Diet and Foraging Ecology of Roseate Terns and Lesser Noddies Breeding Sympatrically on Aride Island, Seychelles

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Abstract.—Inferences on seabird ecology from stable isotopes ratios ($\delta^{13}C$, $\delta^{15}N$) and mercury concentrations analysis of feathers have been made for temperate and polar species but are far more rare for tropical species. In this paper, we used this approach combined with analysis of regurgitations and feeding observations at colonies to examine diet segregation between Roseate Terns (*Sterna dougallii*) and Lesser Noddies (*Anous tenuirostris*) breeding sympatrically on Aride Island (Seychelles), western Indian Ocean. Our results indicated extensive overlap between the two species in trophic level and foraging area during the breeding season. Goatfish predominated (93-97%) in all diet samples of adults and chicks collected in the colonies, except in prey fed to mates by Roseate Terns, of which scad and tuna comprised 20%. The isotopic analyses of feathers replaced by adults during molt (primary and body feathers) suggested, however, that the two species differ in foraging ecology during the nonbreeding period. Roseate Tern adults had consistently lower $\delta^{15}N$ values than Lesser Noddies which, in turn, had $\delta^{15}N$ values comparable to those of chick feathers grown on Aride. Moreover, low but similar mercury levels were found in body feathers of Lesser Noddy adults and Roseate Tern chicks, whereas Roseate Tern adults were significantly more contaminated. Overall, these results support the hypothesis that the Lesser Noddy is largely sedentary, being associated with the same food web in the vicinity of the colonies year-round. In contrast, Roseate Terns rely on distinct prey during the molting (nonbreeding) season which may be also consistent with a change in food web (i.e., a migratory regime) although the assignment of potential wintering areas remain difficult without isotopic basemaps currently available for the Indian Ocean. *Received 19 July 2007, accepted 23 October 2007.*

Key words.—*Anous tenuirostris*, diet, stable isotopes, *Sterna dougallii*, mercury, western Indian Ocean.

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Studies examining the feeding ecology of seabird species during the breeding season are often based on conventional sampling methods such as chick provisioning and analysis of pellets or regurgitations (Catry *et al.* 2006; Paiva *et al.* 2006), but these techniques are limited during the nonbreeding (molting) period when birds are difficult to capture or their wintering sites are unknown or inaccessible. The measurement of stable carbon and nitrogen isotopes in feathers has recently provided a way to infer dietary and foraging ecology information for the nonbreeding period (e.g., Cherel *et al.* 2000) because metabolically inert tissues such as feathers register the isotopic signature of the bird's food at the time of growth (Hobson and Clark 1992; Evans Ogden *et al.* 2004). Previous studies have shown that there is a small enrichment in carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) stable isotope ratios between predator tissues and their prey, known as trophic fractionation factors ($\Delta\delta^{13}C$, $\Delta\delta^{15}N$), since at each successive level of the food chain consumers selectively retain the heavy isotope while releasing the light one (Michener and Schell 1994). The stable-carbon isotope ratio may be a good indicator of inshore (^{13}C-enriched) vs. offshore, pelagic (^{13}C-depleted)

feeders, while $\delta^{15}N$ is enhanced at each successive step in the food chain, thus providing a good indicator of the trophic level (Hobson *et al.* 1994; Hobson 1999).

Birds accumulate mercury from their food and excrete much of it into their plumage in the form of organic (methyl) mercury during feather growth (Thompson and Furness 1989).The levels of mercury in bird feathers have been used to indicate the degree of environmental contamination (Burger *et al.* 1992). Moreover, mercury is, unlike other heavy metals, bioamplified at each successive level in the food chain so that higher concentrations have often been related to individuals feeding at higher trophic level (Bearhop *et al.* 2000a; Becker *et al.* 2002).

Inferences on seabird ecology from ^{13}C and ^{15}N stable isotopes and mercury concentration analysis of feathers have been made for temperate and polar species (e.g., Sydeman *et al.* 1997; Becker *et al.* 2002; Forero *et al.* 2003) but are far more rare for tropical species. In this paper, we compare both diet and foraging ecology of Roseate Terns (*Sterna dougallii*) and Lesser Noddies (*Anous tenuirostris*) that breed sympatrically on Aride Island, Seychelles, equatorial western Indian Ocean. On Aride, both species are present at the colonies during May-August (southeast monsoon), while, during the nonbreeding season (Sept-April), there is currently no information on their whereabouts. We formulated three hypotheses/predictions:

(1) In Western Australia, both species are sympatric during the breeding season, their diets are essentially similar, and their foraging areas overlap (Surman and Wooller 2003). To test whether this is also true on Aride, analysis of regurgitations and feeding observations were compared between both species. We predicted also that similar stable isotope signals (^{13}C, ^{15}N) and mercury concentrations found in chick feathers of both species would support a 'common diet and foraging area' hypothesis.

