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## Niche partitioning among and within sympatric tropical seabirds revealed by stable isotope analysis

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1 STABLE ISOTOPES SUGGEST NICHE PARTITIONING AMONG  
2 SYMPATRIC TROPICAL SEABIRDS

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13  
14 **Running Head:** Stable isotopes show resource partitioning in tropical seabirds

15 **Keywords:** resource partitioning, stable isotopes, foraging ecology, tropical seabirds,

16  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$

17  
18

19 **ABSTRACT**

20 Despite the low productivity and ephemeral and patchy nature of resources in tropical  
21 waters, stable isotopic data from this study suggests that substantial resource partitioning  
22 occurs among tropical seabird communities. In this study we compared  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
23 levels in feathers across eight sympatric tropical seabird species; for a subset of these  
24 species we also compared isotopic levels in blood, and examined variation across years  
25 and sexes. We found that while there is low total variation in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  across  
26 the eight seabird species examined, all species occupied a distinct isotopic niche when  
27 both breeding and non-breeding periods were evaluated. There was only slight variation  
28 in the pattern of resource partitioning between breeding and non-breeding periods.  
29 Notably, there was a strong correlation between body mass, wing span, and wing loading  
30 ratios on foraging area, evaluated by  $\delta^{13}\text{C}$  levels, which is also coincident with estimates  
31 of field metabolic rate. Isotopic separation by age and year, within species was also  
32 observed; however separation by sex appeared to be relatively uncommon even in  
33 sexually dimorphic species. As a group, seabirds were isotopically distinct both from  
34 their prey and from other marine predators. Overall, the results are generally consistent  
35 with what is known about the at sea distribution and diet of these seabirds, and with  
36 patters of stable isotope partitioning among these species in other locations. Still, several  
37 results, including low  $\delta^{13}\text{C}$  of black noddies (*Anous minutus*), high  $\delta^{15}\text{N}$  of white terns  
38 (*Gygis alba*), and strong correlation of  $\delta^{13}\text{C}$  to body size and metabolic rate merit further  
39 examination. More research on isotopic cartography of tropical oceans, species specific  
40 fractionation rates, and stable isotopes of prey are needed to evaluate the usefulness of  
41 stable isotopes in identifying resource partitioning in tropical marine environments  
42

43 **INTRODUCTION**

44 Open oceans in tropical environments generally have low productivity, patchy and  
45 unpredictable distribution of prey, and low structural complexity (Ballance et al 1997,  
46 Longhurst and Pauly 1987, Weimerskirch 2007). High level marine predators thus face  
47 many foraging challenges in locating prey and are generally physiologically constrained  
48 for energetically efficient travel and foraging behavior (Weimerskirch et al 2004,  
49 Bertrand et al 2002). For tropical seabirds this has generally limited them to foraging  
50 within the first several meters of the sea surface, and they are often reliant on subsurface  
51 predators to drive food to the surface, further increasing patchy nature of food resources  
52 (Ballance et al 1997). Yet, despite these strong constraints, diverse predator, and  
53 particularly seabird communities, occur; this leads to questions about the degree, nature,  
54 and mechanisms of resource partitioning in these extremely homogenous and resource  
55 poor environments.

56 Resource partitioning in tropical oceanic environments has been well documented  
57 for temperate and polar seabird species (Ainley et al 1992, 1994), but remains an area of  
58 much inquiry for tropical seabird species particularly in open ocean environments  
59 (Harrison and Seki et al 1987, Catry et al 2009). Tropical seabird diets are more diverse  
60 than their temperate and polar counterparts, and there can be a high degree of overlap in  
61 diets and foraging areas (Ainley and Boekelheide 1990, Ballance et al 1997, Catry et al  
62 2009). Thus, these observations have led to questions about the degree to which tropical  
63 seabird species are able to partition resources.

64 There have been multiple studies of diets of seabird communities in tropical  
65 environments, but these have generally been constrained to the breeding season (Ashmole

66 and Ashmole 1967, Diamond 1983, Harrison et al 1983, Catry et al 2009). The only study  
67 to comprehensively explore the diet of non-breeding tropical seabird communities found  
68 higher degrees of resource partitioning than found in a similar study of polar seabirds  
69 (Spear et al 2007). They found partitioning by species, sex, age, foraging strategy, and  
70 body size. However, at-sea surveys of seabird diets have some inherent limitations for  
71 answering questions about resource partitioning. Since seabirds are typically sampled  
72 lethally, each animal contributes only a single data point in space and time, and it is thus  
73 not possible to examine changes in individual foraging behavior across space and time.  
74 Also, since reproductive status cannot be confirmed, it is not possible to link foraging  
75 behavior to reproductive status, although it is clear that reproductive status influences  
76 foraging ability. Spatially extensive survey efforts may also cross community boundaries  
77 for both seabirds and prey species, resulting in comparisons of foraging ecology of  
78 species that have limited co-occurrence. Collections across longer time periods may  
79 compare foraging across heterogeneous temporal periods.

80 Data on resource partitioning of tropical seabirds is also available from direct  
81 comparisons of foraging behavior across species via various methods of electronic  
82 tracking (Burger and Shaffer 2008, Weimerskirch et al 2005, 2006a, 2006b, Young et al.  
83 2010). However, cost, size, and logistical constraints associated with these methods have  
84 been generally limited to comparisons involving two or three species, with emphasis on  
85 larger species during breeding periods (Ropert-Coudert and Wilson 2005).

86 The usefulness of stable isotope analysis (SIA) as a tool for understanding  
87 resource partitioning is providing a low impact way to examine resource partitioning,  
88 both spatially and by trophic level. Stable isotopes of nitrogen and carbon in seabird

89 tissue reflect those values seen in their prey and give insight into origin and type of prey  
90 consumed. Stable carbon isotopes of seabirds and seabird prey show evidence of an  
91 increasing enrichment in inshore as compared to offshore feeding animals in both tropical  
92 and temperate areas (Hobson et al 2004, Cherel et al 2008). Stable nitrogen isotopes  
93 increase in a predictable manner with each trophic exchange, and thus indicate trophic  
94 position of a consumer (Vanderklift and Ponsard 2003). Crucial to seabird studies, since  
95 different tissues integrate these stable isotopes over different periods of time, a single bird  
96 can provide integrated information on diet over a period of time ranging from days to  
97 even years, depending on the tissue or tissues analyzed (Dalerum and Angerbjörn 2005).

