep ocean are more depleted in $^{13}C$ than those found in the Beaked Salmon/Anchovy post-larvae consumed by the Brown Noddies. This suggests that their foraging area is closer to the coast and likely associated with a relatively nutrient-enriched shelf-edge feature. By comparison, the $\delta^{13}C$ and $\delta^{15}N$ values of the sardines (Fig. 2) indicate a more coastal prey species (enriched $^{13}C$) in a nitrate-deficient (depleted $^{15}N$) environment.

The $\delta^{13}C$ and $\delta^{15}N$ values from the Black-spotted Goatfish post-larvae suggest that Bridled Terns forage in relatively oligotrophic and unproductive environments. Such conditions are typical of much of the southwestern Australian continental shelf (Feng *et al.* 2009). The ability of Bridled Terns to utilise relatively unproductive environments may reduce competition with other dark terns, particularly the Lesser Noddy.

![Diagram](image-url)
Bridled Terns breeding on islands of southwestern Australia spend the austral winter in the northwest Sulawesi Sea between about 4°N and 7°N (Dunlop & Johnstone 1994), where they undergo the basic moulting. The high δ13C value in the adult primaries relative to the chick feathers from the breeding area reflects the relative enrichment in 13C of tropical low-latitude waters. Its larger congener, the Sooty Tern, has higher δ13C and δ15N values in its primary feathers. This almost certainly reflects the Sooty Terns’ tendency to forage over relatively productive water masses (Jaquemet et al. 2007) rather than any difference in latitude. Tuna also aggregate in such areas, providing foraging opportunities for Sooty Terns. Again, Bridled Terns appear to be foraging over less productive waters, in this case in the wintering area, than other dark terns.

The δ13C values in the primary feathers of adult Brown Noddies confirms that they occupy lower latitude waters outside the breeding season, but these waters are not as close to the equator as those occupied by the Bridled or Sooty Terns. Detailed δ13C “isoscapes” are not yet available for the eastern Indian Ocean, but Brown Noddiess breeding off southwestern Australia likely winter closer to the sub tropics.

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REFERENCES