(2) Lesser Noddies remain in the vicinity of the colonies year-round in western Australia (Higgins and Davies 1996), and hence can be considered sedentary. Conversely, the Roseate Tern is essentially a migratory species, including other tropical (Caribbean) populations (Cramp 1985; Gochfeld *et al.* 1998). If the same is true for the Aride populations (i.e., both species segregate their foraging grounds and/or diets during the molting period), we predicted that different stable isotope ratios should be found in adult feathers grown during the nonbreeding season.

(3) Given the relative isolation of Aride Island from anthropogenic sources of mercury compared to Europe and North America, we predicted that contaminant levels in feathers grown by Roseate Tern chicks should be lower than those reported in their temperate counterparts.

METHODS

Study Area

Aride Island (4°10'S, 55°40'E, Fig. 1) Nature Reserve, Seychelles, holds one of the largest Roseate Tern breeding colonies known in the western Indian Ocean (*c.* 1,200 pairs) and the largest world population of Lesser Noddies (*c.* 150,000 pairs; Bowler *et al.* 2002). There, the two species have been intensively studied during the

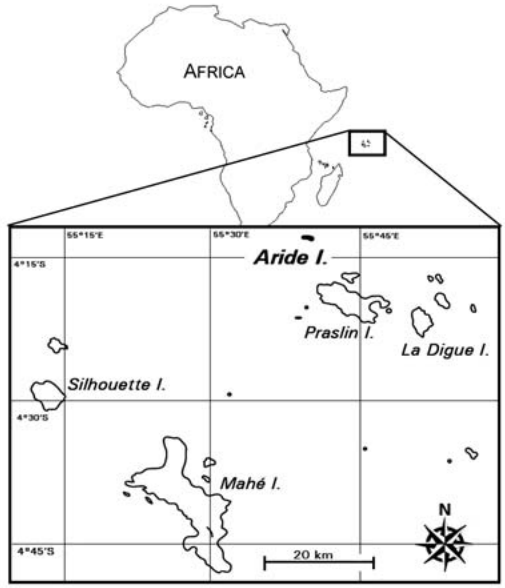

Figure 1. Location of Aride, showing the central group of granitic islands in The Seychelles.

breeding season (May-August, southeast monsoon) since 1997 (Ramos *et al.* 2002, 2004) but little is known about dispersal of adults and fledglings during the nonbreeding season (Sept-April).

Diet Sampling

Diet of both species was assessed in the colonies in 2004 and 2005 by recording: (1) prey displayed to mate during incubation and delivered to chicks, and (2) prey found during daily visits to marked nests in study quadrats and regurgitated by adults during ringing. Diet of Lesser Noddies was assessed only with method (2). From 18 May to 8 June 2005, prey used in display to Roseate Tern mates was recorded daily for two to three h with binoculars from vantage points located around the colony area. Prey delivery to eight to ten Roseate Tern chicks was observed between 07.00-09.00 h daily from 6 to 30 June 2004. Roseate Terns feed mostly on goatfishes (Mullidae), and observers were very familiar with that fish family (Ramos 2000). Genera *Upeneus* and *Parupeneus* could not be separated in the field and were grouped in the data. Other fish observed were identified at least to family by comparison with identified specimens collected in 2004 (8 June-22 July) around tern nests. Mullid samples dropped by Roseate Terns were collected, measured to nearest 1.0 mm (Mean standard length: 38.2 ± (SD) 5.1 mm), weighed with Pesola balances, and stored at -20°C for stable isotope analysis.

Collection of Feathers

Most feather samples were obtained during the 2004 breeding season (Table 2; May-August). Lesser Noddy chicks were sampled mostly in 2006. Most feather samples were collected from dead individuals: six to ten feathers were plucked from breast and the outermost primary (p10) feathers was collected from the right wing from different individuals (Table 2). For chicks, wing length was measured so that age could be inferred from wing/age curves obtained in previous studies (Maul 1998). Supplementary feather samples were also collected in 2003 and 2005 (Table 2).