98 Multiple studies have now used these SIA to understand resource partitioning  
99 among seabird communities (REFS). SIA have now yielded important insights into subtle  
100 changes in foraging ecology based on reproductive stage (e.g. Awkerman et al 2007), age  
101 (e.g. Forero et al 2002), colony location (e.g. Jaquemet et al 2008), sex (e.g. Bearhop et al  
102 2006), migratory patterns (e.g. Cherel et al 2000), as well as other factors (e.g. Cherel et  
103 al 2005, Phillips et al 2009). These studies have been consistent with data observed via  
104 direct tracking both in temperate and tropical systems (Phillips et al 2009, Weimerskirch  
105 et al 2009b, Young et al 2010). Since SIA allows for fairly robust, low impact method to  
106 resolve spatial and trophic separation among species, it is a promising tool to examine  
107 resource partitioning among seabirds in tropical environments, particularly for those  
108 species (e.g. terns, noddies, and small petrels) that are too small for current tracking  
109 methods. There have been a few studies that used SIA to examine resource partitioning  
110 on a community scale in the tropics (Cherel et al 2008, Catry et al 2008, Kojadinovic  
111 2008). Those studies, all conducted in Southern Indian Ocean, reached very different

112 conclusions, both in the degree of resource partitioning and the usefulness of isotopes as  
113 a tool for identifying foraging patterns in the tropics. Our study site, Palmyra Atoll  
114 (equatorial Pacific), is quite different from the other studies in that Palmyra is far (1000's  
115 km) from any continental shelf or coastal habitat, and has lower heterogeneity in oceanic  
116 conditions (productivity, SST, bathymetry) and thus may more typify open ocean  
117 conditions experienced by many tropical seabirds (Weimerskirch et al 2005, Catry et al  
118 2008).

119 The aims of the present study are 1) determine if there is significant isotopic  
120 partitioning in tropical seabirds living in an open ocean environment; 2) compare SIA  
121 results to data from conventional stomach content analyses, at-sea surveys, and known  
122 natural history to evaluate the usefulness of SIA as a tool for examining resource  
123 partitioning in among sympatric tropical seabirds; 3) compare patterns of isotopic  
124 partitioning in blood and feathers to evaluate differences in partitioning in breeding (from  
125 blood) and non-breeding (from feathers) periods; and 4) compare isotopic levels among  
126 different age classes and sexes of the same species and over multiple consecutive years.  
127 Specifically, we examined stable isotopes of carbon and nitrogen from nine species of  
128 sympatric seabirds at Palmyra Atoll. This included multiple congeneric species, and  
129 species with similar foraging strategies, where fine-scale niche partitioning might be  
130 particularly important for mitigating competitive interactions.

131

## 132 **METHODS**

133 Our research was conducted at Palmyra Atoll National Wildlife Refuge (5.867° N,  
134 162.067° W). Palmyra Atoll is a low-lying tropical atoll located in the Line Island chain

135 of the central Pacific Ocean. It is situated at the boundary of the eastern cool tongue and  
136 western warm pools of the Pacific, on the boundary of the intertropical convergence zone  
137 (Longhurst and Pauly 1987). Palmyra is composed of a ring of calcium carbonate  
138 derived islets encircling three saltwater lagoons. The land of Palmyra is predominantly  
139 forested; *P. grandis* and *T. argentea* forest provide extensive nesting habitat for tree  
140 nesting birds and occasional herbaceous and bare patches (including two maintained  
141 areas) serve as nesting areas for ground nesting birds (Young et al 2010). The  
142 surrounding waters are uniformly low in productivity (mean of 0.14 mg chlorophyll *a*  
143 /m<sup>3</sup>), warm (mean sea surface temperature of 21.3°C), and deep (except in immediate  
144 vicinity of the Line Island chain, surrounding waters are > 1000 m). The seabird  
145 community at Palmyra consists of 10 breeding species from 1) Order Charadriiformes -  
146 sooty terns *Sterna fuscata* (125,000-220,000 pair), white terns *Gygis alba* (~200 pair),  
147 brown noddies *Anous stolidus* (~500 pair), black noddies *A. minutus* (~1000 pair), and 2)  
148 Order Pelecaniformes - greater frigatebird *Fregata minor* (~250 pair), red-footed boobies  
149 *Sula sula* (~2500 pairs), brown booby *S. leucogaster* (~400 pairs), masked booby *S.*  
150 *dactylatra* (~35 pairs), and red-tailed tropicbirds *Phaethon rubricauda* (~150 pairs), and  
151 white-tailed tropicbirds *P. lepturus* (~10 pairs) (Fefer 1987, Young et al *unpublished*  
152 *data*). At Palmyra these birds breed asynchronously throughout the year.

153

#### 154 ***Sample collection***

155 We collected feather samples from 9 of the 10 species that breed at the atoll (all except  
156 white-tailed tropicbirds). Samples were collected from breeding adults (either incubating  
157 or chick rearing), with the exception of samples from white terns, where reproductive



158 status was unknown. All samples were collected in July 2009, except for sooty terns,  
159 which did not breed in summer 2009. Samples from sooty terns were thus collected in  
160 July 2008. For red-footed boobies, additional samples were collected from breeding  
161 adults in two previous years (July 2007 and July 2008) for interannual comparisons. For  
162 five species we also analyzed feathers collected from chicks in 2009. Feather tissue from  
163 brown noddies and wedge-tailed shearwaters (not a breeding species at Palmyra) were  
164 not included in statistical analyses due to small sample sizes. Birds were sexed using  
165 voice, plumage, and/or molecular sexing methods (Young et al 2010). We used  
166 unbraided underwing contour feathers (Jaeger et al 2009). Body masses of remaining  
167 species, plus wingspan and wingloading for all species were estimated from Hertel and  
168 Ballance (1999) and Spear and Ainley (1999). Field metabolic rate (kJ/day) was  
169 estimated from allometric equations for Pelicaniformes, Charadriiformes, and  
170 Procellariiformes (Shaffer in review).

171 For the three boobies, the frigatebird, and the sooty tern, blood was also collected  
172 from a brachial vessel from a subset of the individuals that were sampled for feathers.  
173 Muscle tissue (breast) was collected from red-footed boobies, masked boobies, black  
174 noddies, and sooty terns (chicks only) found dead in the breeding colony.

175 Diet samples were collected when spontaneously regurgitated. The best-  
176 preserved specimens of the common *Exocoetidae* (flying fish) and *Ommastrephidae*  
177 (flying squids) from these diet samples were used for the isotopic analyses. Muscle  
178 tissue of *Clupeiformes* (herring and anchovy), small baitfish common in the diets of many  
179 of these species (Catry et al 2009) was directly collected from below a seabird feeding  
180 aggregation immediately off the atoll. Muscle tissue from pelagic fish predators (wahoo,

Hillary 2/13/10 9:17 PM

**Comment [1]:** Scott – I don't mention the black noddy wingspan measurements by Melinda. Do you think I should?

181 *Acanthocybium solandri*; yellowfin tuna, *Thunnus albacores*) was collected from animals  
182 captured from within 3km of the reef immediately surrounding the atoll. *Sthenoteuthis*  
183 *spp.* (jumbo flying squid) was captured approximately 700 km from the atoll.

