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RESEARCH ARTICLE

Resource partitioning between species and sexes in Great Frigatebirds and Lesser Frigatebirds

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ABSTRACT

Seabirds inhabiting large, multispecies colonies face intraspecific and interspecific competition for prey and this often results in foraging strategies that partition resources. Here, we identified mechanisms that facilitate partitioning of resources between 2 congeneric tropical seabirds, Great Frigatebirds (*Fregata minor*) and Lesser Frigatebirds (*F. ariel*), for which traditional research methods have documented high levels of resource overlap. Stable isotope analysis (SIA) indicated that throughout the breeding cycle, male and female Great Frigatebirds consumed prey with higher $\delta^{15}\text{N}$ compared to male Lesser Frigatebirds. This trend was not significant when comparing $\delta^{15}\text{N}$ values of male and female Great Frigatebirds to female Lesser Frigatebirds. During the breeding period, GPS tracking and SIA indicated considerable spatial overlap among species and sexes. This contrasted with SIA of samples that provide insight into nonbreeding resource acquisition because these indicated that male Great Frigatebirds and male Lesser Frigatebirds had lower $\delta^{13}\text{C}$ values than females of each species, signifying greater use of offshore foraging grounds by males of both species. Together these results suggest that body size differences influence trophic position of the prey consumed. Furthermore, central-place foraging constraints, and spatially unpredictable resource distribution, limit potential for spatial differences in foraging strategies when breeding. By contrast, spatial distribution of foraging differs during the nonbreeding period as the requirement for central-place foraging is lifted.

Keywords: diet, feeding zones, foraging ecology, kernel analysis, marine predators, niche differentiation, prey specificity, reverse sexual dimorphism

Repartición de recursos entre especies y sexos en *Fregata minor* y *Fregata ariel*

RESUMEN

Las aves marinas que habitan colonias grandes y con varias especies se enfrentan a competencia intra- e interespecífica por sus presas, lo que frecuentemente resulta en estrategias de forrajeo que reparten los recursos. En este trabajo identificamos los mecanismos que facilitan la repartición de recursos entre dos especies de aves tropicales congénicas, *Fregata minor* y *F. ariel*, para las que los métodos tradicionales de investigación han documentado altos niveles de superposición en recursos. Los análisis de isótopos estables (AIE) indicaron que durante todo el ciclo reproductivo los machos y hembras de *F. minor* consumieron presas con valores más altos de $\delta^{15}\text{N}$ en comparación con los machos de *F. ariel*. Esta tendencia no fue significativa cuando comparamos los valores de $\delta^{15}\text{N}$ de machos y hembras de *F. minor* con los de las hembras de *F. ariel*. Durante la temporada reproductiva, el seguimiento por GPS y los AIE indicaron una superposición espacial considerable entre especies y sexos. Esto contrasta con los AIE de las muestras que brindan información sobre la adquisición de recursos no reproductivos debido a que éstos indicaron que los machos de *F. minor* y los machos de *F. ariel* tuvieron valores de $\delta^{13}\text{C}$ menores que las hembras de cada especie, lo que significa que hay un mayor uso de terrenos de forrajeo fuera de la costa por parte de los machos de ambas especies. En conjunto, estos resultados sugieren que las diferencias en el tamaño corporal afectan la posición trófica de las presas que están siendo consumidas. Además, las restricciones en el sitio central de forrajeo y la distribución espacial impredecible de los recursos limitan el potencial para que haya diferencias espaciales en las estrategias de forrajeo durante la reproducción. En contraste, la distribución espacial del forrajeo fue diferente durante el periodo no reproductivo ya que no se requiere un sitio central de forrajeo.

Palabras clave: análisis Kernel, depredadores marinos, dieta, diferenciación de nicho, dimorfismo sexual reverso, ecología del forrajeo, especificidad en las presas, zonas de alimentación

INTRODUCTION

Organisms that use shared resources cannot persist in sympatry if ecological overlap with respect to a limiting resource is too great (Gause 1934, Hutchinson 1959, Hardin 1960, MacArthur and Levins 1967). To alleviate this potential conflict, community members partition resources by adopting a diversity of ecological strategies (MacArthur 1957). With respect to food resources, morphological, physiological, and behavioral factors are influential in determining the type of prey consumed, spatial aspects of the foraging strategy, and foraging method used.

During the breeding season, seabirds are central-place foragers because they must periodically return to their colony to undertake incubation duties and to provision young. Range limits resulting from this requirement are further mediated by individual body condition and the condition of their offspring (Chaurand and Weimerskirch 1994, Weimerskirch 1998). The resulting pattern of prey use can generate relatively intense foraging close to the colony (Elliott et al. 2009). In these circumstances, prey resources in the waters surrounding large seabird colonies can become depleted due to sustained foraging activity by the seabird assemblage (Ashmole 1963, Furness and Birkhead 1984, Birt et al. 1987, Lewis et al. 2001). Resource depletion leads to conditions that induce competition.

Many polar, temperate, and tropical seabird assemblages display resource partitioning where there is competition for prey resources. A number of attributes including prey species or prey size specificities (Ashmole and Ashmole 1967, Rayner et al. 2008), foraging location (Henkel 2009, Wakefield et al. 2013), diving capacity (Linnebjerg et al. 2015), or diel patterns in foraging (Spear et al. 2007) facilitate resource partitioning among members of the seabird community. These attributes may be contrasted between different species (Weimerskirch et al. 1988) or within a single species between different populations, sexes, or age classes (González-Solís et al. 2000, Grémillet et al. 2004, Steenweg et al. 2011, Wakefield et al. 2013). Primary productivity strongly influences how these contrasts manifest (Young et al. 2010b, Kappes et al. 2011). Primary productivity is also important for structuring the distribution of seabirds when not breeding. At the cessation of breeding, adults no longer support dependent offspring and migration or dispersal away from the colony may further diminish competition for resources (Ashmole 1963). Migrating or dispersing individuals often track regions of high primary productivity with greater prey availability (González-Solís et al. 2007, Egevang et al. 2010, Jessopp et al. 2013, McKnight et al. 2013).

Tropical marine systems are one area where primary productivity is generally low and the distribution of resources is often more patchy and unpredictable than in temperate

locations (Ainley and Boekelheide 1984, Weimerskirch 2007). Many tropical seabirds have evolved wing morphology conducive to efficient flight that enables them to cover large areas when searching for unpredictable prey resources (Brewer and Hertel 2007). This morphology is not suited to underwater propulsion and constrains most tropical seabirds to surface foraging (Spear et al. 2007). Surface foraging and low productivity further interact to increase levels of competition and thus drive strong selection for foraging strategies that effectively partition prey resources.