Molt

Roseate Tern. The molt of adults may include up to three successive wing series, from the innermost (p1) towards the outermost (p10) primary feather (Ginn and Melville 1983). Only the first series is completed upon arrival on breeding grounds which imply that the p10 is replaced only once during the nonbreeding period (Pyle 2008). O'Neill *et al.* (2005) found, in an Asian population breeding in May-July, birds in active molt with the first series renewed from p1 to p7 in January. This suggests that the outermost (p10) flight feather is more likely to be replaced towards the end of the nonbreeding period (Pyle 2008). Roseate Tern adults show their typical pinkish breast-feathers throughout the year, but information is still scant on their precise timing of molt (Hays *et al.* 2006), which is presumably restricted to the nonbreeding season.

Lesser Noddy. Molt in this species (Higgins and Davies 1996) and in the congeneric Black Noddy (*Anous minutus*) on Ascension Island (Ashmole 1962) is achieved exclusively during the nonbreeding season, hence adult feathers (body feathers and p10) sampled on Aride in May-August are considered to be presumably grown during the previous September-April period (Ramos *et al.* 2004). Moreover, Higgins and Davies (1996) suggest that p10 is molted last and may be growing just before the breeding season.

Stable Isotope and Mercury Analysis

Feather samples for isotopic measurements were washed in a 2:1 chloroform: methanol preparation to remove surface contaminants, rinsed in deionized water, and oven dried for at least 72 h at 50°C before being grounded into a homogenous powder. The same procedure was used to prepare samples of dorsal muscle tissue (*ca.* 0.5 g) excised from each fish (mullids; N = 5), with multiple rinses in 2:1 chloroform: methanol applied to remove lipids that would otherwise lower the $d^{13}C$ signature (Hobson and Clark 1992). A small amount (*ca.* 1.5-1.8 mg) of each feather and fish samples was loaded in a miniature tin cup for combustion in a C-N-S elemental analyzer (Carlo Erba, Italy). Automated analyses were performed using a V. G. Optima (Micromass) isotope ratio mass spectrometer (V.G. Instrument, UK). Experimental precision was ≤0.3 and 0.4‰ for carbon and nitrogen, respectively. Stable isotope ratios are expressed as d (delta) values (in parts per thousand; ‰), relative to the vPDB (Vienna Peedee Belemnite) standard for carbon and to atmospheric N_2 for nitrogen, according to:

$$\delta^{13} \text{ or } \delta^{15}N = \left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right) * 10^3$$

$$\text{where } R = \frac{^{13}C}{^{12}C} \text{ or } \frac{^{15}N}{^{14}N}$$

Reference materials from the International Atomic Energy Agency were IAEA-N_1 ($\delta^{15}N$ = +0.4 ± 0.2‰) and IAEA CH-6 (sucrose) ($\delta^{13}C$ = -10.4 ± 0.2‰).

Because most mercury in feathers is methylmercury, analyses of total mercury concentration in feathers (i.e., without excluding inorganic mercury) were performed (Thompson and Furness 1989). Total mercury concentration was determined by Cold Vapor Atomic Absorption Spectroscopy using a Perkin-Elmer 50B spectrophotometer and by thermal atomization followed by Atomic Absorption Spectroscopy using AMA 254 spectrophotometer for a small number of samples. Samples were prepared following a standard method previously described for Little Tern feathers (*S. albifrons*; Tavares *et al.* 2005). Results were compared between equipments, and no significant differences were found (t-test, $P > 0.05$). Relative Standard Deviation (RSD) values of 5 ± 3% were found for reproducibility using Perkin-Elmer 50B. RSD values of 2 ± 1% were found for reproducibility using AMA 254. Accuracy was monitored with reference materials and considered as the closeness of a measured value to a known certified value. Accuracy was within 10% of the certified values. Reference material for feather analysis was NIES-5 Human Hair (National Institute for Environmental Studies; certified value 4.4 ± 0.4 μg g^{-1}).