184

#### 185 ***Sample preparation and isotopic analyses***

186 Feathers were washed in DI water, dried at 60°C for storage, and subsequently cut into  
187 fine pieces for analysis. Blood, diet, and muscle tissue samples were all preserved frozen  
188 at -80°C. They were then freeze dried and ground to a fine powder. We did not extract  
189 lipid from any tissues as C:N ratios were always less than 4.0, and usually less than 3.5,  
190 suggesting lipid levels were low across all samples (Post et al 2007).

191 Stable isotopic ratios of C and N were analyzed at the Stanford Stable Isotope  
192 Biogeochemistry Laboratory (SIBL) using a Thermo Finnegan Delta-Plus XP IRMS.  
193 Replicate laboratory standards of graphite (USGS 24), ammonium sulfate (IAEA N1),  
194 and acetalanalide internal to each run show analytical error of less than 0.2‰ for both C  
195 and N.

196

#### 197 ***Isotopic interpretations***

198 The interpretation of carbon isotope values presented in this paper, are based on the  
199 assumption that the established inshore/offshore gradient of carbon-13 in seabird diets  
200 (Cherel and Hobson 2007, Graham et al 2009) is likely the primary driver for changes in  
201 stable carbon isotopes observed in this study. Benthic to pelagic gradients in carbon  
202 isotopes may partially cause this pattern; however the steep drop off in waters  
203 immediately surrounding Palmyra, and the fact that all seabirds in this study consume

204 prey found on or near the ocean surface, make it unlikely to be the primary driver of  
205 differences in carbon isotopes. Changes in carbon isotopes due to trophic level  
206 differentiation are generally small in seabirds, and given the limited range of  $\delta^{15}\text{N}$   
207 measured and the lack of correlation between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  observed in this study, it is  
208 not likely to be an important explanatory factor here. Variation in  $\delta^{15}\text{N}$  within a tissue  
209 type is likely primarily due to sequential enrichment in consumer tissues, such that  $\delta^{15}\text{N}$   
210 is interpreted as a measurement of trophic position. However, since there are established  
211  $\delta^{15}\text{N}$  gradients on large scales across the Pacific Ocean (Graham et al 2009) we also  
212 consider the possibility that  $\delta^{15}\text{N}$  changes could be caused by these spatial gradients.

213 We further assume that there is no size or age specific fractionation of either  
214 carbon ( $\Delta\text{C}$ ) or nitrogen ( $\Delta\text{N}$ ) isotopes within seabirds (Cherel et al 2005). We do not  
215 directly compare  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  across tissue types, given different isotopic signatures and  
216 fractionation rates of these tissues (Cherel et al 2005). The period of isotopic integration  
217 in blood is assumed to be days to weeks, such that blood taken from a breeding bird is  
218 assumed to give diet information on the breeding period (Hobson and Clark 1992a,  
219 1992b). Since feathers are usually molted after reproduction, and are inert thereafter,  
220 feather samples were assumed to represent the composition of the diet during the  
221 nonbreeding period (Bearhop et al 2002). Muscle tissue likely integrates over  
222 intermediate time periods (4-6 weeks) (Hobson and Clark 1992a, 1992b).

223

#### 224 ***Statistical analyses***

225 To examine differences in resource partitioning among species, we used multivariate  
226 analysis of variance (MANOVA), with subsequent univariate ANOVA tests of  $\delta^{13}\text{C}$  and

227  $\delta^{15}\text{N}$  difference, with post-hoc Tukey HSD analyses. Statistical analyses were performed  
228 in JMP 7 (SAS Institute, Cary, NC, USA). When necessary to meet assumptions of  
229 normality, data was transformed using Box-Cox transformation. All figures/tables depict  
230 untransformed data. All mean values are shown with  $\pm 1$  SD, also untransformed.

231

## 232 **RESULTS**

### 233 ***Species comparisons***

234 The nine species of adult seabirds showed significant overall isotopic segregation in  
235 feather samples (MANOVA, Wilks' lambda,  $F_{16,288} = 12.49$ ,  $p < 0.0001$ ; Fig 1A).  
236 Univariate tests of feathers also show significant difference both by  $\delta^{13}\text{C}$  (ANOVA,  $F_{7,145}$   
237  $= 30.41$ ,  $p < 0.0001$ ) and by  $\delta^{15}\text{N}$  (ANOVA,  $F_{7,145} = 5.20$ ,  $p < 0.0001$ ). Results from post  
238 hoc Tukey pairwise comparisons show significant differences in  $\delta^{13}\text{C}$  among most  
239 species, although there is some overlap (Table 1). For  $\delta^{15}\text{N}$ , the three booby species  
240 were all significantly different from the white tern and the great frigatebird; there are no  
241 other significant differences (Table 1).

242 The five species sampled for blood also showed significant overall isotope  
243 segregation (MANOVA, Wilks' lambda,  $F_{8,90} = 36.63$ ,  $p < 0.0001$ ). Univariate tests  
244 showed significant differences both by  $\delta^{13}\text{C}$  (ANOVA,  $F_{4,46} = 129.10$ ,  $p < 0.0001$ ) and by  
245  $\delta^{15}\text{N}$  (ANOVA,  $F_{4,46} = 30.41$ ,  $p < 0.0001$ ). In post hoc analyses, all seabird species  
246 partitioned separately for  $\delta^{13}\text{C}$ , except for greater frigatebirds, which were  
247 indistinguishable from either masked or red-footed boobies. For  $\delta^{15}\text{N}$ , greater  
248 frigatebirds and brown boobies were distinct from the other three species (Fig 1B).

249 All seabirds differed from one another in at least one of the two stable isotopes  
250 measured in blood or feathers. The total variation in values among species was between  
251 1.2‰ (in feathers and 1.8‰ (in blood) in  $\delta^{13}\text{C}$  and between 2.5‰ (in feathers) and 2.3‰  
252 (in blood) in  $\delta^{15}\text{N}$ . The pattern of trophic partitioning among species changed somewhat  
253 between blood and feathers, with great frigatebirds having a relatively lower  $\delta^{13}\text{C}$ , in  
254 feathers compared to blood, and brown boobies had a relatively higher  $\delta^{13}\text{C}$  in feathers  
255 compared to blood.

256 Comparison of  $\delta^{13}\text{C}$  by mean body mass per species yielded a significant positive  
257 relationship ( $R^2 = 0.67$ ,  $p < 0.01$ ), with more enriched  $\delta^{13}\text{C}$  for larger birds (Fig 2A). The  
258 relationship improved significantly when  $\delta^{13}\text{C}$  was compared to wing loading ( $R^2 = 0.82$ ,  
259  $p < 0.01$ ), where birds with lower wing loading were more enriched with  $\delta^{13}\text{C}$  (Fig 2B).  
260 There was also a strong positive relationship between estimated field metabolic rate and  
261  $\delta^{13}\text{C}$  ( $R^2 = 0.74$ ,  $p < 0.01$ ). There were no significant relationships between any of the  
262 above variables and  $\delta^{15}\text{N}$  values.