Frigatebirds (*Fregata* spp.) are seabirds with a pantropical distribution. They display reverse sexual dimorphism, with females ~30% larger than males (Mott et al. 2015). At many breeding colonies 2 or more frigatebird species occur in sympatry (Diamond 1975, King 1986, James and McAllan 2014). Unlike other seabirds, the plumage and wing structure of frigatebirds renders them incapable of settling on the sea surface (Mahoney 1984, Orta 1992, Weimerskirch et al. 2004). When foraging they remain airborne and rely on the activity of subsurface predators such as tunas and dolphins to drive prey to the surface and enable prey capture (Au and Pitman 1986, Spear et al. 2007). As such, foraging opportunities are expected to be even more restricted for frigatebirds when compared with other tropical seabirds, resulting in heightened competition for prey. It is therefore counterintuitive that previous studies have indicated high levels of resource overlap between sympatric frigatebird species (Pocklington 1979, Dunlop et al. 2001), leading some to conclude that frigatebirds display the highest degree of niche overlap of any seabird species-pair (Diamond 1975).

With recent developments in tracking technologies and the application of stable isotope analysis, it is now possible to investigate patterns of seabird resource use at a level of detail previously unattainable (Bearhop et al. 2004, Cooke et al. 2004, Ropert-Coudert and Wilson 2005, Inger and Bearhop 2008). Furthermore, these techniques allow investigation of resource use patterns over extended temporal periods. These developments present opportunities to reexamine questions where traditional methods such as direct identification of dietary items and at-sea survey have been unable to resolve patterns of resource partitioning. Here, we sought to apply these techniques to determine how sympatric populations of Great Frigatebirds (*Fregata minor*) and Lesser Frigatebirds (*F. ariel*) partition available prey resources. In doing so we also sought to identify mechanisms that facilitate coexistence of these remarkably similar congeners.

METHODS

Study Site

Fieldwork was conducted at Ashmore Reef (12.27°S, 123.03°E), an Australian territory in the Timor Sea.

Ashmore Reef is recognized by BirdLife International as an Important Bird Area (IBA) (BirdLife International 2013) and supports 16 species of breeding seabirds with more than 100,000 individuals (Clarke et al. 2011). Great Frigatebirds (65 individuals) and Lesser Frigatebirds (4,196 individuals) both breed at Ashmore Reef (Clarke et al. 2011, Clarke and Herrod 2014). Great Frigatebirds nest in small *Heliotropium foertherianum* shrubs, whereas Lesser Frigatebirds nest on the ground among low grassy and/or herbaceous vegetation. Breeding of both species in this basin is seasonally predictable with laying occurring mid-February through May (Clarke et al. 2011).

Bird Capture and Sampling

Adult birds were captured at their nests during incubation and early chick-rearing periods in March and April of 2014. Birds were captured at night to reduce incidences of heat stress. Individuals were sexed based on plumage characteristics (Marchant and Higgins 1990), weighed (Salter Super Samson, Springvale, Victoria, Australia) and fitted with a metal leg band supplied by the Australian Bird and Bat Banding Scheme. A global positioning system (GPS) device programmed to record a position every 5 min was attached with Tesa tape to 3 central rectrices of the tail (CatTrack 1, Catnip Technologies, Hong Kong: Great Frigatebird $n = 6$, Lesser Frigatebird $n = 26$) or by a Teflon leg-loop harness (HARIER-4L, Ecotone Telemetry, Sopot, Poland: Great Frigatebird $n = 6$, Lesser Frigatebird $n = 9$) (Mott et al. 2015). CatTrack devices were archival-type loggers sealed in waterproof heatshrink. HARIER-4L devices were capable of transmitting stored data via UHF frequencies to a base station established on the island, thus negating the need to recapture a bird to recover data. Bird-borne devices had a total mass of ~ 26 g for CatTrack devices and 15 g for HARIER-4L devices. The minimum and maximum percentage of body mass for any logger deployment were 0.97% and 2.68%, respectively, for Great Frigatebirds, and 1.61% and 3.92%, respectively, for Lesser Frigatebirds. At initial capture, 5 breast feathers were plucked from each bird for later analysis and a blood sample (~ 0.5 mL) was collected from the brachial vein using a 23-gauge needle and syringe. Whole blood was immediately transferred to a 2 mL microtube and centrifuged to separate plasma from red blood cells (RBCs). The plasma portion was pipetted into a second microtube and ethanol was added to both tubes. These samples were refrigerated during field trips then stored at -20°C in the laboratory. Seven individuals spontaneously regurgitated prey remains during handling. Prey remains were archived individually and stored at -20°C soon after collection. The small number of regurgitation samples limited capacity for population-wide inference and these results, along with mixing models constructed using isotopic values from regurgitated prey, are provided in an

appendix (Appendix Table 2 and Appendix Figures 4, 5, and 6).

Laboratory Analysis

Stable isotope analysis and methodological considerations. Various extrinsic and intrinsic factors may influence isotopic values of a consumer. The discrimination factor between a source and a consumer varies with tissue type and species (Caut et al. 2009). However, discrimination factors of blood and feather tissues in piscivorous seabirds have little specific variation (Cherel et al. 2005). Consequently, it is possible to infer respective trophic positions of species by direct comparison of $\delta^{15}\text{N}$ values.

Isotopic values of feathers indicate dietary assimilation at the time of feather formation (Hobson and Clark 1992), which in frigatebirds occurs during the nonbreeding period (Nelson 1975), estimated to be Dec–Feb in breeding populations in this study. Conversely, RBCs reflect diet 2–4 weeks prior to sampling (Quillfeldt et al. 2008) and plasma reflects integration over the week preceding sampling (Hobson and Clark 1993). Here, RBCs and plasma are indicative of diet during courtship and incubation stages of the breeding cycle.

Feather samples were rinsed in a 2:1 chloroform:methanol bath followed by 2 further rinses in methanol solution. They were air dried for >48 hr and homogenized using scissors and a pizza cutting wheel. The resulting coarse powder was weighed (range: 0.7–0.9 mg) into tin capsules for analysis. Ethanol was evaporated off plasma and RBC samples before being freeze dried, ground, and weighed (range: 0.7–0.9 mg) into tin capsules for analysis. No lipid extraction was undertaken due to the small volume of plasma obtained in some cases. Instead, for tissue-types where the ratio of the mass of carbon to nitrogen was >3.5 , we corrected $\delta^{13}\text{C}$ values using the following equation:

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{bulk}} - 3.32 + (0.99 \times \text{C} : \text{N})$$

where $\delta^{13}\text{C}_{\text{normalized}}$ equates to the lipid-free $\delta^{13}\text{C}$ value, $\delta^{13}\text{C}_{\text{bulk}}$ is the measured carbon isotopic value, and C:N is the ratio of the mass of carbon to nitrogen in the sample (Post et al. 2007, Cherel et al. 2014). Feather and RBC samples consistently returned C:N values <3.5 indicating low lipid content and no mathematical correction was applied (Post et al. 2007).

Sample analysis was conducted on an ANCA-GSL2 elemental analyser with resultant CO_2 and N_2 gases analyzed by a Hydra 20:22 isotope-ratio mass spectrometer (Sercon, Cheshire, UK). Isotopic abundances were derived using the equation $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1$; where R = the ratio of the heavy isotope to light isotope ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in the sample or standard. Interna-

tional standards Vienna Pee Dee Belemnite and atmospheric N_2 were used for carbon and nitrogen isotopic ratios, respectively. All results are presented in delta (δ) notation in per mill (‰) units.