Statistical Analyses

$\delta^{13}C$, $\delta^{15}N$ and mercury values were normally distributed (Kolmogorov-Smirnov test, all three tests with p >

0.2) with homogeneous variances among sampling feather groups. Factorial analyses of variance (Type III sums of squares) were used to segregate mean $\delta^{13}C$ and $\delta^{15}N$ values by species, age (chick vs. adult), and type of feather (p10 vs. body). Factorial ANOVA was used to compare the three groups (Roseate Tern adult, Lesser Noddy adult, and Roseate Tern chick) for which mean mercury measurements were available, testing for the effect of feather type. Feathers collected in different years were initially compared with *t*-tests but later pooled during ANOVA due to the small inter-annual variation differences often observed during the paired comparisons. Significant correlations between $\delta^{13}C$, $\delta^{15}N$ and mercury values were checked with Pearson correlation coefficients. For Roseate Terns, a regression analysis was performed also to assess the influence of age, expressed as wing length (WL), on mercury levels found in chick feathers. Differences between isotope values found in fish samples and chick feathers were assessed with one-way ANOVA. Statistical analysis was performed using Statistica software (StatSoft 2001). Values are presented as mean ± SD.

RESULTS

Diet and Stable Isotopes During the Breeding Season

Diet composition (%, number of items) using conventional methods showed strong similarities between year (2004-2005) and species (Table 1). Mullids predominated (93-97%) in all diet samples of adults and chicks, except in prey fed to mates by Roseate Terns, of which scad and tuna comprised 20% (Table 1). Stable $\delta^{13}C$ and $\delta^{15}N$ isotope ratios found in chick feathers are given in Table 2. For Roseate Tern chicks, flight feathers collected in 2004 and 2005 showed no inter-annual variations in $\delta^{13}C$ ($t_9 = 1.66$, $P = 0.13$) and $\delta^{15}N$ ($t_9 = 0.88$, $P = 0.39$) values. Similarly, the single Lesser Noddy chick feather collected in 2004 was within the range of those sampled in 2006, hence suggesting little inter-annual variation (Table 2). For all chick feathers pooled, mean $\delta^{13}C$ values were similar between both species but differed from goatfish muscle ($F_{2,44} = 10.5$, $P < 0.0001$). The fractionation of isotopes ($\Delta\delta^{13}C$) from fish to predator averaged 0.9 and 1.1‰ for Roseate Terns and Lesser Noddies, respectively (Table 2). There was also a significant difference between $\delta^{15}N$ values in chick feathers and goatfish ($F_{2,44} = 50.1$, $P < 0.0001$), the fractionation factors being of the magnitude of 3.0‰ for Roseate Tern and 3.7‰ for Lesser Noddy chicks.

Table 1. Diet composition (% no. of items) of Roseate Tern and Lesser Noddy on Aride Island, Seychelles, during the 2004-2005 breeding seasons. Data are based on (1) observations of prey displayed to mate during incubation and to chicks during the rearing period (eight to twelve chicks observed daily) for Roseate Terns, and (2) prey items regurgitated or dropped around the nest by adults and chicks for both species.

	Roseate Tern			Lesser Noddy
Prey species	% items delivered to mates (18 May-8 June 2005)	% items delivered to chicks (6-30 June 2004)	% items dropped by chicks/adults around nests (8 June-22 July 2004)	% items dropped by chicks/adults around nests (8 June-22 July 2004)
Mullidae (goatfish) *Upeneus and Parupeneus* spp.	77.0	93.4	92.7	97.4
Carangidae (scad) *Selar crumenophthalmus*	8.9	4.8	3.7	2.0
Scombridae (tuna) *Auxis* sp.	11.1		0.9	
Caesionidae (fusilier) *Dipterygonotus balteatus*	1.5	0.9	0.9	
Exocoetidae (flyingfish) *Parexocoetus* sp.	0.4	0.2		0.3
Engraulidae (anchovy) *Stolephorus indicus*			0.9	
Clupeidae (herring) *Spratelloides delicatulus*			0.9	
Undetermined prey	1.1	0.7[a]		0.3
Total no. of prey items (N)	269.0	563.0	110.0	303.0

[a]Includes 0.2% of squid.

Table 2. Mercury concentrations (μg g^{-1}) and stable isotope ratios (‰) in fish samples and feathers of Roseate Terns and Lesser Noddies collected on Aride Island, Seychelles.