263 Although there were few muscle tissue samples per species, there were significant  
264 differences in isotope levels between species in this tissue. Black noddies had lower  $\delta^{15}\text{N}$   
265 in muscles than sooty terns ( $F_{3,12} = 4.64$ ,  $P = 0.02$ ). For  $\delta^{13}\text{C}$  black noddies were  
266 significantly more depleted than either red-footed or masked boobies.

267

### 268 *Effects of year, age, and sex within species*

269 There was a slight but significant interannual difference in  $\delta^{13}\text{C}$  for breeding adult red-  
270 footed boobies (MANOVA, Wilks' Lambda,  $F_{4,126} = 4.10$ ,  $p < 0.01$ ), where boobies in  
271 2007 had slightly higher  $\delta^{13}\text{C}$  values than birds in either 2008 or 2009 (ANOVA,  $F_{2,50} =$

272 3.61,  $p = 0.03$ ; Fig 3). No such trend was detected in  $\delta^{15}\text{N}$ . There were slight differences  
273 in feather isotope levels across age classes for red-footed boobies within 2009  
274 (MANOVA, Wilks' lambda,  $F_{4,44} = 3.21$ ,  $p = 0.02$ ), where chicks had slightly higher  
275  $\delta^{15}\text{N}$  values ( $F_{2,23} = 5.49$ ,  $p = 0.01$ ) than either adult or juvenile birds. No such trend was  
276 apparent in  $\delta^{13}\text{C}$ .

277 Of the five species for which adult and chick feathers were compared, four  
278 showed significantly higher  $\delta^{15}\text{N}$  values in chicks than in adults (black noddy,  $t = 2.47$ ,  $p$   
279  $= 0.02$ ,  $df = 24$ ; red-footed booby  $t = 2.92$ ,  $p = 0.01$ ,  $df = 18$ ; red-tailed tropicbird,  $t =$   
280  $5.63$ ,  $p < 0.0001$ ,  $df = 39$ ; brown booby  $t = 2.71$ ,  $p = 0.01$ ,  $df = 29$ ) and one, great  
281 frigatebirds showed marginally significant increases ( $t = 1.82$ ,  $p = 0.08$ ,  $df = 24$ ; Fig 4).  
282 Only one species, red-tailed tropicbirds showed significant differences in  $\delta^{13}\text{C}$  by age,  
283 with adult birds having lower  $\delta^{13}\text{C}$  than chicks ( $t = 5.63$ ,  $p < 0.0001$ ,  $df = 39$ ).

284 Comparisons by sex (among adult birds from the same year) were conducted for  
285 red-footed, masked, and brown boobies, as well as greater frigatebirds. The only species  
286 that showed significant differences by sex were brown boobies where males had lower  
287  $\delta^{13}\text{C}$  ( $t = 4.23$ ,  $p < 0.001$ ,  $df = 14$ ) and lower  $\delta^{15}\text{N}$  ( $t = 2.40$ ,  $p = 0.03$ ,  $df = 14$ ) than  
288 females.

289

### 290 *Comparisons to prey and other marine predators*

291 Comparisons among seabirds, other marine predators, and prey only included the five  
292 species for which blood data was available. As a group, seabirds were segregated in  
293 trophic space both from their prey and from other large pelagic predators (MANOVA,  
294 Wilks' Lambda,  $F_{6,298} = 23.26$ ,  $p < 0.0001$ ; Fig 5). Seabirds and predatory fish (wahoo,

295 yellowfin tuna) had higher  $\delta^{15}\text{N}$  than prey (flying fish, squid, and anchovies) or than large  
296 predatory invertebrates (jumbo flying squid) ( $F_{6,149}=15.87$ ,  $p < 0.0001$ ). The patterns of  
297  $\delta^{13}\text{C}$  was different, with the large predatory fish having higher  $\delta^{13}\text{C}$  than seabirds, seabird  
298 prey, or predatory invertebrates ( $F_{6,149} = 64.93$ ,  $p < 0.0001$ ).

299 Post-hoc analysis on a species by species comparison, showed less clear patterns  
300 of partitioning among seabirds and their prey. With regard to prey, diet items from  
301 seabird stomachs (flying fish, squid) had large SD ( $\pm\text{XX}$ ), particularly in  $\delta^{15}\text{N}$ , and were  
302 significantly elevated in  $\delta^{15}\text{N}$  over anchovy. Squid were indistinguishable in  $\delta^{15}\text{N}$  from  
303 any of the seabird species, although  $\delta^{13}\text{C}$  distinguished them from all seabird species  
304 except red-footed boobies and greater frigatebirds. Flying-fish were indistinguishable in  
305 either parameter from red-footed and masked boobies.

306 Seabirds had relatively little overlap with other pelagic predators. Only the brown  
307 boobies and yellowfin tuna, and red-footed boobies and jumbo flying squid were  
308 indistinguishable from each other in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

309

## 310 DISCUSSION

### 311 *Resource partitioning by species*

312 The eight sympatric seabird species studied each occupy a distinct ecological niche  
313 across the breeding and non-breeding periods. The degree of partitioning observed in  
314 non breeding period was greater than that detailed by at-sea surveys and diet analyses  
315 (Surman and Wooler 2003, Spear et al 2007).

316 The patterns observed in  $\delta^{13}\text{C}$  in non-breeding period were generally consistent  
317 with data from tracking and at-sea surveys, where sooty terns and greater frigatebirds

318 being highly pelagic, white terns and red-footed boobies less pelagic, followed red-tailed  
319 tropicbirds, brown and masked boobies, the least pelagic (Ballance et al 1997, Jaquemet  
320 et al 2005). The one surprising result based on carbon isotope levels was the highly  
321 pelagic signal of black noddies (i.e. values were more negative than that of any other  
322 species). This species is generally considered to be an opportunistic nearshore feeder that  
323 is often seen foraging near jacks and in lagoons (Ashmole 1968, Seki and Harrison 1989).  
324 Yet values of carbon isotope levels in lagoons at Palmyra are particularly elevated, and  
325 black noddy isotope levels do not resemble those of reef jacks at Palmyra (McCauley et  
326 al unpublished data). Given the small total range of  $\delta^{13}\text{C}$  observed, controlled  
327 measurements of species-specific fractionation rates would be helpful to confirm that  
328 species-specific fractionation rates do not drive these patterns (Becker et al 2007).  
329 Likewise, while  $\delta^{13}\text{C}$  maps available for the equatorial Pacific Ocean do not suggest high  
330 variation in  $\delta^{13}\text{C}$  around this region, that is based on limited sampling near Palmyra  
331 (Graham et al 2007); better isotopic sampling of oceans in this region would help  
332 interpret these results.