Statistical Analysis

Body mass of sampled birds. Differences in recorded body mass for each species by sex category (hereafter referred to as cohorts) were compared using a one-way ANOVA with pairwise post hoc Tukey HSD tests.

Stable isotope analysis. Reverse sexual dimorphism and interspecies size differences are plausible drivers for variation in foraging behavior. Each cohort was therefore treated as a separate subject group in statistical analysis. Where data conformed to underlying assumptions, a multivariate analysis of variance (MANOVA) test was used to compare means of each cohort. When this overall test indicated that significant differences existed among cohorts, univariate one-way analysis of variance (ANOVA) tests with post hoc Tukey's HSD pairwise comparisons were used for $\delta^{13}C$ and $\delta^{15}N$ values to attribute causation to a particular cohort or cohorts (e.g., Cherel and Hobson 2007). When necessary, a nonparametric permutational multivariate analysis of variance (PERMANOVA) based on a Euclidean distance similarity index was undertaken using the *vegan* package in R (e.g., Elsdon et al. 2010). Univariate Kruskal–Wallis tests with pairwise post hoc Nemenyi tests followed where PERMANOVA indicated significant differences were present to determine which cohorts were responsible for the difference. The R package *siar* (Parnell and Jackson 2013) was used to assess niche overlap between each cohort by constructing standard ellipses. Standard ellipses represent 40% of the data and are equivalent to core isotopic niche. We used the SEA_c metric rather than SEA because the former corrects for small sample sizes and loss of an extra degree of freedom associated with analysis of bivariate data (Jackson et al. 2011). Similarity of niche widths was quantified by generating density plots showing credible intervals (50, 75, 95%) of standard ellipse areas in the R package *SIBER* (Jackson et al. 2011).

Tracking data. Analysis was constrained to tracking data obtained during the early breeding period (March, April, and May). Location data were projected into a Lambert Equal-Area Azimuthal projection and filtered to remove erroneous locations where successive locations required a transit speed exceeding 65 km h^{-1} (Weimerskirch et al. 2004, Weimerskirch et al. 2010). Filtered data were assigned to individual foraging trips. A foraging trip consisted of any movement beyond the reef platform during which 5 or more locations were recorded (i.e. 20+ min over open ocean). Track segments within the area encompassed by the reef platform were excluded as no foraging activity of frigatebirds has been observed within the reef during fieldwork. Likewise,

points within the reef platform of nearby Adele Island were also excluded as these are likely to be associated with short-term roosting/visitation on this island as opposed to foraging activity.

Foraging effort was compared between species by extracting the maximum range, trip duration, path distance, and path sinuosity of each foraging trip using ArcMap 10.3 (ESRI, Redlands, California, USA). Path sinuosity was defined as path distance/($2 \times$ maximum range) with higher values indicating a less linear path. These attributes were compared using mixed effects models with species and sex included as fixed factors and individual included as a random factor. We did not weight data so that each individual contributed an equal amount of data to the analyses. \log_{10} transformations of the response variable were undertaken when data showed heteroscedasticity or deviations from normality. Likelihood ratio tests were computed for each foraging trip attribute comparing a full model with a null model lacking the fixed factor species to determine whether the effect of species was significant using the *lme4* R package. The distal bearing of each foraging trip was extracted using ArcMap. To avoid pseudo-replication only data relating to the distal bearing of the first trip for each individual were included in a Rayleigh test to determine whether orientation of foraging trips was clustered. Mean bearings for foraging trips that had clustered orientations were compared with a Watson–Williams test to indicate whether cohorts oriented trips in a similar direction. This was implemented in R using the package *circular*.

Kernel density analysis. First passage time (FPT) analysis using the *fpt* function of the R package *adehabitatLT* (Calenge 2006) was undertaken to identify the scale at which foraging activity of the tracked birds occurred. This value was used as the bandwidth in kernel density analysis following Lascelles et al. (2016). Core foraging areas (50% utilization distribution) and home range (95% utilization distribution) were constructed for each foraging trip using kernel density analyses in the R package *adehabitatHR* (Calenge 2006). Individual foraging trips were analyzed independently to remove any influence of convergence of multiple flight paths at the colony.

The habitat attributes sea-surface temperature (SST), chlorophyll- α concentration (Chl- α), and bathymetry were used to determine whether Great Frigatebirds and Lesser Frigatebirds exploited different environmental conditions, thereby facilitating resource partitioning. Eight-day composites of SST and Chl- α data were obtained from NASA's MODIS aqua database (available from the NASA Physical Oceanography Distributed Active Archive Center at <http://podaac.jpl.nasa.gov/> and NASA Giovanni Portal at <http://giovanni.gsfc.nasa.gov/giovanni/>, respectively). These datasets have a resolution of 4 km and SST data represent measurements taken at night. Bathymetric data were