Sampling group	Sampling year	Sample size[a]	Mean $\delta^{13}C \pm SD$	Mean $\delta^{15}N \pm SD$	Mean Hg ± SD
Goatfish muscle		5	-17.6 ± 0.3	10.9 ± 0.2	
Roseate Tern					
Chick primary 10[b]	2004	8 (8)	-17.0 ± 0.5	13.4 ± 1.5	0.28 ± 0.04
Chick primary 10	2005	3	-16.5 ± 0.1	14.2 ± 0.2	—
Chick body-feathers[c]	2004	6 (12)	-16.5 ± 0.3	14.3 ± 0.3	0.69 ± 0.32
Adult primary 10	2004	19 (21)	-16.9 ± 0.6	10.7 ± 0.7	0.56 ± 0.17
Adult body-feathers	2004	19 (20)	-16.4 ± 0.3	11.4 ± 0.8	1.29 ± 0.26
Lesser Noddy					
Chick primary 10	2004	1	-17.1	14.0	—
Chick primary 10[d]	2006	12	-16.9 ± 0.4	14.7 ± 0.5	—
Chick body-feathers[d]	2006	12	-16.1 ± 0.3	14.6 ± 0.3	—
Adult primary 10	2004	11 (11)	-16.9 ± 0.4	13.4 ± 0.6	0.67 ± 0.15
Adult body-feathers	2003	7 (10)	-16.6 ± 0.2	13.6 ± 0.7	0.87 ± 0.18
Adult body-feathers	2004	5 (14)	-16.9 ± 0.2	13.6 ± 0.6	0.95 ± 0.25

[a]Sample sizes for mercury analyses in parentheses.
[b]Chicks aged twelve to 17 d.
[c]Chicks aged five to 17 d.
[d]Chicks aged 20-30 d.

Stable Isotopes Outside the Breeding Season

To assess inter-annual variations in diet and/or foraging areas of Lesser Noddy adults during the nonbreeding period, body feathers were compared between 2003 and 2004 (Table 2). Similar mean $\delta^{15}N$ values ($t_{10} = 0.04$, $P = 0.96$) were found, while the 2003-feathers were only slightly enriched in ^{13}C ($t_{10} = 2.75$, $P = 0.02$). When individual samples collected in different years were pooled, no segregation by species and age was apparent with the ANOVA (Table 3), suggesting that $\delta^{13}C$ values for Roseate Tern adults, Lesser Noddy adults, and their chicks were roughly of the same magnitude (Fig. 2). Type of feather was the only significant factor explaining differences in $\delta^{13}C$ values ($F_{1,96} = 37.3$, $P < 0.0001$), with body feathers being consistently ^{13}C-enriched compared to primary 10, irrespective of age and species (no significant interaction terms; Table 3). For $\delta^{15}N$, the ANOVA suggested that Lesser Noddies were, on average, feeding at a higher trophic level than Roseate Terns ($F_{1,96} = 102.1$, $P < 0.0001$), while adults had a tendency to feed at a lower trophic level outside the breeding season compared to their chicks ($F_{1,96} = 172.5$, $P < 0.0001$; Table 3). In fact, there was a highly significant interaction be-

Table 3. Results of factorial ANOVA (Type III) testing the effect of species (LN = Lesser Noddy vs. RT= Roseate Tern), age (Chick vs. Adult), feather-type (P10 = primary 10 vs. Body = body feathers), and first order interaction terms on $\delta^{13}C$ and $\delta^{15}N$ values in feathers collected on Aride Island, Seychelles. Sampling groups with feathers collected in more than one year (see Table 2) were pooled.

	$\delta^{13}C$			$\delta^{15}N$		
Variable	$F_{1,96}$	P	Effect size	$F_{1,96}$	P	Effect size
Species	0.5	0.5	—	102.1	<0.0001	LN > RT
Age	2.7	0.1	—	172.5	<0.0001	Ad. < Chick
Type of feather	37.3	<0.0001	Body > P10	6.3	0.01	Body > P10
Species*age	3.2	0.1	—	34.1	<0.0001	—
Species*type of feather	0.0	0.8	—	4.1	0.04	—
Age*type of feather	2.2	0.1	—	0.1	0.73	—

tween species and age because Roseate Tern adults were well separated from the remaining Roseate Tern chick and Lesser Noddy adult/chick groups, suggesting that Roseate Tern adults feed consistently at a lower $\delta^{15}N$ level (body + flight feathers) during the non-breeding season (Fig. 2). There was also a significant effect of the type of feather, with ^{15}N-enriched body feathers (Table 3), but this difference was mainly attributable to Roseate Terns (adults and chicks; Fig. 2). The magnitude of the difference in $\delta^{15}N$ between Roseate Tern and Lesser Noddy adults ranged from 2.2‰ (body) to 2.7‰ (primary 10), which corresponds 2/3 of one trophic level (see above; Table 2).