333         Species level changes in  $\delta^{13}\text{C}$  were highly correlated to body mass, wing loading  
334 and metabolic rates; small species with high metabolic rates and species with low wing  
335 loading exhibit a more pelagic signature than larger species and species with high wing  
336 loading. Generally, birds with low body mass and high wing loading should have low  
337 costs of flight, perhaps enabling a more pelagic lifestyle (Pennycuik 1989). However,  
338 since these factors covary with metabolic rate, it is also possible that metabolic rate  
339 drives this pattern.



340 Nitrogen isotopes from non-breeding periods showed the greater frigatebird to  
341 have elevated  $\delta^{15}\text{N}$  levels over many species including all the boobies (consistent with  
342 Cherel et al. 2008). Although direct analysis of diets of non-breeding greater frigatebirds  
343 is quite similar to red-footed boobies, these birds also often consume pulli of sooty terns  
344 and noddies, potentially explaining this variation (Schreiber and Hensley 1986, Megyesi  
345 and Griffin 1996, Spear et al 2007). Kleptoparasitism which seems to be of particular  
346 importance in non-breeding birds could potentially explain these elevated  $\delta^{15}\text{N}$  values, as  
347 these partially digested food items may have elevated  $\delta^{15}\text{N}$  levels (Gilardi 1994). As in  
348 the Seychelles (Catry et al 2008), the white tern also showed high  $\delta^{15}\text{N}$  levels. While  
349 Catry et al suggested that this might be reason to discount results of  $\delta^{15}\text{N}$ , the consistency  
350 across studies perhaps merits further consideration for biologically valid explanations. It  
351 is possible that these high levels may be due to the large portion of its diet (>40%)  
352 composed of small, predatory Scombridae (*Euthynnus* sp; Spear et al 2007). This  
353 predatory species might well be higher in  $\delta^{15}\text{N}$  than flying fish and squid dominating diet  
354 of other species; direct measurements of  $\delta^{15}\text{N}$  of these prey would be necessary to resolve  
355 this. The three booby species, which feed primarily on flying fish and squid (Schreiber  
356 and Hensley 1986, Spear et al 2007) show particularly low  $\delta^{15}\text{N}$  values. Controlled  
357 studies of species specific fractionation patterns would help understand if physiological  
358 or ecological factors drive  $\delta^{15}\text{N}$  patterns (Becker et al 2007)

359 Examination of blood samples, representing the breeding interval, also showed  
360 distinct niches for each of the species examined. There were small changes in foraging  
361 areas in non-breeding as opposed to breeding periods, with greater frigatebirds and brown  
362 boobies looking comparatively less pelagic than during non-breeding interval. For the

363 two species for which tracking data is available at Palmyra (red-footed and masked  
364 booby), the  $\delta^{13}\text{C}$  results are high consistent with tracking results, even though the  
365 differences in foraging distances was not extremely large (Young et al in press).

366 The relative positions of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in both breeding and non-breeding periods  
367 observed at Palmyra were highly consistent with those observed in Europa Island and in  
368 the Seychelles (Catry et al 2008, Cherel et al 2008) suggesting that niche partitioning is  
369 consistent in very different parts of the species' ranges. The absolute values of  $\delta^{13}\text{C}$  were  
370 also consistent in both studies in nonbreeding interval, but slightly depleted at Palmyra  
371 during breeding interval, perhaps due to more oceanic location of Palmyra itself which  
372 might lead to lower  $\delta^{13}\text{C}$  values (Graham et al 2009). In contrast, absolute values of  $\delta^{15}\text{N}$   
373 observed at Palmyra were greatly elevated (by about 2‰) over that observed at Europa in  
374 both breeding and non-breeding periods. This suggests a higher baseline of nitrogen at  
375 Palmyra than at Europa; similar results were seen in comparison of Seychelles to  
376 Mozambique Channel (Jaquemet et al 2008). This is consistent with latitudinal variations  
377 of  $\delta^{15}\text{N}$  in isotopic cartography. This suggests that while it is possible to compare  
378 relative  $\delta^{15}\text{N}$  positions across studies, to compare absolute values of  $\delta^{15}\text{N}$  strong good  
379 knowledge of baseline  $\delta^{15}\text{N}$  is needed (Graham et al 2009).

380 [There was a relatively few samples of muscle tissue, but patterns were fairly  
381 consistent with that seen in feathers and blood. Only the  $\delta^{15}\text{N}$  of black noddies were  
382 significantly different (lower in  $\delta^{15}\text{N}$ ).

383

384 *Partitioning within species*

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**Comment [2]:** What about dropping muscle tissue altogether? It's not really adding much and it will cut length a little...

385           Comparison of adult feathers to chick feathers shows elevated levels of  $\delta^{15}\text{N}$  in  
386 chicks across all five species examined. This varies from the pattern seen for greater  
387 frigatebirds in Europa Island, but is consistent with results seen for sooty terns at the  
388 same site (Cherel 2008). This could reflect a shift to higher trophic level prey items  
389 during the breeding period, selective feeding of food items to young, age specific  
390 fractionation, or some effect of regurgitation of food. Other studies have shown  
391 differential provisioning of chicks with higher quality food, or different trophic level food  
392 sources (Hodum and Hobson 2000, Cherel 2008). While seabird studies have not  
393 documented changes in  $\Delta\text{N}$  by age, this has been seen in other taxa and could be a viable  
394 explanation (Roth and Hobson 2000). Even without different  $\Delta\text{N}$ , by feeding on partially  
395 digested food, they may be incorporating  $\delta^{15}\text{N}$  from their parents' bodies, thus explaining  
396 higher  $\delta^{15}\text{N}$  values. Direct comparison of adult and chick blood and diets (not taken  
397 here) would help resolve this. The lack of any shift in  $\delta^{13}\text{C}$  from adults to chicks was  
398 unexpected given that breeding places constraints on seabird foraging distances, but is  
399 consistent with lack of change seen in Seychelles (Catry et al 2008).

400           We saw relatively little resource partitioning by sex. Of the four species, all  
401 exhibiting reverse sexual dimorphism, for which sex differences in foraging were  
402 examined, we saw differences only for one (brown booby). The larger females of brown  
403 boobies showed higher  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , indicating higher trophic level and less pelagic  
404 food sources. This is consistent with other evidence of niche partitioning by sex in brown  
405 boobies (Gilardi 1992, Weimerskirch et al 2009b). Likewise, the lack of resource  
406 partitioning by sex in red-footed boobies, and masked boobies is also consistent other  
407 studies (Weimerskirch et al 2009a, Young et al *in press*), although sexual differences

408 have been observed in the red-footed booby in other locations (Weimerskirch et al  
409 2006b).