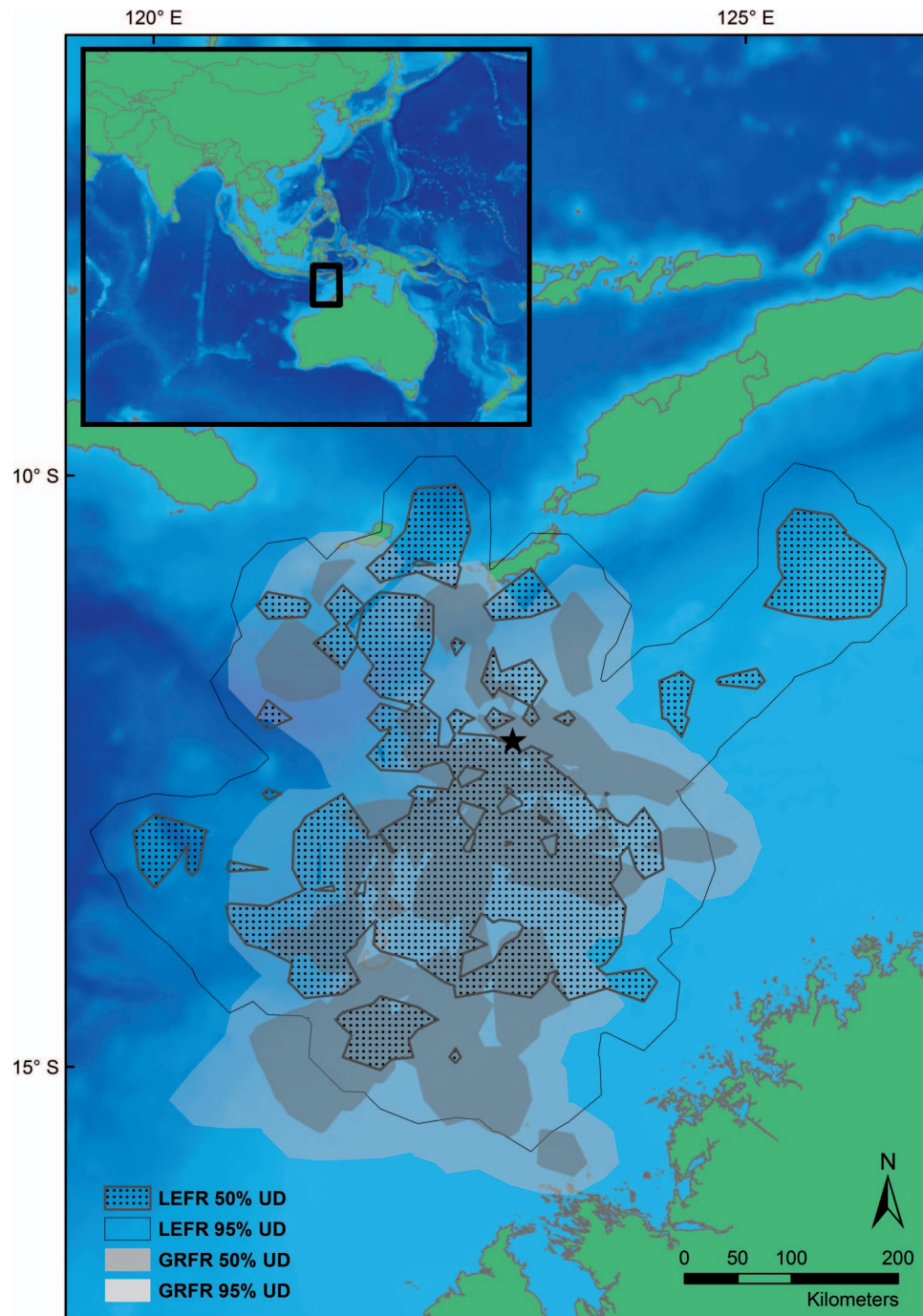


FIGURE 1. Study region showing Ashmore Reef, the location of tracking device deployment (star), and core (50% utilization distribution) and home range (95% utilization distribution) kernel density plots for Great Frigatebirds (GRFR) and Lesser Frigatebirds (LEFR). Inset: location of study region in a broad geographical context with the extent of the main map demarcated by black rectangle.

obtained from Geoscience Australia's Australian Bathymetry and Topography Grid (Whiteway 2009). The starting date of each foraging trip was used to define which 8-day composite best represented the conditions experienced on that foraging trip.

Outputs of kernel density analysis were imported into ArcMap 10.3 and the median value for each environmental variable within the kernel envelope of individual trips was extracted. For very small kernels that did not contain environmental point data, the nearest point for each

TABLE 1. Mean body masses of sampled frigatebird cohorts at Ashmore Reef.

Species	Sex	<i>n</i>	Mass \pm SE (g)
Great Frigatebird	Female	7	1,403.6 \pm 50.4
	Male	5	1,075.8 \pm 46.9
Lesser Frigatebird	Female	22	899.0 \pm 13.1
	Male	9	778.8 \pm 17.4

variable was manually assigned. To compare environmental variables within kernel areas, linear mixed effects models with species, sex, and environmental variables treated as fixed effects and individual as a random effect were used (Young et al. 2010b, Kappes et al. 2011, Ceia et al. 2015).

All values are reported as means \pm SE.

RESULTS

Body Mass

Differences in body mass between cohorts were found ($F_{3,40} = 81.3$, $P < 0.001$). All pairwise post hoc comparisons were significant at the 0.05 level with cohorts assorting from heaviest to lightest in the order female Great Frigatebirds, male Great Frigatebirds, female Lesser Frigatebirds, and male Lesser Frigatebirds (Table 1).

Stable Isotope Analysis

Isotopic values derived from the nonbreeding period (i.e. from feather samples) differed significantly among cohorts (MANOVA: $F_{3,27} = 5.8$, $P < 0.001$) and these were driven by the higher mean $\delta^{15}\text{N}$ value of male Great Frigatebirds than male Lesser Frigatebirds ($P = 0.02$) (Figure 2). Male Great Frigatebirds and male Lesser Frigatebirds also had a lower $\delta^{13}\text{C}$ value than female Lesser Frigatebirds ($P = 0.02$ and $P = 0.03$, respectively), but no significant differences were found between these cohorts and female Great Frigatebirds (Figure 2). Analysis of samples indicative of the early breeding season showed that significant differences were driven by higher mean $\delta^{15}\text{N}$ value of female and male Great Frigatebirds compared to male Lesser Frigatebirds and that this pattern was consistent for both RBC and plasma samples (PERMANOVA; RBC $F_{3,27} = 6.0$, $P = 0.001$; Plasma $F_{3,27} = 6.0$, $P = 0.001$) (Figure 2). For all 3 tissue types, both Great Frigatebird sexes had a higher $\delta^{15}\text{N}$ value than female Lesser Frigatebirds, but in no case were these differences significant (Figure 2).

Isotopic niche width varied little during the breeding season among cohorts (Figure 3). The smaller niche width of female Lesser Frigatebird plasma samples compared to niche width of plasma samples from male Lesser Frigatebirds was the only significant difference among breeding season samples (Figure 3). Niche width during the nonbreeding period was larger than during the breeding period for all comparisons except female Great Frigatebirds