Mercury Concentrations

Mercury values did not differ between body feathers of Lesser Noddy adults collected in 2003 and 2004 (t_{22} = 0.88, P = 0.38; Table 2). The ANOVA revealed a significant effect for Roseate Tern adults, which had higher mercury values in their feathers compared to Lesser Noddy adults and Roseate Tern chicks ($F_{2,90}$ = 26.5, P < 0.0001; Table 2). There was also a significant effect of feather-type ($F_{1,90}$ = 91.3, P < 0.0001) because mercury levels were always lower in primary feathers (Table 2). This was particularly marked in Roseate Tern adults whose body feathers were almost three times more contaminated than flight feathers. Hg levels for this latter type of feathers were positively correlated with $\delta^{15}N$ for Roseate Tern adults (r = 0.618, N = 19, P = 0.005), while Lesser Noddy adults showed a similar but negative correlation between Hg and $\delta^{15}N$ (r = - 0.681, N = 11, P = 0.021).

Hg levels in Roseate Tern chick feathers were negatively correlated with age expressed as wing length, but while the relation was significant for body feathers (Fig. 3), it was not significant for primary 10 (Hg = 0.396 – 0.001 × WL (wing length), r^2 = 0.25, N = 8, P = 0.21). However, in the latter case the data set covered a restricted range of wing-lengths (73-114 mm).

DISCUSSION

Isotopic Signatures

Diet sampling on Aride Island suggested that Roseate Tern and Lesser Noddy parents rely mostly on a single prey (goatfish, family mullidae) to feed their young during the chick-rearing period (93.4-97.4%; Ramos 2000). This pattern had been previously documented in the 1970s on the nearby Cousin Island for Lesser Noddies (>93% of diet samples was goatfish; Diamond 1983). The diet of Roseate Tern adults was slightly more diverse, but it was nevertheless dominated by goatfish. Lesser Noddy and Roseate Tern

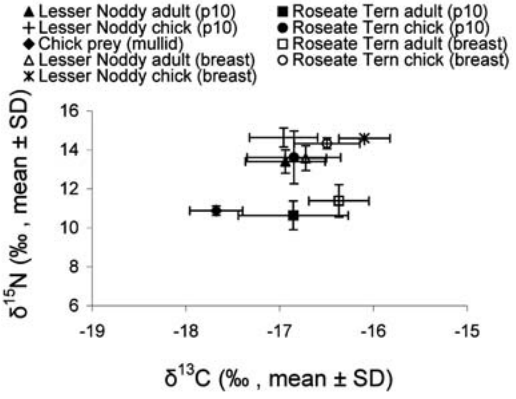

Figure 2. Stable carbon ($\delta^{13}C$) versus nitrogen ($\delta^{15}N$) isotope ratios in Roseate Tern and Lesser Noddy feathers collected on Aride Island, Seychelles. Stable isotope ratios of the main fish prey taken by both species (fam. *Mullidae*) are also shown (see also Table 2).

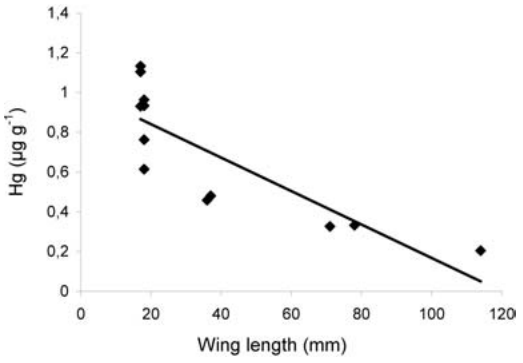

Figure 3. Linear regression of mercury concentrations in body feathers on wing measurements for Roseate Tern chicks (Hg = 1.009 – 0.008*WL, r^2 = 0.66, N = 12, P < 0.001).