410 In the one species for which we compared data across multiple years, we saw  
411 small but significant differences in  $\delta^{13}\text{C}$  for one of the three years. This may point to  
412 small variability in food sources across time even in tropical resources. While it is not  
413 always possible to gather simultaneously, this suggests cautions in interpreting data from  
414 seabirds gathered different years in isotopic analyses.

415

#### 416 ***Comparisons with prey and predators***

417 We saw clear distinctions among seabirds, their prey, and other marine predators.  
418 The relatively little overlap between pelagic predators and seabirds on a species by  
419 species basis was unexpected, given that many of these seabirds feed so heavily in flocks  
420 over schools of predators. The primary differences in seabirds and other predatory fish  
421 was  $\delta^{13}\text{C}$  and may reflect integration of benthic food sources into fish diets. However, it  
422 could also represent other differences in diet, as other studies of seabird and predator  
423 diets have shown substantial variation, even though they forage together (Catry et al  
424 2009). The difference in  $\delta^{15}\text{N}$  between *Sthenoteuthis spp.* and seabirds may reflect lower  
425 trophic diet of *Sthenoteuthis spp.* (Shchetinnikov 1992).

426 Seabirds were also not isotopically distinct from individual prey types in  $\delta^{15}\text{N}$ ,  
427 which was unexpected given known fractionation rates for seabirds between 3 and 5 ‰  
428 (REFS). This may be due to use of muscle/mantle from diet samples rather than whole  
429 animals; whole fish have been shown to have lower  $\delta^{15}\text{N}$  levels (REFS). This may also  
430 be due to partial digestion of diet samples analyzed. Although diet samples selected

431 appeared to be in excellent condition, and interior muscle samples were, minimizing  
432 potential contamination with seabird digestive enzymes, SD was very high in these  
433 samples and overall  $\delta^{15}\text{N}$  levels were high. Muscle from Clupeiformes from beneath bird  
434 foraging flocks did not show this elevated  $\delta^{15}\text{N}$  or the high SD. We suggest care should  
435 be used in determining diet items based on items from prey items gathered via stomach  
436 contents. Analysis of whole additional diet items gathered directly, and sorted to lower  
437 taxonomic levels would be a good resource for future use of isotopes in diet analyses of  
438 tropical seabirds. This would also help resolve lingering questions about the merit of  
439  $\delta^{15}\text{N}$  in assessing food sources of tropical seabirds (Catry et al 2008)

440

#### 441 ***Stable isotopes as a tool for evaluating resource partitioning in tropical seabirds***

442         There has been some discussion about the merit of using stable carbon and  
443 nitrogen in examining niche partitioning among tropical seabirds in open ocean sites. In  
444 this study, we find high consistency in species specific patterns of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  across  
445 tissue types in this study, and between this study and other studies despite widely  
446 different habitats (Catry et al 2008, Cherel et al 2008). For the two species for which  
447 tracking data is available at this site, stable isotope levels are consistent (both within and  
448 across species) with tracking data and appear to be able to detect small scale changes in  
449 foraging (Young et al *in press*). Alignment of tracking, at-sea surveys, and isotope data  
450 is also seen from various work in the Mozambique Channel (Jaquemet et al 2005, Cherel  
451 et al 2008). Also, for the great majority of analyses, patterns of partitioning are in  
452 keeping with the data available from at-sea surveys and stomach content analyses. All of

453 these factors appear to provide evidence for reliability of isotopes for identifying foraging  
454 patterns of tropical species.

455         However the anomalously low  $\delta^{13}\text{C}$  of black noddies and the strong correlation of  
456  $\delta^{13}\text{C}$  to field metabolic rate, does raise possibility that species specific fractionation rates  
457 might be an alternative explanation for significant variation observed in isotopes across  
458 species (repeated across both space and time). Other potential explanations (i.e.  
459 nutritional stress causing differential fractionation, mixing of benthic  $\delta^{13}\text{C}$  signals, local  
460 variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) would be unlikely to be consistent across spatially and  
461 temporally distinct studies. However analyses of prey item isotope levels, controlled  
462 laboratory experiments of species specific fractionation rates, and better isotopic maps for  
463 the region would help confirm the interpretations presented here.

464

#### 465 **Conclusions**

466         In general this study supports the idea that there is high niche partitioning among  
467 tropical seabirds even in ocean environments. Resource partitioning is not complete  
468 unless considered across both breeding and non-breeding periods. Partitioning appears to  
469 occur within species, as well as among species – with different isotopic signatures  
470 observed by sex, age, and year. Sexual partitioning of resources did not appear to be  
471 common even among species that had relatively high sexual dimorphism, consistent with  
472 tracking data from this site (Young et al *in press*). Total trophic range of seabird diet was  
473 small, and both seabirds and their diet showed substantially higher levels of  $\delta^{15}\text{N}$  in this  
474 study than in studies from other sites despite apparently similar diets, pointing to  
475 potential variability in space in this value. There was a strong correlation between body

476 size, wing loading, and metabolic rate on  $\delta^{13}\text{C}$ ; there are multiple possible explanations  
477 for this pattern.

478 While variability in both isotopes was smaller in this study than in comparable  
479 polar or temperate studies, the results suggest that niche partitioning is at least as  
480 prevalent in this system. This is despite more limited foraging techniques of tropical  
481 seabirds studied here, and despite patchier resources in the tropical ocean. The apparent  
482 ability to detect small differences in foraging changes via isotopes in tropical  
483 environments, continues to further suggestions of others that this minimally invasive tool  
484 can offer powerful insight to niche partitioning in tropical seabirds.

485

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497

Hillary 2/15/10 12:25 PM

**Comment [3]:** Could cut this entire paragraph, basically just summarizes previous statements...

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**Comment [4]:** Weimerskirch et al 2007 reference missing.