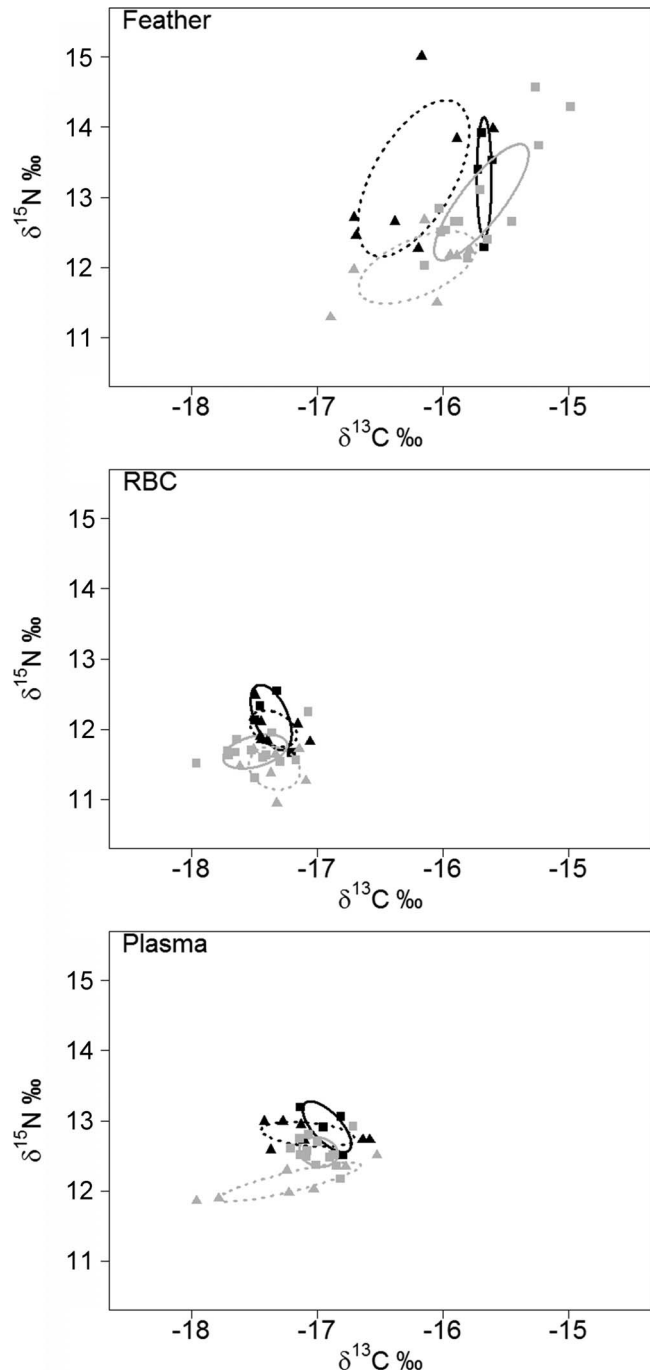


FIGURE 2. Bi-plots depicting isotopic values of Great Frigatebirds (female: black square; male: black triangle) and Lesser Frigatebirds (female: gray square; male: gray triangle) for feather, red blood cells (RBC), and normalized plasma (Plasma). Standard ellipses (SEA_c) are also shown with Great Frigatebirds and Lesser Frigatebirds represented by black ellipses and gray ellipses, respectively. Females are indicated by solid lines and males by dotted lines.

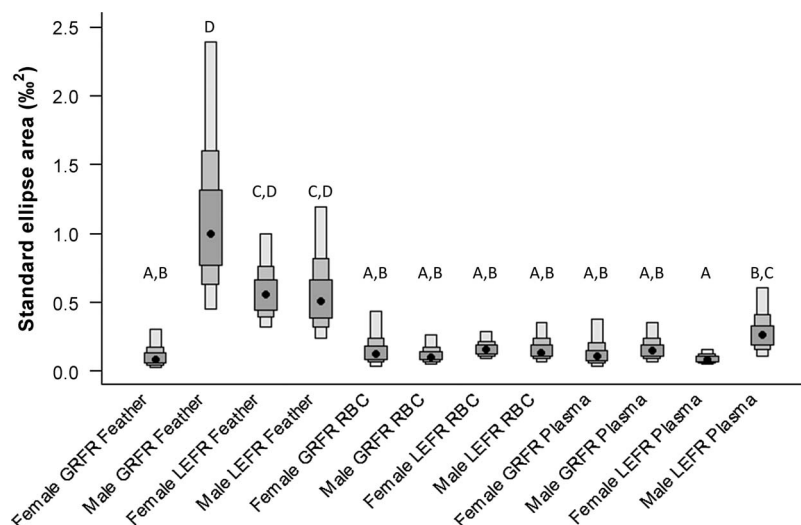


FIGURE 3. Density plot displaying the mean standard ellipse area (black circle) of each sex of Great Frigatebirds (GRFR) and Lesser Frigatebirds (LEFR) for the 3 tissue types. Shaded boxes depict the 50, 75, and 95% confidence intervals associated with the mean from dark gray to light gray. Shared letters indicate that the mean value of one or both cohorts is contained within the 95% confidence interval of the other cohort.

(Figure 3). The niche width of female Great Frigatebird feather samples was smaller in comparison to male Great Frigatebirds and both sexes of Lesser Frigatebird and similar in size to all cohorts during the breeding season (Figure 3). The position of the isotopic niche of male Lesser Frigatebirds did not overlap with either sex of Great Frigatebirds for plasma samples and it did not overlap the isotopic niche of feather samples of female Great Frigatebirds (Figure 2). With the exception of isotopic niches indicated by feather samples of female and male Great Frigatebirds, all other cohorts had some degree of overlap in isotopic niche with greatest overlap between male and female Great Frigatebirds for both breeding season sample types (Figure 2).

Tracking Data

Tracking data consisted of 108 trips by 7 Great Frigatebirds (GRFR) and 102 trips by 16 Lesser Frigatebirds (LEFR). There was no difference in mean range of foraging trips (GRFR: 76.4 ± 10.1 km, LEFR: 123.2 ± 10.4 km; $\chi^2 = 3.4$, $P = 0.07$), path distance (GRFR: 364.8 ± 68.9 km, LEFR: 601.1 ± 78.4 km; $\chi^2 = 3.2$, $P = 0.07$), or sinuosity (GRFR: 1.8 ± 0.1 , LEFR: 2.0 ± 0.1 ; $\chi^2 = 2.0$, $P = 0.16$) between species. However Lesser Frigatebirds undertook trips of a significantly longer duration (GRFR: 0.9 ± 0.2 days, LEFR: 1.6 ± 0.2 days; $\chi^2 = 4.3$, $P = 0.04$).

Foraging trips undertaken by male Great Frigatebirds, and female and male Lesser Frigatebirds, had a clustered orientation (male Great Frigatebird Rayleigh test statistic = 0.62, $P < 0.001$; female Lesser Frigatebird Rayleigh test statistic = 0.4, $P < 0.001$; and male Lesser Frigatebird Rayleigh test statistic = 0.6, $P = 0.001$). Importantly, orientation of these clustered foraging trips was similar

(Watson–Williams test $F_{2,128} = 1.9$, $P = 0.16$) across all 3 cohorts with mean bearing of foraging trips centred toward the south-southwest of the colony (male Great Frigatebirds 202.9° ; female Lesser Frigatebirds 184.2° ; and male Lesser Frigatebirds 215.6°). The distal bearing of foraging trips of female Great Frigatebirds did not display a clustered orientation (Rayleigh test statistic = 0.1, $P = 0.65$).

Extensive spatial overlap in home range areas used by the 2 species was evident, with 84% of Great Frigatebird home range area occurring within Lesser Frigatebird home range area, whereas 68% of the home range of Lesser Frigatebirds occurred within that of Great Frigatebirds (Figure 1). Areas of core use showed less extensive overlap whereby 43% of Great Frigatebird core area and 41% of Lesser Frigatebird core area occurred within that of the other species (Figure 1).

Median SST within core foraging ranges did not differ between species ($\chi^2 = 0.2$, $P = 0.67$). Core areas of Great Frigatebird foraging trips had significantly higher median Chl- α concentration ($\chi^2 = 11.1$, $P < 0.001$) and were located over waters with shallower bathymetry ($\chi^2 = 6.4$, $P = 0.01$) than core areas of Lesser Frigatebird foraging trips.