chicks showed closely related isotopic signals, which was expected from the high diet similarities observed between both species (Cherel *et al.* 2002). We note that the small differences in ^{15}N values may actually reflect slightly diverse diets because stable isotope measurement is a more integrative method that conventional approaches. Making the assumption of a whole diet based on goatfishes, the trophic fractionation factors found from prey to predator (chick feathers) ($\Delta\delta^{13}C$ 0.9-1.1‰; $\Delta\delta^{15}N$ = 3.0-3.7‰) agree with previous studies in aquatic food webs (*c.* 0.8‰ for $\Delta\delta^{13}C$, and *c.* 3.4‰ for $\Delta\delta^{15}N$; Vander Zanden and Rasmussen 2001). Overall, the diets of adults and chicks of both species overlapped extensively, which is consistent with our hypothesis 1.

We found no inter-annual differences in $\delta^{15}N$ during the nonbreeding season in Lesser Noddy adults, suggesting that this species did not change trophic level between years. Also, the year-to-year changes in $\delta^{13}C$ were slight, presumably reflecting the same foraging habitat use between years. Assuming that the physiological processes involved in diet-feather fractionation are similar for chicks and adults (Cherel *et al.* 2000), then similar $\delta^{13}C$ and $\delta^{15}N$ in Lesser Noddy adults and chick feathers would suggest that adults probably remain in areas around the breeding colony during the molting period (hypothesis 2). The strong $\delta^{15}N$ difference between Roseate Tern adults and their chicks must be explained, however, by a change in diet during the nonbreeding season. $\delta^{13}C$ and $\delta^{15}N$ signatures in adult feathers grown during the molting period differed also between Roseate Terns and Lesser Noddies, but while differences in $\delta^{13}C$ were not significant (maximum of 0.5‰ between body feathers in 2004), there was a strong segregation for $\delta^{15}N$, with Roseate Terns showing consistently lower values for both types of feathers sampled. Thus, it is tempting to suggest that during the nonbreeding season, Roseate Terns feed at a lower trophic level than noddies. For instance, Roseate Tern adults may shift diet from carnivorous goatfishes (breeding season); towards invertebrate- or zooplankton-feeding fishes that display lower $\delta^{15}N$ values (e.g., Das *et al.* 2003). However, because $\delta^{15}N$ signatures (and $\delta^{13}C$) may differ between ocean systems (Saino and Hattori 1985), it may be difficult to tease out a change in trophic level within the same food web from a physical change in foraging location (Hobson 2005). The distinct $\delta^{15}N$ signatures found between both species might, therefore, be explained by either a difference in diet, in foraging areas, or both.

In marine systems, particulate organic matter (POM) is assumed to be the baseline value representing the first trophic level for a given food chain (Hobson *et al.* 1994), but the $\delta^{15}N$ of POM has been found to vary temporally and spatially due to the changes in $\delta^{15}N$ of source nitrogen and of isotopic fractionation during N processing (Kumar *et al.* 2004). Depending on these changes the baseline $\delta^{15}N$ value may be affected which, in turn, may be transmitted up the food chain (Sherwood and Rose 2005). POM measurements from the northern Indian Ocean showed a spatial variation between 2.1-10.1‰ in $\delta^{15}N$ (Saino and Hattori 1980), but there is no systematic basemaps of isotopic values currently available for the western Indian Ocean.

Tree (2005) suggested recently that Roseate Terns breeding in Kenya and Somalia may belong, together with the Seychelles, to the same northwestern Indian Ocean population. Single unringed individuals trapped along the east African coast have been also assigned to the small, pale *S. d. arideensis* form (Tree and Klages 2003) typically found on Aride and in other western Indian Ocean colonies (Tree 2005). This raises the possibility of regional movements from Aride Island to the productive oceanic waters along the eastern African coastline during the nonbreeding season. However, despite intensive ringing of adults and fledglings on Aride Island since 1997, there is no ring-recovery data outside the breeding season to confirm this hypothesis. The absence of isotopic baseline maps for our geographical area precludes also any confirmation of this hypothesis from the data available in this paper. The lack of isotopic mapping of marine systems has been previously found to preclude direct assignment of winter areas in other seabird

species such as Audouin's Gulls (*Larus audouini*) breeding in the Mediterranean region (Sanpera *et al.* 2007).