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662

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FEATHERS: SEABIRDS	<i>n</i>	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$		C:N	
Black noddy	18	14.79	1.90 (AB)	-16.87	0.32 (A)	3.34	0.07
Brown noddy †	3	16.35	0.31	-16.12	0.25	3.37	0.01
Sooty tern	21	14.7	2.80 (AB)	-16.30 ± 0.28	(B)	3.23	0.03
White tern	20	16.20 ± 1.69	(A)	-15.91 ± 0.29	(C)	3.16	0.04
Brown booby	21	14.08	1.39 (B)	-15.43	0.31 (DE)	3.18	0.03
Masked booby	15	14.17	0.98 (B)	-15.22	0.24 (E)	3.18	0.03
Red-footed booby	12	13.85	1.25 (B)	-15.73	0.34 (CD)	3.22	0.03
Great frigatebird	19	16.03 ± 1.09	(A)	-16.26	0.20 (B)	3.27	0.03
Red-tailed tropicbird	26	15.35 ± 1.70	(AB)	-15.61 ± 0.27	(D)	3.14	0.03
Wedge-tailed shearwater †	1	9.31		-16.62		3.34	
BLOOD: SEABIRDS							
Sooty tern	17	14.29 ± 1.52	(A)	-18.02 ± 0.13	(A)	3.33	0.11
Brown booby	10	15.67	0.72 (B)	-17.20	0.12 (B)	3.30	0.03
Masked booby	9	14.21 ± 0.61	(A)	-17.15 ± 0.18	(C)	3.40	0.06
Red-footed booby	11	13.79 ± 0.44	(A)	-17.42 ± 0.09	(D)	3.31	0.04
Great frigatebird	5	16.07	0.72 (B)	-17.20	0.12 (CD)	3.41	0.03
MUSCLE: SEABIRDS							
Black noddy	3	10.89 ± 0.17	(A)	-18.34	0.02 (A)	3.79	0.04
Masked booby	3	14.09 ± 0.01	(A)	-16.88	0.45 (B)	3.34	0.12
Red-footed booby	7	13.46 ± 1.44	(A)	-17.48	0.37 (AB)	3.89	0.07
Sooty tern (chick)	4	14.57 ± 4.05	(A)	-17.50	0.54 (AB)	3.47 ± 0.24	
MUSCLE: PREDATORS & PREY							
<i>Clupeiformes</i>	15	11.00	0.46	-17.80	0.46	3.35	0.09
<i>Exocetidae</i>	26	13.06	2.39	-17.34	0.29	2.66	0.05
<i>Ommastrephidae</i>	12	14.64	1.28	-17.61	1.02	3.26	0.22
<i>Acanthocybium solandri</i>	15	14.53	3.15	-16.21	1.24	3.15	0.06
<i>Thunnus albacores</i>	25	14.63	0.96	-16.68	0.36	3.16	0.15
<i>Sthenoteuthis spp.</i>	11	12.82	1.02	-17.62	0.27	3.18	0.05



666

667 **Table 1:** Stable isotopic ratios of carbon and nitrogen and mass ratio of C:N in feathers,  
668 blood, and muscle tissue of seabirds, and muscles of other pelagic predators and prey..

669 Letters following mean values denote significant differences among species in post-hoc  
670 analyses, values (within tissue type and isotopic ratio) not connected with the same letter  
671 are significantly different. Species marked with † are not considered in statistical  
672 comparisons due to small sample size. Values are mean  $\pm$  SD

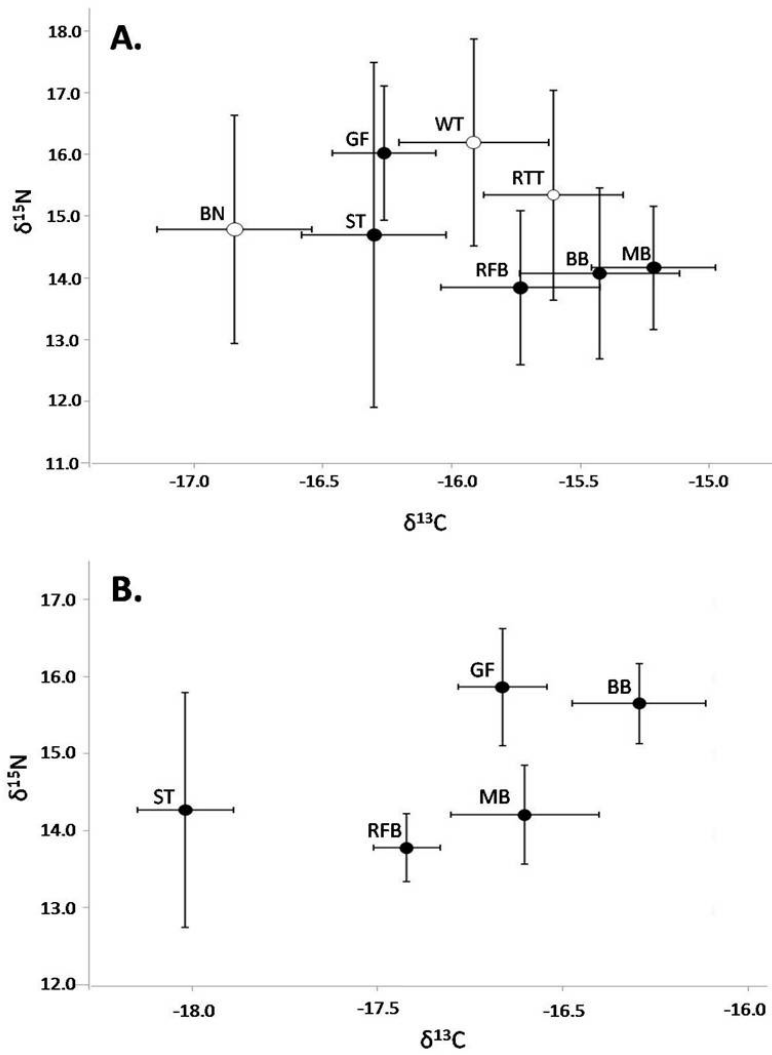
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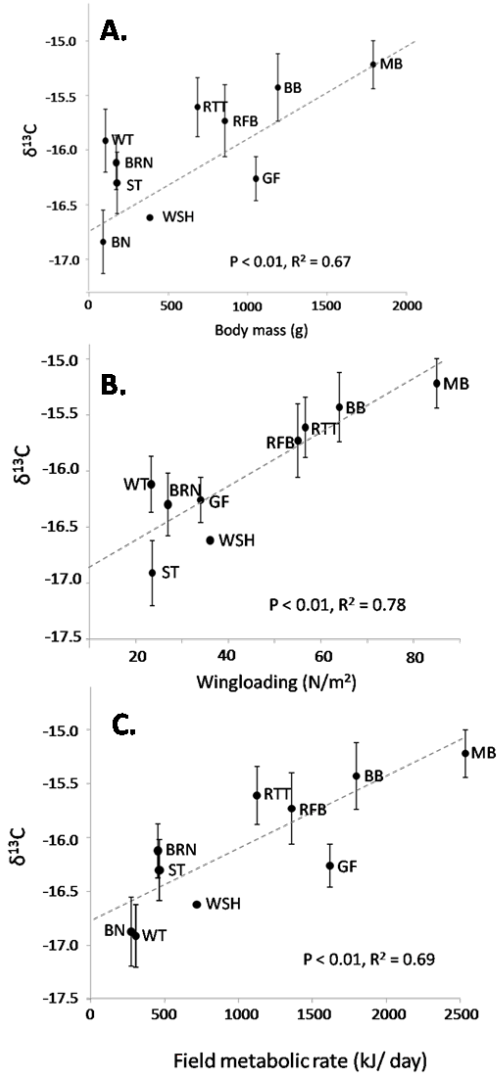
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679 **Figure 1:** Stable carbon and nitrogen isotope values (mean ± SD) from eight seabird  
 680 species from Palmyra Atoll. Panel A shows values from feathers; solid black symbols  
 681 denote those species for which isotopic values of blood are also presented panel B. BB =  
 682 brown booby, BN = black noddy, MB = masked booby, GF = great frigatebird, RFB =  
 683 red-footed booby, RTT = red-tailed tropicbird, ST = sooty tern, WT = white tern.