DISCUSSION

Important differences in dietary and spatial aspects of the foraging strategy of Great Frigatebirds and Lesser Frigatebirds were revealed. SIA demonstrated some dietary differences are maintained year-round, whereas tracking and SIA indicated similarity in spatial attributes of foraging during the breeding season. For each tissue type one or both sexes of Great Frigatebird had a higher mean $\delta^{15}\text{N}$ value compared to male Lesser Frigatebirds. The same

trend was apparent, though not significant, for both sexes of Great Frigatebird relative to female Lesser Frigatebirds. Cherel et al. (2008) found similar interspecific differences between $\delta^{15}\text{N}$ values of Great Frigatebirds and Lesser Frigatebirds during the nonbreeding period, but not the breeding period. They found no significant differences between sexes for Great Frigatebirds and did not test for between-sex differences in Lesser Frigatebirds. Pooling of data across sexes by Cherel et al. (2008) may have contributed to the breeding season disparity between their findings and those presented here.

Year-round Trophic Differences

Our observation that male Lesser Frigatebirds consistently fed on prey with a lower $\delta^{15}\text{N}$ when compared with other frigatebird cohorts is best explained by body size. Great Frigatebirds are larger than Lesser Frigatebirds (Marchant and Higgins 1990, this study) and frigatebirds display reversed sexual dimorphism (Marchant and Higgins 1990, Lagarde et al. 2004, Mott et al. 2015, this study). Body size can mediate trophic position by enabling larger individuals to capture larger prey items (Cohen et al. 1993, Scharf et al. 2000). In marine food chains, body size of a fish is correlated with its $\delta^{15}\text{N}$ value and this correlation is particularly strong in flying fish (Mancini et al. 2014, Mancini and Bugoni 2014). Flying fish are a major component of frigatebird diet (Diamond 1975, Harrison et al. 1983, Cherel et al. 2008), a feature confirmed by regurgitation samples obtained here (Appendix Table 2). Therefore, Great Frigatebirds, with their larger body size, may have captured a larger proportion of large-bodied, high $\delta^{15}\text{N}$ prey items leading to their comparatively high $\delta^{15}\text{N}$ value. Alternatively, their larger body size may have enabled them to exclude the smaller-bodied Lesser Frigatebird from profitable foraging opportunities and forced Lesser Frigatebirds to forage on a prey base of lower value (Persson 1985, Ballance et al. 1997). However, the smaller number of Great Frigatebirds within the Ashmore study region suggests that it would be difficult to have maintained levels of interference competition sufficient to sustain this effect (Young et al. 2010b). Finally, energetic cost of flight and flight speed of a bird are proportional to body mass and wing loading, respectively (Ellington 1991, Ballance et al. 1997). Although flight costs are low for frigatebirds (Weimerskirch et al. 2003, Weimerskirch et al. 2016), the larger body size of Great Frigatebirds would have incurred higher flight costs relative to the smaller Lesser Frigatebird. In combination with any difference in wing loading between these species, this may have imposed energetic constraints on foraging trips whereby exploiting a foraging location where a prey type or prey size class was particularly abundant was viable for only one of the two species (Shaffer et al. 2001, Phillips et al. 2004, Lewis et al. 2005). Although there are several plausible proximate

mechanisms, observed size differences between Great Frigatebirds and Lesser Frigatebirds remain the likely ultimate mechanism leading to differences in resource use. Similar patterns of size-mediated differences in foraging ecology occur in other tropical seabirds (Lewis et al. 2005, Young et al. 2010a, Young et al. 2010b). However, there is no information available to indicate whether body size-mediated differences in prey exploitation we observed occurred in response to limited prey availability or whether these 2 species were simply using prey resources they were best adapted to exploit (Linnebjerg et al. 2013).

Breeding Season Foraging Ecology

Dietary assimilation during the breeding period as inferred through stable isotope analyses (plasma and RBC samples) suggested sampled individuals, irrespective of species or sex, shared similar foraging locations. Similarly, GPS tracking demonstrated striking similarities between foraging strategies of breeding Great Frigatebirds and Lesser Frigatebirds. These conclusions applied to both measures of foraging effort (range, path distance) and spatial usage (home range overlap, clustered orientation of the distal bearing of foraging trips, path sinuosity). Central-place foraging imposes restrictions on foraging range that likely necessitated some degree of spatial convergence in foraging strategy (Phillips et al. 2007). Moreover, these similarities may explain why previous attempts to identify spatial mechanisms facilitating resource partitioning using vessel-based at-sea surveys were unable to resolve interspecific differences (e.g., Pocklington 1979).

Stable isotope analysis and home range estimation are coarse indicators of spatial parameters and coarse-scaled sampling units limit the potential to detect differences in foraging parameters (Haney and Schauer 1994). By contrast, when GPS outputs were considered at the finer resolution of core foraging areas it appears that there were some subtle differences in habitat affinities of the 2 species. Median chlorophyll- α concentration of waters within core foraging areas for both frigatebirds was low relative to the range of chlorophyll- α concentrations available within the foraging range. However, median chlorophyll- α concentration in core areas of Great Frigatebird foraging trips was significantly higher than in core areas of Lesser Frigatebirds. The waters within core foraging areas of Great Frigatebirds also had a significantly shallower median depth. By contrast, in other locations frigatebirds forage preferentially over waters with the highest available productivity (Weimerskirch et al. 2004, Jaquemet et al. 2005, Weimerskirch et al. 2010). Reaching waters with high relative productivity during the present study would have required frigatebirds to depart the colony into a headwind based on prevailing wind conditions (MERRA Model MATMNXLV v5.2.0 data available from NASA Giovanni Portal at <http://giovanni.gsfc.nasa.gov/giovanni/>). Many

species of seabirds display behaviors that minimize energy expended flying into a headwind (Weimerskirch et al. 2000, Grémillet et al. 2004, Weimerskirch et al. 2005), and frigatebirds may also have oriented foraging trips to capitalize on wind conditions rather than oriented foraging trips toward waters with higher relative productivity (Young et al. 2010b).

Nonbreeding Season Foraging Ecology

Differences in feather sample $\delta^{13}\text{C}$ values between sexes indicated male frigatebirds include a greater proportion of prey sourced from pelagic locations than female frigatebirds when not breeding (Hobson et al. 1994). This could have resulted from periodic movements over offshore waters or relocation to oceanic islands, whereas females foraged preferentially over inshore waters or relocated to roosting islands in neritic locations. No isoscape information exists for this region to assess the strength of the ^{13}C enrichment gradient between inshore and offshore locations and inform which of these scenarios was most probable. The biennial breeding cycle of frigatebirds that successfully reproduce would result in a large proportion of the population in a nonbreeding phase at any one time (Nelson 1975). Large numbers of nonbreeding birds are not present at this colony during the breeding season (Clarke and Herrod 2014), suggesting post-breeding dispersal from the colony. Migration is a strategy to cope with seasonal variation (Cohen 1967) and post-breeding movements are undertaken by tropical seabirds, including Barau's Petrels (*Pterodroma baraui*), Cape Verde Shearwaters (*Calonectris edwardsii*), and Wedge-tailed Shearwaters (*Puffinus pacificus*) (Catry et al. 2009, González-Solís et al. 2009, Pinet et al. 2011). Cherel et al. (2008) found no difference between the sexes in $\delta^{13}\text{C}$ value at any stage of the breeding cycle for Great Frigatebirds at Europa Island. Year-round breeding of frigatebirds at Europa Island (Le Corre 2001) indicates that suitable foraging conditions for frigatebirds persist year-round there, possibly negating the need for post-breeding dispersal in that system.