Mercury Concentrations

The fact that Roseate Tern feathers grown on Aride had low mercury values (Table 4) should reflect the uncontaminated oceanic environment around the Island (Bearhop *et al.* 2000b) (hypothesis 3). Field observations showed that Roseate Tern adults spend several weeks in the vicinity of Aride Island prior to laying (Maul 1998, pers. obs.), suggesting that mercury levels in small Roseate Tern chicks may partly reflect the contamination of prey taken by females (Becker *et al.* 1994). The negative relation between mercury levels and chick age should be, however, related to physiological processes: although the body burden can be enhanced in larger chicks due to food intake, its concentration is decreased by the fast mass increment during the growing period (i.e., a dilution effect; Becker *et al.* 1994), which may explain the age relation observed. In contaminated areas, an opposite relation is expected because mercury inputs by food cannot be counterbalanced by the dilution effect (Tavares *et al.* 2004, 2005).

Mercury concentrations measured in body feathers of adults were consistently higher than those found in wing-feathers, which could be connected to molt. The tenth (outermost) primary feather is grown over a short period (weekly scale), when the body pool of accumulated mercury has presumably been depleted by incorporation in feathers grown early in the molting sequence (p1 to p9). However, the six to ten body feathers analyzed for each individual bird represent an average over a longer time scale (monthly scale) than for primary feathers (Thompson *et al.* 1998).

Mercury concentrations in Lesser Noddy adult body feathers were lower than those reported for the congeneric Black Noddy in the Great Barrier Reef, Australia (Table 4), but comparable to that found in chick feathers grown on Aride. In contrast, Roseate Tern adults displayed higher mercury values in their body feathers. Therefore, the compari-

Table 4. Comparison of total mercury concentrations in body feathers of Roseate Tern and Lesser/Black Noddy adults and chicks from various populations.

Species/Population	Period of feather growth/Location	Age class (N)	Mean ($\mu g\ g^{-1}$)	Min - Max ($\mu g\ g^{-1}$)	Source
Roseate Tern					
Temperate Atlantic Ocean (USA)	Breeding/Cedar Beach	adult (8)	7.5 ± 1.2	—	Burger *et al.* 1992
	Breeding/Cedar Beach	fledgling (15)	1.5-2.0	1.0-3.0	Burger and Gochfeld 1997[a]
	NB[b]/S. America	adult (8)	2.7 ± 1.0	—	Burger *et al.* 1992
Temperate Atlantic Ocean (Azores)	Breeding/Azores	chick (13)	1.2 ± 0.2	0.4-2.7	Monteiro *et al.* 1995
	Breeding/unknown	adult (21)	2.2 ± 0.2	0.5-3.9	Monteiro *et al.* 1995
Tropical Atlantic Ocean (Caribbean)	NB/S. America[c]	adult (15)	2.2 ± 0.3	—	Burger and Gochfeld 1991
Indian Ocean (Seychelles)	Breeding/Aride Island	chick (12)	0.7 ± 0.1	0.2-1.0	This study
	NB/unknown	adult (20)	1.3 ± 0.1	0.7-1.8	This study
Lesser and Black Noddy				—	
Indian Ocean (Seychelles)	NB/unknown	adult (24)	0.9 ± 0.1	0.5-1.4	This study
Pacific Ocean (Australia)	NB/unknown	adult (15)	1.6 ± 0.3	—	Burger and Gochfeld 1991

[a]These data were only available graphically in the paper.
[b]NB: nonbreeding season.
[c]Hays *et al.* 1999.

son with Lesser Noddy adults suggests different levels of exposure to mercury contaminants during the nonbreeding season by the two species. The relative exposure of Roseate Tern adults may also vary during the nonbreeding period, being lower in the period preceding their return to the colony when primary 10 is replaced (hence explaining the lower Hg values in flight feathers). We also found different correlations between mercury and $\delta^{15}N$ for both species: Roseate Terns feeding at a high trophic level presumably consumed more contaminated prey, but Lesser Noddies showed an opposite relationship, which further supports the idea that adults of both species may rely on a different food web/trophic level during the nonbreeding season. High mercury levels found in food items taken by Roseate Tern adults may reflect high methylation rates and/or prey taken in coastal ecosystems under anthropogenic influence (Nisbet *et al.* 2002), although the mercury levels found in this study remain largely below the values reported at Cedar beach, northeastern United States, where birds are exposed to pollution from industrial sources (Table 4; Burger *et al.* 1992).

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