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686 **Figure 2:** Stable isotope values of carbon compared to (a) body mass (b) wing loading

687 and (c) estimated field metabolic rate. Species codes are the same as in Figure 1, plus

688 BRN = Brown noddy; WSH = Wedge-tailed shearwater. Statistics here include all

689 species depicted.

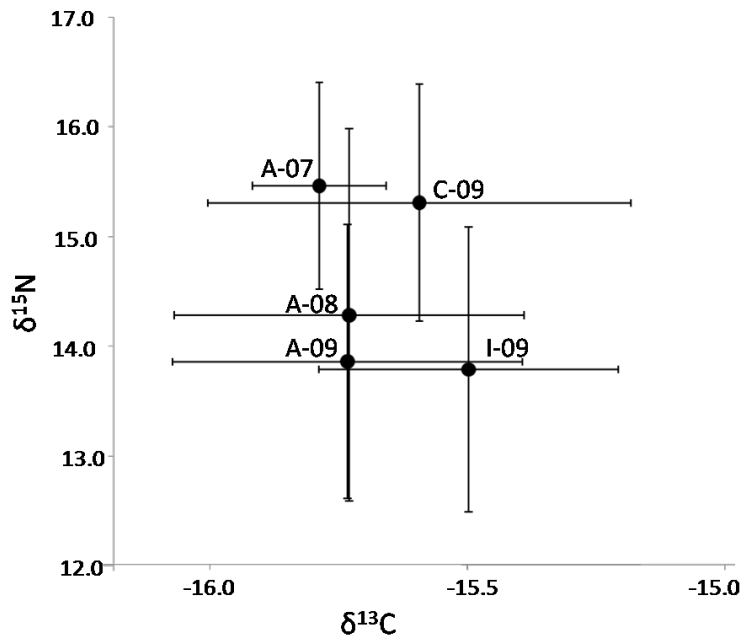
Hillary 2/13/10 5:58 PM

**Comment [5]:** Probably can drop at least one of these as they all covary – but which?

Hillary 1/29/10 11:42 AM

**Comment [6]:** In text I report values w/o brownnoddy and wedge tailed shearwater. Should I clarify? Or remove? Keep consistent?

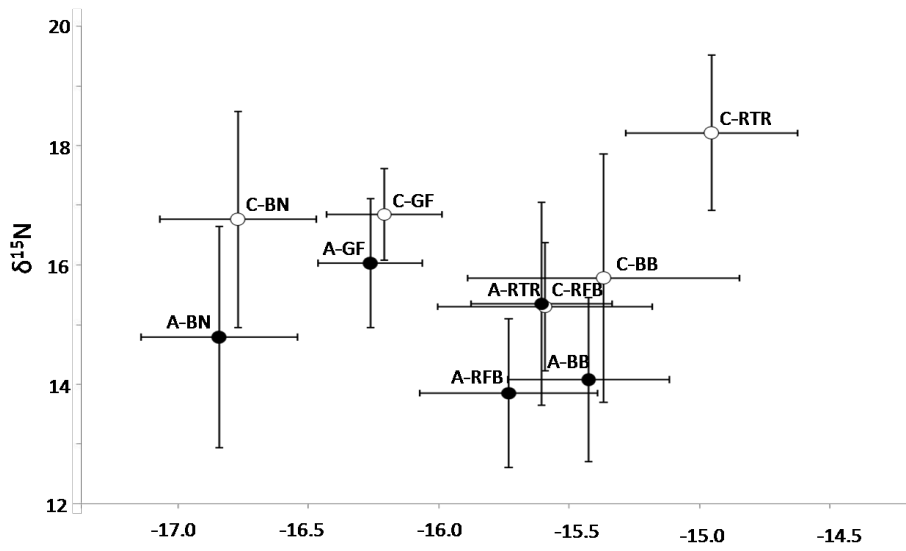
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693 **Figure 3:** A comparison of stable carbon and nitrogen isotope values for feathers from  
694 red-footed boobies across multiple years and age classes. The first letter indicates age  
695 class (A= adult, I = immature, C = chick) and the number indicates the year samples were  
696 collected (2007, 2008, or 2009).



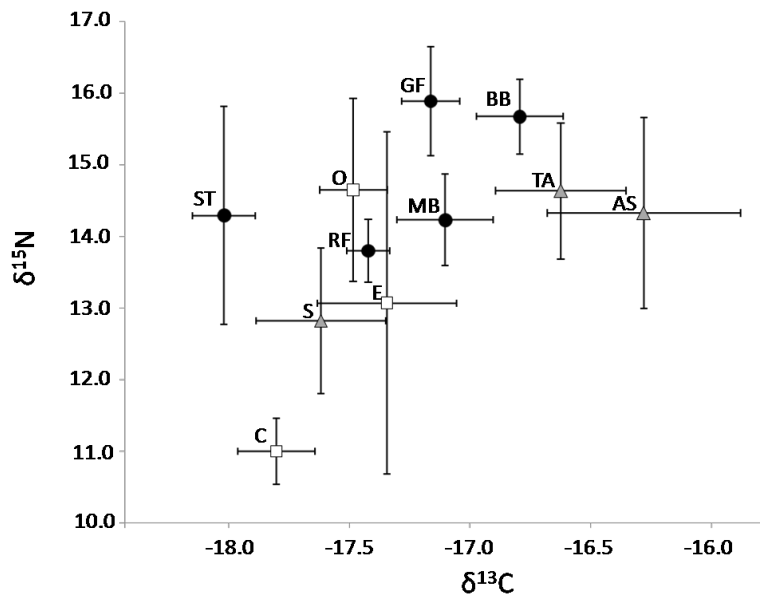
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699 **Figure 4:** Stable carbon and nitrogen isotope values of feathers compared across age  
 700 classes for multiple seabird species. Adults (A) are indicated by unfilled shapes and  
 701 chicks (C) are indicated by filled shapes. Different species are indicated by codes (as  
 702 same as in Figure 1) and shape.

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707 **Figure 5:** Stable carbon and nitrogen isotope values of seabirds (filled circles), their prey

708 (open squares), and other pelagic predators around Palmyra Atoll (grey triangles). AS=

709 *Acanthocybium solandri* (wahoo); TA = *Thunnus albacores* (yellowfin tuna); E =

710 Exocetidae (flying fish, various); C = Clupeiformes (anchovy and herring); S =

711 *Sthenoteuthis spp.* (jumbo flying squid, various). Seabird codes are the same as in Fig 1.

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