The isotopic niche width of male Great Frigatebirds and male and female Lesser Frigatebirds was larger during the nonbreeding period (feather samples) than the breeding season (plasma and RBC samples) for all cohorts. Although it is important to consider that the time frame over which isotopic information is integrated into feathers differs from red blood cells and plasma, large isotopic niche width during the nonbreeding period occurs in other tropical, and polar, seabird assemblages (Cherel et al. 2007, Cherel et al. 2008). Species including Light-mantled Albatross (*Phoebastria palpebrata*), Common Diving-Petrel (*Pelecanoides urinatrix*), and Wilson's Storm-Petrel (*Oceanites oceanicus*) can have large isotopic variation in feather samples indicative of broad geographical ranges during the nonbreeding period (Cherel et al. 2006, Phillips et al. 2009,

Connan et al. 2014). Concomitant trophic differences may also occur, reflecting divergent foraging patterns in different parts of the nonbreeding range (Connan et al. 2014). Broadening of the isotopic niche has been attributed to release from constraints of central-place foraging (Cherel et al. 2007) and results suggest that frigatebirds also increase variation in foraging parameters once breeding has ceased. However, isotopic niche width of female Great Frigatebirds did not increase and this was primarily a result of the low variation in $\delta^{13}\text{C}$ values within the cohort. Although sample size is small, this suggests low variation in the spatial distribution of this cohort (Ceia et al. 2014), which could be related to habitat specificity during this period.

The results identified dietary partitioning as an important mechanism facilitating year-round partitioning of resources between these congeneric seabirds. When constrained during the breeding season by the requirements of central-place foraging, differences in spatial attributes of the foraging strategy of these species are limited. However, when not breeding, between-sex differences in location of foraging emerge that may further diminish resource overlap among members of this colony.

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APPENDIX

Identification of Regurgitated Prey Remains

Each regurgitated prey item was identified to the lowest taxonomic unit possible. Food and Agriculture Organization species identification sheets (Food and Agriculture Organization of the United Nations 1974), Allen et al. (2009), the online resource Fishbase (available at <http://www.fishbase.org>), and a photographic reference collection of known identity prey remains were used to assist visual identification. Identification of otoliths involved compar-

ison with a reference collection extracted from fish of known identity and the resources of Furlani et al. (2007) and Fishbase. Cephalopod beaks were identified primarily using Lu and Ickeringill (2002), but also Wolff (1982, 1984), Nateewathana (1992), Xavier and Cherel (2009), and Chen et al. (2012). Cuttlebones were identified using Norman and Reid (2000). It was not possible to identify all ingested items to species level due to partial digestion of some items and results are subsequently grouped at the family level.

The importance of individual taxa in the diet of frigatebird species was assessed by calculating frequency of occurrence and numerical abundance (Polito et al. 2011, Connan et al. 2014). Frequency of occurrence was calculated as the proportion of regurgitation samples that contained the given prey. Numerical abundance was calculated as the total number of individuals of a given prey taxon across all regurgitation samples as a percentage of the total number of identified prey items.

Results of Identification of Prey Remains

Exocoetid and hemiramphid fishes were present in both Great and Lesser frigatebird regurgitate samples (Appendix Table 2). Piscivorous predators of the families Scombridae and Carangidae were present only in regurgitate samples of Great Frigatebirds (Appendix Table 2). Conversely, remains of ommastrephid squid were present only in Lesser Frigatebird regurgitate samples (Appendix Table 2).

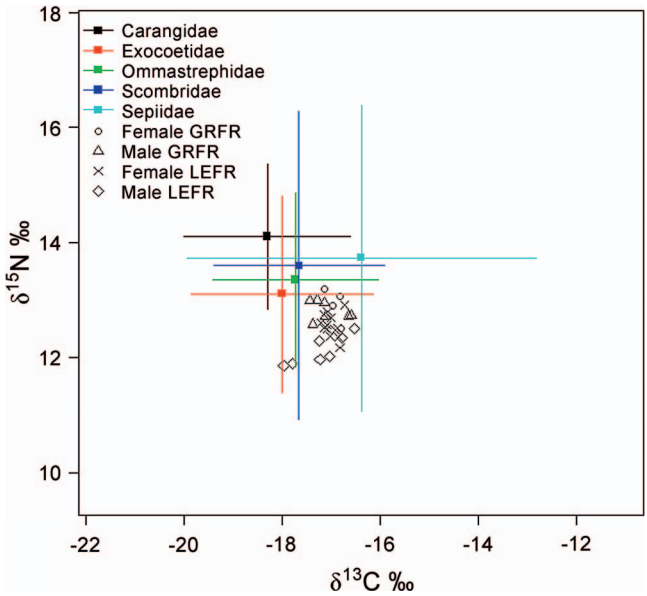
Regurgitation sample preparation for stable isotope analysis. Regurgitated remains of prey from 5 families that occur most frequently in regurgitation samples of frigatebirds in this region were subjected to SIA (hemiramphids were not included because of limited undigested tissue). Sample preparation followed Logan et al. (2008). A sample of muscle was removed from the caudal region of fish or the mantle of cephalopods. Samples were rinsed in deionized water before being finely minced and oven-dried at 60°C for 48 hr until constant mass was attained. Dried samples were then ground with a mortar and pestle and the resulting powder separated into 2 subsamples per prey item. The first set of subsamples was immediately prepared for SIA (referred to hereafter as bulk samples), whereas other subsamples were subjected to a lipid extraction. Lipid extraction consisted of immersing the sample in a 2:1 chloroform:methanol solution, mixing by vortexing for 30 s before standing for 30 min. Each sample was subsequently centrifuged at 1318 g for 10 min and the supernatant was discarded with the aid of a pipette. This immersion process was repeated 3 or more times until the supernatant was no longer colored or cloudy. Lipid extracted samples were again oven dried at 60°C for 48 hr. Bulk samples and lipid extracted samples were freeze

APPENDIX TABLE 2. Composition of regurgitation samples of Great Frigatebirds (GRFR) and Lesser Frigatebirds (LEFR) in terms of frequency of occurrence (FO) and numerical abundance (NA) of prey families.

Species		FO (%)	NA (%)
GRFR (<i>n</i> = 3 (8 items))	Carangidae	33.3	25.0
	Exocoetidae	33.3	25.0
	Hemiramphidae	33.3	25.0
	Ommastrephidae	0.0	0.0
	Scombridae	33.3	12.5
	Unidentifiable fish	33.3	12.5
LEFR (<i>n</i> = 4 (14 items))	Carangidae	0.0	0.0
	Exocoetidae	50.0	14.3
	Hemiramphidae	50.0	14.3
	Ommastrephidae	25.0	7.1
	Scombridae	0.0	0.0
	Unidentifiable fish	75.0	64.3

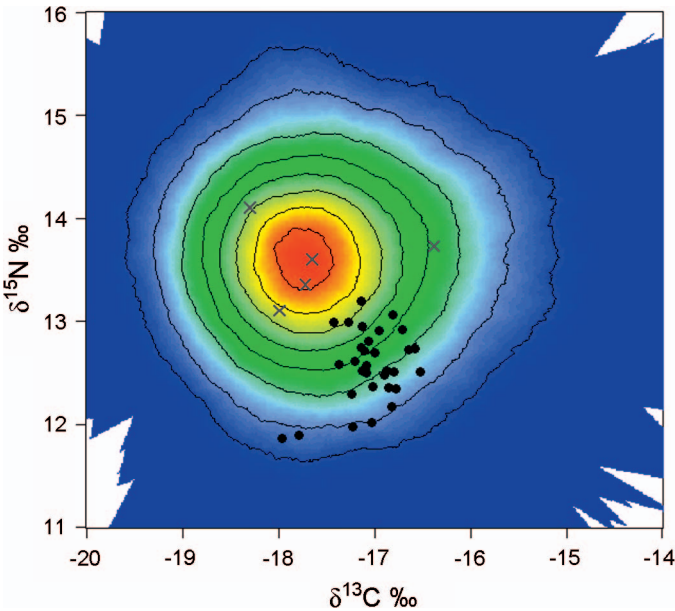
dried and weighed (range: 0.4–0.6 mg) into tin capsules for analysis.

Mixing model generation. Stable isotopic values obtained from regurgitated prey remains commonly occurring in the diet of frigatebirds were used to estimate proportional contribution of prey families to the diet of Lesser and Great frigatebirds. This was achieved using mixing models solved within the SIAR Bayesian framework with a non-informative Dirichlet prior distribution (Jackson et al. 2009) and Markov chain Monte Carlo (MCMC) simulations. SIAR mixing models generate a

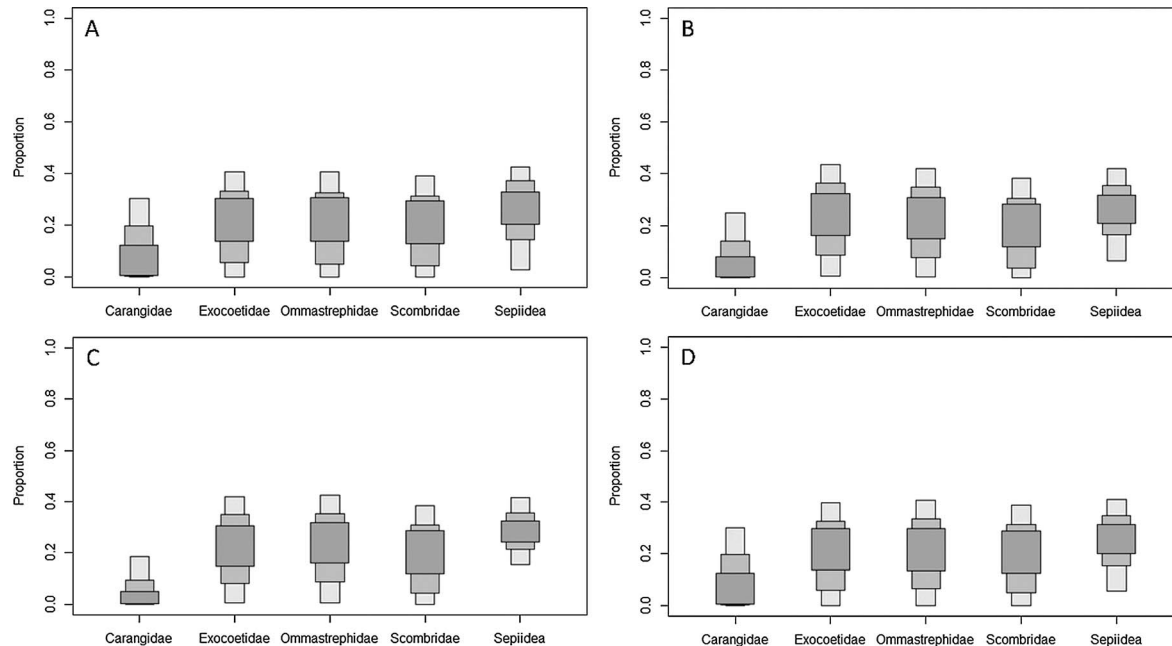


APPENDIX FIGURE 5. Isotopic bi-plot depicting the position in isotopic space of frigatebirds in relation to mean position of prey families in their diet after the trophic enrichment factors presented in Stauss et al. (2012) have been added to isotopic values of dietary sources. Error bars of prey families depict standard error.

true probability density function for the parameter of interest. Default SIAR MCMC parameters (iterations = 2×10^5 , burning = 5×10^4 , thinning = 15) were used for modelling. No trophic enrichment factor has been



APPENDIX FIGURE 4. Mixing region displaying the probability of the data fitting the MCMC mixing model following Smith et al. (2013). Contours depict the probability of a viable solution existing with the outermost contour representing a probability of 0.05 and the remaining contours increasing from 0.1 to 0.7 in 0.1 increments. Gray crosses indicate dietary sources and black circles depict the location of frigatebird plasma samples in isotopic space. Trophic enrichment factors of Stauss et al. (2012) ($\Delta^{15}\text{N} = 2.25 \pm 0.61$ and $\Delta^{13}\text{C} = 0.24 \pm 0.79$) have been added to the raw isotopic data of sources.



APPENDIX FIGURE 6. Mixing model-derived estimates of the proportional contribution of each prey family to the diet of (A) female Great Frigatebirds, (B) male Great Frigatebirds, (C) female Lesser Frigatebirds, and (D) male Lesser Frigatebirds. Shaded boxes indicate 50, 75, and 95% credibility intervals from dark gray to light gray, respectively.

determined for any species of frigatebird so we applied the values of Stauss et al. (2012) to mixing models for another Suliform seabird, the Northern Gannet (*Morus bassanus*). These were $\Delta^{13}\text{C} = +0.24 (\pm 0.79)$ and $\Delta^{15}\text{N} = +2.25 (\pm 0.61)$. Simulated mixing polygons were generated following Smith et al. (2013) using the packages *sp* and *splancs* in program R to make an a priori assessment of the goodness-of-fit of the data to the mixing model. No sampled birds were excluded as all were within the 0.05 contour (Appendix Figure 4) indicating that a viable

mathematical solution for the mixing model existed (Smith et al. 2013).

Mixing model outputs. In relation to among-group separation, variation in isotopic value of all 5 prey families considered was large in both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ directions resulting in substantial overlap in the spread of samples (Appendix Figure 5) and a mixing model with little discriminating power. Consequently the model indicated approximately equal contributions of each prey family to the diet of males and females of both species (Appendix Figure 6).